

A NEW SPECIES OF *Panderevela* (GASTROPODA: HETEROBRANCHIA: SACOGLOSSA) FROM PHUKET ISLAND, THAILAND

Kathe R. Jensen

Natural History Museum of Denmark (Zoological Museum), DK-2100 Copenhagen Ø, Denmark
Corresponding author: krjensen@snm.ku.dk

ABSTRACT: The first species of the sacoglossan genus *Panderevela* from the Indo-Pacific region is described and named in honor of the late Prof. Jørgen Hylleberg. It is small, less than 2 mm long preserved, darkly pigmented, and associated with the green alga *Avrainvillea*. It was collected at Rawai Beach, Phuket Island, Thailand, in November 1986 and November 1990. Although searches have been made on several other occasions in the same location, the species has not been found since then, so it appears to be rare. The morphological characters defining the genus *Panderevela* are discussed and the anatomy is compared to other species of the family Costasiellidae. All specimens collected were fixed in formalin, so DNA analysis has not been possible.

Keywords: Costasiellidae, Sacoglossa, comparative anatomy, morphology, new species

INTRODUCTION

Sacoglossan sea slugs (Mollusca, Gastropoda, Heterobranchia) from Thailand have been described in a number of papers. Bergh (1902) included specimens of *Plakobranthus ocellatus* van Hasselt, 1824, from the Gulf of Thailand. Jensen (1989) described *Cylindrobulla phuketi*, which only later was included in the Sacoglossa (Mikkelsen, 1998). Jensen (1998) described the anatomy of three species, *Plakobranthus ocellatus*, *Thuridilla ratna* (Marcus, 1965), and *Elysia pusilla* (Bergh, 1872) (as *Elysiella pusilla*) from Phuket Island, and listed prior records of *Elysia* cf. *marginata* (Pease, 1871) (as *E. ornata* (Swainson, 1840)) and *Ercolania translucens* Jensen, 1993. Swennen (1998, 2001, 2007) described two new species of *Elysia*, *E. siamensis* and *E. bangtawaensis*, two new species of *Gascoignella*, *G. nukuli* and *G. jabae*, and one new species of *Costasiella*, *C. coronata*, from the southern Gulf of Thailand. Swennen (2011) recorded *Elysia leucolegnote* Jensen, 1990, also from the Gulf of Thailand, and Swennen *et al.* (2001) recorded *Ercolania tentaculata* (Eliot, 1917) and an unidentified *Ercolania* sp. (probably *E. gopalai* (Rao, 1937)) from the Gulf of Thailand. Jensen *et al.* (2014a) described *Ercolania halophilae* Jensen, Kohnert, Bendell and Schrödl, 2014 from several localities on the Andaman Sea coast of Thailand.

Mehrotra and Scott (2016) recorded six species of Sacoglossa of which three (*Costasiella usagi* Ichikawa, 1993, *Elysia asbecki* Wägele, Stemmer, Burghardt and Händeler, 2010, and *Plakobranthus papua* Meyers-Muñoz and van der Velde, 2016 (as *Plakobranthus ianthobaptus* Gould, 1852)) were new records for Thai waters. Most recently two new species, *Plakobranthus noctisstellatus* Mehrotra, Caballer Gutiérrez, Scott, Arnold, Monchanin and Chavanich, 2020 and *Elysia aowthai* Mehrotra, Caballer Gutiérrez, Scott, Arnold, Monchanin and Chavanich, 2020, have been described (Mehrotra *et al.* 2020), and a new genus, *Swennenia*, has been created for *Gascoignella jabae* Swennen, 2001 (Buatip and Tan 2020).

The genus *Panderevela* Moro and Ortea, 2015 was described for two new species, *P. dacilae* Moro and Ortea, 2015 from the Canary Islands, and *P. ipse* Ortea, Moro and Espinosa in Moro and Ortea, 2015 from Cuba, which had previously been confused with *Costasiella nonatoi* Marcus and Marcus, 1960 from various localities in the Caribbean. The genus is distinguished from *Costasiella* Pruvot-Fol, 1951, by having median eyes behind rather than between the rhinophores, no pedal tentacles or protruding foot corners, and rhinophores with lateral extensions continuing onto the front of the head to form crests bordering a marked cleft (Moro and Ortea 2015).

The present study describes the first species of *Panderevela* from the Indo-Pacific region. It is associated with the siphonalean green alga *Avrainvillea*, and has been collected from Rawai Beach, Phuket Island, on the Andaman Sea coast of Thailand. It is compared to other species of the genus *Panderevela* and its affiliation with the family Costasiellidae is discussed.

MATERIALS AND METHODS

Many thalli of the siphonalean green alga *Avrainvillea* spp. were collected in shallow water at low tide at Rawai Beach at the southern end of Phuket Island, Thailand, in November 1986, April 1989, November 1990, September 1997, and July 2010. The seaweed was transported to the Reference Collection at Phuket Marine Biological Center and carefully examined with a magnifying lens or under a dissection microscope. Several specimens of the sacoglossan genus *Costasiella* were found on all occasions. These have subsequently been identified as belonging to the species complex named *Costasiella* cf. *kuroshimae* because of their similarity to *C. kuroshimae* Ichikawa, 1993 from Japan (Jensen 2009; 2015; Jensen *et al.* 2014b; Krug *et al.* 2015).

A few tiny specimens of what was thought to be another species of *Costasiella* were found when breaking up the often sand-encrusted stipes of the *Avrainvillea* thalli in November 1986. They were transferred to petri dishes, photographed, and observed for a few days before being fixed in 4% neutral formaldehyde. The specimens were transferred to 80% ethanol before being transported to the Zoological Museum in Copenhagen to await collection of more specimens for formal description of the species. A single specimen was carried alive in seawater to Copenhagen and preserved in January 1987. No specimens were found in April 1989, a single specimen was collected in November 1990, and none since then. A final attempt to find specimens that could be preserved for DNA analysis in July 2010 was also unsuccessful.

In 1988 one specimen was embedded in epoxy resin, serially sectioned, and stained with toluidine blue. Recently two specimens were dissected and digital photographs taken at various stages of dissection. The pharynx was removed and the tissues dissolved in a weak sodium hypochlorite

solution. The radula was photographed before being dehydrated in ethanol, dried, and placed on a SEM-stub. As the first radula disappeared in the adhesive pad on the SEM-stub, an eyebrow hair was used to prevent the second tiny radula from sinking into the adhesive. The penis was also removed, photographed, dehydrated, dried, and placed on a SEM-stub. Radular teeth and penis were sputter coated with a platinum-palladium alloy and scanned in a JEOL JSM-6335F scanning electron microscope.

Due to the small size and the low number of specimens available, description of this species has been postponed till now. In the meantime, the genus *Panderevela* has been separated from *Costasiella* by Moro and Ortea (2015), and the present specimens clearly belong to that genus, which will be discussed in this paper.

SYSTEMATICS

Order Sacoglossa von Ihering, 1876
Superfamily Plakobranchoidea Gray, 1840
Family Costasiellidae Clark, 1984
Genus *Panderevela* Moro and Ortea, 2015

Type species: *Panderevela dacilae* Moro and Ortea, 2015; type locality Tenerife, Canary Islands.

***Panderevela hyllebergi* sp. nov.**

Figs. 1-5

Zoobank registration (species): urn:lsid:zoobank.org:act:CD7AA51E-E015-4BB2-9170-301FAC15933F.

Zoobank registration (publication): urn:lsid:zoobank.org:pub:60C4C65B-F995-49D8-AC25-F927587B932E.

Holotype. 1.9 mm long - almost all cerata intact (Fig. 1); no white spot on pericardium. Rawai Beach, Phuket, Thailand, Nov. 1986. Phuket Marine Biological Center Reference Collection, registration number: PMBC 21217.

Paratypes. One specimen 1.7 mm long, most cerata intact; same locality - preserved Jan. 1987 after maintaining in laboratory since collection (Nov. 1986), deposited in the Natural History Museum of Denmark (registration number: NHMD- 868310). One specimen (length not recorded), same locality, sectioned and stained with toluidine blue (NHMD-

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868311). Two specimens (0.8 and 1 mm long preserved, most cerata autotomized) dissected; penis of both specimens on SEM stubs (NHMD-868312 and NHMD-868313); radula of 0.8 mm specimen lost, radula of 1 mm specimen on SEM-stub (NHMD-868313) with penis of same specimen.

Additional material examined. 2 specimens - 1.7 and 1.0 mm preserved lengths, most cerata autotomized, same locality, Nov. 1986; 1 specimen, same locality, Nov. 1990.

Etymology. *Panderevela hyllebergi* is named in honor of the late Prof. Jørgen Hylleberg, a long-time friend and colleague, who introduced me to marine biology in Thailand, the Phuket Marine Biological Center and the Tropical Marine Mollusc Programme.

Description

External features. Alive the dominant color of this species is intense black (Fig. 2). The anterior groove of the head, the tips of the cerata, the foot sole, a pair of rather large patches surrounding the eyes, and the lateral surfaces of the head are devoid of pigmentation and appear white (Fig. 3A). Black bands extend along the anterior crests of the head (Fig. 3B). Cerata are fusiform with a sub-terminal orange band. The tip of the cerata is transparent with a black spot on one side (Fig. 3C). The rhinophores are cylindrical, black to the tips, which are white in most of the preserved specimens. The pericardium is round to ovoid, short, pigmented, and in most specimens with a white spot or stripe posteriorly. The central part of the dorsum, behind the pericardium and between the cerata (not visible in living specimens) is unpigmented. Longitudinal dark stripes just medial to the cerata look like dorsal vessels, but only digestive gland tubules underlie these stripes. A small white spot lies behind the eyes in the black area, probably the anus. On the right side, the penial opening lies in the black area below the rhinophoral base, anterior to the eye. The oviducal opening lies behind and dorsal to the penial opening. No vaginal opening was discernible in the preserved specimens.

Internal anatomy (based mostly on serial sections). The oral tube is short and surrounded by glands. The pharynx is barrel-shaped with indistinctly septate muscle dorsally (Fig. 3D). The ascus-muscle

surrounding the descending limb of the radula (Figs 3D, 4A) is attached to the ventral surface of the pharynx for most of its length. There is a large pharyngeal pouch of almost solid muscle (Figs 3D, 4B). The radula of the 0.8 mm specimen had five fully formed teeth and one ghost tooth in the ascending limb and five teeth plus four pre-radular teeth in the descending limb (Fig. 3E); the 1 mm specimen had six fully formed teeth plus one ghost tooth in the ascending limb and eight teeth in the descending limb; the pre-radular teeth of this specimen were not visible. The teeth are very small, 30-40 μm long, but appear to be blade-shaped with smooth cutting edges (Fig. 5A); the base is slightly less than half the total length (Fig. 3E). The leading tooth of the 0.8 mm specimen was 29.4 μm long, and that of the 1 mm specimen 39.4 μm long. The esophagus is very narrow anteriorly until after it passes through the nerve-ring. There is a large muscular esophageal pouch in front of the small, thin-walled stomach (Fig. 4C). The intestine arises from the anterior part of the stomach leading to the anus, which is located at the anterior right corner of the pericardial prominence. The digestive gland forms two main longitudinal ducts, which send lateral branches into the cerata (Fig. 4D). The digestive gland tubules in the cerata are unbranched. Digested material appears to be delivered into the lumen surrounded by a cellular membrane (Fig. 4D). Salivary glands surround the esophagus and their ducts enter the pharynx next to the esophagus.

The pericardial prominence is located anteriorly (Fig. 3A, B). It is short and slightly ovoid. Unfortunately the serial sections were torn at this part, so the anatomy of these structures have only been observed in the dissected specimens. Under the pigmented epidermis is the thin-walled pericardial sac and inside this sac, the muscular, almost spherical, ventricle is located anteriorly. It has a circular opening antero-ventrally for the aorta. The auricle is short, broad and thin-walled and is located behind the ventricle. It was not possible to distinguish the connection between the pericardium and the kidney, which is located posterior to the pericardium with its anterior end extending above posterior pericardium.

The nervous system consists of large, paired, cerebro-pleural ganglia (Fig. 4B) connected by a short commissure; the large, paired, pedal ganglia are connected by a longer commissure and bear

distinct statocysts dorsally. The large eyes have spherical lenses, and the optic ganglia are located immediately underneath the basal epithelium of the eyes. Small buccal ganglia are located at the point of origin of the esophagus, and they seem to give rise to a tiny “gastric” ganglion attached to the esophageal pouch. The visceral chain is short, and it was not possible to see whether there are two or three separate ganglia. From the sections it appears that the sub-esophageal and visceral ganglia are fused, or at least located adjacent to each other.

The penis is located to the right of the pharynx (Fig. 4B). It is unarmed, muscular, and conical

(Figs. 4F, 5B). In the 1 mm specimen it was approximately 0.2 mm long and 80 μ m in diameter at the base. The vas deferens coils posteriorly and receives the duct from the bi- or tri-lobed prostate shortly after its separation from the hermaphrodite duct. It has not been possible to accurately follow all the tiny reproductive ducts as some sections were lost, torn, or folded. The sections show a rather voluminous seminal receptacle with a muscular wall (Fig. 4D) running ventrally along the median line of the body; it connects to the small fertilization chamber close to the entrance of the proximal part of the mucus gland (Fig. 4E). The thin-walled, almost spherical, genital

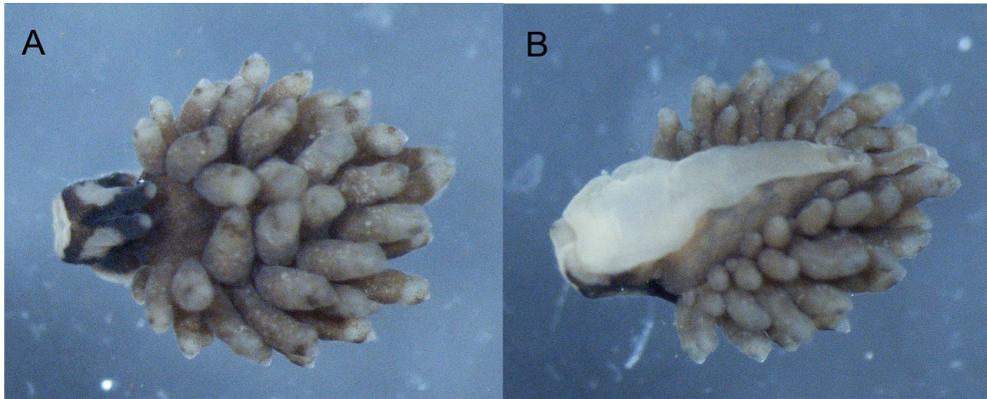


Figure 1. Preserved holotype of *Panderevela hyllebergi* sp. nov. Length of specimen 1.9 mm. A. Dorsal view; B. Ventral view.

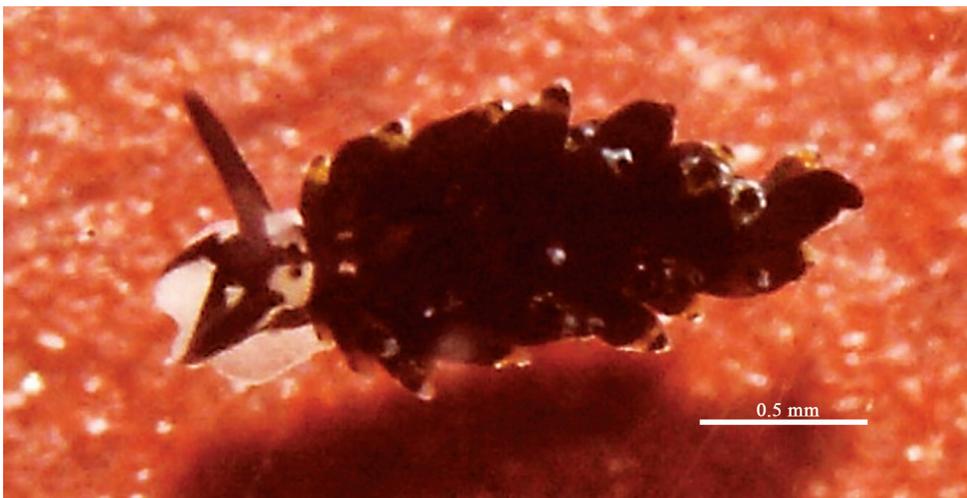


Figure 2. Live specimen (length ca. 2 mm) of *Panderevela hyllebergi* sp. nov. photographed in November 1986 and scanned from old color slide in 2020.

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receptacle lies on the left side of the body at approximately the level of the esophageal pouch (Fig. 4C) and contains a mass of unidentifiable material. The thin duct connects to the central reproductive area, presumably the fertilization chamber. The albumen gland of sacoglossans usually follows the course of the digestive gland tubules, but such a gland was not discernible in *P. hyllebergi*. In the sections there were two thin-walled sacs present on the right side of the body, filled with the blue stain; these could be albumen glands, but they have no similarity to such a gland of other sacoglossans and are most likely a staining artefact of possibly lobes of the prostate or salivary glands, both of which are located just anterior to these sacs. The hermaphrodite follicles are located in the posterior part of the body, ventral to the digestive gland tubules. Their tiny ducts connect

to a central, wide ampulla, running parallel to the seminal receptacle.

DISCUSSION

Panderevela hyllebergi sp. nov. is the first species of the genus to be described from the Indo-Pacific region. However, a similar, possibly identical, species has been found in Guam; it does not have the sub-terminal orange band and black spot on the tip of each ceras. Its cerata have pale yellowish transparent tips, and its rhinophores appear relatively longer. It has been included in molecular analyses of sacoglossans (Jensen *et al.* 2014b; Krug *et al.* 2015) as *Costasiella* sp. 4, and it is possibly also this species that is listed as *Costasiella* sp. 2 by Christa *et al.* (2014). Because cryptic spe-

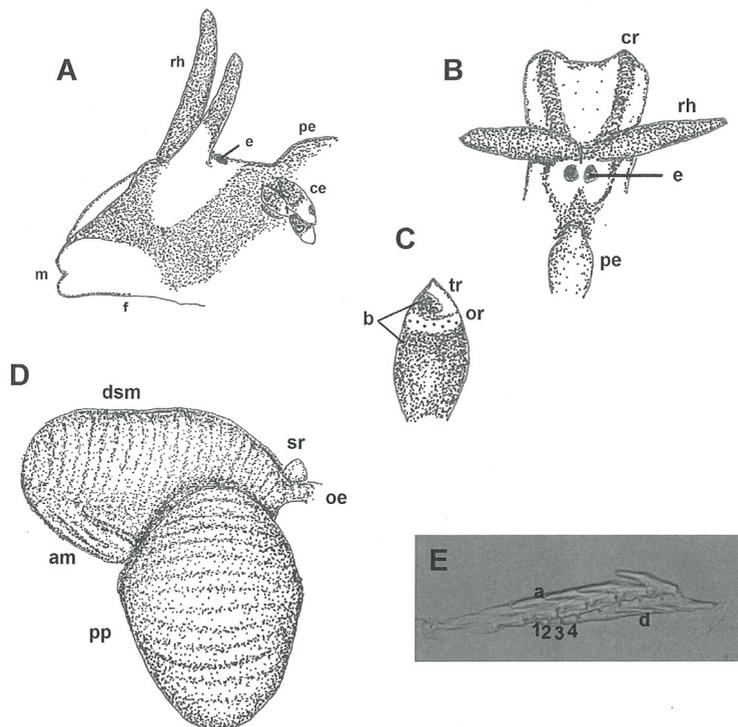


Figure 3. *Panderevela hyllebergi* sp. nov. A. Left lateral view of head drawn from live specimen; B. Dorsal view of head drawn from live specimen; C. Ceras drawn from live specimen; D. Pharynx of 1 mm specimen drawn from digital photo, lateral view; length of pharynx 235 μ m; E. Light micrograph of radula of 0.8 mm specimen; numbers indicate pre-radular teeth; length of leading tooth 29.4 μ m. Abbreviations: a = ascending limb; am = ascus muscle; b = black; ce = cerata; cr = anterior crests of head; d = descending limb; dsm = dorsal septate muscle; e = eye; f = foot; m = mouth; oe = esophagus; or = orange band; pe = pericardial prominence; rh = rhinophore; sr = salivary reservoir; tr = transparent.

cies complexes are so common in heterobranch sea slugs, including the Sacoglossa (e.g., Krug *et al.* 2015; McCarthy *et al.* 2019), it is considered prudent to consider the Guam specimens a separate, yet unnamed species.

When Clark (1984) created the family Costasiellidae, the species previously allocated to *Costasiella* had had a complicated history of generic affiliations, some being described as *Stiliger* [i.e., *S. (Ercolania) illus* Marcus, 1965 and *S. lilianae* Marcus and Marcus,

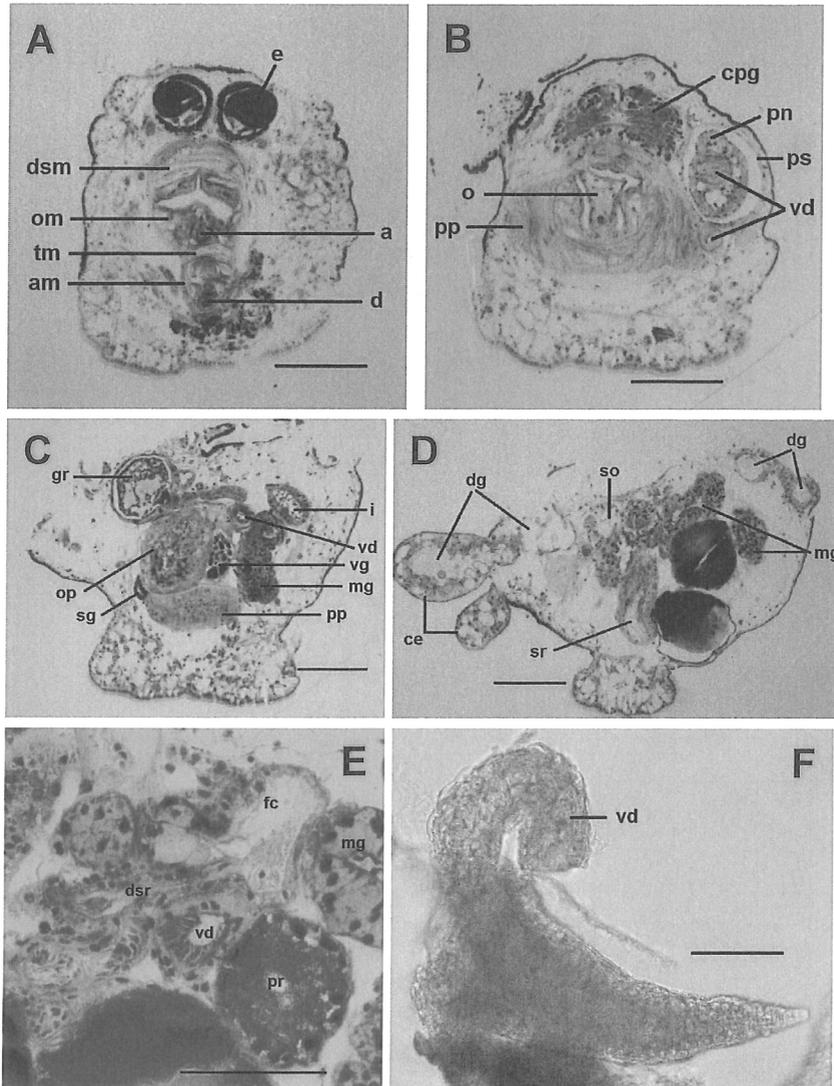


Figure 4. Sections and light micrograph of penis of *Panderevela hyllebergi* sp. nov. All sections are oriented dorsal side up and right side to the right. A. at level of eyes; B. at level of middle part of penis; C. at level of genital receptacle; D. at level of stomach; E. close-up of fertilization area; F. Light micrograph of penis of 0.8 mm specimen. Abbreviations: a – ascending limb of radula; am – ascus muscle; ce – cerata; cpg – cerebro-pleural ganglion; d – descending limb of radula; dg – digestive gland tubules; dsm – dorsal septate muscle; dsr – duct from seminal receptacle; e – eye; fc – fertilization chamber; gr – genital receptacle; i – intestine; mg – mucus gland; o – odontophore; om – odontophore muscle; op – esophageal pouch; pn – penis; pp – pharyngeal pouch; pr – prostate; ps – penial sheath; sg – salivary gland; so – stomach; sr – seminal receptacle; tm – transverse muscle; vd – vas deferens. Scale bars: A – D: 100 μ m; E – F: 50 μ m.

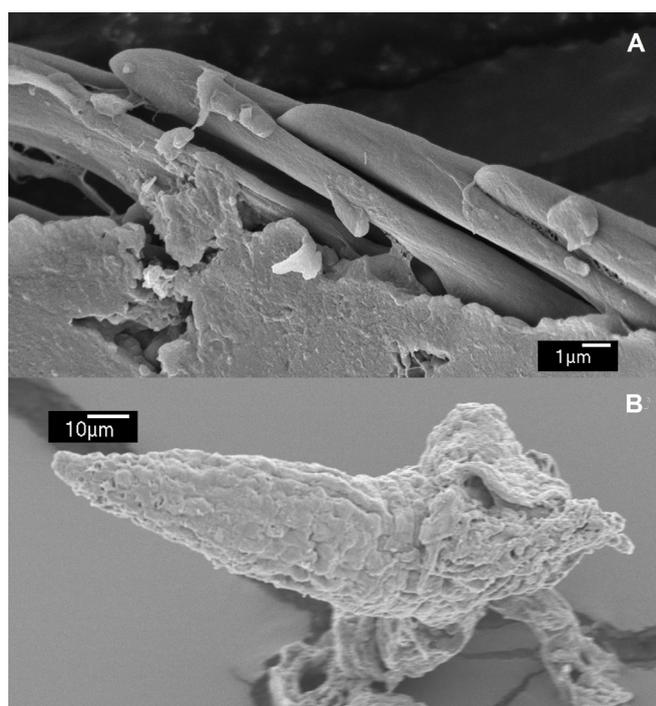


Figure 5. SEM micrographs of *Panderevela hyllebergi* sp. nov. A. Radula of 1 mm specimen; B. Penis of 0.8 mm specimen.

1969], and one species, *C. nonatoi*, had been transferred to *Placida*; even *Ercolania* has been mentioned in synonymy, although only as a subgenus. Marcus (1982) transferred *Stiliger* (*Ercolania*) *illus* to *Costasiella* and confirmed the inclusion of *C. nonatoi* and *C. lilianae* in the genus. She also suggested that *Doto* (?) *ocellifera* Simroth, 1895 was a *Costasiella*, later confirmed by Clark (1984) who synonymized it with *C. lilianae*. Clark (1984) also described a species from Bermuda, which he identified as *C. nonatoi*, and his description has been used to identify similar specimens from Florida, Panama, and the Bahamas (Rudman 2004; Jensen *et al.* 2014b; Christa *et al.* 2014; Espinoza *et al.* 2014; Krug *et al.* 2015). However, these records all refer to the species now known as *Panderevela ipse*. Table 1 summarizes the morphologies of *Panderevela hyllebergi* sp. nov., the type species of *Costasiella*, *C. virescens* Pruvot-Fol, 1951, the species of this genus previously recorded from Thailand, and of the two known species of *Panderevela*. The remaining species of *Costasiella* have been compared previously (see Table 2 in Jensen *et al.* 2014b).

Phylogenetic analyses based on molecular data sometimes place the Costasiellidae as a monophyletic group at the base of the Plakobranchoidea (Christa *et al.* 2015). At other times, the two genera *Panderevela* and *Costasiella* seem paraphyletic, their relative positions depending on the other species included in the analysis (Krug *et al.* 2015; Krug *et al.* 2018). Clearly the anatomy of the other species of *Panderevela* and *Costasiella* need to be examined, and specimens for DNA analysis should be collected.

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Table 1. Comparison of morphological characters of *Panderevela hyllebergi* sp. nov. and other species of the genus, the type species of *Costasiella* (*C. virescens*) and species of that genus recorded from Thai waters. *Type species of *Panderevela*. ? no data available.

Species	Rhinophores	Eyes	Cerata	Pericardium	Tail	Anterior foot	Pharyngeal pouch	Teeth (a, ascending; d, descending; as, ascus)	Esophageal pouch	CNS, no. visceral	Penis	number of genital openings
<i>C. virescens</i> Pruvot-Fol, 1951	Slightly flattened	Large, median between rhinophores	Fusiform; w. albumen gland	Tall, ovoid	Not constricted	W. tentacles	?	Smooth, blade-shaped; 5a, 15d, 5as; up to 70 µm	?	3	unarmed	2
<i>C. usagi</i> Ichikawa, 1993	Simple, thick	Large, in protuberance between rhinophores	Fusiform w. thin longitudinal lines; no albumen gland	Tall, short	Not constricted	W. thin tentacles	Small	Smooth, blade-shaped; 7a, 8d, ? as	?	2?	spiral stylet	2
<i>C. cf. kuroshimae</i> Ichikawa, 1993	Simple	Large, median between rhinophores	Fusiform w. orange & iridescent blue spots; w. albumen gland	Tall, ovoid dorsal vessels present	Like ceras	Rounded	Large	Smooth, blade-shaped; 7a, 6d, x as	?	?	unarmed	?
<i>C. coronata</i> Swennen, 2007	Simple, flattened at base	Median, between rhinophores	Flattened; w. albumen gland	Small; w. large renal shield	Not constricted	Pointed or rounded corners	Absent	Smooth, blade-shaped; 5-8a, 18-27d, 3 prerad; 85-100µm	Present	?	unarmed	3
<i>Panderevela dactilae</i> Moro & Ortea, 2015*	Cylindrical, flattened at bases, white tips	Large, median behind rhinophores	Fusiform, black w. brilliant blue dots; ? albumen gland	Small, with long renal tube	Not constricted	Rounded, bilobed	?	Blade-shaped, smooth; 7a, 8d; 30-35 µm	?	?	unarmed	?
<i>P. ipse</i> Ortea, Moro & Espinosa, 2015	Cylindrical, flattened at base, white tips	Large, median behind rhinophores	Fusiform, black w. white dots; ? albumen gland	Small, w. renal tube	Not constricted	Rounded	?	Blade-shaped, smooth; 40 µm	?	?	?	?
<i>P. hyllebergi</i> sp. nov	Cylindrical, flattened at base, ± white tips	Large, median behind rhinophores	Fusiform, black, sub-terminal orange band, white tip with black spot; no albumen gland	Ovoid, short	Not constricted	Rounded	Large	Narrowly blade-shaped, smooth; 5-6a, 5-8d, 4 prerad; 25-40 µm	Present	2	unarmed	2

REFERENCES

- Bergh, R. 1902. Gastropoda opisthobranchiata. The Danish Expedition to Siam 1899-1900. I. Gastropoda opisthobranchiata. Det Kongelige Danske Videnskabernes Selskabs Skrifter, 6. Række, naturvidenskabelig og matematisk Afdeling XII. **2**: 155–218, plates 1–3.
- Buatip, S. and S.K. Tan. 2020. A new genus *Swennenia* for *Gascoignella jabae* Swennen, 2001, a small rare mangrove dwelling sea slug in the Gulf of Thailand, with notes on the species (Gastropoda: Sacoglossa: Plakobranchoidea). Raffles Bull. Zool. **68**: 629–635.
- Christa, G., S.B. Gould, J. Franken, M. Vleugels, D. Karameinski, K. Händeler, W.F. Martin and H. Wägele. 2014. Functional kleptoplasty in a limapontioidean genus: phylogeny, food preferences and photosynthesis in *Costasiella*, with a focus on *C. ocellifera* (Gastropoda; Sacoglossa). J. Moll. Stud. **80(5)**: 499–507. [<https://doi.org/10.1093/mollus/eyu026>]
- Christa, G., K. Händeler, P. Kück, M. Vleugels, J. Franken, D. Karameinski and H. Wägele. 2015. Phylogenetic evidence for multiple independent origins of functional kleptoplasty in Sacoglossa (Heterobranchia, Gastropoda). Org. Div. Evol. **15**: 23–36. [<https://link.springer.com/content/pdf/10.1007/s13127-014-0189-z.pdf>]
- Clark, K.B. 1984. New records and synonymies of Bermuda opisthobranchs (Gastropoda). Nautilus. **98**: 85–97.
- Espinoza, E., A. DuPont and A. Valdés. 2014. Molecular data reveal an undescribed cryptic species of *Costasiella* Pruvot-Fol, 1951 (Euthyneura: Sacoglossa: Limapontidae) in the Bahamas. Am. Malacol. Bull. **32(2)**: 173–182. [<https://doi.org/10.4003/006.032.0208>]
- Jensen, K.R. 1989. A new species of *Cylindrobulla* from Phuket, Thailand, with a discussion of the systematic affiliation of the genus. Phuket Mar. Biol. Cent. Res. Bull. **52**: 1–11.
- Jensen, K.R. 1998. Anatomy of some opisthobranch molluscs from Phuket, Thailand, with a list of Opisthobranchia recorded from Thailand. Phuket Marine Biological Center Special Publication **18(2)**: 243–262.
- Jensen, K.R. 2009. Sacoglossa (Mollusca: Gastropoda: Opisthobranchia) from Singapore. Raffles Bull. Zool., Suppl. **22**: 207–223.
- Jensen, K.R. 2015. Sacoglossa (Mollusca: Gastropoda: Heterobranchia) from northern coasts of Singapore. Raffles Bull. Zool., Suppl. **31**: 226–249.
- Jensen, K.R., P. Kohnert, B. Bendell and M. Schrödl. 2014a. Life on a leaf: 3D-reconstruction and description of a new limapontioid sacoglossan (Gastropoda: Heterobranchia: 'Opisthobranchia') living on the seagrass *Halophila ovalis*. J. Moll. Stud. **80(5)**: 624–641. [DOI: 10.1093/mollus/eyu071]
- Jensen, K.R., P.J. Krug, A. Dupont and M. Nishina. 2014b. A review of taxonomy and phylogenetic relationships in the genus *Costasiella* (Heterobranchia: Sacoglossa), with a description of a new species. J. Moll. Stud. **80(5)**: 562–574. [DOI: 10.1093/mollus/eyu048]
- Krug, P.J., J.E. Vendetti, R.A. Ellingson, C.D. Trowbridge, Y.M. Hirano, D.Y. Trathen, A.K. Rodriguez, C. Swennen, N.G. Wilson and Á.A. Valdés. 2015. Species selection favors dispersive life histories in sea slugs, but higher per-offspring investment drives shifts to short-lived larvae. Syst. Biol. **64(6)**: 983–999. [<https://doi.org/10.1093/sysbio/syv046>]
- Krug, P.J., N.L.W.S. Wong, M.R. Medina, T.M. Gosliner and Á.A. Valdés. 2018. Cryptic speciation yields remarkable mimics: A new genus of sea slugs that masquerade as toxic algae (*Caulerpa* spp.). Zool. Scr. **47**: 699–713. [<https://doi.org/10.1111/zsc.12310>]
- McCarthy, J.B., P.J. Krug and Á.A. Valdés. 2019. Integrative systematics of *Placida cremoniana* (Trinchese, 1892) (Gastropoda, Heterobranchia, Sacoglossa) reveals multiple pseudocryptic species. Mar. Biodiv. **49**: 457–371. [<https://doi.org/10.1007/s12526-017-0812-2>]
- Marcus, E. deB.-R. 1982. Systematics of the genera of the order Ascoglossa (Gastropoda). J. Moll. Stud., Suppl. **10**: 1–31.
- Marcus, Ev. and Er. Marcus. 1960. Opisthobranchs from American Atlantic warm waters. Bull. Mar. Sci. **10**: 129–203.

- Mehrotra, R. and C.M. Scott. 2016. Species inventory of sea slugs (Gastropoda: Heterobranchia) for Koh Tao, Thailand, with 25 first records for Thai waters. *Mar. Biodiv.* **46**: 761–771. [DOI: 10.1007/s12526-015-0424-7]
- Mehrotra, R., M. Caballer Gutiérrez, C.M. Scott, S. Arnold, C. Monchanin and S. Chavanich. 2020. On the Plakobrachidae (Gastropoda, Sacoglossa) from soft sediment habitats of Koh Tao, Gulf of Thailand, with descriptions of two new species. *ZooKeys* **969**: 85–121. [DOI: 10.3897/zookeys.969.52941]
- Mikkelsen, P.M. 1998. *Cylindrobulla* and *Ascobulla* in the western Atlantic (Gastropoda, Opisthobranchia, Sacoglossa): Systematic review, description of a new species, and phylogenetic reanalysis. *Zool. Scr.* **27**: 49–71.
- Moro, L. and J. Ortea. 2015. Nuevos taxones de babosas marinas de las islas Canarias y de Cabo Verde (Mollusca: Heterobranchia). *Vieraea* **43**: 21–86.
- Rudman, W.B. 2004. *Costasiella nonatoi* Marcus & Marcus, 1960. In: Sea Slug Forum. Australian Museum, Sydney. Available from <http://seaslugforum.net/find/costnona>. (accessed on 16/10/2020).
- Swennen, C. 1998. Two new gastropods, *Elysia bangtawaensis* and *E. siamensis* from southern Thailand (Opisthobranchia, Sacoglossa, Elysiidae). *Bull. Zool. Mus. Univ. Amsterdam* **16(6)**: 33–39.
- Swennen, C. 2001. Two new sacoglossans (Gastropoda: Opisthobranchia) from Thailand. *Beaufortia Bull. Zool. Mus. University of Amsterdam* **51(3)**: 75–81.
- Swennen, C. 2007. *Costasiella coronata*, new species, and a revised diagnosis for the family Costasiellidae (Mollusca: Opisthobranchia: Sacoglossa). *Raffles Bull. Zool.* **55(2)**: 355–362.
- Swennen, C. 2011. Large mangrove-dwelling *Elysia* species in Asia, with descriptions of two new species (Gastropoda: Opisthobranchia: Sacoglossa). *Raffles Bull. Zool.* **59(1)**: 29–37.
- Swennen, C., R.G. Moolenbeck, N. Ruttanadaku, H. Hobbelink, H. Dekker and S. Hajisamae. 2001. The Molluscs of the Southern Gulf of Thailand. Thai Studies in Biodiversity No. 4. The Biodiversity Research and Training Program, Bangkok, Thailand. 210 pp.

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