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# Sacoglossa (Mollusca: Gastropoda: Heterobranchia) from northern coasts of Singapore

Kathe R. Jensen

Abstract. This paper describes three new species and several new records of Sacoglossa, the sap-sucking sea slugs, (Mollusca: Gastropoda: Heterobranchia) from the northern shores of Singapore. One new species, *Berthelinia singaporensis* represents the first record of the bivalved family Juliidae in Singapore. The second new species, *Volvatella maculata*, was described previously as *Volvatella* sp. Two other shelled species, *Ascobulla fischeri* and *Volvatella ventricosa*, both originally described from Australia, are also first records from Singapore, as is *Lobiger viridis*, a widespread Indo-west Pacific species. *Elysia tomentosa*, also originally from Australia, is another new record for Singapore. Based on a single, tiny specimen from Changi Point, a new genus and species of limapontiid is named *Kerryclarkella inconspicua* and provisionally described. New anatomical details are given for *Volvatella vigourouxi, Elysia bangtawaensis, E. ornata, E. singaporensis, E. verrucosa* and *Costasiella* cf. *kuroshimae*.

Key words. Sacoglossa, anatomy, new species, taxonomy, Singapore

#### INTRODUCTION

The Sacoglossa is a highly specialised group of sap-sucking gastropods, previously included in the molluscan sub-class Opisthobranchia. Recent research on phylogeny has shown that Opisthobranchia is not a monophyletic group, but relationships among the taxa traditionally included in that group remain open for discussion (Dinapoli & Klussmann-Kolb, 2010; Jörger et al., 2010; Schrödl et al., 2011; Kocot et al., 2013; Wägele et al., 2014). The Sacoglossa is one of the traditional opisthobranch taxa that have been excluded from the group, but its relationship to the newly erected Panpulmonata remains unclear (Jörger et al., 2010; Dayrat et al., 2011; Zapata et al., 2014). A major problem in these phylogenetic analyses is the taxon sampling and the fact that a large proportion of species remain undescribed and unnamed. Also, recent molecular analyses have shown a high proportion of cryptic species or "species complexes" within most traditional opisthobranch taxa (Krug et al., 2011, 2013; Jörger et al., 2012; Ornelas-Gatdula et al., 2012; Carmona et al., 2011, 2014; Takano et al., 2013; Espinoza et al., 2014). It is therefore important to continue field collection and describe new species to obtain a stable classification of heterobranch gastropods.

Sacoglossans are characterised by a muscular, suctorial pharynx and a uniseriate radula composed of an ascending (dorsal) limb, a descending (ventral) limb and an ascus

Zoological Museum (Natural History Museum of Denmark), Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark; Email: krjensen@snm.ku.dk

© National University of Singapore ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print) containing used teeth either rolled into a spiral still attached to the radular ribbon, or in an irregular heap dislodged from the radular ribbon. The most recently formed tooth is usually not mineralised and appears indistinct and soft; this tooth is called a ghost tooth. The teeth consist of a base, articulating with the tooth in front and behind, and a cusp of variable shape, which usually interlocks with the tooth in front. The tooth located at the tip of the odontophore is called the leading tooth, and is usually the only tooth involved in piercing the cell wall of the food algae. The oldest teeth, formed in the larval stage, do not have cusps and are called preradular teeth. Tooth shape and size are important characters for distinguishing species and also have phylogenetic importance (Jensen, 1996b). Other characters used for taxonomic purposes have been summarised in Jensen (1996b).

Singapore has a rich marine flora of siphonalean green algae (Pham et al., 2011), the preferred food of Sacoglossa. The northern coast along the Johor Strait also has a high variety of habitats, ranging from relatively high energy sandy beaches at Changi Point to sheltered mangroves at Sungei Buloh, thus offering opportunities to collect sacoglossans with different food and habitat requirements.

During the international workshop at Pulau Ubin in Johor Strait, Singapore in October 2012 a total of 17 species of Sacoglossa were collected. This included the first record of the bivalved family Juliidae and the shelled genus *Ascobulla*. Furthermore, three species and one genus are new to science and are here named and described. Nine of the species have been recorded and anatomically described from Singapore previously (Jensen, 2009). Additional information on distribution, anatomy and/or biology of these species is also given. One additional species, also a new record for

Singapore, was collected shortly after the workshop and has been included in the present paper.

#### MATERIAL AND METHODS

A few specimens were hand-collected in the field, but the majority were found by collecting different seaweeds in plastic bags and sorting through these with a magnifying lens at the outdoor sorting laboratory set up at OBS Pulau Ubin. Specimens were kept alive in small containers and observed under a dissecting microscope. Specimens were also routinely photographed through the microscope, sometimes only after relaxing in MgCl2. In a few cases short video sequences were also made. Subsequently specimens were preserved following the procedure of Jensen (2009). Anatomy was studied by fine dissection. Digital pictures were taken at various stages of dissection to document the position of individual structures before taking them apart. Radulae were prepared for SEM by dissecting out the pharynx and dissolving the musculature in NaOH-solution. Radulae were then rinsed, dehydrated and dried as described in Jensen (2009) and placed on SEM stubs. Penial stylets, where present, were prepared for SEM by dissecting out the penis, dehydrating in ethanol followed by acetone (Jensen, 2009), after which it was air-dried and placed on an SEM stub. Specimens were observed in a JEOL JSM-6335F Scanning Electron Microscope. For the larger and most common species samples were taken out for later molecular analysis, but for several species only a single specimen was found and this was preserved for morphological description only.

#### **TAXONOMY**

#### **VOLVATELLIDAE Pilsbry, 1895**

#### Ascobulla Marcus, 1972

Type species – *Ascobulla ulla* (Marcus & Marcus, 1970) by original designation.

This genus was separated from *Cylindrobulla* by possessing a typical sacoglossan radula with large articulating teeth, including a rod-like preradular tooth (Marcus, 1972). At the same time the Japanese species *Cylindrobulla japonica* Hamatani, 1969, was also transferred to the genus *Ascobulla*. Marcus (1972) maintained that both genera should remain in the family Cylindrobullidae within the order Cephalaspidea. Most other authors included at least *Ascobulla* (Jensen, 1996a, b) or both genera in the Sacoglossa (Mikkelsen, 1998), and this has been confirmed by molecular data (Maeda et al., 2010; Neusser et al., 2011), although *Cylindrobulla* still has its own family, Cylindrobullidae, whereas *Ascobulla* belongs in the family Volvatellidae (Jensen, 1996b).

# Ascobulla fischeri (Adams & Angas, 1864) (Figs. 1A, 2, 3)

Material examined. 1 specimen, shell length 4.2 mm, shell width 2 mm (dissected), Changi Point (station SW33),

18 October 2012, from fine sediment around rhizoids of *Caulerpa* spp.

**Colour alive.** The only visible colouration is the orange colour of digestive gland visible through visceral epidermis, mantle and transparent shell (Fig. 1A). Head and foot all white.

External features. Shell very fragile; it cracked from contraction of adductor muscle when animal tried to burrow into the sediment in a shallow petri-dish in the laboratory. Apical area filled with detritus entrapped in mucus exuded from mantle cavity, hence protoconch could not be separated in preserved specimen. Cephalic shield consists of two separate lobes with distinct groove in between (Fig. 2A). Narrow ciliated groove on right side, extending from female genital papilla to mouth area (Fig. 2C). This is a spawn groove in which eggs are transported during spawning. Foot short and rounded, somewhat narrower posteriorly (Fig. 2B) and separated from the neck by a groove. Eyes not visible from the outside.

Mantle organs. Gill forms conspicuous broad band of longitudinal folds extending across mantle cavity, forming a >360° spiral with the innermost part located under the infrapallial lobe and reflected inner lip of shell (Fig. 2A, B). Shell adductor muscle attached at anterior right corner of mantle fold, running diagonally across neck attached to lower edge of diaphragm separating cephalic part of body from visceral mass. Oval osphradium located at posterior margin of adductor muscle on mantle fold (Fig. 3A). Pericardium located in front of gill. Auricle thin-walled, ventricle small, muscular, heart-shaped, with an aorta descending anteriorly into visceral mass. Behind the gill is a band containing numerous white glands, probably corresponding to the hypobranchial gland. Behind this is a ciliated band, and at the posterior end of the mantle fold is a second band of white glands. The mantle margin contains the shell gland, and along the narrow part of the shell aperture as well as along the infrapallial lobe, is a series of glandular bosses. The floor of the mantle cavity contains the female genital papilla at the right anterior end (Fig. 2C). The left anterior end contains the white mucus gland of the female reproductive system. The majority of the mantle floor covers the digestive gland, which extends into the infrapallial lobe. The intestine runs for a short distance on the surface of the mantle floor and the anus is located in front of the ventral ciliated ridge, which is located opposite the dorsal ciliated band. Both these bands continue into the upper whorls of the shell.

**Internal anatomy.** Oral tube short. Pharynx large, muscular with short, indistinctly demarcated, collar-like, muscular pharyngeal pouch posteriorly. Odontophore located rather far towards posterior end of pharynx. Paired salivary glands very long and coiling around wide, transparent anterior oesophagus. Large salivary reservoirs located next to exit of oesophagus from pharynx. Posterior ends of salivary glands firmly attached to oesophageal pouch in preserved specimen (Fig. 3B), but there are no separate oesophageal glands.

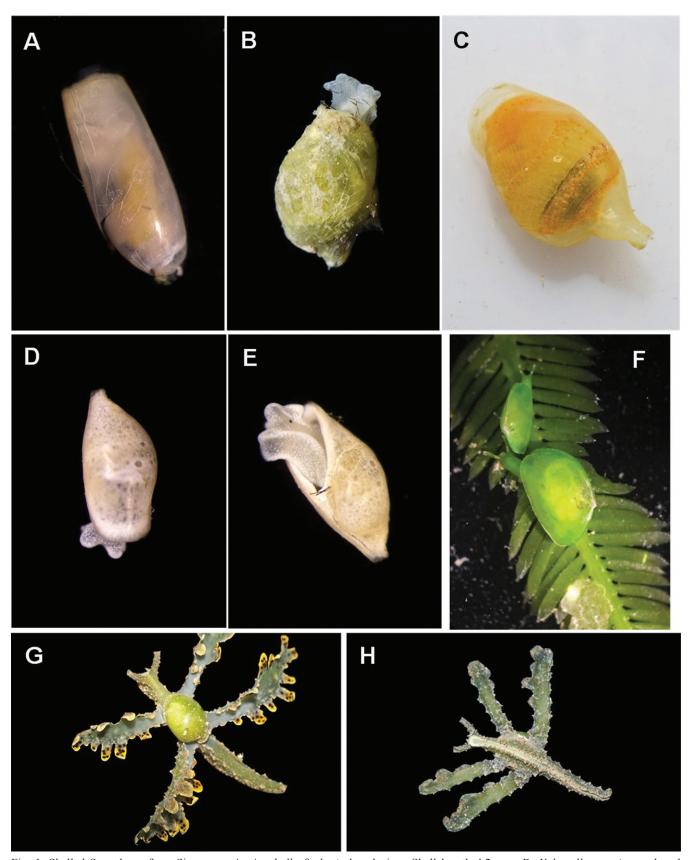


Fig. 1. Shelled Sacoglossa from Singapore. A, *Ascobulla fischeri*, dorsal view. Shell length 4.2 mm; B, *Volvatella ventricosa*, dorsal view. Shell length 7.5 mm; C, *Volvatella vigourouxi*, dorsal view. Shell length 12.5 mm; D, *Volvatella maculata*, new species, dorsal view. Shell length 5 mm; E, same, ventral view; F, *Berthelinia singaporensis*, new species, two specimens (shell lengths approximately 2.5 and 3 mm) on Caulerpa frond; G, *Lobiger viridis*, dorsal view with open parapodia. Shell length 14.5 mm. H, Same, ventral view. Photographs by Rene Ong.

Oesophageal pouch immediately in front of diaphragm, and posterior oesophagus, which penetrates the diaphragm, much narrower than anterior part. Nervous system with paired cerebro-pleural ganglia connected by long commissure and paired pedal ganglia are closely adjacent. Distinct double connectives between cerebro-pleural and pedal ganglia on either side. Visceral loop long, containing three ganglia: a small sub-oesophageal ganglion on the left side towards ventral surface of oesophagus, an abdominal ganglion closely attached to diaphragm, and a supra-oesophageal ganglion, slightly smaller than abdominal one, and located towards dorsal surface of oesophagus on right side. It sends a nerve to the osphradium. Connective from left cerebro-pleural to sub-oesophageal ganglion shorter than that from right cerebro-pleural to supra-oesophageal ganglion. Penis is long (1.6 mm), almost cylindrical (diameter about 0.2 mm), forming a U-turn and tapering gradually towards tip (Fig. 3C). Penial stylet completely enclosed in penial musculature, but presumably eversible (Fig. 3D).

**Observations on living specimen.** When placed in a petridish with sand from the beach, *A. fischeri* attempted to dig into the sediment. The lobes of the cephalic shield and the foot formed a cone and extended into the sediment, which unfortunately was not deep enough for the animal to drag the shell and visceral mass into it. The shell cracked during the attempt and after that the animal had difficulties moving

around in the plastic container. The pumping movements of the shell caused by contracting the shell adductor muscle were no longer efficient to ventilate the gill.

Remarks. Two species of Ascobulla are known from the Indo-west Pacific region. The best known anatomically is A. fischeri (Adams & Angas, 1864), which was re-described by Jensen & Wells (1990). For the other species, A. japonica (Hamatani, 1969) only external morphology and radula have been described. For several of the species described as Cylindrobulla only shells are known and thus it is not possible to assign them to this genus or to Ascobulla. Anatomy has also been described for the Caribbean Ascobulla ulla (Marcus & Marcus, 1970) (Marcus & Marcus, 1956, 1970, Marcus, 1972, Jensen, 1996a, Mikkelsen, 1998), and in part for A. fragilis (Jeffreys, 1856) from the Mediterranean (Jensen, 2011). The present specimen is tentatively identified as A. fischeri because the anatomy is almost identical. However, as the anatomy of the other Indo-Pacific species is unknown, the identification remains tentative.

#### Volvatella Pease, 1860

Type species – Volvatella fragilis Pease, 1860 (by monotypy).

The original description of this genus was very short and without illustrations. There is a type specimen in the Natural

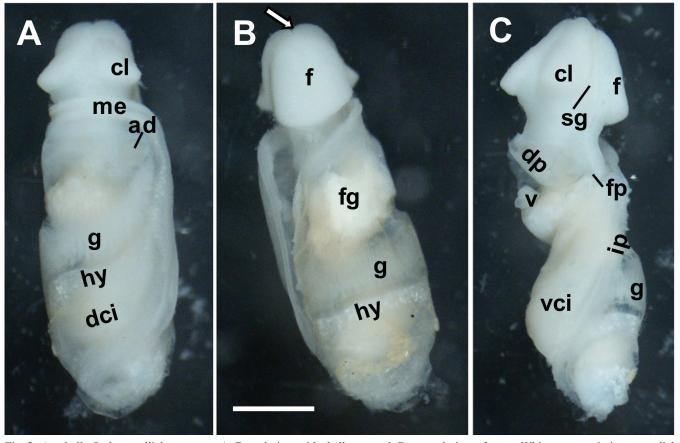


Fig. 2. *Ascobulla fischeri*, pallial structures. A, Dorsal view with shell removed; B, ventral view of same. White arrow pointing to medial notch between cephalic lobes; C, Lateral view after removal of shell and mantle fold. Legend: ad – adductor muscle; cl – posterior right lobe of cephalic shield; dci – dorsal ciliated band; dp – diaphragm; f – foot; fg – female gland mass; fp – female genital papilla; g – gill; hy – hypobranchial gland; ip – infrapallial lobe; me – mantle edge; sg – spawn groove; v – ventricle of heart; vci – ventral ciliated ridge. Scale bar = 1 mm.

History Museum in London, but it is in so poor a condition that it is not possible to assign it to any species for which soft parts known. The genus is characterised by having a posterior shell spout of varying length. Some species have green mantle folds, but most are white or have yellow, orange or red spots in variable numbers and positions. A cephalic shield is apparently absent, but whether this is a primary absence or a secondary loss is unknown.

# Volvatella ventricosa Jensen & Wells, 1990 (Fig. 1B)

**Material examined.** 1 specimen, Tuas (station SW16) on *Caulerpa* spp., 16 October 2012.

**Colour alive.** Shell appears green due to colour of mantle fold (Fig. 1B). Head and foot white.

**External features.** Shell length 7.5 mm and maximum width 4 mm. Posterior shell spout located on right side of shell; very

short, barely extending beyond inflated body whorl. Deep "umbilicus" where aperture narrows. No cephalic shield, just a pair of short triangular processes dorsally on head and anteriorly a pair of broad, grooved tentacles, joining at the bases in a median notch. Eyes visible laterally beneath anterior tentacles. Foot short and broadly triangular.

Remarks. This is a new record for Singapore. With only one specimen available the internal anatomy has not been examined. Two species with green mantles are known from the Indo-west Pacific region: *Volvatella viridis* Hamatani, 1976 from Japan and *V. ventricosa* Jensen & Wells, 1990 from Australia. *Volvatella viridis* has subsequently been found in Australia (Rudman, 2002: http://www.seaslugforum.net/find/7452) and Hong Kong (Jensen, 2003), and *V. ventricosa* has been reported from Hawaii (http://seaslugsofhawaii.com/species/Volvatella-ventricosa-a.html). The two species are about the same size, but *V. ventricosa* has a shorter shell spout, which is also more skewed to the right side of the shell, and the ventral part of the body whorl is more inflated

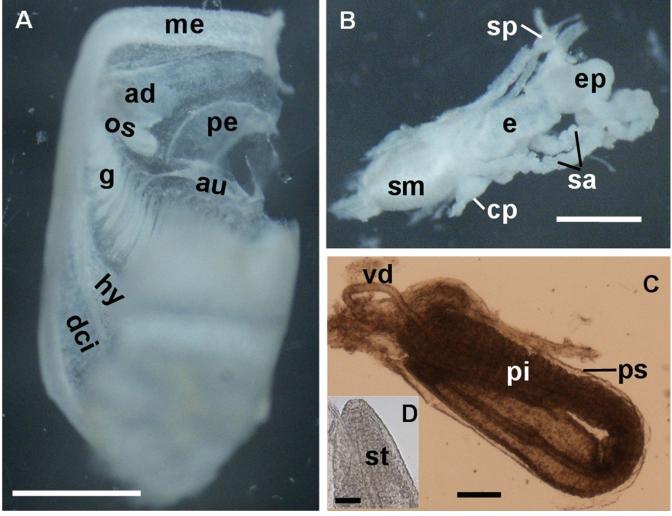


Fig. 3. Ascobulla fischeri, anatomy. A, Cut off mantle fold viewed from inside; B, Pharyngeal complex; C, Penis; D, Tip of penis with stylet inside. Legend: ad – adductor muscle; au – auricle of heart; cp – cerebropleural ganglion; dci – dorsal ciliated band; e – oesophaus; ep – oesophageal pouch; g – gill; hy – hypobranchial gland; me – mantle edge; os – osphradium; pe – pericardium; pi – penis; ps – penial sheath; sa – salivary glands; sp – supra-oesophageal ganglion; sm – dorsal septate muscle of pharynx; st – penial stylet; vd – vas deferens. Scale bars = 1 mm [A]; 0.5 mm [B]; 0.1 mm [C]; 50 µm [D].

than in *V. viridis*. Several species of *Volvatella* are only known from their shells and hence the colours of the mantle of the living animals remain undescribed.

#### Volvatella vigourouxi (Montrouzier in Souverbie, 1861) (Fig. 1C)

**Material examined.** 16 specimens (2 dissected), Chek Jawa (station SW42), 19 October 2012, from *Caulerpa* spp. collected by volunteers. 1 specimen, Sekudu (SW24), 17 October 2012 (Toh Chay Hoon).

Internal anatomy. As the species was described from Singapore before (Jensen, 2009), only a few additional comments on the internal anatomy will be added here. Shell length varied from 2.5 mm to 12 mm and shell width from 1.2 mm to 6.5 mm. A specimen with shell length 6 mm dissected. Protoconch completely covered by callus and hidden inside hollow columella. Pharynx with rather flat dorsal septate muscle. Radula (Table 1) and teeth were described previously (Jensen, 2009). Thin-walled oesophagus extending across large muscular pharyngeal pouch, and circum-oesophageal nerve ring located ventrally of pharyngeal complex. Paired salivary glands long and tubular, entering pharynx laterally to oesophagus. Oesophageal pouch behind circum-oesophageal nerve ring, and shortly behind this oesophagus passes through diaphragm separating head-foot from visceral mass. Unarmed penis with long extensible flagellum completely retracted in dissected specimens.

Remarks. This species was also found in 2006 in Singapore (Jensen, 2009). It appears to be very common in certain places. In 2006 fourteen specimens were collected at Pulau Tekukor, and in 2012 sixteen specimens were collected at Chek Jawa. Sizes of the specimens differ widely, but were within the same range in 2006 and 2012, indicating that reproduction takes place throughout the year.

# Volvatella maculata new species (Figs. 1D, E, 4, 5A–C)

Volvatella sp. - Jensen, 2009: p. 208, figs 1D, E, 3E

**Material examined.** Holotype: 1 specimen, shell length (including spout) 4 mm, shell width 2 mm, Chek Jawa, 17 October 2012 (ZRC.MOL.5788). Paratypes (both dissected): 1 specimen, same locality and date as holotype; 1 specimen, Sekudu (station SW24), 17 October 2012.

**Shell.** Shell transparent and extremely fragile. Periostracum yellowish, transparent, and rather tough. Shell breaking into numerous fragments when attempting to separate soft parts. Some fragments remain firmly attached to mantle. Anterior part of aperture wide, accommodating head and foot of animal when retracted. Posteriorly outer lip overlapping upper whorls forming short posterior spout. Deep umbilicus, and inner lip covered by thin callus secreted by infrapallial lobe. Protoconch completely hidden in sunken spire, covered by callus and extremely fragile.

Colour alive. Colour pattern was described for the single specimen collected in 2006 (Jensen, 2009). General body colour white. Mantle with numerous circular, transparent spots of variable sizes (Fig. 1D). These are visible through transparent shell, but disappear in preserved specimens. Eyes visible laterally in groove formed by anterior cephalic lobes (Fig. 1E).

External features. This has been described for the single specimen collected in 2006 (Jensen, 2009). Head and foot can be completely retracted into shell. No cephalic shield, just two pairs of highly motile cephalic lobes. Anterior pair grooved and larger than more dorsally positioned, triangular, posterior pair. Foot short and narrow, rounded posteriorly and with broad, rounded anterior lobes (Fig. 1E). Ciliated spawn groove running from female genital papilla towards mouth area. Gill forming a band of longitudinal lamellae across mantle roof (Fig. 4A) and underneath infrapallial lobe. Shell adductor muscle attached to mantle fold at right anterior corner, traversing neck along diaphragm separating cephalic region from visceral mass, and attaching ventrally to inner lip of shell just in front of umbilicus. Small osphradium at dorsal attachment of adductor muscle (Fig. 4A).

Internal anatomy. Pharynx with large, almost spherical, muscular pharyngeal pouch (Fig. 4B, C), asymmetrically attached to pharynx posteriorly. Length of pharynx (excluding pouch) 0.4 mm, height behind ascus 0.3 mm. Diameter of pharyngeal pouch 0.4 mm. Radula with 5 teeth in ascending limb, 13 in descending limb and one rodshaped preradular tooth (Fig. 4D, 5B). Length of leading tooth 81 µm of which base was 26 µm. Length of preradular tooth 30µm. Radular teeth are elongate with narrow triangular cusps equipped with coarse denticles along distal half of edges (Fig. 5A). Base rather short and low. Penis located in front of pharyngeal pouch (4B), dorsal to pharynx; almost cylindrical and equipped with a thin, flexible, almost straight stylet (Figs 4E, 5C). Vas deferens connecting to an almost spherical, muscular seminal vesicle (Fig. 4E). Female gland complex (mucus and albumen glands) located in anterior left part of visceral mass (Fig. 4B).

**Remarks.** A single specimen of this species was collected in 2006 and described externally as *Volvatella* sp. (Jensen, 2009). This species occurs in the same habitats as *V. vigourouxi*, but is much rarer. It differs from *V. vigourouxi* in colouration, more slender shape of radular teeth and the presence of a penial stylet. Jensen (1997b) compared the species of *Volvatella* known at the time. The teeth of the present species are most similar to those of *V. cf. candida* Pease, 1868, as described by Jensen (1997a), and this species also had a penial stylet. However, the shell is very different, a posterior spout being nearly absent, whereas the present species has a distinct spout. Table 1 compares the known species of *Volvatella*. The present species is different from all other known species and is described as new to science.

**Etymology.** The specific epithet *maculata* refers to the circular spots on the mantle of this species.

#### JULIIDAE E.A. Smith, 1885

#### Berthelinia Crosse, 1875

Type species – *Berthelinia elegans* Crosse, 1875 by monotypy.

The discovery of living bivalved sacoglossans, described as *Tamanovalva limax* Kawaguti & Baba, 1959, in Japan created a sensation in malacology and the subsequent transfer of a whole family, Juliidae, from Bivalvia to the Sacoglossa

(Keen & Smith, 1961) spawned the collection of several living species of this family from different parts of the world, e.g., Australia (Burn, 1960, 1965), Gulf of California (Keen, 1960), Hawaii (Kay, 1962), Jamaica (Edmunds, 1962), India (Rao, 1965), Fiji (Burn, 1966). The similarity of the Japanese species and the fossil, Eocene genus *Berthelinia* was soon pointed out (Keen, 1960), and also the genus *Edenttellina* was included in the synonymy (Cox & Rees, 1960). However, some scientists maintain *Tamanovalva* as a valid genus (Burn, 1998). *Berthelinia* species have a thin bivalve shell with the protoconch located along the dorsal

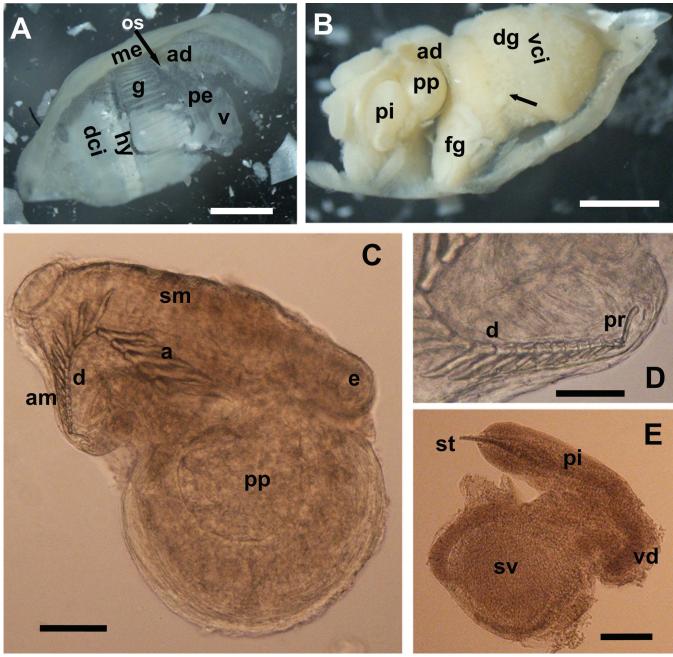


Fig. 4. *Volvatella maculata* new species, anatomy. A, cut off mantle fold viewed from inside; B, body after removal of shell, mantle fold and diaphragm (latero-dorsal view). Arrow points to anus; C, pharynx, partly dissolved in NaOH; D, close-up of descending limb of radula and rodshaped preradular tooth; E, penial complex. Legend: a – ascending limb of radula; ad – adductor muscle; am – ascus-muscle; d – descending limb of radula; dci – dorsal ciliated band; dg – digestive gland; e – oesophagus; fg – female gland mass; g – gill; hy – hypobranchial gland; me – mantle edge; os – osphradium; pe – pericardium; pi – penis; pp – pharyngeal pouch; pr – rodshaped preradular tooth; sm – dorsal septate muscle of pharynx; st – penial stylet; sv – seminal vesicle; v – ventricle of heart; vci – ventral ciliated ridge; vd – vas deferens. Scale bars = 1 mm [A, B]; 0.5 mm [C, E]; 50 μm [D].

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Table 1. Comparison of species of *Volvatella*. Legend:  $\mathbf{a}$  – teeth in ascending limb of radula;  $\mathbf{d}$  – teeth in descending limb of radula;  $\mathbf{pr}$  – preradular teeth.

Species	Pharynx	Radula	Penis	Reference
Volvatella fragilis Pease, 1860	?	?	?	
Volvatella vigourouxi (Montrouzier, 1861)	Pharynx about same size as pharyngeal pouch	11a, 15d	tubular stylet (Baba); unarmed (Jensen)	Baba, 1966; Jensen, 2009
Volvatella candida Pease, 1868	Large, with larger pharyngeal pouch	5(+1)a, 20d, 1pr	short stylet	Jensen, 1997a
Volvatella pyriformis Pease, 1868	?	?	?	
Volvatella cincta Nevill &Nevill, 1869	?	?	?	
Volvatella laguncula Sowerby, 1894	?	6a, 15d, 1pr	unarmed	Thompson, 1979
Volvatella kawamurai Habe, 1946	?	?	?	
Volvatella elioti (Evans, 1950)	Large pharyngeal pouch	?	?	Evans, 1950
Volvatella evansi (Kay, 1961)	?	?	?	
Volvatella ficula Burn, 1966	?	6a, 4+xd	?	Burn, 1966
Volvatella ayakii Hamatani, 1972	?	8-10a, 15-19d, 1pr	unarmed	Hamatani, 1972
Volvatella viridis Hamatani, 1976	?	6-7a, 16d, 1pr	unarmed	Hamatani, 1976
Volvatella bermudae Clark, 1982	Large, asymmetrical pharyngeal pouch	8a, 19d, 1pr	retractable stylet	Clark, 1982
Volvatella ventricosa Jensen & Wells, 1990	Pharyngeal pouch larger than pharynx	4(+1)a, 14d, 1pr	short stylet	Jensen & Wells, 1990
Volvatella angelinianae Ichikawa, 1993	?	?	?	
Volvatella australis Jensen, 1997	Pharyngeal pouch smaller than pharynx	7a, 17d, 1pr	unarmed	Jensen, 1997a
Volvatella maculata new species	Pharyngeal pouch slightly larger than pharynx	5a, 13d, 1pr	long, thin, flexible stylet	Present study

edge of the left valve, rolled rhinophores, a long, narrow foot and eyes on a tiny prominence behind the rhinophores.

# Berthelinia singaporensis new species (Figs. 1F, 5D, E, 6, 7)

Material examined. Holotype: 1 specimen, shell length 4 mm, height 2.7 mm, Chek Jawa 19 October 2012 (ZRC. MOL.5789). Paratypes: 5 specimens (2 dissected), Tuas (station SW16), 16 October 2012; 2 specimens (dissected), Chek Jawa, 17 October 2012; 6 specimens (2 dissected), Chek Jawa, 19 October 2012 (SW42).

**Shell.** Bivalved shell broadly rounded anteriorly, more narrowly rounded posteriorly. Protoconch located in posterior half of left valve (Fig. 6A). Protoconch with 1.5 whorls and tilted towards right valve. External surface of shell smooth and glossy with indistinct concentric growth lines and fine radial striae (Fig. 6A, C); internally with a silky gloss and more distinct radial striae than on outer surface (Fig. 6B, D). Tallest point of shell in anterior half, in front of protoconch.

Ligament or hinge line a thickened rim on either side of protoconch on left valve and in corresponding site of right valve. Left valve hinge line forking posteriorly and with a small tooth anteriorly (Fig. 6B), fitting into corresponding anterior fork and posterior tooth on right valve. Shell lengths of present specimens between 2.5 mm and 6 mm.

Colour alive. Shell and soft parts appear bright green. Shell retaining some green colour after removal of soft parts, but most green coloration due to pigmentation of mantle fold and visceral mass. Protoconch white (Fig. 7A). Tips of rhinophores sprinkled with white dots (Fig. 1F). Some specimens with sprinkling continuing down rhinophores. Small black eyes located in small transparent protuberance behind rhinophores.

**External features.** Animal can be completely withdrawn into shell. Head-foot region narrow; thin foot-sole slightly wider than head and neck. Foot sole extending posteriorly below visceral mass forming a short pointed tail. Anterior foot margin deeply notched centrally forming highly motile

pedal lobes. Anterior foot corners rounded. Rhinophores rolled, with external groove. On right side of neck and head a ciliated spawn groove extending from female genital papilla inside mantle cavity to mouth area. Due to contracted state of preserved specimens, penial opening not visible externally on the right side.

Pallial structures. Osphradium indistinct, close to adductor muscle. Gill forming a broad band of longitudinal lamellae. Heart located dorsally in mantle cavity, anterior to gill. Behind gill is a glandular band and a narrow ciliated ridge. Mantle edge rather thick and probably glandular.

**Internal anatomy.** Pharynx tall and rather narrow. Length of pharynx in 4 mm specimen 0.8 mm and height 0.6

mm. Radular sac where new teeth are formed protruding posteriorly under the oesophagus (Fig. 7B). Salivary glands apparently absent, and pharyngeal pouches are simple tubules with large lumen, entering pharynx next to oesophagus. Radular teeth blade-shaped with lateral flanges having a row of hair-like denticles along sides (Fig. 5D); bases short and stout, tips with a small knob but not bifid. Radula of one specimen with 10 fully formed teeth plus one ghost tooth in ascending limb, 26 teeth in descending limb plus one long rod-shaped preradular tooth (Fig. 7C); another specimen with 11 fully formed plus one ghost teeth in ascending limb, 30 teeth in descending limb plus one rod-shaped preradular tooth. Leading tooth 118 µm long of which the base was 25 µm. Posterior part of descending limb curls up in the ascus. Penis with flexible stylet having peculiar lateral flanges

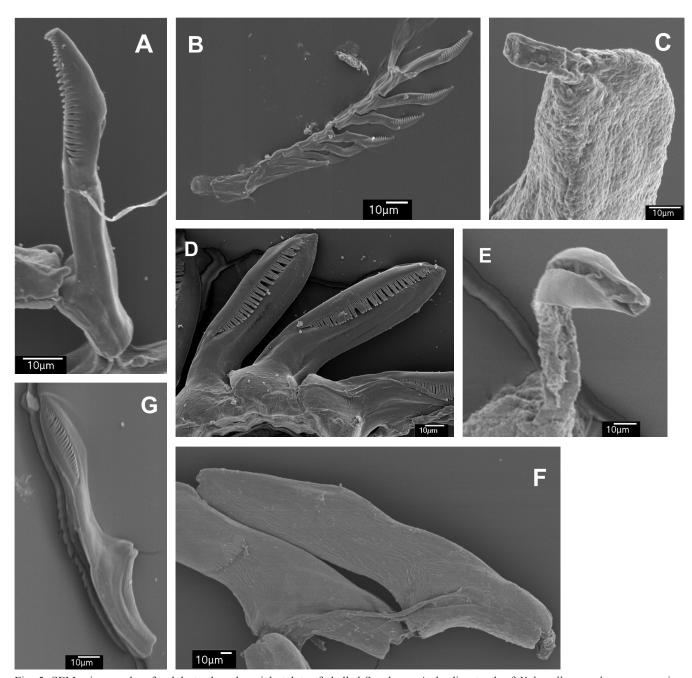


Fig. 5. SEM micrographs of radula teeth and penial stylets of shelled Sacolossa. A, leading tooth of *Volvatella maculata* new species; B, posterior end of descending limb of radula of same; C, tip of penis with stylet of same; D, teeth of *Berthelinia singaporensis*, new species; E, penial stylet of same. F, teeth from tip of radula of *Lobiger viridis*. G, tooth from ascus of same.

(Figs 5E, 7D). Bursa copulatrix immediately behind female genital papilla.

**Observations on living animals.** The animals moved around in small dishes in the laboratory for a few days, but apparently the *Caulerpa* that was used for food, turned bad and the animals became moribund. The development of a single egg mass that had been deposited could not be traced as the algae with the attached egg mass had to be discarded. The egg mass was flat, without discernible whorls, containing more than 200 eggs.

**Remarks.** This is a new record of the genus and family from Singapore. Externally this species is very similar to B. limax (Kawaguti & Baba, 1959) as well as to B. babai (Burn, 1965) and B. darwini Jensen, 1997. However, penial armature is different. The penial stylet is most similar to that of B. australis (Burn, 1960) (as Midorigai australis) (Gascoigne, 1974, 1993). Externally the latter is rather different from all other species of Berthelinia (Burn, 1960, 1965, 1966; Baba, 1961; Sarma, 1975; Jensen, 1997a, b). Previous descriptions of anatomy of Berthelinia species have always included a pair of muscular pharyngeal pouches in addition to salivary glands. In the present species pharyngeal pouches are thin-walled, and salivary glands appear to be absent. Table 2 compares the anatomy of known species of Berthelinia. Unfortunately the anatomy of the species described from India (Sarma, 1975) is unknown. The present

species differs from all the known species and is therefore described as new to science.

**Etymology.** *Berthelinia singaporensis* refers to the species being discovered first in Singapore.

#### OXYNOIDAE H. Adams & A. Adams, 1854

#### Lobiger Krohn, 1847

Type species – *Lobiger philippii* Krohn (by monotypy). Synonym – *L. serradifalci* (Calcara, 1840)

Lobiger viridis Pease, 1863 (Figs. 1G, H, 5F, G, 8)

Lobiger sp. Pease, 1861 Lobiger picta Pease, 1868: pp. 75–76, pl. 8, fig. 3.

Material examined. 1 specimen collected on 14 December 2012 at Changi East (Rene Ong); 1 specimen (dissected) collected on 26 April 2013 at Pulau Tekukor (Rene Ong).

**Shell.** Shell length of largest (dissected) specimen 14.5 mm. Shell covers only visceral mass though head can be almost completely retracted into it. Outer lip greatly flared and spire completely hidden under callus of inner lip (Fig. 8A, B).

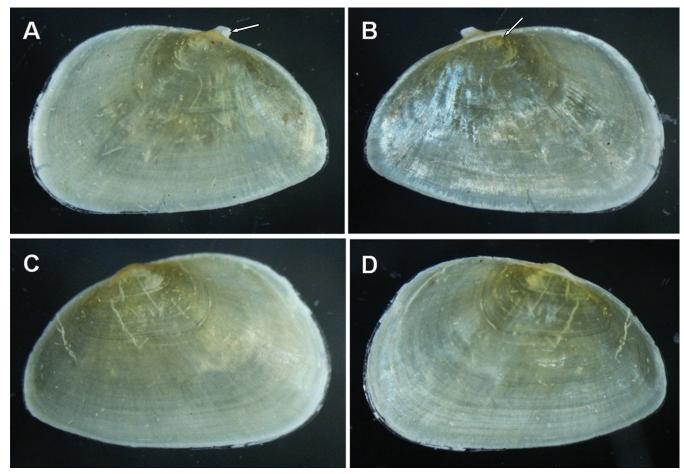


Fig. 6. Shell valves of *Berthelinia singaporensis* new species. A, left valve, external surface. Arrow points to protoconch; B, left valve, internal surface. Arrow points to hinge tooth; C, right valve, external surface; D, right valve, internal surface. Shell length: 4.3 mm.

Table 2. Comparison of species of *Berthelinia*. Legend:  $\mathbf{a}$  – teeth in ascending limb of radula;  $\mathbf{d}$  – teeth in descending limb of radula;  $\mathbf{pr}$  – preradular teeth.

Species	Pharynx	Radula	Penis	Reference
Berthelinia schlumbergeri Dautzenberg, 1895	?	?	?	
Berthelinia typica (Gatliff & Gabriel, 1911)	?	6a, 23d; teeth smooth with bifid tips	Long, curved, flexible stylet with basal spur	Baba, 1961; Gascoigne, 1974
Berthelinia chloris Dall, 1918	?	?	?	
Berthelinia corallensis Hedley, 1920	?	?	?	
Berthelinia limax (Kawaguti & Baba, 1959)	Paired pharyngeal pouches	5–7a, 30–35d	Unarmed	Baba, 1961
Berthelinia australis (Burn, 1960)	?	5a, 34d, 1pr	Long, flexible stylet with vane	Burn, 1960; Gascoigne, 1974; Gascoigne & Sartory, 1974
Berthelinia caribbea Edmunds, 1963	Dorsal pouch on pharynx plus large paired crops	5–6a, 19–26d	unarmed?	Edmunds, 1963
Berthelinia pseudochloris Kay, 1964	?	?	?	
Berthelinia babai (Burn, 1965)	?	9a, 32d, 1pr	?	Burn, 1960; Gascoigne & Sartory, 1974
Berthelinia fijiensis (Burn, 1966)	Cylindrical with short pouches	5a, 25–30d	?	Burn, 1966
Berthelinia ganapati Sarma, 1975	Cylindrical with short, slender crops	7a, 35d	?	Sarma, 1975
Berthelinia waltairensis Sarma, 1975	Cylindrical with short slender crops	7a, 25d	?	Sarma, 1975
Berthelinia rottnesti Jensen, 1993	Short, muscular pharyngeal pouches	4–6a (?1 ghost), 22–23d, 1pr	Unarmed	Jensen, 1993
Berthelinia darwini Jensen, 1997	Short pharyngeal pouches	7a, 20–24d, 1pr	Long, coiled stylet	Jensen, 1997a,b
Berthelinia singaporensis new species	Thin-walled pouches	10–11a (+ 1 ghost), 26–33d, 1pr	Long stylet with flexible flanges	Present study

Colour alive. General body colour green (Fig. 1G, H). Papillae light brown as are tips of rhinophores. Along foot margin a row of dark brown or bluish spots. These also surround the mouth area, tentacular lobes and mantle edge. Inside of parapodia strikingly coloured. Lateral lobes bright orange with black spots. Outside of lobes pale brown.

**External features.** The dissected specimen was about 30 mm long preserved, including the tail. Four elongate parapodia, usually held vertically or somewhat posteriorly and folded so the inner surface is invisible. Parapodial margins deeply lobed. Rhinophores long and rolled with flared tips; medial margin continuing ventrally to form a folded process, almost like oral tentacles. Entire body surface covered by irregular papillae. Inner surface of parapodia and mantle smooth. Foot sole narrow and smooth, extending to long, muscular tail.

Anterior foot corners rounded and only slightly wider than remaining foot sole.

Internal anatomy. Pharynx with flat dorsal septate muscle (Fig. 8C). Anteriorly are two muscular pads surrounding the pharyngeal opening. Ventral ascus-muscle long and with distinct longitudinal muscle-bands. It ends in a transparent, thin-walled ascus packed with discarded teeth (Fig. 8E). Very long, coiled, muscular pharyngeal pouch attached ventrally to pharynx. Oesophagus leaving pharynx posteriorly, and a pair of salivary glands entering pharynx next to oesophagus. Long (2.5mm) oesophageal pouch with a papillose surface, possibly glandular (Fig. 8C). Radula with 5 fully formed teeth plus one ghost tooth in ascending limb, 8 in descending limb and a heap of densely packed teeth in ascus (Fig. 8D). Teeth blade-shaped with notched tips (Fig. 5F). Those in

ascending and descending limbs with smooth edges, those in ascus with fine denticles laterally (Fig. 5G). Leading tooth broke before it could be measured, but teeth in ascending limb 410–420  $\mu$ m long with bases 126–137  $\mu$ m long.

**Spawning.** The specimen collected in December 2012 spawned in the laboratory. This has been described in a separate paper (Jensen & Ong, 2015).

**Remarks.** This species is a new record for Singapore. Pease (1861) described a *Lobiger* without giving it a specific name, just a question mark. Later he discovered his mistake and sent a note to the editor, and this as well as some other mistakes were published as notes in which the species was named *Lobiger viridis* (see Pease, 1863). In 1869 another species was named *L. viridis* by Nevill & Nevill (1869).

This was then renamed *L. nevilli* by Pilsbry (1896). In 1868 Pease named his species L. picta without commenting on his prior naming in 1863. The synonymy of several species of Lobiger has been proposed. Lobiger sagamiensis Baba, 1952 from Japan and Hong Kong has denticulate teeth in the descending limb of the radula (Jensen, 1985). It has been synonymised with L. souverbii Fischer, 1856 and with L. nevilli by Baba (1974). The latter two species have black lines and sometimes iridescent blue spots on the mantle, which have not been seen in L. viridis. Lobiger souverbii has teeth almost identical to those of L. viridis, but the parapodial lobes of L. souverbii have only slight crenulations along the edges and there are no black dots along the orange inside margins. In L. sagamiensis the parapodial lobes have deep, irregular lobules along the margins. Until molecular analyses can confirm synonymy, it is considered prudent

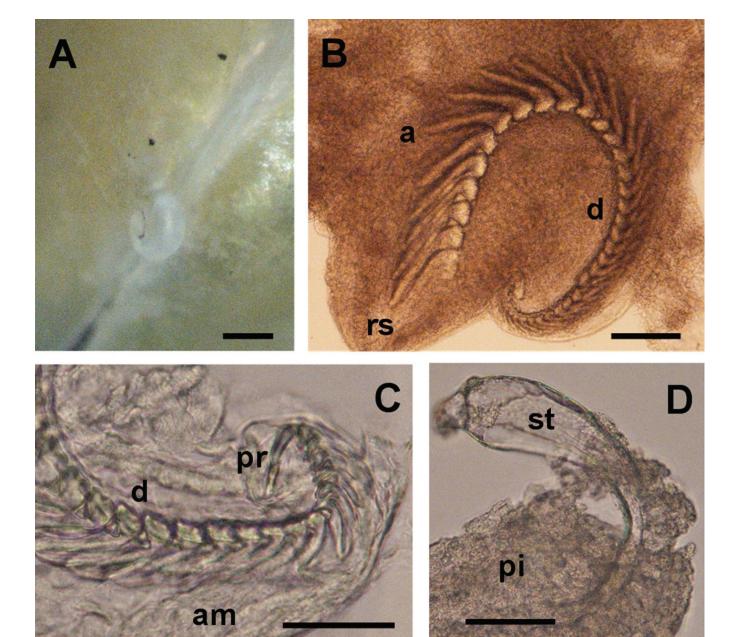


Fig. 7. Berthelinia singaporensis new species, anatomy. A, hinge view of shell with protoconch; B, pharynx (partly dissolved in NaOH); C, posterior end of descending limb of radula with rodshaped preradular tooth; D, tip of penis with stylet. Legend: a – ascending limb of radula; am – ascus-muscle; d – descending limb of radula. pi – penis; pr – rodshaped preradular tooth; rs – radular sac; st – penial stylet. Scale bars = 0.1 mm [A, B]; 50 μm [C, D].

to continue calling the widespread Indo-Pacific species *L. viridis*. Pease (1861) described four cephalic tentacles in *L. viridis*, but probably he mistook the large folded extensions from the rhinophores for separate tentacles.

### PLAKOBRANCHIDAE Gray, 1840

#### Elysia Risso, 1818

Type species – Elysia timida Risso, 1818 by monotypy.

This genus is characterised by wing-like parapodia laterally, which are usually folded over the dorsal surface. A renopericardial prominence is located anteriorly, and a number of dorsal vessels branch from this towards the edges of the parapodia. The function of the vessels is unknown, but the number of vessels as well as the shape and size of the renopericardial swelling are important characters for identifying species. The complex reproductive system is also important; albumen and prostate glands both form branching tubules extending into the parapodia alongside the digestive gland tubules. Some species produce extra-capsular yolk, and egg mass structure and development pattern are also important characters. Most species have planktotrophic veliger larvae, but some have lecithotrophic veligers or intra-capsular

metamorphosis (sometimes called direct development), and poecilogony has also been described (Clark & Jensen, 1981; Jensen, 1985, 1992, 1996b).

### Elysia bangtawaensis Swennen, 1998 (Figs. 9A, 10A, 11A)

**Material examined.** 6 specimens (3 dissected) collected on 26 October 2012 at Sungei Mandoi Besar (SW97) by Ria Tan; 5 specimens collected on 30 October 2012 at Sungei Buloh (SW135) by Ria Tan.

Colour alive. General body colour dark green. Several orange/red spots are found along parapodial margins (Fig. 9A). White dots are scattered over the entire body, fewer on the inside of the parapodia than elsewhere. Tips of rhinophores white.

**External morphology.** The dissected specimens were 14, 15 and 18 mm long preserved. Rhinophores rolled, eyes behind rhinophores. Pericardium short and wide. One large pair of dorsal vessels extending from posterior end, and one or two thinner vessels extend from either side, sometimes asymmetrically. All vessels branch repeatedly towards the parapodial margins (Fig. 9A). A vaginal opening visible

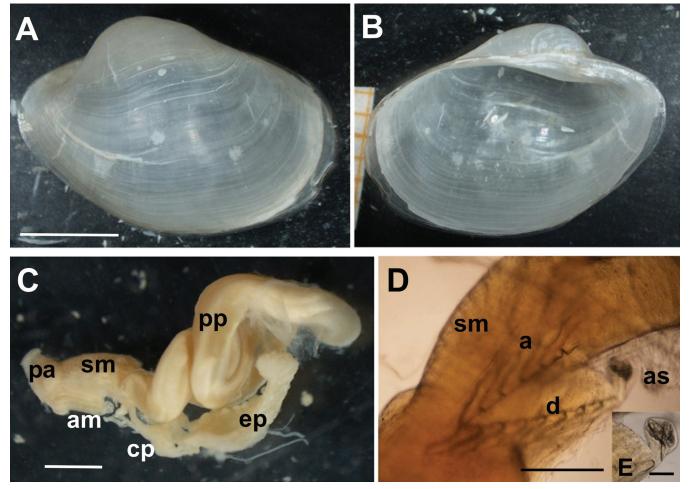


Fig. 8. Lobiger viridis, anatomy. A, shell, external view; B, shell, internal view. C, pharyngeal complex. D, pharynx, partly dissolved in NaOH; E, close-up of thin-walled ascus. Legend: a – ascending limb of radula; am – ascus-muscle; as – thin-walled ascus; cp – cerebropleural ganglion; d – descending limb of radula; ep – oesophageal pouch; pa – anterior muscle pads on pharynx; pp – pharyngeal pouch; sm – dorsal septate muscle of pharynx. Scale bars = 5 mm [A, B]; 1 mm[C]; 0.5 mm [D]; 0.1 mm [E].

in some specimens on outer side of right parapodium near its anterior attachment. Anterior foot corners somewhat protruding with pointed tips, giving a spatulate appearance.

Internal anatomy. Long, folded oral tube surrounded by densely arranged follicles of oral glands. Pharynx small (0.5 mm long and 0.5 mm high in the 18 mm specimen) relative to size of head and completely embedded in fibrous connective tissue. A dark brown line along lateral edges of pharyngeal cavity (Fig. 11A). Ascus-muscle rather short and attached to ventral surface of pharynx throughout its length. Ascending limb of radula diagonal in odontophore musculature. The dissected specimens had 8 teeth in the ascending limb, 8 teeth attached to radular ribbon in descending limb and 3 loose teeth behind this (18 mm specimen); 9 (+1 ghost) teeth in ascending limb and 8 attached plus two loose teeth in the descending limb (14 mm specimen); 8 teeth in the ascending limb, 7 in the descending one plus 3 loose teeth (15 mm specimen); the ascus was detached from the ascus-muscle in all three specimens, but contained numerous teeth densely packed in a transparent sac. The teeth are blade-shaped with fine denticles along cutting edge (Fig. 10A). The leading tooth was 63 µm long of which the base was 21 µm in 18 and 14 mm specimens. There was a small oesophageal pouch behind the circum-oesophageal nerve ring. The penis was unarmed and cylindrical in one specimen, conical in another, about 0.8 mm in widest diameter in both.

**Remarks.** This species was originally described from the southern Gulf of Thailand (Swennen, 1998), but has also been found in Singapore (Swennen, 2011) and in India (Jagtap et al., 2009). Here only a few additions to the descriptions have been added, including SEM of the radular teeth. Swennen (2011) described the ascus as vestigial. The present specimens had large asci densely packed with used teeth. However, the asci separated from the pharynx when it was dissected out.

*Elysia ornata* (Swainson, 1840) (Figs. 9B, 10B, C, 11B)

**Material examined.** 1 specimen collected on 17 October, 2012 at Sekudu (station SW24) by Toh Chay Hoon.

Colour alive. Ground colour green with numerous black spots of varying size scattered on the whole body surface (Fig. 9B). Parapodial margins black with a submarginal orange band. Some white spots scattered over body surface, but there is no white band or line at the parapodial margins. Tips of rhinophores orange and there is a black line along fold of rhinophores. Posterior part of renopericardial hump white with some black spots.

**External features.** The preserved specimen was about 35 mm long. Alive it had been more than 70 mm long. The pericardium is short and rather narrow. One pair of branching vessels enter the pericardium posteriorly and one or two more along each side of the pericardium. Anus and oviducal

opening are located in the groove along the right parapodial attachment to the neck. This groove continues across the foot sole to the left parapodium. The posterior part of the foot sole is not distinctly demarcated. The tail is rounded.

Internal anatomy. Pharynx very small in relation to the size of the animal (pharynx length 1.3 mm, height 1 mm); completely embedded in fibrous connective tissue. Group of oral glands located on dorsal side, just above pharyngeal opening. Ascus-muscle rather short, only about half the length of the pharynx (Fig. 11B). Dorsal septate muscle well developed, therefore oesophagus is attached to pharynx lower than in other species. Conspicuous paired salivary glands winding around oesophagus, and prominent muscular oesophageal pouch located behind circum-oesophageal nerve ring. Radula rather short, with 7 teeth in ascending limb, 8 in descending limb and a heap of at least 12 teeth in ascus. Teeth blade-shaped, apparently with some very fine denticles along cutting edge (Fig. 10B, C). Leading tooth 155 µm of which base was 55 µm. Smallest teeth in ascus were 17–20 μm with 10-11 μm bases. Thus bases relatively longer in juvenile teeth.

**Spawn.** The animal produced a strange-looking egg mass in the laboratory. It was a long, irregularly coiled string containing many oocytes without capsules towards one end, and several oocytes in one capsule through most of its length. However, it had the usual white streaks of extracapsular material along the external surface. As the animal had been on its own in the laboratory for about 10 days, the eggs were probably not fertilised, though some did undergo a few divisions.

**Remarks.** The confusion about the identity of Indo-Pacific Elysia species with black and orange marginal bands on parapodia and rhinophores has been discussed previously (Jensen, 1992, 2009). Most recently a complex of species has been indicated by molecular studies (Krug et al., 2013). However, the species illustrated in that paper are very different from the Singaporean specimens (Jensen, 2009, present study), which are almost identical to specimens from the Atlantic in colour pattern. Also, the egg mass had white streaks of extra-capsular material, as in Atlantic specimens of E. ornata, and hence it is here identified as that species, which is assumed to have circum-tropical distribution (Jensen, 1992). The finely denticulate teeth may indicate that E. grandifolia (Kelaart, 1858) should also be included in the synonymy. Kelaart's colour illustration published in Eliot (1906) indicates continuous orange and black marginal bands, and Eliot observed fine denticles on the radular teeth of Kelaart's original material. The large body size appears to be common in specimens that are found alone and not given the opportunity to reproduce. Repeated spawning usually cause shrinking in body size though feeding continues during the spawning period, and variation in body size of mature specimens may be caused by differences in reproductive state.

# Elysia pusilla (Bergh, 1872)

**Material examined.** 1 specimen, 16 October, 2012, Tuas (SW16).

Remarks. The specimen appeared in a tray containing *Udotea* collected at the above mentioned station. It was only 3 mm long preserved. Jensen (1992) synonymised several species of *Halimeda*-associated *Elysia* species under the name *Elysiella* pusilla Bergh, 1872. Later molecular analysis rendered *Elysiella* a junior synonym of *Elysia*, and most recently it has been shown that there may be a species complex, or at least two sibling species, *E. pusilla* and *E. macnaei* Marcus, 1982 (see Händeler & Wägele, 2007). Also, poecilogony has been described in *E. pusilla* from different localities (Vendetti et al., 2012).

Elysia singaporensis Swennen, 2011 (Figs, 9C, 10D, E, 11C, D)

**Material examined.** 4 specimens (2 dissected) collected on 28 at Lim Chu Kang (SW106) by Ria Tan & team; 6 specimens on 28 October 2012 at Lim Chu Kang (SW110) Ria Tan; 1 specimen, 30 October, 2012, Sungei Buloh (SW135); 3 specimens no data on label.

Colour alive. The general body colour is bright green. There is a thin yellow or orange line along the dorsal surface of the rhinophores (Fig. 9C). Orange and white dots are scattered on the body. Some specimens have white dots concentrated in a dorsal stripe on head from between rhinophores to anterior edge of pericardial prominence.

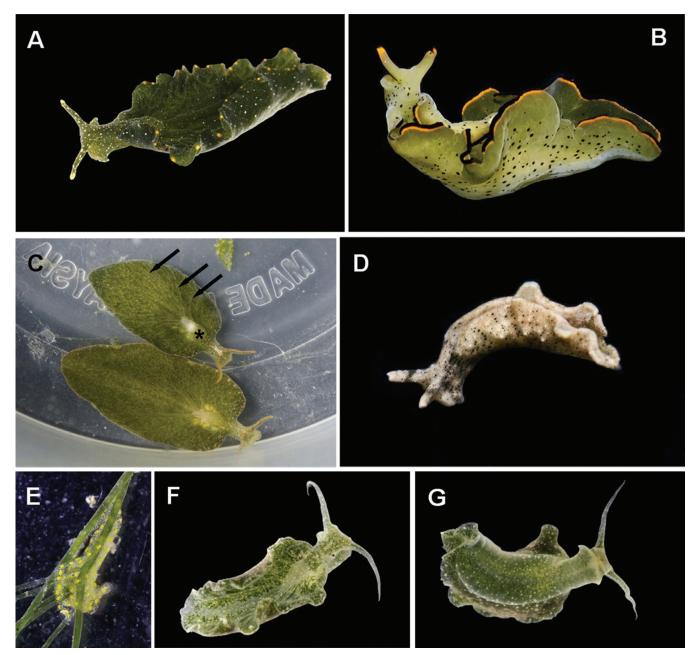


Fig. 9. Elysia species from Singapore. A, Elysia bangtawaensis. Length approximately 30 mm; B, Elysia ornata. Length approximately 70 mm; C, Elysia singaporensis. Length of largest specimen approx. 20 mm; D, Elysia cf. verrucosa. Length approximately 10 mm; E, Egg mass of Elysia cf. verrucosa. Yellow spots are extra-capsular yolk, white dots are the embryos; F, Elysia sp.; G, Ventral view of same. Photographs by Rene Ong

**External features.** Preserved length about 10 mm. Two vessels extending from right side of pericardium and three on left side (Fig. 9C). When parapodia are held open the shape of the animal resembles a mangrove leaf.

**Internal anatomy.** Length of pharynx 0.5 mm, height slightly under 0.5 mm (Fig. 11C). Radula with 4 teeth in ascending limb, 8 in descending limb (two of which were not attached to the radular ribbon). Ascus (Fig. 11D) was dislodged from pharynx when this was removed from specimen. Length of leading tooth 91  $\mu$ m with a base of 37  $\mu$ m. The teeth are blade-shaped with a denticulate cutting edge and pointed tips (Fig. 10D, E).

**Remarks.** This species was described only a few years ago, but seems to be rather common in mangroves of Singapore. So far it has not been found elsewhere, but it is too early to state that it is truly a Singaporean endemic. The teeth of the present specimen are smaller than in the original description, but the animals were also smaller. In other respects the present specimens agree with the original description (Swennen, 2011).

# Elysia tomentosa Jensen, 1997 (Figs. 10F, G, 11E, F)

**Material examined.** 1 specimen (dissected) 16 October 2012, Tuas (station SW16)

Colour alive. The general body colour was dark green. There was a thin dark line along inner and outer margins of parapodia. Between the two lines the parapodial margins were cream-coloured. Numerous black dots, some of them ocellate, were distributed on the body surface, including head and rhinophores. Dots absent on foot sole.

**External features.** The specimen was juvenile and the typical composite papillae along the parapodial margin were indistinct. The pericardium had a long renal ridge with several branching vessels extending towards the parapodial edges.

Internal anatomy. The pharynx was large, almost spherical (1.1 mm long, 0.9 mm high), the dorsal septate muscle taking up more than half of the sphere (Fig. 11E). The ascus-muscle containing the descending limb of the radula was thin and only about half the length of the pharynx. The radula had 4 teeth in the ascending limb, 17 in the descending limb, and ended in a small spiral in the ascus with 3 preradular teeth at the tip (Fig. 11F). The leading tooth was 130  $\mu$ m long with a base of 42  $\mu$ m. The teeth were blade-shaped with small denticles along cutting edge (Fig. 10F, G). The penis was short, 0.4 mm, and conical, probably capable of great extension. Nervous system with three distinct ganglia on the visceral loop.

Remarks. This species was originally described from the Houtman Abrolhos Islands, Western Australia (Jensen, 1997a), but has subsequently been recorded from most of the Indo-West Pacific region (Eastern Australia, New Caledonia, Sulawesi (Indonesia), Western India, Hawaii,

Japan and probably introduced in Turkey (see: http://www. seaslugforum.net/showall/elystome); Réunion and Mayotte (see: http://seaslugs.free.fr/nudibranche/a elysia tomentosa. htm); Eniwetak Atolls (see: http://www.underwaterkwaj.com/ nudi/sacoglossans/e475.htm); Philippines (see: http://www. philippine-sea-slugs.com/Sacoglossa/Elysia tomentosa.htm). However, these records may not all be of this species (Krug et al., 2013; http://sacoglossa.lifedesks.org/pages/34287). It is therefore important to describe the anatomy of specimens collected from other places. The present specimen differs from the original description in having a shorter descending limb of the radula. However, this can be explained by the much smaller size of the animal, obviously a juvenile. *Elysia* tomentosa feeds on Caulerpa spp. (Jensen, 1997a; Burfeind et al., 2009), and has probably been introduced to the eastern Mediterranean with the invasive Caulerpa taxifolia or C. racemosa (Yokes & Rudman, 2004).

# Elysia cf. verrucosa Jensen, 1985 (Figs. 9D, E; 10H; 11G)

**Material examined.** 3 specimens (2 dissected) collected on 16 October 2012 at Tuas (SW16).

**Colour alive.** The general body colour was greyish green with numerous small black spots scattered over the whole surface (Fig. 9D). Also, there were many tiny orange or red dots. There was a dark band or spot subterminally on the rhinophores and also some weak pigmentation on the anterior surface of the head and the anterior part of the foot sole. White pigment was concentrated on papillae, along parapodial margins, and at the tips of the rhinophores.

**External features.** Specimens were 3.5, 4 and 5 mm long after preservation. The pericardium was short and narrow with two pairs of rather indistinct branching vessels extending posteriorly and laterally towards parapodial edges. The male genital opening was at the base of the right rhinophore, the female genital aperture and anus in the ciliated groove on the right side of the neck. The groove continues ventrally across the foot sole. The foot is weakly notched at the anterior margin. The eyes are comma-shaped, located behind the folded rhinophores.

Internal anatomy. The mouth opening is surrounded by a ring of dark pigment, possibly indicating a labial cuticle. The pharynx is very big, 0.8 mm long and 0.6 mm high in the 3.5 mm specimen. The dorsal septate muscle constitutes slightly over half of the total height, and there is a pigmented line along its attachment to the odontophore on either side (Fig. 11G). The radula is very small compared to the size of the pharynx, reaching less than half way down the odontophore musculature. The radula contained 8 teeth in the ascending limb, 10 in the descending limb, and a heap of at least 8 teeth in the ascus. The teeth are blade-shaped with denticles along the cutting edge (Fig. 10H). The leading tooth was 88 μm long with a base of 36 μm.

**Spawn.** An egg mass was deposited in the laboratory on 21 October 2012. It was irregularly coiled, and the number of

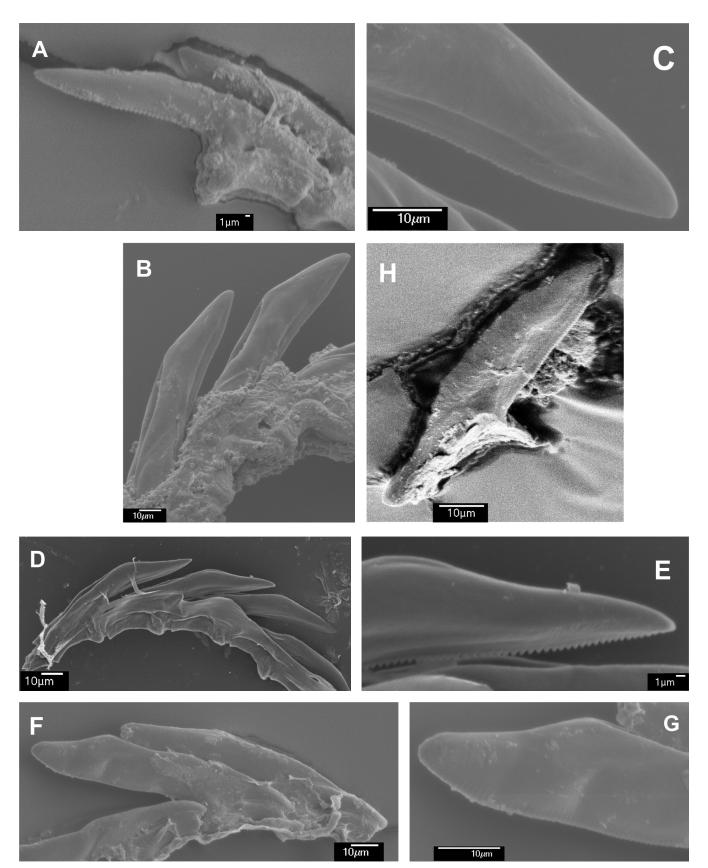


Fig. 10. SEM micrographs of radula teeth of *Elysia* species. A, *Elysia bangtawaensis*; B, *Elysia ornata*; C, close-up of cutting edge of same; D, *Elysia singaporensis*; E, close-up of cutting edge of same; F, *Elysia tomentosa*; G, close of tip of tooth of same; H, *Elysia* cf. *verrucosa*.

eggs was estimated to be about 750 (30 eggs per mm of a 25 mm egg mass). It had blotches of yellow extra-capsular material along the external surface (Fig. 9E). The eggs had gone through several divisions before the egg mass was observed. Egg capsules were measured after preservation, and probably were slightly larger alive. Capsules measured  $170\pm20~\mu m$  by  $136\pm19~\mu m$  (N = 20).

Remarks. This species was originally described from Hong Kong, but two specimens were collected in Singapore in 2006 (Jensen, 1985, 2009). One of these specimens was 30 mm long, but the much smaller specimens collected in the present study were sexually mature and produced an egg mass. In the original description the radular teeth were described as having rounded tips (Jensen, 1985), but in specimens from Singapore they have rather pointed tips (Jensen, 2009, present study). As the tooth illustrated in the original description is almost identical to that of *E. japonica*, there is a possibility that it was actually that of a pale variety of *E. japonica* and that

the radula of *E. verrucosa* from Hong Kong has been lost. However, there is also the possibility that the Singaporean specimens represent a separate, unnamed species.

*Elysia* sp. (Fig. 9F, G)

**Material examined.** 1 specimen collected on 30 October 2012 at Sungei Buloh (SW135) by Ria Tan.

**Colour alive.** General body colour green. Numerous small white spots scattered over body, including rhinophores. Parapodial margins, rhinophores and pericardium transparent.

**External features.** The specimen had very long simple (neither rolled nor grooved) rhinophores. Only the bases were green from digestive gland tubules. Three to four dorsal vessels branch from either side of the pericardium. Foot sole distinctly demarcated from parapodia. Transverse

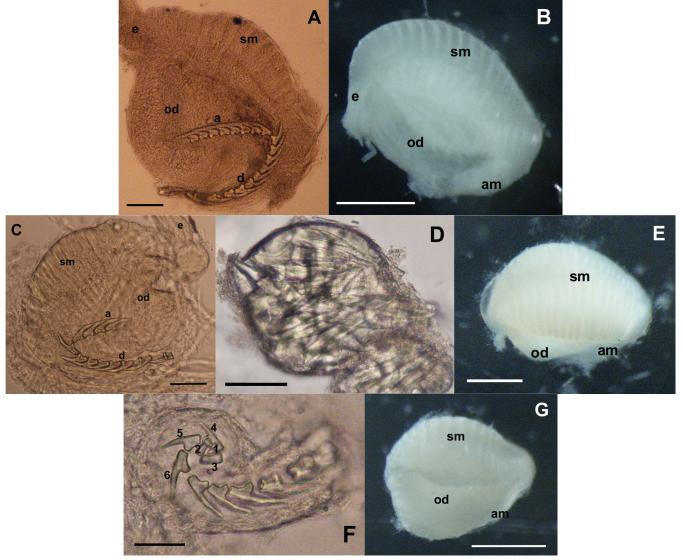


Fig. 11. Pharynx anatomy of *Elysia* species. A, *Elysia bangtawaensis*, pharynx partly dissolved in NaOH; B, *Elysia ornata*, pharynx; C, *Elysia singaporensis*, pharynx partly dissolved in NaOH; D, close-up of dislodged ascus of same. E, *Elysia tomentosa*, pharynx; F, close-up of ascus with preradular teeth of same; G, *Elysia* cf. *verrucosa*, pharynx; Legend: a – ascending limb of radula; am – ascus-muscle; d – descending limb of radula; e – oesophagus; od – odontophore; sm – dorsal septate mucle. Numbers 1 to 3 – preradular teeth; 4 to 6 – oldest juvenile teeth. Scale bars = 0.1 mm [A, C]; 0.5 mm [B, E, G]; 50 μm [D]; 25 μm [F].

groove across foot at level of parapodial attachment. Tail short, rounded. Anterior foot corners pointed.

**Remarks.** Only one specimen of this species was collected. It is not possible to assign this specimen to any known species of *Elysia*. Numerous undescribed species of the genus exist, but without more material for anatomical study, a proper description cannot be made.

# **COSTASIELLIDAE Clark, 1984**

#### Costasiella Pruvot-Fol, 1951

Type species – *Costasiella virescens* Pruvot-Fol, 1951 by monotypy.

The family Costasiellidae has recently been resurrected (Espinoza et al., 2014; Jensen et al., 2014a). Species of this genus have large eyes located close together and usually

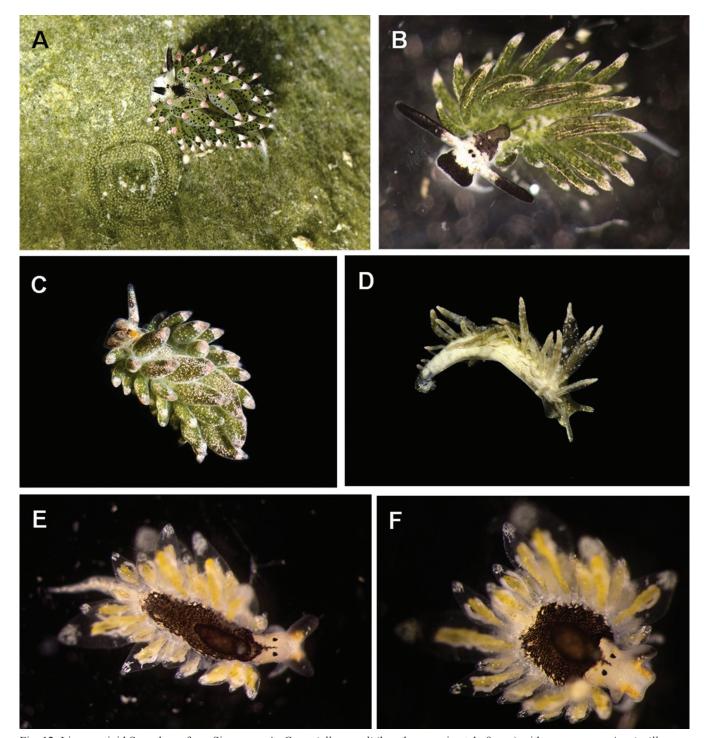


Fig. 12. Limapontioid Sacoglossa from Singapore. A, *Costasiella paweli* (length approximately 8 mm) with egg mass on *Avrainvillea* sp.; B, *Costasiella usagi*. Length approximately 2 mm; C, *Costasiella* cf. *kuroshimae*. Length approximately 3 mm; D, *Placida daguilarensis*. Length approximately 7 mm; E, *Kerryclarkella inconspicua*, new genus, new species, dorsal view. Length approximately 2 mm; F, same, frontal view.

between the rhinophores. They have fusiform cerata, often with mammillate tips and a large, tall pericardial prominence. Some species have pedal tentacles, some have the tail shaped as a ceras, some have branches of albumen gland extending into the cerata, some have penial armature, and some have four genital openings.

# Costasiella paweli Ichikawa, 1993 (Fig. 12A)

**Material examined.** 3 specimens collected on 17 October 2012 at Chek Jawa (SW23)

**Spawn.** The animals produced several egg masses in the laboratory. Egg masses were regular spirals (Fig. 12A). One preserved egg mass contained about 1100 eggs in blastulastage. Egg capsules were almost spherical. The capsules measured 139±8.6 by 120±4.2μm (N=20).

**Remarks.** This species was also collected in Singapore in 2006 and described anatomically (Jensen, 2009). It seems to be fairly common and larger than the other two species of *Costasiella* occurring in Singaporean waters. The present specimens were about 7–8 mm long. Reproductive pattern varies within the genus and poecilogony has been described in at least one species (Clark & Jensen, 1981; Miles & Clark, 2002; Vendetti et al., 2012; Espinoza et al., 2014).

# Costasiella usagi Ichikawa, 1993 (Fig. 12B)

**Material examined.** 1 specimen collected on 16 October 2012 at Tuas (SW16).

**Remarks.** This appears to be a rare species compared to the other two *Costasiella* species occurring in Singapore. Only one specimen (length about 2 mm) was collected during the present study.

# Costasiella cf. kuroshimae Ichikawa, 1993 (Fig. 12C)

**Material examined.** about 24 specimens collected on 16 October 2012 at Tuas (SW16).

**Remarks.** This species has been recorded from Singapore previously and its anatomy described (Jensen, 2009). However, there seems to be a species complex in the Indowest Pacific region (Jensen et al., 2014a). The present specimens were about 1 to 4 mm long.

#### **LIMAPONTIIDAE Gray, 1847**

#### Placida Trinchese, 1877

Type species – *Placida tardyi* (Trinchese, 1873) (as *Laura tardy*), by subsequent designation (Iredale & O'Donoghue, 1923).

This genus is characterised by a combination of blade-shaped radular teeth, a curved penial stylet, and a limapontiid reproductive system. Digestive gland tubules usually extend into head and rhinophores and most species have branches of the albumen gland in the cerata.

# Placida daguilarensis Jensen, 1990 (Fig. 12D)

**Material examined.** 4 specimens collected on 18 October at Changi Point (SW33).

**Remarks.** This species has been recorded from Singapore previously (Jensen, 2009). It feeds on *Bryopsis* spp., and is found where this alga is abundant. It was originally described from Hong Kong (Jensen, 1990) and has also been recorded from Japan (Hirano et al., 2006). It may be more widespread in the Indo-west Pacific region, but photographs of animals need to be confirmed with anatomical studies.

# Kerryclarkella inconspicua, new genus, new species (Figs. 12E, F, 13)

**Material examined.** Holotype: 1 specimen, 1.5 mm long preserved, collected on 18 October 2012 at Changi Point among rhizomes of seagrass *Halophila* (ZRC.MOL.5790).

Colour alive. The dorsal surface between the cerata, including the pericardium, is dark brown (Fig. 12E). A thin line of this pigment extends forwards between the relatively large black eyes. The cerata are transparent and a yellow digestive gland tubule plus two white albumen gland tubules are visible in each. At the tips of the cerata a cluster of white dots are found. Yellow spots are also found on the bases of the rhinophores and the anterior edges of the head (Fig. 12F). A dark stripe is also seen inside the fold of the rhinophores. White dots are scattered on most parts of the body, especially the tail. In the preserved specimen a dark band is also seen below the cerata (Fig. 13B). There is a distinct melanin-black vesicle at the right anterior corner of the pericardium seen only in the preserved specimen (Fig. 13A). Next to the mouth is a pair of small black dots (Fig. 13B).

External features. The specimen was only about 1 mm long when collected, and appeared to have lost most cerata. Fortunately it grew somewhat bigger and developed new cerata during the following days is the laboratory. The rhinophores are longitudinally folded and broad, the bases touching one another at the anterior margin of the head. The eyes are located behind the rhinophores. No digestive gland tubules extend into head and rhinophores. The pericardium is tall, elongate, almost half the length of the body. The anus is located on a papilla on top of the pericardium anteriorly. The cerata are arranged in two to three longitudinal rows along the sides of the body. The largest cerata are those in the middle of the body of the innermost row. The foot sole is narrow and has long pedal tentacles at the anterior corners. The pedal tentacles are curved backwards when the animal crawls. There is a long, thin tail without any cerata. In the preserved specimen the rhinophores are short and triangular.

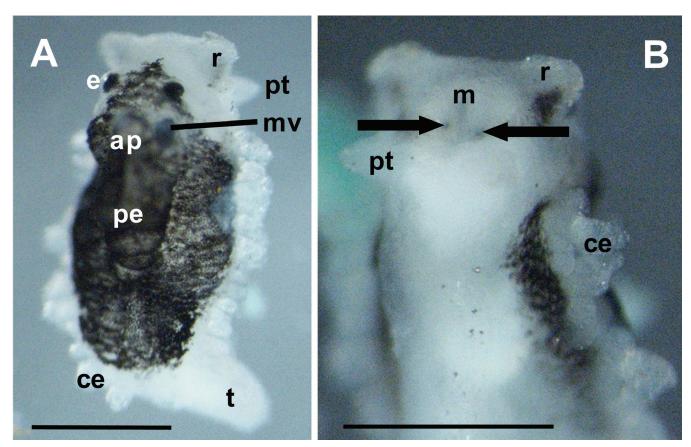


Fig. 13. *Kerryclarkella inconspicua*, new genus, new species. A, dorsal view of preserved holotype; B, ventral view of anterior body of preserved holotype. Arrows point to black dots flanking mouth. Legend: ap – anal papilla; ce – ceras; e – eye; m – mouth; mv – melanin-black vesicle; pe – pericardial ridge; pt – pedal tentacle; r – rhinophore; t – tail. Scale bars = 0.5 mm.

White pedal glands are visible through epidermis of anterior foot sole between pedal tentacles. No genital apertures were visible in preserved specimen.

**Observations on living specimen.** The animal was found in the sediment surrounding the rhizomes of the seagrass *Halophila*. It was kept in the laboratory in a small dish with fragments of this seagrass and several filamentous algae, but feeding was not observed. It moved very fast and was difficult to observe under the stereomicroscope. The bright yellow content of the digestive gland could be an indication of a diet of diatoms or possibly eggs of small invertebrates.

**Remarks.** This species is of such remarkable colour pattern and external morphology that it cannot be assigned to one of the existing sacoglossan genera. It shows some similarities to Costasiella, such as pedal tentacles and tall pericardium, but also to some species of Ercolania or Placida, such as anus on papilla on top of pericardium and branches of albumen gland in cerata. The latter also occurs in some species of Costasiella. Small black dots flanking the mouth have been described in several species of Costasiella (Jensen, 2009) and also in some species of Ercolania, e.g., E. halophilae Jensen, Kohnert, Bendell & Schrödl, 2014 (Jensen et al., 2014b). With only one specimen available it has not been possible to examine the radular teeth or penial armature, which might indicate affiliation to one of the above genera. Costasiella and Placida have blade-shaped radular teeth, and Ercolania has sabot-shaped teeth (Jensen, 1996b). The bright yellow

coloration of the content of the digestive gland tubules in the cerata is unique among the Sacoglossa. The presence of a melanin-black vesicle near the pericardium may indicate that the specimen is a juvenile. This structure has been interpreted as the remains of a larval kidney. However, the presence of albumen gland branches in the cerata indicates that the animal is sexually mature. Without further material a proper diagnosis of the new genus cannot be given. Preliminarily the genus *Kerryclarkella* has the characters of the only known species, *K. inconspicua*.

**Etymology.** The generic name is in honour of the late Kerry B. Clark whose work on sacoglossans from Florida and the Caribbean has been instrumental to subsequent research on this group of heterobranchs, and for his friendship and support of the research of the present author. The specific epithet is to indicate the minute size and obscure habitat of the species.

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#### LITERATURE CITED

- Adams H & Adams A (1854) The genera of Recent Mollusca. Vol. II. John Van Voorst, London.
- Adams ARN & Angas GF (1864) Descriptions of new species of shells, chiefly from Australia, in the collection of Mr. Angas. Proceedings of the Zoological Society of London, 1864: 35–40.
- Baba K (1949) Opisthobranchia of Sagami Bay. Collected by His Majesty the Emperor of Japan. Iwanami Shoten, Tokyo.
- Baba K (1952) Record of a rare sacoglossan mollusk, Lobiger (Lobiger) sagamiensis n.sp. from Sagami Bay, Japan. Zoological Magazine (Dobutsugaku Zasshi), 61(11): 337–338.
- Baba K (1961) On the identification and the affinity of *Tamanovalva limax*, a bivalved sacoglossan mollusc in Japan. Publications of the Seto Marine Biological Laboratory, 9: 37–62, pl 1–4.
- Baba K (1966) Gross anatomy of the specimens of the shelled sacoglossan *Volvatella* (=*Arthessa*) collected from Okino-Erubu Island, southern Kyushu, Japan (Nudibranchia). Publications of the Seto Marine Biological Laboratory, 14: 197–205, pls 7–10.
- Baba K (1974) Some comments on *Lobiger souberbii* Fischer, 1856, re-identified, of Japan. Veliger, 16: 253–257.
- Bergh R (1872) Malacologische Untersuchungen. In: Semper C (ed.), Reisen im Archipel der Philippinen, 2(3-4): 137–203, pls 17–24
- Burfeind DD, Tibbetts IR & Udy JW (2009) Grazing rates of *Elysia tomentosa* on native and introduced *Caulerpa taxifolia*. Hydrobiologia, 632: 355–358.
- Burn R (1960). Australian bivalve gastropods. Nature, 187: 44–46. Burn R (1965) Rediscovery and taxonomy of *Edenttellina typica* Gattliff & Gabriel. Nature, 206: 735–736.
- Burn R (1966) The opisthobranchs of a Caulerpan microfauna from Fiji. Proceedings of the Malacological Society of London, 37: 45–65.
- Burn R (1998) Order Sacoglossa. In: Beesley PL, Ross GJB & Wells A (eds.) Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5: 961-974 CSIRO Publishing: Melbourne, Part B, viii 565–1234.
- Calcara P (1840) Monografie dei generi Clausilia e Bulimo coll'aggiunta di alcune nuove specie di conchiglie siciliane esistenti nella collezione della Sig. Teresa Gargotta in Salinas. Palermo, Muratori, 54pp.
- Carmona L, Malaquias MAE, Gosliner TM, Pola M & Cervera JL (2011) Amphi-Atlantic distributions and cryptic species in sacoglossan sea slugs. Journal of Molluscan Studies, 77: 401–412.
- Carmona L, Lei BR, Pola M, Gosliner TM, Valdés Á & Cervera JL (2014) Untangling the *Spurilla neapolitana* (Delle Chiaje, 1841) species complex: a review of the genus *Spurilla* Bergh, 1864 (Mollusca: Nudibranchia: Aeolidiidae). Zoological Journal of the Linnean Society, 17: 132–154.
- Clark KB (1982) A new *Volvatella* (Mollusca: Ascoglossa) from Bermuda, with comments on the genus. Bulletin of Marine Science, 32:112–120.
- Clark KB (1984) New records and synonymies of Bermuda opisthobranchs (Gastropoda). Nautilus, 98: 85–97.

- Clark KB & Jensen KR (1981) A comparison of egg size, capsule size, and development patterns in the order Ascoglossa (Sacoglossa) (Mollusca: Opisthobranchia). International Journal of Invertebrate Reproduction, 3: 57–64.
- Cox LR & Rees WJ (1960) A bivalve gastropod. Nature, 185: 749–751.
- Crosse H (1875) Description du nouveau genre, *Berthelinia*. Journal de Conchyliologie, 23: 79–81.
- Dautzenberg P (1895) De l'existence du genre *Berthelinia* Crosse à l'époque actuelle. Bulletin de la Societé zoologique de France, 20: 37–38.
- Dayrat B, Conrad M, Balayan S, White TR, Albrecht C, Golding R, Gomes SR, Harasewych MG & Martins AMF (2011) Phylogenetic relationships and evolution of pulmonate gastropods (Mollusca): New insights from increased taxon sampling. Molecular Phylogenetics and Evolution, 59: 425–437.
- Dinapoli A & Klussmann-Kolb A (2010) The long way to diversity Phylogeny and evolution of the Heterobranchia (Mollusca: Gastropoda). Molecular Phylogenetics and Evolution, 55: 60–76.
- Edmunds M (1962) Bivalved gastropod from Jamaica. Nature, 195: 402
- Edmunds M (1963) *Berthelinia caribbea* n.sp., a bivalved gastropod from the West Atlantic. Journal of the Linnean Society of London, Zoology, 44: 731–739.
- Eliot C (1906) On the nudibranchs of Southern India and Ceylon with special reference to the drawings by Kelaart and collections belonging to Alder and Hancock preserved in the Hancock Museum at Newcastle-on-Tyne. Proceedings of the Zoological Society of London, 1906: 636–691.
- Espinoza E, DuPont A & Valdés Á (2014) Molecular data reveal an undescribed cryptic species of *Costasiella* Pruvot-Fol, 1951 (Euthyneura: Sacoglossa: Limapontidae) in the Bahamas. American Malacological Bulletin, 32(2): 173–182.
- Evans TJ (1950) A review of Pease's genus *Volvatella*, together with a preliminary report on a new sacoglossan genus. Proceedings of the Malacological Society of London 28: 102–106.
- Fischer P (1856) Description d'espèces nouvelles. Journal de Conchyliologie, 5: 273–277, plates 8 and 11.
- Gascoigne T (1974) A note on some sacoglossan penial styles (Gastropoda: Opisthobranchia). Zoological Journal of the Linnean Society, 55: 53–59.
- Gascoigne T (1993) Stylets, Styles, and other cuticular extensions of the male duct in the order Sacoglossa (Gastropoda). Bollettino Malacologico, Milano, 29: 139–146.
- Gascoigne T & Sartory PK (1974) The teeth of three bivalved gastropods and three other species of the order Sacoglossa. With an appendix on *Calliopaea oophaga* n.sp., a new sacoglossan by H. Lemche. Proceedings of the Malacological Society of London, 41: 109–126.
- Gray JE (1840) Synopsis of the contents of the British Museum, 42nd edition. Pp. 1–370.
- Gray JE (1847) A list of the genera of recent Mollusca, their synonyma and types. Proceedings of the Zoological Society of London, 15: 129–219.
- Hamatani I (1969) A new species of the rare shelled sacoglossan genus *Cylindrobulla* from Middle Japan. Publications of the Seto Marine Biological Laboratory, 17: 171–174, pls 5–6.
- Hamatani I (1972) A new species of *Volvatella* Pease 1860, found in the "Caulerpan microfauna" in the province of Kii, middle Japan (Opisthobranchia, Sacoglossa). Publications of the Seto Marine Biological Laboratory, 21: 13–20, pls. 2–3.
- Hamatani I (1976) Preliminary account of a new species of *Volvatella* Pease, 1860, *V. viridis* sp. nov., found in the Caulerpan microfauna in Japan (Opisthobranchia: Ascoglossa). Publications of the Seto Marine Biological Laboratory, 22: 371–376, pl. 6.

- Händeler K & Wägele H (2007) Preliminary study on molecular phylogeny of Sacoglossa and a compilation of their food organisms. Bonner Zoologische Beiträge, 55(3/4): 231–254.
- Hirano YJ, Hirano YM & Trowbridge CD (2006) Record of a common but cryptic sacoglossan, *Placida daguilarensis* Jensen, 1990, from Japan. Memoirs of the National Science Museum, Tokyo, 40: 279–290.
- Ichikawa M (1993) Saccoglossa (Opisthobranchia) from the Ryukyu Islands. Publications of the Seto Marine Biological Laboratory, 36: 119–139
- Iredale T & O'Donoghue C (1923) List of British nudibranchiate Mollusca. Proceedings of the Malacological Society of London, 15: 195–233.
- Jagtap TG, Shenai-Tirodkar PS, Savant SB, Kulkarni VA & Ansari ZA (2009) Elysia bangtawaensis Swennen (Nudibranch) from the mangrove habitat of Mandovi estuary, Goa (central west coast), India. Current Science, 96(1): 30–33.
- Jeffreys JG (1856) On the marine Testacea of the Piedmontese coast. Annals and Magazine of Natural History (2nd series), 17: 155–188, plate II.
- Jensen KR (1985) Annotated checklist of Hong Kong Ascoglossa (Mollusca: Opisthobranchia), with descriptions of four new species. In: Morton B & Dudgeon D (eds.), Proceedings of the Second International Workshop on the Malacofauna Hong Kong and Southern China, Hong Kong 1983. Hong Kong University Press, Hong Kong, Volume 1. Pp. 77–107.
- Jensen KR (1990) Three new species of Ascoglossa (Mollusca, Opisthobranchia) from Hong Kong, and a description of the internal anatomy of *Costasiella pallida* Jensen, 1985.
  In: Morton B (ed.), The Marine Flora and Fauna of Hong Kong and Southern China II. Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 2–24 April 1986.
  Hong Kong University Press, Hong Kong. Pp. 419–432.
- Jensen KR (1992) Anatomy of some Indo-Pacific Elysiidae (Opisthobranchia: Sacoglossa (=Ascoglossa)), with a discussion of the generic division and phylogeny. Journal of Molluscan Studies, 58: 257–296.
- Jensen KR (1993) Sacoglossa (Mollusca, Opisthobranchia) from Rottnest Island and central Western Australia. In: Wells FE, Walker DI, Kirkman H & Lethbridge R (eds.), Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia Western Australian Museum, Perth. Pp. 207–253.
- Jensen KR (1996a) The Diaphanidae as a possible sister group of the Sacoglossa (Gastropoda, Opisthobranchia). In: Taylor JD (ed.), Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, Oxford. Pp. 231–247.
- Jensen KR (1996b) Phylogenetic systematics and classification of the Sacoglossa (Mollusca, Gastropoda, Opisthobranchia). Philosophical Transactions of the Royal Society B, 351: 91–122.
- Jensen KR (1997a) Sacoglossa (Mollusca, Opisthobranchia) from the Houtman Abrolhos Island and central Western Australia. In: Wells FE (ed.), Proceedings of the Seventh International Marine Biological Workshop: The Marine Flora and Fauna of the Houtman Abrolhos Islands, Western Australia. Western Australian Museum, Perth. Pp. 307–333.
- Jensen KR (1997b) Sacoglossa (Mollusca, Opisthobranchia) from the Darwin Harbour area, Northern Territory, Australia. In: Hanley JR, Caswell G, Megirian D & Larson HK (eds.), Proceedings of the Sixth International Marine Biological Workshop: The Marine Flora and Fauna of Darwin, Northern Territory, Australia. Darwin, Australia. Museums and Art Galleries of the Northern Territory and the Australian Marine Sciences Association Pp. 163–186.

- Jensen KR (2003) Distributions, diets and reproduction of Hong Kong Sacoglossa (Mollusca: Opisthobranchia): a summary of data, 1980–2001. In: Morton B (ed.), Perspectives on Marine Environmental Change in Hong Kong and Southern China, 1977–2001. Proceedings of an International Workshops Reunion Conference, Hong Kong 2001. Hong Kong University Press, Hong Kong. Pp. 347–365.
- Jensen KR (2009) Sacoglossa (Mollusca: Gastropoda: Opisthobranchia) from Singapore. Raffles Bulletin of Zoology Supplement, 22: 207–223.
- Jensen KR (2011) Comparative morphology of the mantle cavity organs of shelled Sacoglossa, with a discussion of relationships with other Heterobranchia. Thalassas, 27(2): 169–192.
- Jensen KR, Krug PJ, Dupont A & Nishina M (2014a) A review of taxonomy and phylogenetic relationships in the genus Costasiella (Heterobranchia: Sacoglossa), with a description of a new species. Journal of Molluscan Studies, 80: 562–574.
- Jensen KR, Kohnert P, Bendell B & Schrödl M (2014b) Life on a leaf: 3D-reconstruction and description of a new limapontiid sacoglossan (Gastropoda: Heterobranchia: 'Opisthobranchia') living on the seagrass *Halophila ovalis*. Journal of Molluscan Studies, 80: 624–641.
- Jensen KR & Ong RSL (2015) Spawning observed in a specimen of the shelled sacoglossan *Lobiger viridis* Pease, 1863 from Singapore (Mollusca: Gastropoda: Heterobranchia). Raffles Bulletin of Zoology, in press
- Jensen KR & Wells FE (1990) Sacoglossa (=Ascoglossa) (Mollusca, Opisthobranchia) from southern Western Australia. In: Wells FE, Walker DI, Kirkman H & Lethbridge R (eds.), Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia. Western Australian Museum, Perth. Volume 1. Pp. 297–331.
- Jörger KM, Norenburg JL, Wilson NG & Schrödl M (2012) Barcoding against a paradox? Combined molecular species delineations reveal multiple cryptic lineages in elusive meiofaunal sea slugs. BMC Evolutionary Biology, 12: e245.
- Jörger KM, Stöger I, Kano Y, Fukuda H, Knebelsberger T & Schrödl M (2010) On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. BMC Evolutionary Biology, 10: 323.
- Kawaguti S & Baba K (1959) A preliminary note on a two-valved sacoglossan gastropod, *Tamanovalva limax* n.gen., n.sp., from Tamano, Japan. Biological Journal of Okayama University, 5: 177–184.
- Kay A (1962) A bivalved gastropod from the Hawaiian Islands. Nature, 195: 96–97.
- Keen AM (1960) A bivalve gastropod. Nature, 186: 406–407.
- Keen AM & Smith AG (1961) West American species of the gastropod genus *Berthelinia*. Proceedings of the California Academy of Science, 30: 47–66.
- Kelaart EF (1858) Descriptions of new and little-known species of Ceylon nudibranchiate molluscs and zoophytes. Journal of the Royal Asiatic Society, Ceylon Branch, 3(1): 84–139.
- Kocot KM, Halanych KM & Krug PJ (2013) Phylogenomics supports Panpulmonata: Opisthobranch paraphyly and key evolutionary steps in a major radiation of gastropod molluscs. Molecular Phylogenetics and Evolution, 69(3): 764–771.
- Krohn M (1847) Observations sur deux nouveaux genres de gastéropodes (*Lobiger* et *Lophocercus*). Annales des Sciences Naturelles, Paris (3)7: 52-60, plate 2.
- Krug PJ, Händeler K & Vendetti J (2011) Genes, morphology, development and photosynthetic ability support the resurrection of *Elysia cornigera* (Heterobranchia: Plakobranchoidea) as distinct from the "solar-powered" sea slug, *E. timida*. Invertebrate Systematics, 25: 477–489.

- Krug PJ, Vendetti JE, Rodriguez AK, Retana JN, Hirano YM & Trowbridge CD (2013) Integrative species delimitation in photosynthetic sea slugs reveals twenty candidate species in three nominal taxa studied for drug discovery, plastid symbiosis or biological control. Molecular Phylogenetics and Evolution, 69(3): 1101–1119.
- Maeda T, Kajita T, Maruyama T & Hirano Y (2010) Molecular phylogeny of the Sacoglossa, with a discussion of gain and loss of kleptoplasty in the evolution of the group. Biological Bulletin, 219: 17–26.
- Marcus E & Marcus E (1956) On the tectibranch gastropod Cylindrobulla. Anais da Academia Brasileira de Ciências, 28: 119–128.
- Marcus E & Marcus E (1970) Opisthobranchs from Curação and faunistically related regions. Studies on the Fauna of Curação and other Caribbean Islands, 33: 1–129.
- Marcus E deB-R (1972) On some opisthobranchs from Florida. Bulletin of Marine Science, 22: 284–308.
- Mikkelsen PM (1998) *Cylindrobulla* and *Ascobulla* in the western Atlantic (Gastropoda, Opisthobranchia, Sacoglossa): Systematic review, description of a new species, and phylogenetic reanalysis. Zoologica Scripta, 27: 49–71.
- Miles CM & Clark KB (2002) Comparison of biochemical composition and developmental mode in two populations of *Costasiella* [Opisthobranchia: Ascoglossa (=Sacoglossa)]. Journal of Molluscan Studies, 68: 101–109.
- Montrouzier RP (1861) Lophocercus Vigourouxi. In: Souverbie,
   M. Descriptions d'espèces nouvelle de l'archipel calédonien.
   Journal de Conchyliologie, 9: 271–284, plate 11.
- Neusser TP, Fukuda H, Jörger KM, Kano Y & Schrödl M (2011) Sacoglossa or Acochlidia? 3D reconstruction, molecular phylogeny and evolution of Aitengidae (Gastropoda: Heterobranchia). Journal of Molluscan Studies, 77: 332–350.
- Nevill G & Nevill H (1869) On some new marine Gastropoda from the southern province of Ceylon. Journal of Asiatic Society, Bengal, 38: 65–69.
- Ornelas-Gatdula E, Camacho-Garcia Y, Schrödl M, Padula V, Hooker Y, Gosliner TM & Valdés Á (2012) Molecular systematics of the "Navanax aenigmaticus" species complex (Mollusca, Cephalaspidea): coming full circle. Zoologica Scripta, 41: 374–385.
- Pease WH (1860) Descriptions of new species of Mollusca from the Sandwich Islands, Pt. I. Proceedings of the Zoological Society, London, 1860: 18–36.
- Pease WH (1861) Descriptions of new species of Mollusca from the Pacific Islands. Proceedings of the Zoological Society of London, 1861: 242–247.
- Pease WH (1863) Letter from, on errors and omissions in former communications. Proceedings of the Zoological Society of London, 1863: 510.
- Pease WH (1868) Descriptions of marine Gasteropodae inhabiting Polynesia. American Journal of Conchology, 4: 71–80, pls 7–12.
- Pham MN, Tan HTW, Mitrovic S & Yeo HHT (2011) A checklist of the algae of Singapore, 2<sup>nd</sup> Edition. Raffles Museum of Biodiversity Research, National University of Singapore, Singapore. 99 pp. http://rmbr.nus.edu.sg/raffles\_museum\_pub/singapore\_algae\_checklist\_second\_edition.pdf.
- Pilsbry HA (1895) Manual of conchology: structural and systematic. 15: 181–436, plates 43–50 & 59–61.
- Pilsbry HA (1896) Manual of conchology: structural and systematic. Volume 16. Academy of Natural Sciences, Philadelphia, pp. 7 + 262, frontispiece + pls 1–74.

- Pruvot-Fol A (1951) Étude des nudibranches de la Mediterranée. Arch. Zool. Exper. et Génér. 88: 1–79.
- Rao KP (1965) Record of the bivalve gastropod *Berthelinia limax* (Kawaguti and Baba, 1959) from the Indian Ocean. Nature, 208: 404–405.
- Risso A (1818) Mémoire sur quelques Gastéropodes nouveaux, Nudibranches et Tectibranches observés dans la Mer de Nice (1). Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts, 87 : 368–377.
- Rudman WB (2002) *Volvatella viridis* from Queensland. In : Sea Slug Forum, Australian Museum, Sydney. http://www.seaslugforum.net/find/7452.
- Sarma ALN (1975) Three new species of the bivalved gastropods *Julia* and *Berthelinia* found in Eastern Indian Ocean. Venus (Japanese Journal of Malacology), 34: 11–25.
- Smith EA (1885) Report on the Lamellibranchiata collected by H.M.S. Challenger, during the years 1873–1876. Reports on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876 13(1): 1–341.
- Schrödl M, Jörger KM, Klussmann-Kolb A & Wilson NG (2011) Bye bye "Opisthobranchia"! A review on the contribution of mesopsammic sea slugs to euthyneuran systematics. Thalassas, 27(2): 101–112.
- Swainson W (1840) A treatise on malacology or shells and shell-fish. In: Lardner D (ed.), The Cabinet Encyclopedia.
- Swennen C (1998) Two new gastropods, *Elysia bangtawaensis* and *E. siamensis* from southern Thailand (Opisthobranchia, Sacoglossa, Elysiidae). Bulletin Zoölogisch Museum, Universiteit van Amsterdam, 16(6): 33–39.
- Swennen C (2011) Large mangrove-dwelling *Elysia* species in Asia, with descriptions of two new species (Gastropoda: Opisthobranchia: Sacoglossa). The Raffles Bulletin of Zoology, 59(1): 29–37.
- Takano T, Hirano YM, Trowbridge CD, Hirano YJ & Watano Y (2013) Taxonomic clarification in the genus *Elysia* (Gastropoda: Sacoglossa): *E. atroviridis* and *E. setoensis*. American Malacological Bulletin, 31(1): 25–37.
- Thompson TE (1979) Biology and relationships of the South African sacoglossan molluse *Volvatella laguncula*. Journal of Zoology, London, 189: 339–347.
- Trinchese S (1876) Rendiconti dell'Accademia delle Scienze dell'Istituto di Bologna, 1875-76: 84.
- Vendetti JE, Trowbridge CD & Krug PJ (2012) Poecilogony and population genetic structure in *Elysia pusilla* (Heterobranchia: Sacoglossa), and reproductive data for five sacoglossans that express dimorphisms in larval development. Integrative and Comparative Biology, 52(1): 138–150.
- Wägele H, Klussmann-Kolb A, Verbeek E & Schrödl M (2014) Flashback and foreshadowing a review of the taxon Opisthobranchia. Organisms, Diversity & Evolution, 14: 133–149.
- Yokes B & Rudman WB (2004). Lessepsian opisthobranchs from douthwestern coast of Turkey: Five new records for Mediterranean. Rapport Commissione Internationale Mer Méditerranée, 37: 557.
- Zapata F, Wilson NG, Howison M, Andrade SCS, Jörger KM, Schrödl M, Goetz FE, Giribet G & Dunn CW (2014) Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda. Proceedings of the Royal Society B, 281: 20141739.