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LARGE MANGROVE-DWELLING *ELYSIA* SPECIES IN ASIA, WITH DESCRIPTIONS OF TWO NEW SPECIES (GASTROPODA: OPISTOBRANCHIA: SACOGLOSSA)

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ABSTRACT. − Two large *Elysia* species have been described as specific for mangrove habitats over the last 20 years: *E. leucolegnote* Jensen, 1990 and *E. bangtawaensis* Swennen, 1998. They are usually found aggregated on soft mud without algae in shallow, shaded pools during low tide. Two more species are added in the present paper as *E. singaporensis*, new species, and *E. bengalensis*, new species. The four *Elysia* species are easily recognizable. External and internal characters of the four mangrove-associated *Elysia* spp. are depicted, together with some biological notes, suggesting two morphological groups similar in behaviour and habitat.

KEY WORDS. − *Elysia*, Mangrove, Plakobranchidae, Western and Central Indo-Pacific.

INTRODUCTION

Sacoglossan opisthobranchs have no jaws and their radula consists of a single, longitudinal row of teeth of which the older teeth are kept during their life in an ascus (Pruvot-Fol, 1954). The classification of the Sacoglossa was most recently reviewed by Jensen (1996). The Plakobranchidae (Elysiidae) form the largest family in the Sacoglossa with *Elysia* as the most speciose genus. The most obvious character of *Elysia*, shared with *Plakobranchus* and *Thuridilla*, is the presence of wing-like parapodia bordering the posterior part of the foot. The species have neither shell nor oral tentacles. The majority of the *Elysia* species are smaller than 20 mm, but a few are larger and measure beween 25–50 mm. Several large tropical species from reef habitats were described over 100 years ago [*E. grandifolia* Kelaart, 1858; *E. rufescens* (Pease, 1871); *E. subornata* Verrill, 1901]. However, several large species living in turbid water in mangrove forests have only been discovered during the last 20 years. The first known large mangrove *Elysia* was found in Hong Kong and named *E. leucolegnote* by Jensen in 1990. It was followed by *E. bangtawaensis* Swennen, 1998, found in the Gulf of Thailand. Meanwhile, two other species have been found elsewhere. All are named and depicted herein this paper.

MATERIALS AND METHODS

Specimens of three species were collected by the author in mangrove forests at different sites on separate occasions. Photographs were made of the habitat, and live specimens were described in the laboratory. Although important external characters can be seen in live specimens, details such as apertures and dorsal vessels are more easily examined in carefully relaxed preserved specimens. For this, some specimens were relaxed by placing them in a solution of 71 g $MgCl_2$ in l,000 ml water meanwhile removing mucous accumulation and then fixing them in a 5% formaldehyde-seawater solution. Pharynx, radular teeth, and main details of the digestive system were checked via dissections by hand with fine needles. For permanent storage, some specimens were transferred into 70% ethanol. Specimens of the fourth species were collected and given to me by a colleague working in India. Types of the new species have been deposited in the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore (ZRC) and in the Zoological Museum of the University of Amsterdam (ZMA).

SPECIES ACCOUNT

Elysia leucolegnote Jensen, 1990
(Figs. 1–7)

Material examined. – South China Sea, Hong Kong, inland, south side Starling Inlet, about 22°31'28"N, 114°31'28"E, tens, 11 Mar.2004; Near Ting Kok, about 22°28'14"N, 114°13'01"E, tens, 14 Mar.2004; Hong Kong , Mai Po Nature Reserve, in mangrove forest along Deep Bay (22°29'52"N, 114°01'48"E), tens, Nov.2007; Gulf of Thailand, south of Chumphon at about

Table 1. Live specimens of the four known mangrove *Elysia* species can easily been distinguished by the following characteristics:

1.	Parapodia with white or yellowish border, triangular white-yellowish mark on head. No other colours on skin ..... *E. leucolegnote* Jensen, 1990.
–.	Parapodia with tens of coloured dots ..... 2.
2.	Old rose specks over dorsal and ventral sides including foot sole, forming line over dorsal sides of rhinophores ..... *E. singaporensis*, new species.
–.	No old rose, but white dots on parapodia ..... 3.
3.	Tips of rhinophores pale or orange. Parapodial border with several orange or reddish glandular dots ..... *E. bangtawaensis* Swennen, 1998.
–.	Tips of rhinophores dark. Mainly white dots on parapodia and body ..... *E. bengalensis*, new species

10°22'20"N, 99°10'26"E, tens, 27 – 29 Mar.2007; Near Don Sak at about 9°18'59"N, 99°45'34"E, and 9°18'10"N, 99°48'08"E, about ten, 2 Oct.2007; Pak Phanang Bay, at about 8°35'37"N, 99°58'23"E and 8°29'19"N, 100°11'33"E, tens, 28-29 Sep.2007, 7, 13 Apr. and 30 Sep.2008; Near Bang Tawa, about 06°51'28"N, 101°09'31"E, tens, 30 Sept.2008; same site, 15, 16 Oct.2009; Andaman Sea Thailand, Ko Libong in mangrove at about 07°14'50"N, 99°26'30"E, tens, 9 Oct.2007; mangrove east of Krabi at about 08°03'17"N, 098°53'57"E, tens, 3 Oct.2010.

Live colouration. **–** Narrow white line along parapodial borders, often locally widened. Some have few white spots on renopericardial prominence, rarely few white spots on dorsal sides of parapodia. White triangle on head connected with white line over dorsal sides of rhinophores. Tips of rhinophores and often also posterior side of renocardial prominence lack tubules of digestive gland (Fig. 1). Individuals with digestive gland yellowish starting in the central parts have not fed for some months as confirmed in captivity.

External morphology. **–** Length alive up to 41 mm. Length of renopericardial prominence about three times width. Two major dorsal vessels connected to posterior side (Fig. 2A). Renopore in vaginal aperture anterior right of renopericardinal prominence on dorsum (Fig. 7A).

Internal characteristics. **–** Pharynx small, round, ascus on stalk, length 330-350 µm, height without ascus stalk 280-320 µm (Fig. 3A). Radular teeth: ascending limb 4-6, descending limb 7-9, ascus 8 to 18 (N= 5). Teeth blade-shaped with upwards curved tips, cutting edges denticulate (Fig. 4A). Tooth length up to 63 µm. Oesophagus about 2.8 times length of pharynx. Stomach small compared to intestine (Fig. 5A). Green, glandular tissue of digestive gland starts in main branches far from stomach (Fig. 5A). Penis unarmed, conical with narrow extension, length 400-500 µm (Fig. 6A). Vas deferens convoluted just before entering penis. Gonadal follicles individually connected to ducts.

Biology. **–** Egg strings up to 55 cm long, irregularly curved, but when substrate allows in wide spirals, with yellow string of extra-capsular yolk in the jelly, single ovum per capsule, 11 March 2004 Starling Inlet, 13 April 2008 Pak Phanang Bay. Some specimens were kept in captivity in separate bottles for several years. One large specimen was collected and stayed alive in captivity for 53 months; three others reached four years then accidentally died. Food source is the tiny, siphonal green alga *Boodleopsis* c.f. *pusilla*.

Discussion. **–** It may be the result of a different treatment of the pharynx, but Jensen (1990) described the descending limb of the radula as attached over its whole length, while my specimens showed the ascus on a partly free stalk (Fig. 3A). Jensen (2003) reported that her specimens feed on *Boodleopsis pusilla*, *Cladophora*, *Cladophoropsis* and *Enteromorpha* in the laboratory. Only *Boodleopsis* was taken as food in my experiments. *Cladophora* and *Enteromorpha* were not touched even when the slugs finally lost size and colour. They started feeding when *Boodleopsis* was given and then became green again after a few days.

Elysia singaporensis, new species

(Figs. 1–7)

Material examined. **–** HOLOTYPE: 1 ex. (length alive 23 mm)(ZRC, MOL.2974), coll. Singapore, Western Johor Straits, old mangrove forest bordering east side of Sungei Buloh Wetland Park, about 1°26'47"N, 103º43'57"E, 21 May 2002.
PARATYPES: 3 ex. (ZRC, MOL. 2974); 3 ex. (ZMA, Cat. nr. Moll. 179181), same site and date as holotype.
OTHERS: 22 ex., length alive 20-31 mm, with egg strings, 21 May 2002; same site, 18 Oct.2009, 12 ex. Length alive 15-22 mm, with egg strings.

Etymology. **–** The species name is derived from the island state of Singapore where the specimens were found.

Live colouration. **–** Basic colour green from content of digestive gland. Ruddy specks over dorsal and ventral sides including foot sole, forming line over dorsal sides of rhinophores. Tubules of digestive gland lacking in tips of rhinophores and over posterior part of renopericardial prominence (Fig. 1B).

External morphology of live specimens. **–** Length alive up to 31 mm. Eyes not conspicuous, wide apart behind rhinophores; rhinophores with groove over whole length. Lateral groove on right side from anterior border of right parapodium to foot; transversal groove dividing foot into two parts; anterior foot corners slightly extended, bluntly pointed; frontal border can be kept notched, but also smoothly curved; foot behind transverse groove weakly developed.

Thin tributaries of digestive gland visible over whole body, missing in tips of rhinophores, over eyes, and sometimes partly above renopericardium. Renopericardial prominence long and narrow, tapering posteriorly, length three to four times width. Renal part posterior of cardial part, about 2/3 of total length, posterior with pair of major dorsal vessels and on each lateral side zero to two vessels, varying in number and position (Fig. 2B). Renopore in vaginal aperture on dorsum at anterior right side of pericardium (Fig. 7B). Parapodia and body do not bear protuberances. Male aperture below right rhinophore; anus and oviducal apertures close together in upper part of lateral groove.

***Internal features*. –** Pharynx small, ascus on stalk, length 570-760 µm, height without ascus stalk 550 to 630 µm (three 25 mm long specimens) (Fig. 3B). Radula with 4 to 7 teeth including ghost teeth in ascending row, 6 to 9 in descending row, few in ascus. Teeth narrow blade-shaped (Fig. 4B),

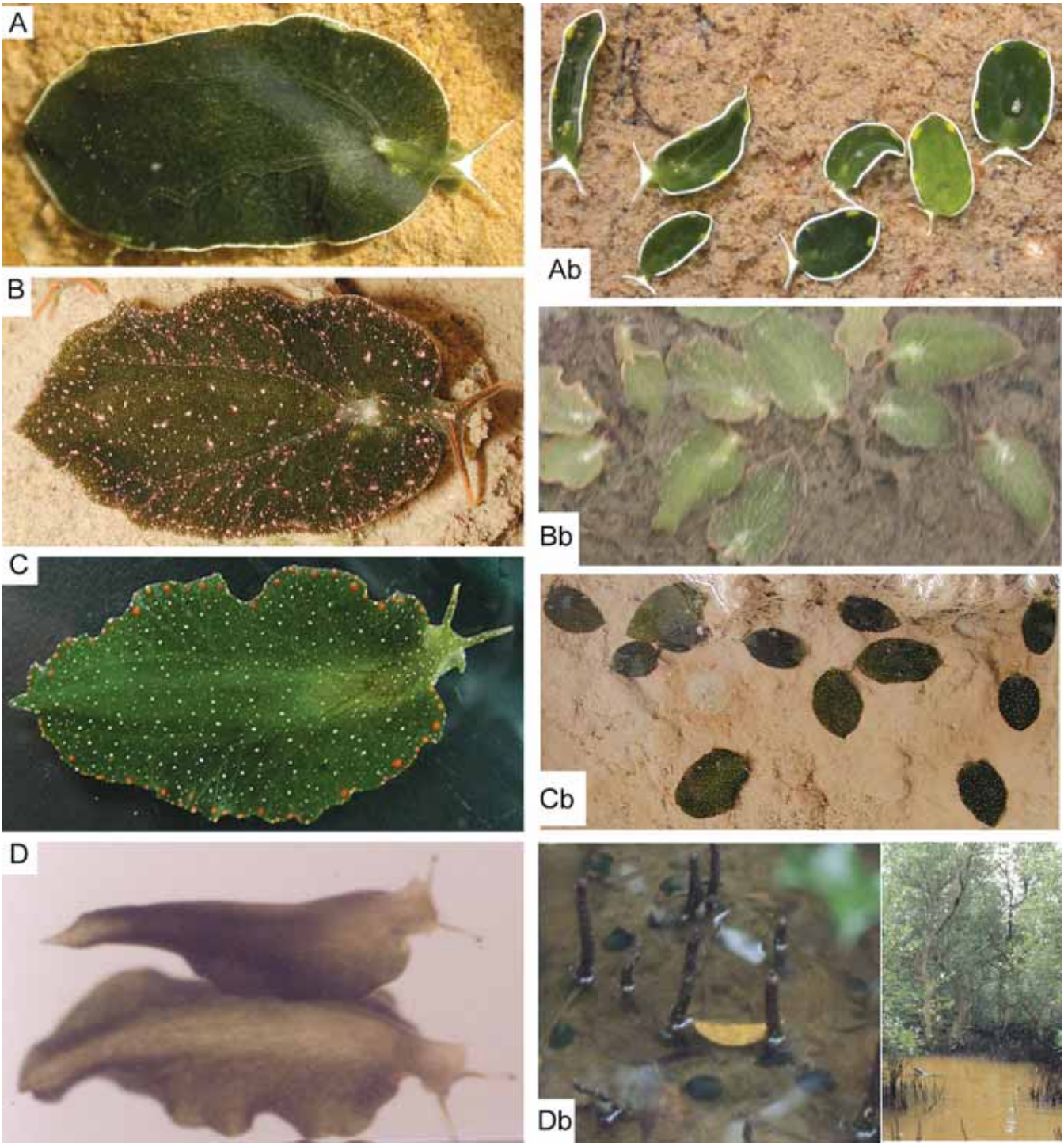

Fig. 1. The four mangrove *Elysia* species: **A**, *E. leucolegnote* Jensen, 1990; **B,** *E. singaporensis*, new species; **C**, *E. bangtawaensis* Swennen, 1998; **D**, *E. bengalensis*, new species. A and B photographed in-situ, respectively Pak Phanang Bay and Singapore, C and D photographed in captivity. **Ab, Bb, Cb, Db** group photographed in-situ, respectively Pak Phanang Bay, Singapore, Bangtawa, and Andhra Pradesh (India). D and Db photographed by Dr. S. Bouillon.

used teeth often with slightly incurved tips, finely denticulate cutting edges. Tooth length 140-180 µm. Oesophagus short about as long as pharynx. Relatively massive intestine plicate near anus. Glandular tissue of digestive gland starts in main branches far from stomach (Fig. 5B). Penis, unarmed, tapered, (Fig. 6B).

Biology. **–** Egg strings have been found in May and October. Strings had 3–4 ova per capsule, but older string had one veliger per capsule. Yellow extra-capsular yolk, in interrupted line over whole length of string (Fig.7F, G). The strings were irregular on algae, but more or less in counter-clockwise, loose spirals on glass in captivity. The longest measured string was 320 mm.

Elysia bangtawaensis Swennen, 1998
(Figs. 1-7)

Syn.: *Elysia bangtawaensis* Swennen, 1997. (Rudman, 2007; Coleman, 2008). Incorrect year of publication due to a difference of the year printed on the volume and the date of distribution of the last issue which is stated as 18 April 1998.

Material examined. **–** Gulf of Thailand. Pak Phanang Bay about 08°36'10"N, 99°58'16"E and 8°29'19"N, 100°10'58"E, 2 respectively 4 specimens near hundreds of *Elysia leucolegnote*, 28-30 Sep.2007; Bang Tawa, about 06°51'28"N, 101°09'31"E, type locality, yearly between Mar.1997 and Oct.2010; Inland ditch near Ban Di, about 6°52'17"N, 101°18'48"E, 5-10 during several visits between 1999 and 2002 (site now converted into shrimp ponds); Inner Pattani Bay, about 6°53'50"N, 101°20'49"E, 2 to 30 individuals during several visits between 1997 and 2007; Straits of Malacca, Johor State, 01°21'30"N, 103°30'37"E, 3 specimens, 17 Oct.2009; Andaman Sea, Thailand, mangrove east of Krabi at about 08°03'17"N, 098 53'57"E, one, 3 Oct, 2010. Arabian Sea, estuary Mandovi River, Goa, India, material seen. [See photo: Jagtap et al., 2009]. Bay of Bengal, Andhra Pradesh, about 20 km south of Kãkinãda, 16°51'40"N, 82°15'10"E, some specimens, 4 Dec.2002 [specimens sent to me by Dr S. Bouillon]; South Pacific Ocean, Australia, Queensland, near Coolangatta, about 28°10'S, 153°32'E, 28 Jul.2007 (photos by G. Cobb in Coleman, 2008).

Live colouration. **–** Prominent reddish to orange, glandular warts along parapodial borders. White spots of different sizes and fine reddish specks dispersed on dorsal and ventral sides, including foot sole. Green ductules of digestive gland cover renal part in most specimens; they do not reach tips of rhinophores. Tips pale or coloured by white and orange spots (Fig. 1C). Individuals with digestive gland yellowish starting in the central parts have not fed for some months as confirmed in captivity.

External characters. **–** Length alive up to 52 mm. Renopericardial prominence oval, length less than twice width. Two major dorsal vessels on posterior side and one,

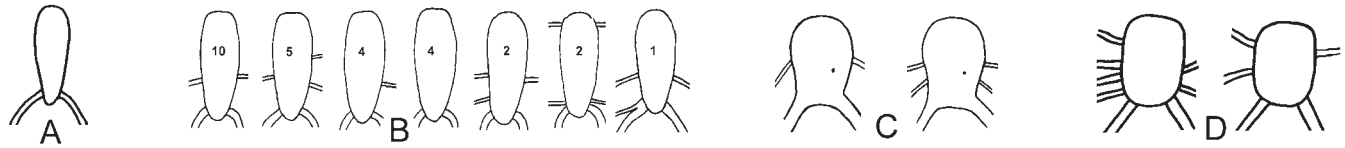

Fig. 2. Renopericardial bulbs and attachments of dorsal vessels of: **A,**: *Elysia leucolegnote*; **B,** *E. singaporensis*, new species; **C**, *E. bangtawaensis*; **D,** *E. bengalensis*, new species. The highest variation in number of vessels is shown by *E. singaporensis*. Figures in the bulbs of this species indicate the number of specimens with that pattern found in a sample of 28 individuals.

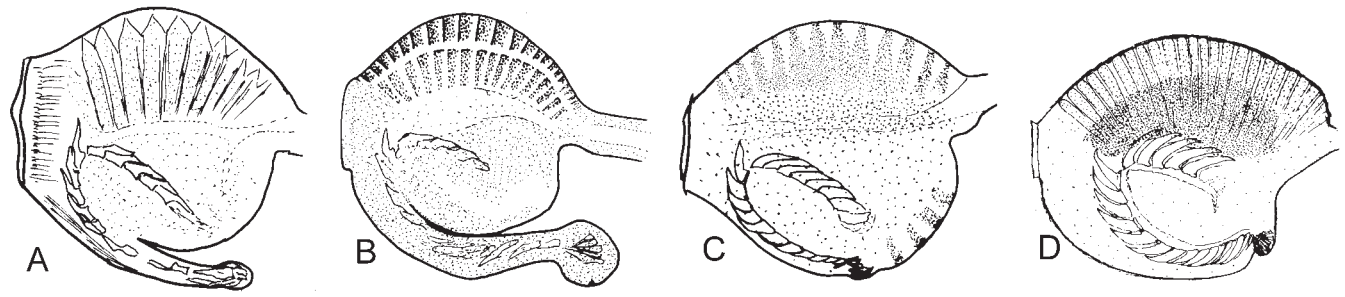

Fig. 3. Lateral view of the shape of the pharynx: **A**, *Elysia leucolegnote*; **B**, *E. singaporensis*, new species; **C**: *E. bangtawaensis*; **D**, *E. bengalensis*, new species.

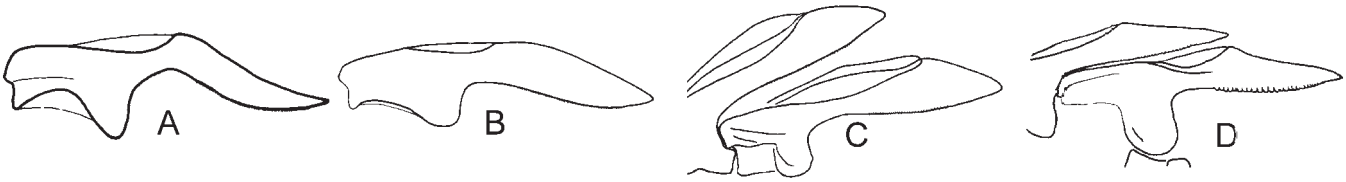

Fig. 4. Lateral view of the radular teeth: **A**, *Elysia leucolegnote*; **B**, *E. singaporensis*, new species; **C**, *E. bangtawaensis*; **D**, *E. bengalensis*, new species.

sometimes two, thinner vessels on both lateral sides (Fig. 2C). Renopore on dorsal side of pericardium in posterior part between heart and renal part (Fig. 2C). Vaginal aperture on ventral side of right parapodium near anterior border (Fig. 7C).

***Internal characteristics*. –** Pharynx small, length about 400 µm, dark pigment band over sides, ascus vestigial (Fig. 3C). Radula with 7 to 9 teeth in ascending limb and same number in descending limbs. Teeth blade-shaped, more than 80 very fine denticles along cutting edge, tooth length in specimens of 23 to 49 mm length alive similar, about 67 µm (Fig. 4C). Oesophagus narrow, length about 2.5 times length of pharynx. Stomach wide, green, glandular tissue of digestive gland starts in stomach. Intestine pale, wide, runs upward from anterior part stomach (Fig. 5C). Penis unarmed, conical (Fig. 6C). Male follicles more central, larger and less numerous than female follicles.

***Biology*. –** Copulation by lying with the right side of the frontal part of the body against the partner. Penis goes into the underside of the right parapodium. At the end they may form a ball when penises withdraw. Egg strings without extra-capsular yolk, up to 720 mm long, irregularly coiled over substrate; in captivity irregular spiral on glass.

During low tide, when there is no water current, the slugs were often found in dense aggregations resembling fallen leaves on bare mud in shallow, water-filled depressions or gullies in mangrove forests. Depression can be as small as a footprint of a water buffalo or human. When a sudden movement in the water occurred (e.g., a foot step), the slugs closed their parapodia and become detached from the floor. Their feet clearly did not strongly adhere to any substrate. The slugs rolled around across the substrate usually to slightly deeper parts from where they can be easily swept out by another foot step. I was unable to determine what

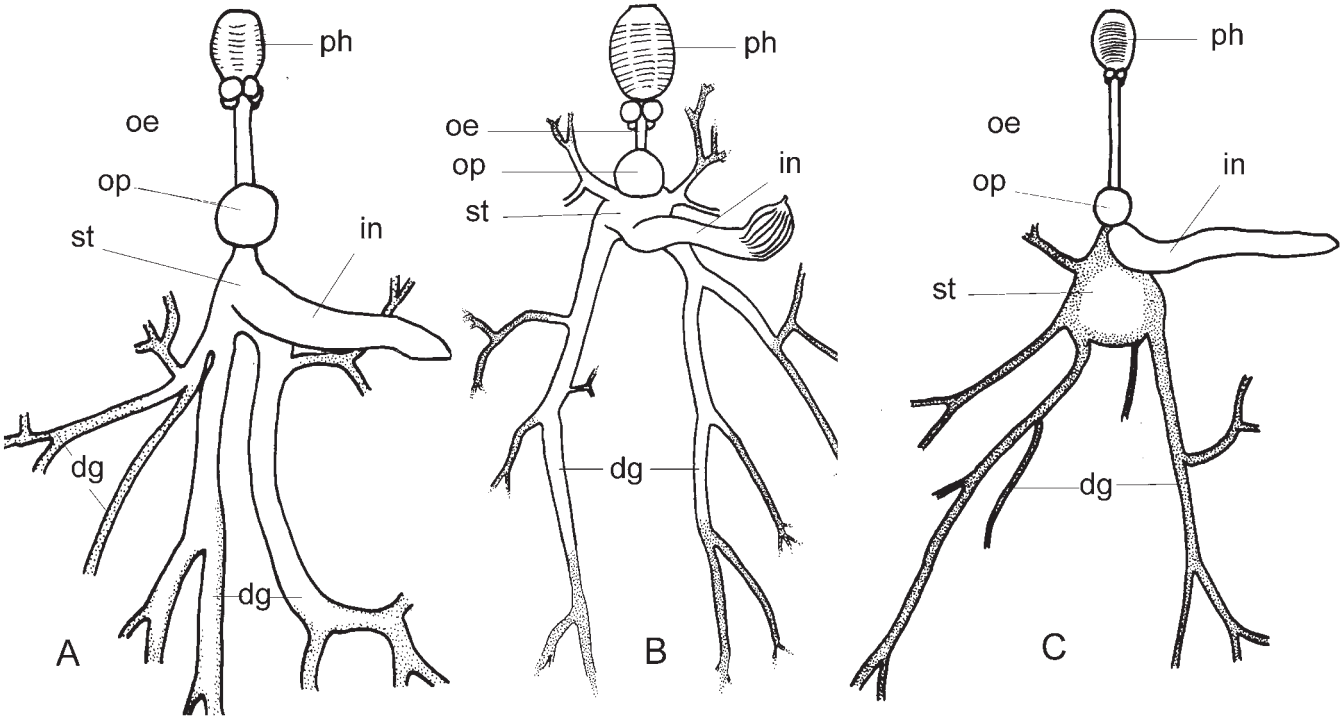

Fig. 5. Dorsal view of the main parts of the digestive systems: **A,** *E. leucolegnote*; **B,** *E. singaporensis*; **C**, *E. bangtawaensis*. Legend: **dg** – digestive gland; **in** – intestine; **oe** – oesophagus; **op** – oesophageal pouch; **ph** – pharynx; **st** – stomach. Note that two specimens per species were studied for making the drawings. They were collected from the same site and day. When the distribution of the coloured glandular parts is influenced by the feeding condition then the differences do not indicate differences between species.

Fig. 6. Shape of the penis of: **A,** *Elysia leucolegnote*; **B,** *E. singaporensis*, new species; **C**, *E. bangtawaensis*; **D,** *E. bengalensis*, new species.

happened when the tide moved in. The movements of the tidal currents are strong and longer lasting than a step; I would expect that they be dislodged from the substrate. However, when the flood came in, the water turbidity was high due to the heavy load of mud particles and visibility immediately decreased to zero. Although the slugs are likely dislocated by the tidal currents, I have no idea how they could select depressions that contain sufficient water for survival during the next low tide.

When discovering *E. bangtawaensis* in March 1997, I had not dealt with sacoglossans since 1959 (Swennen, 1961) and had missed the developments in knowledge since then. Therefore, I wondered what was the meaning of their behaviour and what was their food, because there were no visible algae in the shallow pools with a soft mud bottom. Specimens were put in trays in the laboratory with the local mud and seawater. They soon became immobile and stretched out their parapodia as seen in the field. When undisturbed, they kept the parapodia expanded also during the night. Closing the parapodia over the body occurred when the tray was touched, but also when exposed to direct sunlight that even stimulated them to move to a shaded position such as below other specimens (Swennen, 1998). This made it unlikely that resembling a leaf was procryptic. Feeding trials with algae from outside the forest had no success.

I noticed during a subsequent visit that tiny green algae were present on the dry mud surface between mangrove roots above mean high tide level. Mud and algae could not be separated and were placed in-situ in the trays with the slugs. This time, the slugs were attracted by the algae and appeared to feed on them. At my request, Mr. M. Lavaleye (Royal Netherlands Institute for Sea Research, Texel) conducted phytopigment analyses of an *E. bangtawaensis* and the algae. That showed that the spectra of both organisms were almost identical. Mr. K. A. Sjollema (Laboratory for Electron Microscopy, University of Groningen) made images of a piece of slug

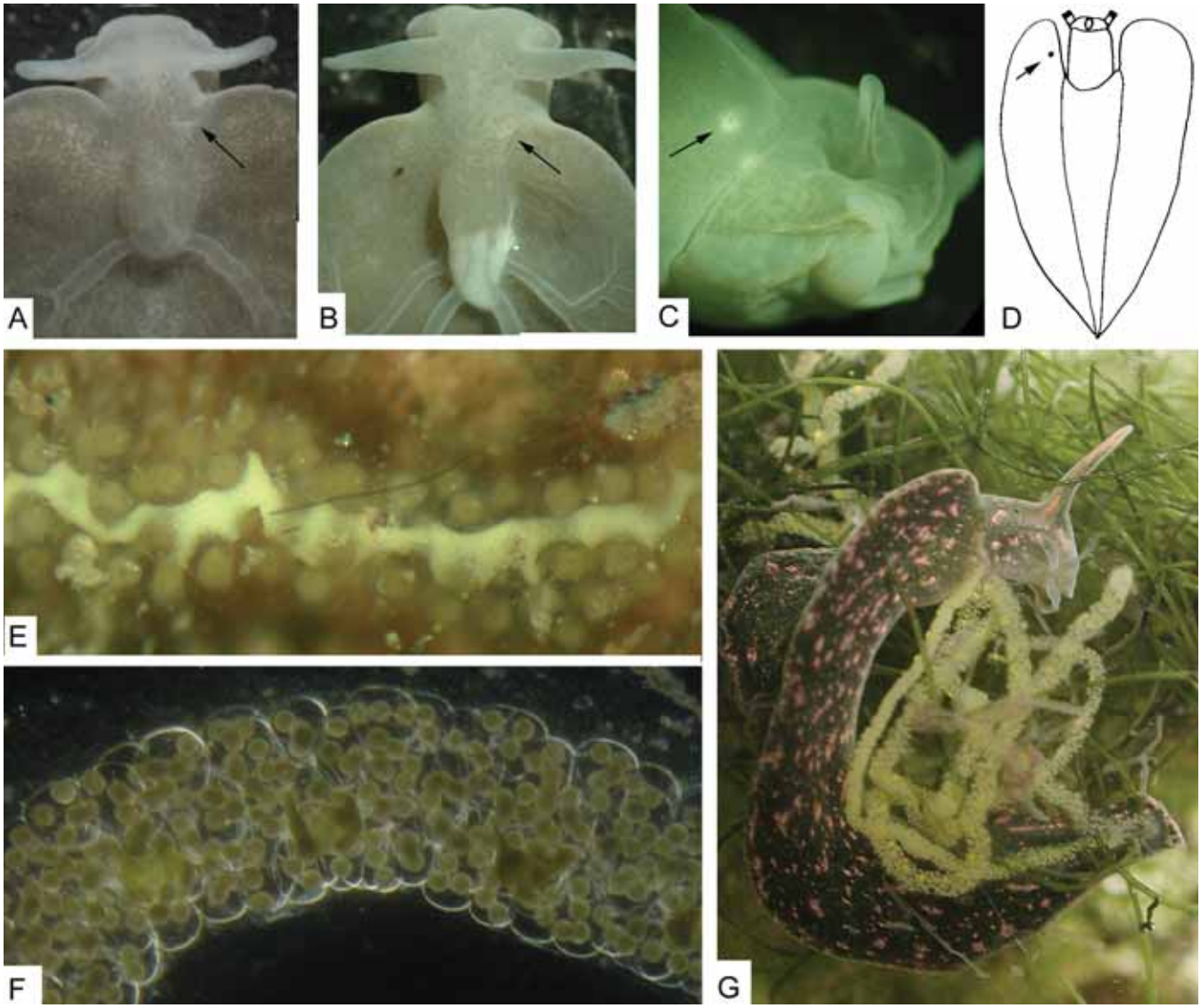

Fig. 7. Position of vaginal apertures in: A, *Elysia leucolegnote*; **B**, *E. singaporensis*, new species; **C**: *E. bangtawaensis*; **D**, *E. bengalensis*, new species. **E**, part of an egg string of *Elysia leucolegnote* showing uninterrupted band of extra-capsular yolk; **F**, part of an egg string of *E. singaporensis* showing interrupted band of extra-capsular yolk and more than one ovum per capsule; **G**, *E. singaporensis*, new species, producing an egg string in algae in aquarium. Position of vaginal apertures indicated by arrow.

Table 2. Differences and similarities of position of vaginal aperture and shape of ascus and radular teeth in the four large mangrove *Elysia* species.

	E. leucolegnote and *E. singaporensis*	*E. bangtawaensis* and *E. bengalensis*
Vaginal aperture	On dorsal side of right parapodium anterior of renopericardium together with renal aperture	On anterior ventral side of right parapodium
Ascus	Prominent on long stalk largely free of ventral side of pharynx	Vestigial on ventral side of pharynx
Radular teeth	Narrow serrate blades	Wide serrate blades

tissue and the alga. They showed that in the cells of the digestive gland of *E. bangtawaensis* several chloroplasts occurred that were similar to the ones in the algae. Then, Dr. W. Stolte (Royal Netherlands Institute for Sea Research) placed a live slug in a respirometer and measured the oxygen from incoming and outgoing seawater. The specimen had a length of 3.4 cm, and had no contact with any algae for 20 days. The space was too small for allowing the slug to fully expand its parapodia in the measuring chamber, but still the measurements in various light conditions showed a gross photosynthesis of 4.2 micromole O_2/h and a respiration of 1.3 micromole O_2/h illustrating that *E. bangtawaensis* can indeed act as a plant with real photosynthesis taking place in dimmed light (117 micromole photons/m^2/s) producing more oxygen than used. This is known under such names as chloroplast retention, kleptoplasty, chloroplast symbiosis, solar-powered slugs. Further investigations were stopped due to lack of time and funding.

Discussion. **–** Specimens from India, Malaysia, Thailand and Australia show the same colour pattern.

Elysia bengalensis, new species
(Figs. 1–7)

Material examined. **–** HOLOTYPE: 1 ex. (length alive 43 mm) (ZRC. MOL.2972), Bay of Bengal, Andhra Pradesh, delta of Godovari River about 20 km south of Kãkinãda, between 16°43'N, 16°52'N and 82°15'E, 82°22'E, May 2001, coll. Steven Bouillon.

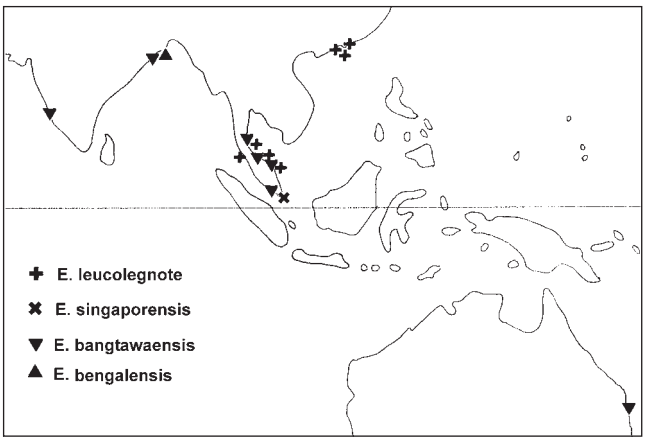

Fig. 8. Map showing the known distribution of the four mangrove *Elysia* species discussed in this paper. The sites in the Gulf of Thailand and Hong Kong were in close proximity and one mark may indicate more than one collection site.

PARATYPES: 2 ex. (ZRC.MOL.2973), same site and date as holotype.
OTHERS: about 7 specimens internally rotten, same site and date as holotype.

Etymology. **–** The species name is derived from the Bay of Bengal into which the Godovari River discharges.

Live colouration. **–** Basic colour green from content of digestive gland. Irregular row of larger white spots along parapodial border. Conspicuous white specks irregularly spaced all over dorsal and ventral sides, not on foot sole. Tips of rhinophores and vaginal aperture dark coloured. Dark remains visible on both areas in specimens stored in 70% ethanol or 6% formaldehyde for five years.

External appearance. **–** Length alive up to 50 mm. Rhinophores with groove over whole length. Parapodia and body smooth. Anterior foot corners slightly extended, bluntly pointed. Renocardial prominence oval, length less than twice width; pair of major dorsal vessels on posterior side of prominence; one to four smaller vessels on each lateral side (Fig. 2D). Renopore could not be detected in available material. Male aperture below right rhinophore; anus and oviducal apertures close together in upper part of lateral groove. Vaginal aperture on ventral side of right parapodium near anterior border as in *E. bangtawaensis*, but black marked (Fig. D).

Internal characteristics. **–** Pharynx small, length about 380 µm, with strong dorsal septate muscle, ascus vestigial. Radula with 7 teeth in ascending row, 10–11 in descending row, and bundle of about 15 worn teeth in ascus. Length of radular teeth 68–80 µm (two individuals). Teeth blade-shaped, blade about 38% of total length, 20-35 denticles on cutting edge (Fig. 4D). Shape of blade slightly differs from *E. bangtawaensis*, but has fewer and larger denticles. Penis unarmed, conical (Fig. 6D).

DISCUSSION

The four large mangrove *Elysia* species can be divided into two groups of two species according to some anatomical differences and similarities (Table 2). The four species live in shaded mangrove habitats and are often found congregated in pools. They are usually found in shallow pools and drains high in the intertidal zone during low tide, but they cannot live amphibiously. All show a similar behaviour as

mentioned in the description of *E. bangtawaensis*, thus can likely be grouped under the name solar-powered slugs. That does not mean that they like direct sun light, they seem to dislike strong light and prefer the shade (Swennen, 1998). Tests showed that *E. bangtawaensis* and *E. leucolegnote* can keep their chloroplasts for months; *E. bengalensis* and *E. singaporensis* could not be tested. Long-term functional chloroplast retention has only been found in the Plakobranchoidea. However, several large *Elysia* species do not have this quality (Händeler et al., 2009).

The food alga of *Elysia leucolegnote* and *E. bangtawaensis* is *Boodleopsis* c.f. *pusilla* that grows in high mud between mangrove roots. Here it becomes not wetted during neap high tides in the summer months in the Gulf of Thailand, when the water level is lower due to the monsoon wind. This means that these slugs cannot reach their food at libitum, but have to wait for spring high tides. Experiments showed that they can feed for many hours and can survive without food for two to three months. However, then they become gradually smaller and their green colour changes into yellowish. This may suggest that they not only need new chloroplasts, but also some additional substances from their food alga. The famished slugs regain their colour and size after they feed on algae. Specimens of *Elysia bangtawaensis, E. leucolegnote,* and *E. singaporensis* that are not green but yellowish, are rarely found among normal specimens of these species in the field. They look similar as specimens that in captivity were deprived of food for more than two months. It remains unclear if this is the results of feeding difficulties or other problems. The noted differences in the extent of the glandular tissue in the main branches of the digestive system (Fig. 5) has been based on the greenish colour in two specimens per species collected from the same site and day. In retrospect, it may be possible that the distribution of the coloured glandular parts has been influenced by the physical condition of the slugs and if so, would not indicate differences among species.

I did not study the reproductive organs in detail. The status of the reproductive cycle seemed to induce large differences in shape and size of albumen gland, bursae, and gonadal follicles. The reproductive periods seemed short and remained unpredictable for me. The long egg strings were not always found in the field nor deposited in captivity. The egg strings of *E. leucolegnote, E. singaporensis* contain a band of yellowish extra-capsular yolk (Boucher, 1983) that is interrupted in *E. singaporensis.* Three to four ova were found per capsule in fresh laid strings of the latter species, but only one veliger in older strings. Perhaps the other eggs were eaten by the developing veliger as no remains were detected, or the string was aberrant. The egg masses of *E. bengalensis* are still unknown.

Damaged specimens were frequently found. They lacked small or large parts along the border of the parapodia or had holes in the parapodia. These specimens behaved normally and small wounds completely healed when kept and fed in captivity. Such damages seemed to occur more often in *E. bangtawaensis* and *E. singaporensis* than in *E. leucolegnote*. Crabs or birds may have damaged these specimens, but tests in captivity showed that *E. bangtawaensis* and *E. leucolegnote* are highly unpalatable for local predatory fish and shrimps. Only the nudibranch *Gymnodoris pattani* Swennen, 1996, swallows them entirely, notwithstanding the *Gymnodoris* was usually much smaller than the *Elysia*. The discussed species have a long life span compared to the small *Elysia siamensis* Swennen, 1998, that reach only the age of three months. Individuals of *E. bangtawaensis* were kept up to 14 months in captivity, and of *E. leucolegnote* up to more than four years.

I am unable to indicate specific differences in habitat preferences among the species. *E. bangtawaensis* was found in the same area as *E. bengalensis* in the Bay of Bengal. *Elysia bangtawaensis* often occurs with *E. leucolegnote* in the same forest patch, and were regularly found mixed on several sites in the Gulf of Thailand. In the Pak Phanang Bay, only a few specimens of *E. bangtawaensis* were found in rather remote sites in the mangrove forest in September 2007, while at the same time *E. leucolegnote* was numerous over most of the area. Therefore, it was a surprise to see both species numerous in April and October 2008. No obvious changes were noted in the habitats. Generally, water in which the slugs were found was clear during low tide, but turbid during high tide. During low tide, the water quality was likely poor due to rotting wood and leaves, but the slugs tolerate it. *Elysia leucolegnote* has even been found in apparently anaerobic water conditions with white colonies and borders of sulphur bacteria around them both in Starling Inlet (Hong Kong) and near Chumphon (Thailand) where the high tides does not reach these sites during neap tides.

The known distribution of the four discussed *Elysia* species is limited to the tropical West Pacific and East Indian Oceans on both sides of the equator to about 22°North and 28°South (Fig. 8). *Elysia bangtawaensis* seems to have the widest distribution. However, the ranges of the species are in fact nearly unknown as turbid intertidal and mangrove habitats are generally poorly studied. Mangrove forests are notoriously difficult to explore due to lack of trails, orientation marks, unobstructed views, and an inclement human environment that include deep soft mud, biting ants, stinging mosquitoes, and skin-cutting oysters. The discoveries of *Elysia leucolegnote* in the Gulf of Thailand and Andaman Sea are the first reports outside Hong Kong. I expect that the four species have a broader distribution than could be reported here.

Although there is still much potential mangrove habitat available where the four mangrove *Elysia* species can occur, these habitats are at increasing risk of reduction. I have observed large-scale destruction of mangrove forests in SE Asia since my first visit in 1984. For example the small remnant of the mangrove forest near the village Bangtawa that was saved by the villagers from being converted into shrimp ponds, and is the type locality of *Elysia bangtawaensis* Swennen, 1998, *Gascoignella nukuli* Swennen, 2001, and *Costasiella coronata* Swennen, 2007; has recently been damaged by mechanically digging a wide ditch with high

dikes along both sides. The site near Ban Di, type locality of *Gascoignella jabae* Swennen, 2001, was converted into shrimp ponds that have already been disused. Today, disused ponds are not restored to their natural condition and remain empty and barren. Dikes, concrete sluices and other man-made constructions around the ponds block tidal flows that could aid in the natural recovery of these areas. On-going conversion of mangrove forests to shrimp ponds put these habitats and associated species at great risk for species loss and possible extinction.

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