

# Six new species of *Horniella* Raffray from the Oriental region (Coleoptera, Staphylinidae, Pselaphinae)

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## Abstract

The Oriental pselaphine genus *Horniella* Raffray, 1905 currently contains 29 species. In this paper, six new species are described: *H. nantouensis* Zhang, Hu & Yin, **sp. nov.** and *H. taiwanensis* Zhang, Hu & Yin, **sp. nov.** from Taiwan, China; *H. bifurca* Zhang & Yin, **sp. nov.** and *H. haucki* Zhang & Yin, **sp. nov.** from Thailand; *H. khasiensis* Zhang & Yin, **sp. nov.** from northern India; and *H. sababensis* Zhang & Yin, **sp. nov.** from eastern Malaysia. In addition, *H. aculeata* Yin & Li, 2015, originally described from Yunnan, China, is newly recorded from Thailand.

## Keywords

Ant-loving beetles, Asia, new record, new taxa, species list, taxonomy

## Introduction

The Oriental pselaphine genus *Horniella* Raffray, 1905 (Tyrini: Somatipionina) currently includes 29 species distributed in China (12 spp.), Thailand (9 spp.), Malaysia (4 spp.), Nepal and India (1 sp.), Sri Lanka (1 sp.), the Philippines (1 sp.), and Indonesia (1 sp.) (Raffray 1905; Yin and Li 2014, 2015; Newton 2020). Members of this genus are easily recognizable by their medium-sized to large body, enlarged maxillary palpomeres 4 that lack an apical palpal cone, presence of a frontal fovea on the head, weakly to greatly developed anterolateral genal projections, pronotum with median and

lateral antebasal foveae that are connected by an antebasal sulcus, and usually medially carinate abdominal tergite 1 (IV) that is longer than tergite 2 (V). The known species were placed in four groups (Yin and Li 2014), which are followed here. The *H. centralis* group, with nine species, is defined by the distinct apicolateral genal projections, the head with a pair of long, curved ocular canthi, and the apical portion of the aedeagal median lobe with the right or left half strongly projecting apically. The *H. burckhardti* group, also containing nine species, is morphologically similar to the *H. centralis* group, but the apical portion of the aedeagal median lobe narrows apically. The *H. hirtella* group, represented by six species, lacks distinct apicolateral genal projections and ocular canthi, and the aedeagus usually has a relatively simple endophallus (membranous structures containing many small denticles). The *H. gigas* group, including three species, lacks obvious apicolateral genal projections or ocular canthi, each of the apical three antennomeres is distinctly elongate, maxillary palpomeres 2 are conspicuously elongate, tarsomeres 2 extend to near the midlength of tarsomeres 3, and the endophallus of the aedeagus has simple sclerites and/or small denticles on a membranous structure. A large number of unassociated females have been listed by Yin and Li (2014, 2015), which indicates that the true diversity of this group still remains underexplored.

Based on an examination of additional material deposited in the Muséum d'Histoire Naturelle, Geneva, Switzerland, and the National Museum of Natural Science, Taichung City, Taiwan, China, we describe here six new species from China (2), Thailand (2), India (1), and Malaysia (1). Thus, the total species number of *Horniella* raises from 29 to 35. Furthermore, new collecting data of *Horniella aculeata* Yin & Li from Thailand are provided.

## Material and methods

The type material of the new species described in this paper is deposited in the Muséum d'Histoire Naturelle, Geneva (**MHNG**), the National Museum of Natural Science, Taichung City, Taiwan (**NMNS**), and the Insect Collection of Shanghai Normal University, Shanghai (**SNUC**).

Dissected parts were preserved in Euparal on plastic slides that were placed on the same pin with the specimen. The habitus images of the beetles were taken using a Canon 5D Mark III camera in conjunction with a Canon MP-E 65 mm f/2.8 1–5× macro lens, and a Canon MT-24EX Macro Twin Lite flash was used as the light source. Images of the morphological details were produced using a Canon G9 camera mounted to an Olympus CX31 microscope under reflected or transmitted light. Zerene Stacker v. 1.04 was used for image stacking. All images were modified and grouped into plates using Adobe Photoshop CC 2020.

The abdominal tergites and sternites are numbered following Chandler (2001) in Arabic (starting from the first visible segment) and Roman (reflecting true morphological position) numerals, e.g., tergite 1 (IV), or sternite 1 (III). Paired structures in the species descriptions are treated as singular.

The collecting data of the material are quoted verbatim. The Chinese translation of each locality is included in parentheses at first appearance in the text. A slash is used to separate different labels. Each type specimen bears the following label: 'HOLOTYPE [red] (or PARATYPE [yellow]), ♂ (or ♀), *Horniella* + specific name sp. n., det. Zhang & Yin, 2021, NMNS (or MHNG, or SNUC)'.

The following abbreviations are applied: **AL** = length of the dorsally exposed part of the abdomen (posterior to elytra) along the midline; **AW** = maximum width of the abdomen; **EL** = length of the elytra along the suture; **EW** = maximum width of the elytra; **HL** = length of the head from the anterior clypeal margin to the anterior margin of the occipital constriction; **HW** = width of the head across eyes; **PL** = length of the pronotum along the midline; **PW** = maximum width of the pronotum. Length of the body is a sum of HL + PL + EL + AL.

## Results

### *Horniella aculeata* Yin & Li, 2015

*Horniella aculeata* Yin & Li, 2015: 110.

**Material examined.** 2 ♂♂, labeled 'Thailand: Nan prov. Doi Phuoka Nat. Park, 28.IV-12.V.2002, Průdek & Obořil lgt.' (MHNG); 1 ♂, labeled 'THAI, 28-31.v.1995, 19.27N, 98.20E, SOPPONG 1500 m, Vit Kubáň leg.' (MHNG).

**Remarks.** *Horniella aculeata* is readily recognizable by the presence of a large spine on the mesal margin of the protibiae (Yin and Li 2015: fig. 2F), and the aedeagus with one elongate, twisted sclerite (Yin and Li 2015: fig. 2K). This species was described based on two male and four female specimens from Yunnan, China, and the present record extends its distribution to Thailand.

**Distribution.** China: Yunnan; Thailand: Nan, Mae Hong Son. **New country record for Thailand.**

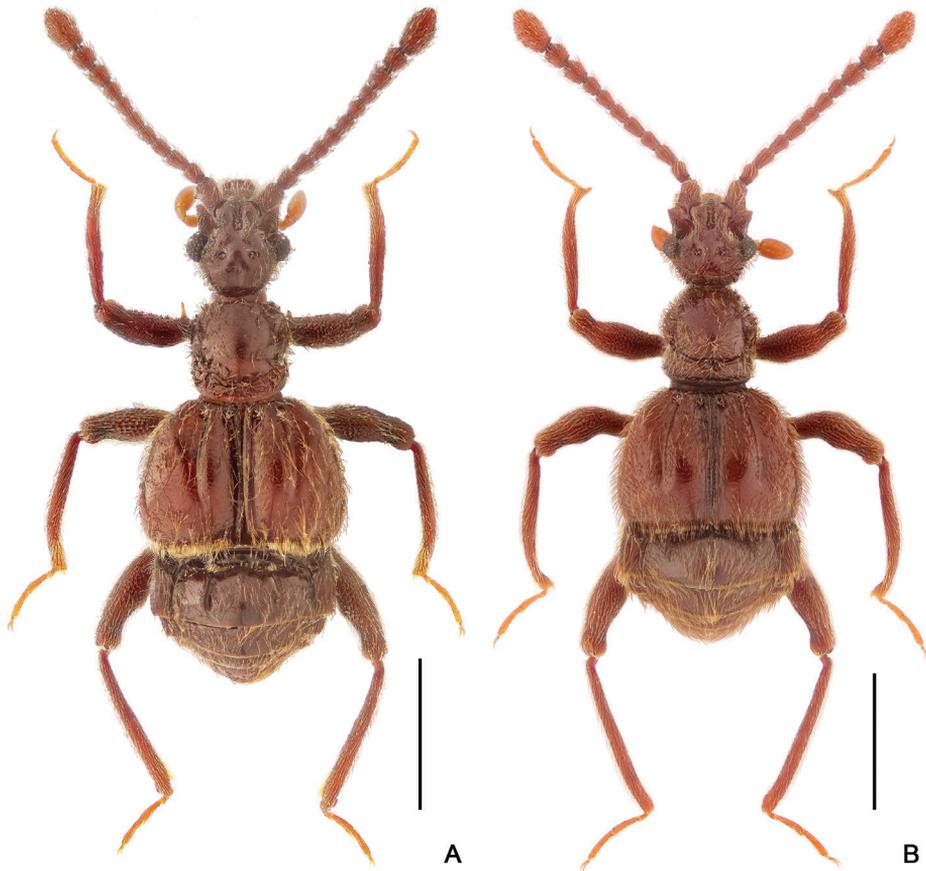
### *Horniella bifurca* Zhang & Yin, sp. nov.

<http://zoobank.org/DD97E152-F782-4FC5-8B59-27D1D383C7A9>

Figures 1A, 2, 10A

**Type material.** **Holotype:** THAILAND: ♂, 'THAILAND: Chiang Mai, Pinh Khong env. 900 m, 19°26.70'N, 99°01.9'E, 14.xi.2012, M. Košťál lgt.' (MHNG). **Paratype:** THAILAND: 1 ♀, same label data as for holotype (MHNG).

**Diagnosis. Male.** Head approximately as long as wide, with distinct anterolateral genal projection, anterior margin of projection roundly emarginate; with long, apically forked ocular canthus; scape angularly expanded at anterolateral margin, antennomeres 9–11 moderately enlarged. Pronotum rounded at anterolateral margins. Protrochanter



**Figure 1.** Dorsal habitus of *Horniella* species **A** *H. bifurca* sp. nov. **B** *H. haucki* sp. nov. Scale bars: 1 mm.

and profemur each with long ventral spine; protibia with small triangular apical spur; mesotrochanter with short but distinct ventral spine. Tergite 1 (IV) with median carina extending posteriorly for approximately 1/4 of tergal length, discal carinae long and thick. Aedeagus with asymmetric median lobe, right half of median lobe greatly protruding apicad, left half strongly curved and forked at apex; endophallus composed of two elongate, twisted sclerites.

**Female.** Similar to male in external morphology, profemur each with two ventral spines near base, protibia lacking preapical spur, mesotrochanter lacking ventral spine; genital complex as in Fig. 10A.

**Description. Male.** Body reddish-brown, length 3.35 mm. Head (Fig. 2A) approximately as long as wide, HL 0.69 mm, HW 0.7 mm; anterolateral genal projection distinct, anterior margin of projection roundly emarginate; antenna 1.7 mm long, scape angularly expanded at anterolateral margin, antennomeres 2–8 slightly elongate or moniliform, club loosely formed by apical three moderately enlarged antennomeres, antennomere 11 largest, approximately as long as antennomeres 9 and 10 combined;



**Figure 2.** Diagnostic characters of *Horniella bifurca* sp. nov. **A** left half of head, in dorsal view **B** head, in lateral view **C** protochanter and profemur **D** protibia **E** mesotrochanter and mesofemur **F** mesotibia **G–I** aedeagus, in dorsal (**G**), lateral (**H**), and ventral (**I**) view. Scale bars: 0.3 mm (**A, C–F**); 0.2 mm (**B, G–I**).

indistinct lateral postantennal pits present; eyes prominent, each composed of approximately 45 large facets, with long, broad forked ocular canthi (Fig. 2B).

Pronotum as long as wide, PL and PW 0.67 mm, widest at apical 1/3; anterolateral margins rounded; disc moderately convex, finely punctate, with distinct median ante-basal and lateral ante-basal foveae connected by complete transverse sulcus.

Elytra much wider than long, EL 0.91 mm, EW 1.36 mm; each elytron with two large, setose basal foveae; discal striae extending from outer basal foveae to apical 3/4 of elytral length.

Legs elongate; protrochanter (Fig. 2C) with elongate ventral spine, profemur (Fig. 2C) with long ventral spine near base, protibia (Fig. 2D) with small triangular apical spur; mesotrochanter (Fig. 2E) with short but distinct ventral spine, mesofemur (Fig. 2E) and mesotibia (Fig. 2F) simple.

Abdomen slightly broader than long, broadest at lateral margins of tergite 1 (IV), AL 1.08 mm, AW 1.22 mm; tergite 1 (IV) largest, as long as tergites 2 and 3 (V and VI) combined, with short median carina extending to near basal 1/4 of tergal length, discal carinae long and thick, with broad basal impression, tergite 2 (V) lacking carina, tergites 2–4 (V–VII) each with small basolateral foveae. Sternite 2 (IV) with broad basal sulcus, lacking mediobasal foveae, basolateral foveae developed as large cuticular pockets, with two pairs of ante-basal protuberances, sternites 3–5 (V–VII) each with basolateral foveae, and one median and two lateral nodules, sternite 7 (IX) with well-sclerotized apical half and membranous basal half.

Aedeagus (Fig. 2G–I) 0.61 mm long, with asymmetric median lobe, right half of median lobe greatly protruding apicad, left half elongate, with strongly curved and deeply forked apical part; endophallus composed of two elongate, twisted sclerites.

**Female.** General morphology similar to male, each eye composed of approximately 30 facets; profemur with two long ventral spines near base, protibia lacking preapical spur, mesotrochanter lacking ventral spine. Measurements (as for male): BL 3.08 mm, HL 0.68 mm, HW 0.61 mm, PL 0.65 mm, PW 0.63 mm, EL 0.79 mm, EW 1.17 mm, AL 0.96 mm, AW 1.2 mm. Genital complex (Fig. 10A) with transverse apical sclerite, and elongate membranous basal portion.

**Comparative notes.** This species is placed as a member of the *H. centralis* group. It can be readily separated from the other members of the group by the long, apically-forked ocular canthi, as well as by the unique shape of the aedeagus.

**Distribution.** Thailand: Chiang Mai.

**Etymology.** The new specific epithet *bifurca* (-us, -um) is a Latin adjective means 'two-pronged', referring to the apically-forked ocular canthus of the new species.

***Horniella haucki* Zhang & Yin, sp. nov.**

<http://zoobank.org/4A4C1B4E-F834-4742-BD77-CA7879983132>

Figures 1B, 3

**Type material. Holotype:** THAILAND: ♂, 'THAI, N, Mae Hong Son prov., SE of Sop-pong, 1500 m, 19°27'N, 98°20'E, 23–27.v.1999, D. Hauck leg.' (MHNG).



**Figure 3.** Diagnostic characters of *Horniella haucki* sp. nov. **A** left half of head, in dorsal view **B** head, in lateral view **C** protochanter and profemur **D** protibia **E** mesotrochanter and mesofemur **F** mesotibia **G–I** aedeagus, in dorsal (**G**), lateral (**H**), and ventral (**I**) view. Scale bars: 0.3 mm (**A, C–F**); 0.2 mm (**B, G–I**).

**Diagnosis. Male.** Head longer than wide, with distinct anterolateral genal projection, anterior margin of projection roundly emarginate; with long ocular canthus; scape angularly expanded at basolateral margin, antennomeres 9–11 moderately enlarged. Pronotum rounded at anterolateral margins. Protrochanter and profemur each with long ventral spine; protibia strongly curved near apex, with long apical projection; mesotrochanter with large sharp ventral spine, mesofemur distinctly arched. Tergite 1 (IV) with median carina extending posteriorly for approximately  $3/4$  of tergal length, discal carinae short and thin. Aedeagus with asymmetric median lobe, left half of median lobe greatly protruding in dorso-ventral view; endophallus composed of three long sclerites.

**Description. Male.** Body reddish-brown, length 3.49 mm. Head (Fig. 3A) slightly longer than wide, HL 0.75 mm, HW 0.7 mm; anterolateral genal projection distinct, anterior margin of projection roundly emarginate; antenna 1.95 mm long, scape angularly expanded at basolateral margin, antennomeres 2–7 slightly elongate, antennomere 8 as long as wide, club loosely formed by apical three moderately enlarged antennomeres, antennomere 11 largest, approximately as long as antennomeres 9 and 10 combined; indistinct lateral postantennal pits present; eyes prominent, each composed of approximately 40 large facets, with long ocular canthi (Fig. 3B).

Pronotum longer than wide, PL 0.74 mm, PW 0.69 mm, widest at apical  $1/3$ ; anterolateral margins rounded; disc moderately convex, finely punctate, with distinct median antebasal and lateral antebasal foveae connected by complete transverse antebasal sulcus.

Elytra much wider than long, EL 0.95 mm, EW 1.35 mm; each elytron with two large, setose basal foveae; discal striae extending from outer basal foveae to apical  $2/3$  of elytral length.

Legs elongate; protrochanter (Fig. 3C) with distinct ventral spine, profemur (Fig. 3C) with long ventral spine near base, protibia (Fig. 3D) strongly curved near apex, with long apical projection; mesotrochanter (Fig. 3E) with long sharp ventral spine, mesofemur (Fig. 3E) strongly arched at middle, mesotibia (Fig. 3F) strongly curved near apex, with small triangular spur.

Abdomen slightly broader than long, broadest at lateral margins of tergite 1 (IV), AL 1.05 mm, AW 1.32 mm; tergite 1 (IV) largest, as long as tergites 2 and 3 (V and VI) combined, with median carina extending to near basal  $3/5$  of tergal length, discal carinae short and thin, tergite 2 (V) lacking carina, tergites 2–4 (V–VII) each with small basolateral foveae. Sternite 2 (IV) with broad basal sulcus, lacking mediobasal foveae, basolateral foveae developed as large cuticular pockets, with two pairs of antebasal nodules, sternites 3–5 (V–VII) with basolateral foveae, one median and two lateral nodules, sternite 7 (IX) with well-sclerotized apical half, and membranous basal half.

Aedeagus (Fig. 3G–I) 0.69 mm long, with asymmetric median lobe, left half of median lobe greatly protruding in dorsal view; endophallus composed of three elongate sclerites close to each other.

**Female.** Unknown.

**Comparative notes.** This new species can be readily separated from all members of the *H. centralis* group primarily by the characteristic shape of the aedeagus,

especially the form of the apical portion of the median lobe, and the configuration of the endophallus.

**Distribution.** Thailand: Mae Hong Son.

**Etymology.** The new species is named after David Hauck (České Budějovice, Czech Republic), collector of the holotype.

***Horniella khasiensis* Zhang & Yin, sp. nov.**

<http://zoobank.org/7DC18538-F16A-4665-ADAA-342B93D6D713>

Figures 4A, 5

**Type material. Holotype:** INDIA: ♂, 'INDIA, Meghalaya State (7+9), E Khasi Hills, 11 km SW Cherrapunjee, Laitkynsew, 25.iv.2008, 25°12'48"N, 91°39'48"E, 735 m, Fikáček, Podskalská, Šípek lgt. / secondary tropical rainforest with young trees + bamboo, below village, thin layer of leaf litter (sifting).' (MHNG).

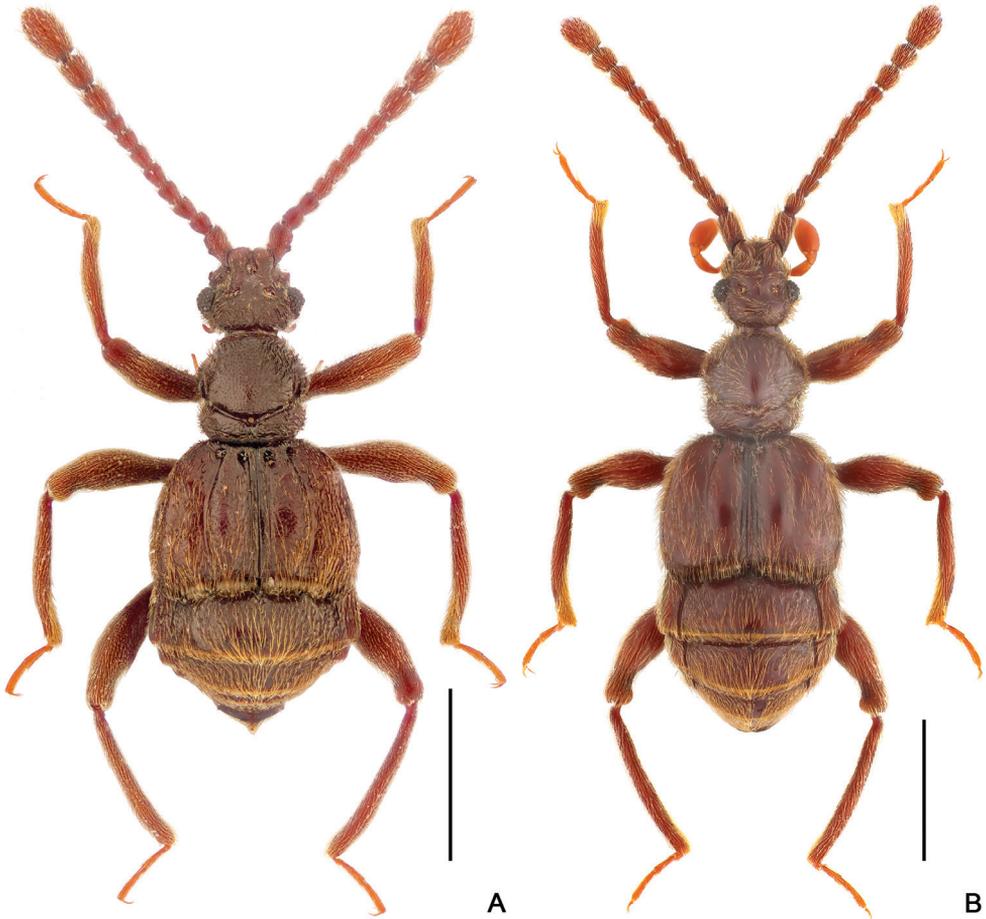
**Diagnosis. Male.** Head wider than long, with distinct anterolateral genal projection, anterior margin of projection roundly emarginate; with markedly long ocular canthus; scape angularly expanded at middle of lateral margin, antennomeres 9–11 enlarged. Pronotum rounded at anterolateral margins. Protrochanter and profemur each with long ventral spine; mesotrochanter with short, small ventral tubercle. Tergite 1 (IV) with median carina extending posteriorly for approximately 1/4 of tergal length, lacking discal carinae, tergite VIII with large medioapical process. Aedeagus with slightly asymmetric median lobe, apex broadly truncate in dorso-ventral view; endophallus composed of three sclerites.

**Description. Male.** Body reddish-brown, length 2.84 mm. Head (Fig. 5A) wider than long, HL 0.56 mm, HW 0.63 mm; anterolateral genal projection distinct, anterior margin of projection roundly emarginate; antenna 1.85 mm long, scape angularly expanded at middle of lateral margin, antennomeres 2–8 slightly elongate or moniliform, club loosely formed by apical three moderately enlarged antennomeres, antennomere 11 largest, slightly shorter than antennomeres 9 and 10 combined; indistinct lateral postantennal pits present; eyes prominent, each composed of approximately 40 large facets, with markedly long and curved ocular canthi (Fig. 5B).

Pronotum as long as wide, PL and PW 0.64 mm, widest anterior to middle; lateral margins rounded; disc moderately convex, finely punctate, with distinct median antebasal and lateral antebasal foveae connected by complete transverse antebasal sulcus.

Elytra much wider than long, EL 0.75 mm, EW 1.2 mm; each elytron with two large, setose basal foveae; discal striae extending from outer basal foveae to near posterior margin of elytra.

Legs elongate; protrochanter (Fig. 5C) with elongate ventral spine, profemur (Fig. 5C) with conspicuously long ventral spine near base, protibia (Fig. 5D) simple; mesotrochanter (Fig. 5E) with short and small ventral tubercle, mesofemur (Fig. 5E) and mesotibia (Fig. 5F) simple.

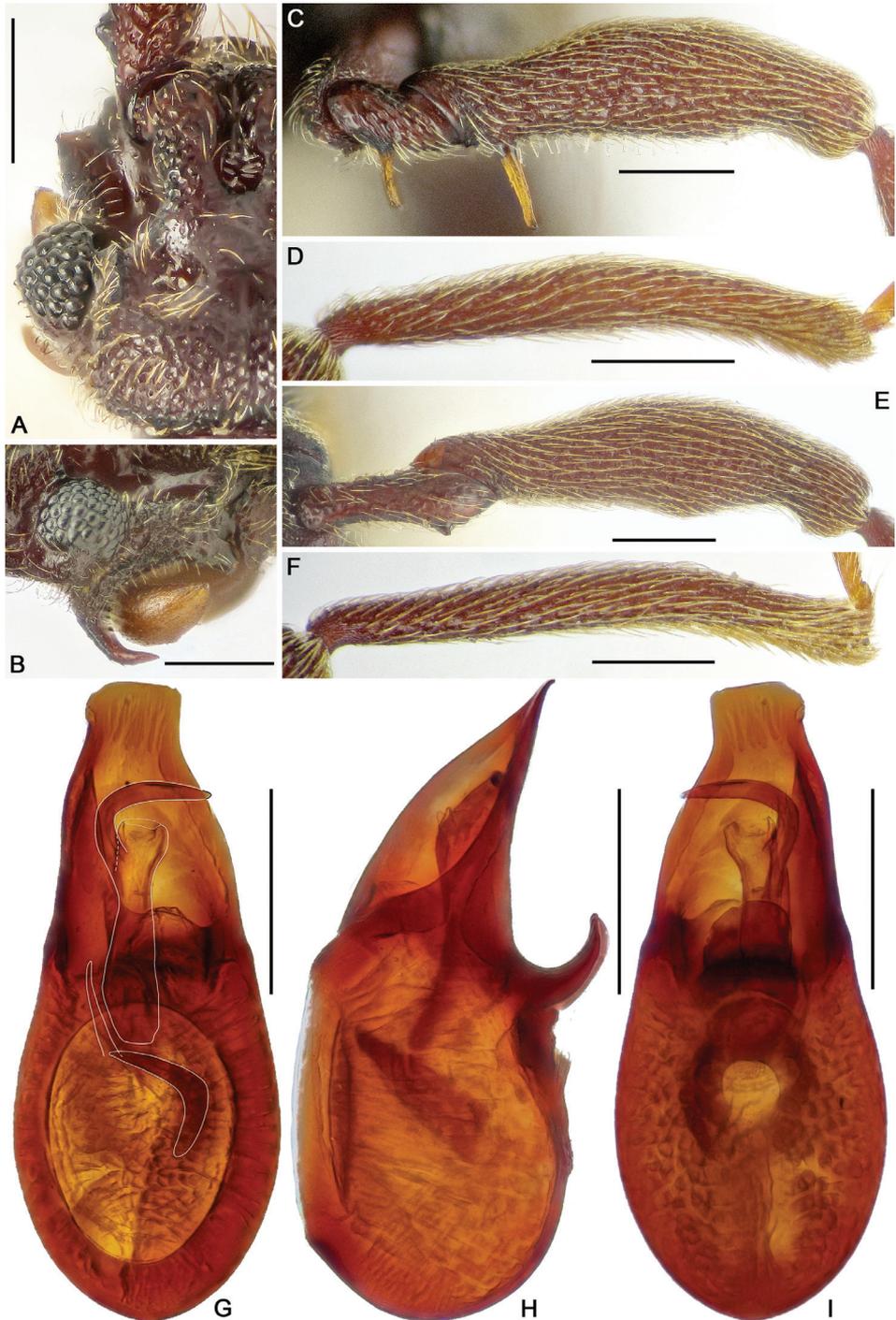


**Figure 4.** Dorsal habitus of *Horniella* species **A** *H. khasiensis* sp. nov. **B** *H. nantouensis* sp. nov. Scale bars: 1 mm.

Abdomen broader than long, broadest at lateral margins of tergite 1 (IV), AL 0.89 mm, AW 1.21 mm; tergite 1 (IV) largest, as long as tergites 2 and 3 (V and VI) combined, with short median carina extending to near basal 1/4 of tergal length, lacking discal carinae, tergite 2 (V) lacking carina, tergites 2–4 (V–VII) each with small basolateral foveae, tergite 5 (VIII) with large medioapical process. Sternite 2 (IV) with broad basal sulcus, lacking mediobasal foveae, basolateral foveae developed as large cuticular pockets, with two pairs of antebasal nodules, sternites 3–5 (V–VII) with basolateral foveae, one median and two lateral nodules, sternite 7 (IX) nearly oval, with well-sclerotized apical half and less sclerotized basal half.

Aedeagus (Fig. 5G–I) 0.59 mm long, median lobe nearly symmetric, apex broadly truncate; endophallus composed of three sclerites: one elongate, plate-like sclerite with curved lobe at apex; one curved sclerite at base, and one much narrower sclerite at left.

**Female.** Unknown.



**Figure 5.** Diagnostic characters of *Horniella khasiensis* sp. nov. **A** left half of head, in dorsal view **B** head, in lateral view **C** protrochanter and profemur **D** protibia **E** mesotrochanter and mesofemur **F** mesotibia **G–I** aedeagus, in dorsal (**G**), lateral (**H**) and ventral (**I**) view. Scale bars: 0.2 mm (**A–I**).

**Comparative notes.** This species is placed as a member of the *H. burckhardtii* group, and is most similar to *H. hongkongensis* Yin & Li in having similar spination of the legs and a general aedeagal form. They can be clearly separated by the more distinctly expanded basolateral margin of the scape, tergite VIII with a large medioapical process, and the different structure of the aedeagal endophallus.

**Distribution.** India: Meghalaya.

**Etymology.** The new species is named after its type locality, the East Khasi Hills.

***Horniella nantouensis* Zhang, Hu & Yin, sp. nov.**

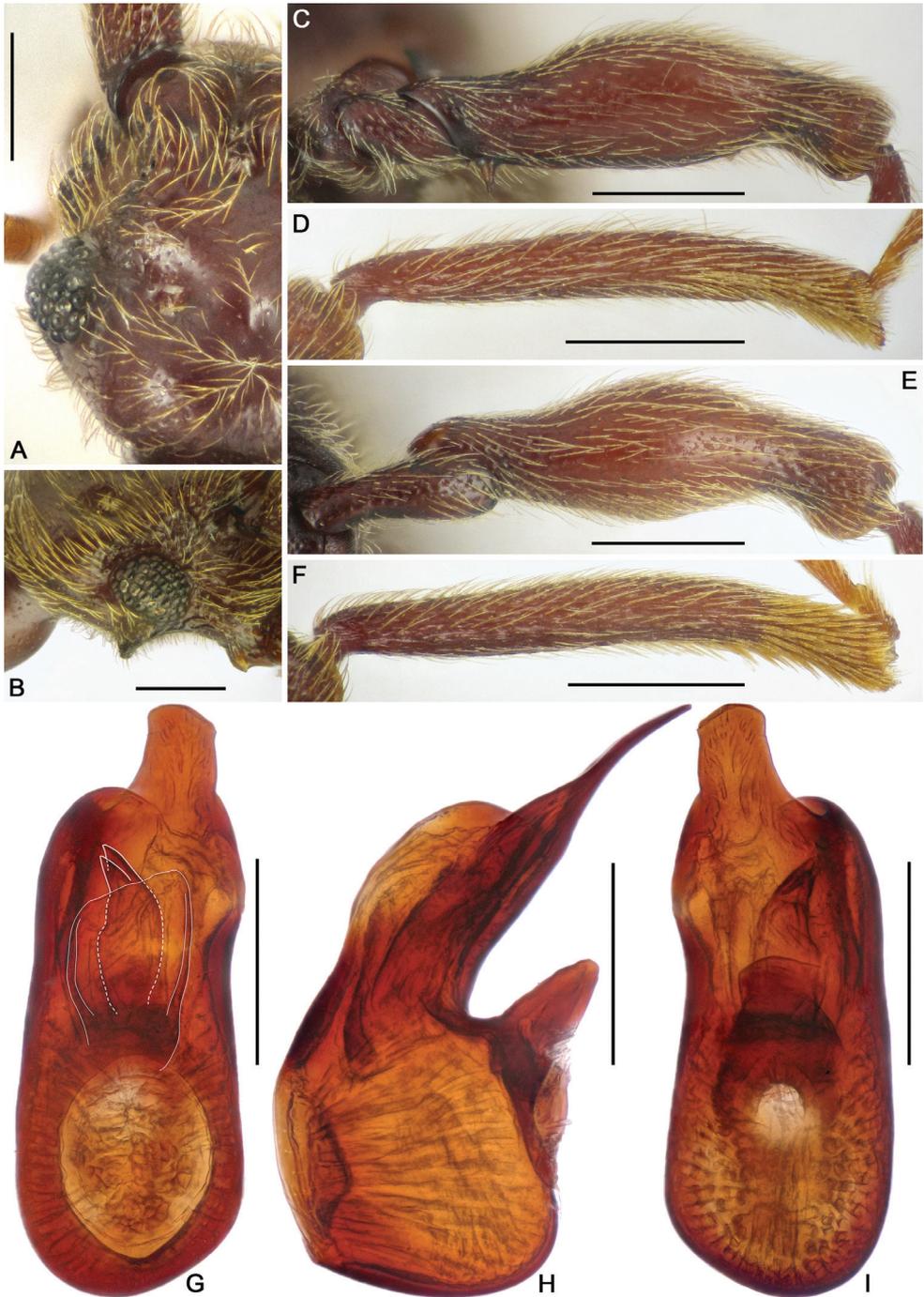
<http://zoobank.org/BAC47C36-A9D6-4D70-9A6D-2B5281C4904F>

Figures 4B, 6, 10B

**Type material. Holotype:** CHINA: ♂, 'TAIWAN: Nantou County, Huisun Forest Reserve [惠荪林场], track to Xiaochushan Mt., 24.0745N, 121.0366E; 1150 m, 4.v.2019; Damaška, Fikáček, Hu & Liu lgt., 2019-TW14 / primary forest on the slope with sparse understory; sifting of small accumulations of leaves / Huisun Leaf Litter Beetles Project, Additional specimen: HS1-034 / *HORNIELLA* sp., P. Hlaváč det., 2019' (NMNS). **Paratypes:** CHINA: 1 ♀, same data as holotype, except 'Huisun Leaf Litter Beetles Project, Additional specimen: HS1-035' (NMNS); 1 ♀, 'same locality and date, except '24.0826N, 121.0316E; 1050 m, 2019-TW15' / sparse secondary forest with dense understory incl. tree ferns on the margin of a tree plantation: sifting / Huisun Leaf Litter Beetles Project, Additional specimen: HS2-041' (NMNS); 1 ♂, 'Tehuashe (900 m), NANTOU, TAIWAN, 南投县德化社 (Tehuashe), 14.xi.2000, Hiroshi Sugaya leg. (in the leaf litter)' (MHNG); 1 ♀, same data as previous, except '4–5.v.(20)01' (MHNG); 2 ♀♀, 'Aowanta (1400 m), NANTOU, TAIWAN, 南投县奥万大, 15.xi.2000, Hiroshi Sugaya leg. (in the leaf litter)' (MHNG).

**Diagnosis. Male.** Head longer than wide, with weakly indicated anterolateral genal projection, anterior margin of projection oblique; with short ocular canthus; lateral margin of scape straight, antennomeres 9–11 slightly enlarged. Pronotum rounded at anterolateral margins. Ventral margin of profemur with one short and acute, and one tiny spine at base; protibia with one small preapical denticle. Tergite 1 (IV) with median carina extending posteriorly for approximately 1/3 of tergal length, lacking discal carinae. Aedeagus with asymmetric median lobe, apical part of median lobe narrowed and protruding apicad, apex nearly rounded in dorsal view. Female. Similar to male in external morphology, profemur with two ventral spines near base; genital complex as in Fig. 10B.

**Description. Male.** Body reddish-brown, length 3.68 mm. Head (Fig. 6A) slightly longer than wide, HL 0.74 mm, HW 0.63 mm; anterolateral genal projection weakly developed, anterior margin of projection oblique; antenna 2.03 mm long, scape lacking expansion at lateral margin, antennomeres 2–8 slightly elongate or moniliform, club loosely formed by apical three moderately enlarged antennomeres, antennomere 11 largest, as long as antennomeres 9 and 10 combined; indistinct lateral postantennal pits present; eyes prominent, each composed of approximately 45 large facets, with pair of short ocular canthi (Fig. 6B).



**Figure 6.** Diagnostic characters of *Horniella nantouensis* sp. nov. **A** left half of head, in dorsal view **B** head, in lateral view **C** protrochanter and profemur **D** protibia **E** mesotrochanter and mesofemur **F** mesotibia **G–I** aedeagus, in dorsal (**G**), lateral (**H**), and ventral (**I**) view. Scale bars: 0.2 mm (**A**, **B**, **G–I**); 0.3 mm in (**C–F**).

Pronotum longer than wide, PL 0.77 mm, PW 0.71 mm; widest at apical 1/3; anterolateral margins rounded; disc moderately convex, finely punctate, with distinct median antebasal and lateral antebasal foveae connected by complete transverse antebasal sulcus.

Elytra much wider than long, EL 0.85 mm, EW 1.33 mm; each elytron with two large, setose basal foveae; discal striae extending from outer basal foveae to middle of elytral length.

Legs elongate; protrochanter (Fig. 6C) simple, profemur (Fig. 6C) with one short and acute, and one tiny ventral spine at base; protibia (Fig. 6D) with small preapical spur; mesotrochanter (Fig. 6E) and mesofemur (Fig. 6E) simple, mesotibia (Fig. 6F) with thick apical setae.

Abdomen slightly longer than broad, broadest at lateral margins of tergite 1 (IV), AL 1.32 mm, AW 1.28 mm; tergite 1 (IV) slightly longer than tergites 2 (V), with median carina extending to near basal 1/3 of tergal length, lacking discal carinae, tergite 2 (V) lacking carina, tergites 2–4 (V–VII) each with small basolateral foveae. Sternite 2 (IV) with broad basal sulcus, lacking mediobasal foveae, basolateral foveae developed as large cuticular pockets, with two pairs of antebasal nodules, sternites 3–5 (V–VII) with basolateral foveae, one median and two lateral nodules.

Aedeagus (Fig. 6G–I) 0.57 mm long, with asymmetric median lobe, apical portion of median lobe narrowed and greatly protruding apically, apex nearly rounded in dorsal view; endophallus composed of broad membranous part with single broad elongate sclerite at middle.

**Female.** General morphology similar to male, each eye composed of approximately 40 facets; profemur each with two distinct ventral spines near base, protibia lacking spur. Measurements (as for male): BL 3.68–3.72 mm, HL 0.74 mm, HW 0.63–0.65 mm, PL 0.72–0.73 mm, PW 0.74–0.75 mm, EL 0.87–0.9 mm, EW 1.33 mm, AL 1.35 mm, AW 1.32–1.33 mm. Genital complex (Fig. 10B) with moderately sclerotized central and membranous lateral parts.

**Comparative notes.** This species is placed as a member of the *H. hirtella* group. The new species is similar to *H. simplaria* Yin & Li by the male having similar anterolateral genital projections, and presence of two ventral spines of profemur. They can be otherwise clearly separated by the larger body size (3.68 mm vs 3.23 mm), lack of a mesal hook-like spine of the protibia (present in *H. simplaria*), and the different shape and structure of the aedeagus of the new species.

**Distribution.** China: Taiwan.

**Etymology.** The new specific is named after its type locality, Nantou County.

***Horniella sabahensis* Zhang & Yin, sp. nov.**

<http://zoobank.org/EC5C6E94-0D2A-461D-8EA7-1C750F093066>

Figures 7A, 8

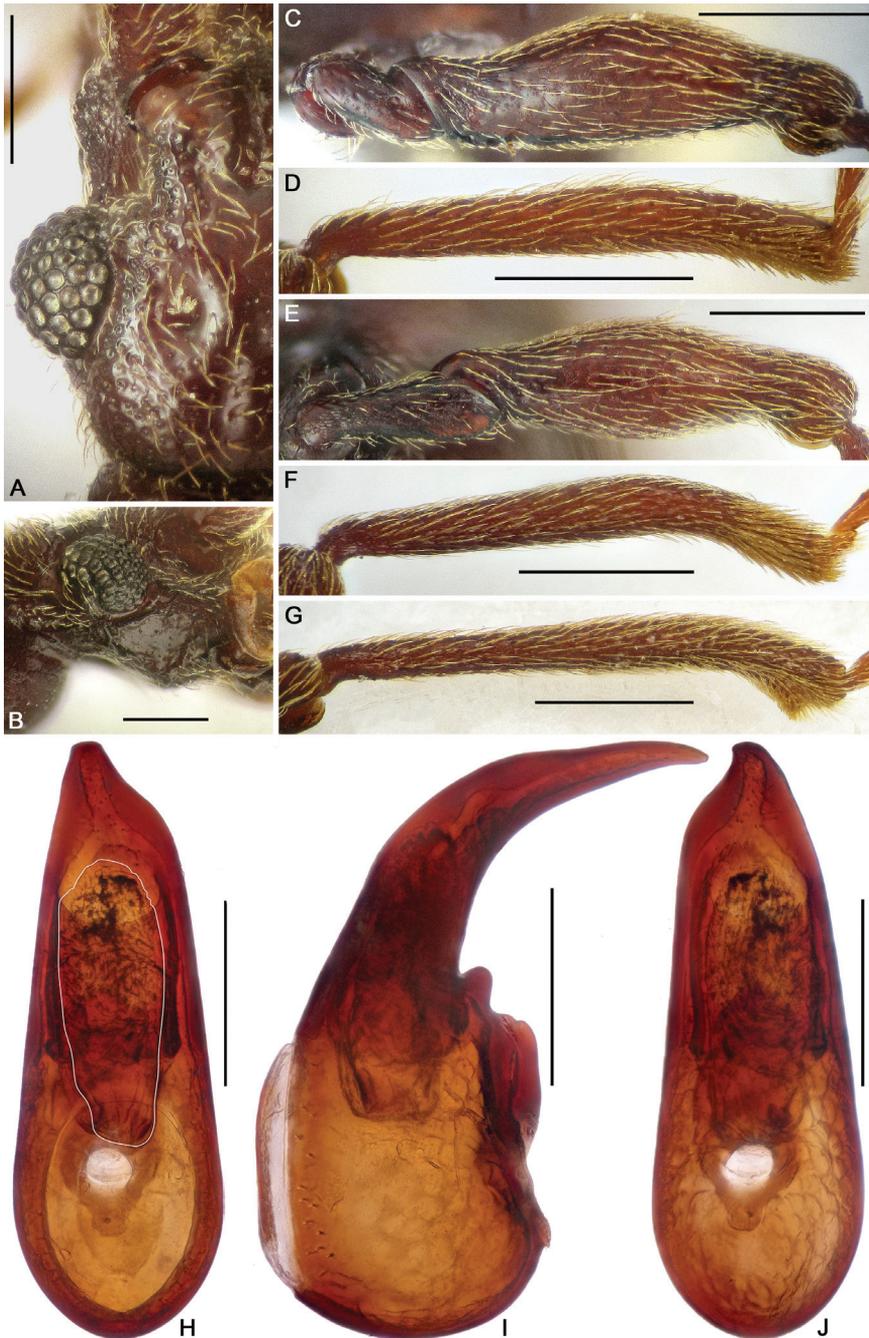
**Type material. Holotype:** EAST MALAYSIA: ♂, 'Borneo: Sabah, Batu Punggul Resort, primary forest, 24.vi.–1.vii.96, Kodada lgt. / vegetation debris and forest floor litter accumulated around large trees near river.' (MHNG).



**Figure 7.** Dorsal habitus of *Horniella* species **A** *H. sabahensis* sp. nov. **B** *H. taiwanensis* sp. nov. Scale bars: 1 mm.

**Diagnosis. Male.** Head longer than wide, anterolateral genal projections weakly developed, anterior margin of projection oblique; scape lacking expansion at lateral margin, antennomeres 9–11 moderately enlarged, forming distinct club. Pronotum rounded at lateral margins. Profemur with two tiny ventral spines near base; metatibia with preapical triangular denticle. Tergite 1 (IV) with median carina extending posteriorly for approximately  $3/4$  of tergal length, lacking discal carinae, tergite 2 (V) with short median carina. Aedeagus with slightly asymmetric median lobe, apical portion of median lobe narrowed, apex truncate in dorso-ventral view; endophallus lacking sclerite, composed of elongate membranous structure with many small denticles.

**Description. Male.** Body reddish-brown, length 3.41 mm. Head (Fig. 8A) longer than wide, HL 0.68 mm, HW 0.59 mm; anterolateral genal projection



**Figure 8.** Diagnostic characters of *Horniella sabahensis* sp. nov. **A** left half of head, in dorsal view **B** head, in lateral view **C** protrochanter and profemur **D** protibia **E** mesotrochanter and mesofemur **F** mesotibia **G** metatibia **H–J** aedeagus, in dorsal (**H**), lateral (**I**), and ventral (**J**) view. Scale bars: 0.2 mm (**A**, **B**, **H–J**); 0.3 mm (**C–G**).

weakly developed, anterior margin of projection oblique; antenna 1.96 mm long, scape lacking expansion at lateral margin, antennomeres 2–8 slightly elongate or moniliform, distinct club formed by apical three enlarged antennomeres, antennomere 11 largest, slightly shorter than antennomeres 9 and 10 combined; indistinct lateral postantennal pits present; eyes prominent, each composed of approximately 40 large facets, usual area of ocular canthus only slightly prominent (Fig. 8B).

Pronotum distinctly longer than wide, PL 0.71 mm, PW 0.6 mm; widest at middle; lateral margins rounded; disc moderately convex, finely punctate, with distinct median antebasal and lateral antebasal foveae connected by complete transverse antebasal sulcus.

Elytra much wider than long, EL 0.77 mm, EW 1.2 mm; each elytron with two large, setose basal foveae; discal striae extending from outer basal foveae to apical 2/3 of elytral length.

Legs elongate; protrochanter (Fig. 8C) simple, profemur (Fig. 8C) with two tiny ventral spines at base, protibia (Fig. 8D) simple; mesotrochanter, mesofemur (Fig. 8E) and mesotibia (Fig. 8F) simple; metatibia (Fig. 8G) with distinct apical triangular denticle.

Abdomen slightly longer than broad, broadest at lateral margins of tergite 1 (IV), AL 1.25 mm, AW 1.16 mm; tergite 1 (IV) largest, slightly shorter than tergites 2 and 3 (V and VI) combined, with median carina extending to near basal 3/4 of tergal length, lacking discal carinae, tergite 2 (V) with median carina extending to near basal 1/4 of tergal length, tergites 2–4 (V–VII) each with small basolateral foveae. Sternite 2 (IV) with broad basal sulcus, lacking mediobasal foveae, basolateral foveae developed as large cuticular pockets, with two pairs of antebasal nodules, sternites 3–5 (V–VII) with basolateral foveae, one median and two lateral nodules, sternite 7 (IX) nearly oval, with well-sclerotized apical half and less sclerotized basal half.

Aedeagus (Fig. 8H–J) 0.57 mm long, with slightly asymmetric median lobe, apical part of median lobe narrowed, apex broadly truncate in dorso-ventral view; endophallus lacking strongly sclerotized structures, composed of broad, elongate membrane with numerous small denticles.

**Female.** Unknown.

**Comparative notes.** *Horniella sabahensis* sp. nov. is placed as a member of the *H. hirtella* group. Males of this species share with *H. prolixo* Yin & Li from Thailand the weakly developed anterolateral genal projections, lack of an expansion at the lateral margin of the scape, and a moderately expanded preapical portion of the metatibia. They can be best separated by the larger body size (3.41 mm vs 2.95–3.02 mm), tergite V with a short median carina (lacking in *H. prolixo*), as well as the much narrower apex of the aedeagus of the new species.

**Distribution.** East Malaysia: Sabah.

**Etymology.** The new species is named after its type locality, Sabah, East Malaysia.

***Horniella taiwanensis* Zhang, Hu & Yin, sp. nov.**

<http://zoobank.org/903D13DA-D767-4259-83A3-3C02BF9DD0E0>

Figures 7B, 9

**Type material.** *Holotype*: CHINA: ♂, 'TAIWAN: Taoyuan City, Northern Cross-island Highway 35.7 k (北横公路35.7 k), Fusing Township, 15-IV-2018, leg. K. X. Zhan' (NMNS). *Paratypes*: CHINA: 1 ♂, 'TAIWAN: Nantou County, Sun Moon Lake (日月潭), Yuchih Township, 13-XII-2016, leg. F. C. Hsu' (NMNS); 1 ♂, 'TAIWAN: Taichung City, Dakeng (大坑), Xinshe Dist., 24.1932, 120.7991, 10-IV-2021, leg. C. T. Hsu (under rock)' (NMNS); 1 ♂, 'Kuantaoshan, NANTOU, TAIWAN, 南投县关刀山, 16.vii.1999, M. Tanikado leg.' (MHNG); 1 ♂, 'Tehuashe (800 m), NANTOU, TAIWAN, 南投县德化社, 2.vii.2000, H. Y. Chu leg. (at light) (MHNG); 1 ♂, 'Taiwan, Nantou, Meifeng (梅峰), 2100 m, 6.v.01 (sifting of litter), Sugaya lgt.' (SNUC).

**Diagnosis. Male.** Head longer than wide, with distinct anterolateral genal projections, anterior margin of projection narrowly emarginate, with long ocular canthus; scape roundly expanded at basolateral margin, antennomeres 9–11 slightly enlarged. Pronotum rounded at anterolateral margins. Protrochanter, profemur and mesotrochanter each with ventral spine; protibia and mesotibia with large apical projection. Tergite 1 (IV) with median carina extending posteriorly for approximately 1/4 of tergal length, lacking discal carinae. Aedeagus with asymmetric median lobe, right half of median lobe greatly protruding apicad, apical margin nearly rounded in dorsal view.

**Description. Male.** Body reddish-brown, length 4.05–4.15 mm. Head (Fig. 9A) slightly longer than wide, HL 0.84–0.87 mm, HW 0.74–0.76 mm; anterolateral genal projection distinct, anterior margin of projection narrowly emarginate; antenna 2.1 mm long, scape roundly expanded at basolateral margin, antennomeres 2–8 slightly elongate or moniliform, club loosely formed by apical three moderately enlarged antennomeres, antennomere 11 largest, slightly shorter than antennomeres 9 and 10 combined; indistinct lateral postantennal pits present; eyes prominent, each composed of approximately 40 large facets, with long ocular canthus (Fig. 9B).

Pronotum slightly longer than wide, PL 0.78–0.82 mm, PW 0.76–0.77 mm; widest at apical 1/3; anterolateral margins rounded; disc moderately convex, finely punctate, with distinct median antebasal and lateral antebasal foveae connected by complete transverse antebasal sulcus.

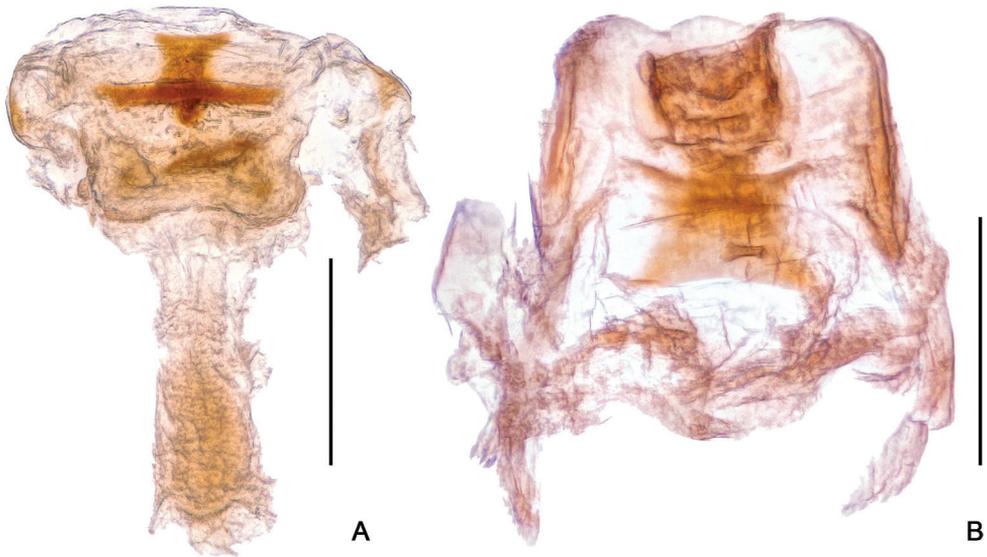
Elytra much wider than long, EL 0.94–1.01 mm; EW 1.51 mm; each elytron with two large, setose basal foveae; discal striae extending from outer basal foveae to apical 2/3 of elytral length.

Legs elongate; protrochanter (Fig. 9C) with short, acute ventral spine, profemur (Fig. 9C) with distinctly long ventral spine near base; protibia (Fig. 9D) with large apical projection; mesotrochanter (Fig. 9E) with sharp ventral spine, mesofemur (Fig. 9E) simple, mesotibia (Fig. 9F) with moderately large projection.

Abdomen approximately as long as broad, broadest at lateral margins of tergite 1 (IV), AL 1.45–1.49 mm, AW 1.47–1.49 mm; tergite 1 (IV) slightly longer than tergites 2 (V), with short median carina extending to near basal 1/4 of tergal length,



**Figure 9.** Diagnostic characters of *Horniella taiwanensis* sp. nov. **A** left half of head, in dorsal view **B** head, in lateral view **C** protrochanter and profemur **D** protibia **E** mesotrochanter and mesofemur **F** mesotibia **G–I** aedeagus, in dorsal (**G**), lateral (**H**), and ventral (**I**) view. Scale bars: 0.2 mm (**A**, **B**, **G–I**); 0.3 mm (**C–F**).



**Figure 10.** Female genitalia of *Horniella* species, in dorsal view **A** *H. bifurca* sp. nov. **B** *H. nantouensis* sp. nov. Scale bars: 0.2 mm.

lacking discal carinae, tergite 2 (V) lacking carina, tergites 2–4 (V–VII) each with small basolateral foveae. Sternite 2 (IV) with broad basal sulcus, lacking mediobasal foveae, basolateral foveae developed as large cuticular pockets, with two pairs of antebasal nodules, sternites 3–5 (V–VII) with basolateral foveae, one median and two lateral nodules, sternite 7 (IX) with well-sclerotized apical half and less sclerotized basal half.

Aedeagus (Fig. 9G–I) 1.01 mm long, with strongly asymmetric median lobe, right half of median lobe greatly protruding apicad, apex broadened, with round apical margin dorso-ventral view; endophallus composed of one elongate, and two much shorter sclerites.

**Female.** Unknown.

**Comparative notes.** This species is placed as a member of the *H. centralis* group and is most similar to *H. sichuanica* Yin & Li in the shapes of the anterolateral genal projections and spination of the legs. They can be clearly separated by the larger body size (4.05–4.15 mm vs 3.58–3.77 mm), the more distinct apical projections of protibia and mesotibia, and the dilated apex of the aedeagal median lobe of the new species.

**Distribution.** China: Taiwan.

**Etymology.** The new specific is named after Taiwan.

### List of *Horniella* species worldwide

*H. aculeata* Yin & Li, 2015: 110. China: Yunnan; Thailand: Nan, Mae Hong Son.

*H. asymmetrica* Yin & Li, 2014: 42. Thailand: Prachin Buri, Chanthaburi.

*H. awana* Yin & Li, 2014: 65. West Malaysia: Pahang.

*H. bifurca* Zhang, & Yin, sp. nov. Thailand: Chiang Mai.

- H. burckhardtii* Yin & Li, 2014: 45. Thailand: Chiang Mai.  
*H. centralis* Yin & Li, 2014: 11. China: Shaanxi.  
*H. cibodas* Yin & Li, 2014: 74. Indonesia: West Java.  
*H. confragosa* Yin & Li, 2014: 14. China: Guangxi, Guizhou.  
*H. dao* Yin & Li, 2014: 17. China: Sichuan.  
*H. falcis* Yin & Li, 2014: 18. China: Guizhou.  
*H. gigas* Yin & Li, 2014: 66. East Malaysia: Sabah.  
*H. haucki* Zhang, & Yin, sp. nov. Thailand: Mae Hong Son.  
*H. himalayica* Yin & Li, 2014: 35. Nepal: Bāgmatī añcal; India: Uttarakhand.  
*H. hirtella* (Raffray, 1901: 30). Sri Lanka: Northern, North Central, Central, Uva.  
*H. hongkongensis* Yin & Li, 2014: 21. China: Hong Kong.  
*H. intricata* Yin & Li, 2014: 47. Thailand: Mae Hong Son, Chiang Mai.  
*H. jinggangshana* Yin & Li, 2015: 113. China: Jiangxi.  
*H. kaengkrachan* Yin & Li, 2014: 50. Thailand: Phetchaburi.  
*H. khaosabap* Yin & Li, 2014: 51. Thailand: Chanthaburi.  
*H. khasiensis* Zhang, & Yin, sp. nov. India: Meghalaya.  
*H. loebli* Yin & Li, 2014: 54. Thailand: Chiang Mai.  
*H. nakhi* Yin & Li, 2014: 25. China: Yunnan.  
*H. nantouensis* Zhang, Hu & Yin, sp. nov. China: Taiwan.  
*H. philippina* Yin & Li, 2014: 63. Philippines: Laguna.  
*H. phuphaman* Yin & Li, 2014: 56. Thailand: Khon Kaen.  
*H. pilosa* Yin & Li, 2014: 69. East Malaysia: Sabah.  
*H. prolixo* Yin & Li, 2014: 60. Thailand: Chiang Mai.  
*H. sabahensis* Zhang, & Yin, sp. nov. East Malaysia: Sabah.  
*H. schuelkei* Yin & Li, 2014: 25. China: Yunnan.  
*H. schwendingeri* Yin & Li, 2014: 60. Thailand: Chiang Mai.  
*H. sichuanica* Yin & Li, 2014: 28. China: Sichuan.  
*H. simplaria* Yin & Li, 2014: 28. China: Guangxi.  
*H. smetanai* Yin & Li, 2014: 72. East Malaysia: Sabah.  
*H. taiwanensis* Zhang, Hu & Yin, sp. nov. China: Taiwan.  
*H. tianmuensis* Yin & Li, 2014: 32. China: Zhejiang.

## Acknowledgements

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# Morphology of the first three zoal stages of the deep-sea caridean shrimp *Heterocarpus fascirostratus* Yang, Chan & Kumar, 2018 (Crustacea, Decapoda, Pandalidae)

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## Abstract

The larvae of the deep-sea pandalid shrimp *Heterocarpus fascirostratus* Yang, Chan & Kumar, 2018 were successfully hatched and cultured to the third zoal stage. The larvae reached the third zoal stage nine days after hatching at a water temperature of  $21 \pm 1$  °C. Although members of *Heterocarpus* A. Milne-Edwards, 1881 have rather diverse body forms and are often separated into many species groups, the early zoal morphology of *H. fascirostratus* follows the general developmental pattern of the species in *Heterocarpus*. The main differences amongst these larvae are body size, spines on the anteroventral margin of the carapace, and the endopod setation of the third maxilliped.

## Keywords

Laboratory rearing, larval development, zoea

## Introduction

The deep-sea pandalid shrimp genus *Heterocarpus* A. Milne-Edwards, 1881 is often considered as having fishery potential (Holthuis 1980; Chan 1998). Thirty species are now known in the genus (Yang et al. 2018) and they have rather high morphological

diversity with at least five species groups recognized to date according to the spination of the pleon and the lateral carinae on the carapace (Crosnier 1988; Yang et al. 2010, 2018; Liao et al. 2019). Larval development, however, has only been reported in four species of *Heterocarpus*; namely *H. abulbus* Yang, Chan & Chu, 2010 (Jiang et al. 2014 [Zoea I]; 2016 [ZI–ZIX]), *H. ensifer* A. Milne-Edwards, 1881 (Landeira et al. 2010 [ZI–ZIV]), *H. hayashii* Crosnier, 1988 (Jiang et al. 2014 [ZI]), and *H. sibogae* de Man, 1917 (Iwata et al. 1986 [ZI–ZV]; Jiang et al. 2014 [ZI]).

*Heterocarpus fascirostratus* Yang, Chan & Kumar, 2018 is the last species described in the genus and belongs to a different species group from those species of the same genus with known larval morphology. *Heterocarpus fascirostratus* only has pleonite III bearing an overhanging spine. *Heterocarpus ensifer*, *H. hayashii* and *H. sibogae* have posterior spines on both pleonites III and IV. *Heterocarpus abulbus* completely lacks a spine on the pleon. In the present work, an ovigerous female of *H. fascirostratus* was collected off the South China Sea and its hatching larvae were cultured for the first time until the third zoeal stage.

## Materials and methods

An ovigerous female of *H. fascirostratus* was captured by the research vessel ‘Ocean Researcher I’ (station CP 4128) with a French beam trawl at depths of 420–444 m off Dongsha Island (Pratas, Taiwan, 20°44.857'N, 116°08.010'E) in the South China Sea. The ovigerous female was maintained in sea water (35 ± 1‰ salinity) at 14 ± 1 °C in the laboratory. After hatching, ~ 200 actively swimming larvae each were transferred to two beakers (5 L) with aerated seawater, temperature at 21 ± 1 °C and natural photoperiod. The larvae were fed daily with *Artemia* nauplii and rotifers from Zoea I to III and with water changed every day. Specimens of each zoeal stage were collected immediately after the larvae molted and subsequently preserved in a 70% ethylene glycol solution. About five larvae were sampled each day to check for moults. At least two larvae from each stage were dissected, mounted on glass slides and examined under a stereo microscope (OLYMPUS SZX12) using fine entomological needles. Appendages were drawn using a *camera lucida* installed on a compound microscope (Olympus BX50). About 80% of the larvae developed to Zoea II, but only two larvae moulted to Zoea III and the rearing terminated then.

The descriptions and figures were arranged according to the standards proposed by Kamanli et al. (2018). Morphological terminology follows Yang and Ko (2004), Landeira et al. (2010), Clark and Cuesta (2015), Kamanli et al. (2018) and Almeida et al. (2021). Zoea I is completely described in detail; however, only appendage changes were described in the subsequent stages. Abbreviations of larval measurements are as follows: carapace length (**CL**), from the postorbital margin to the posteromedian end of the carapace; body length (**BL**), from the postorbital margin of the carapace to the posterior end of the telson; and total length (**TL**), from the tip of the rostrum to the tip of the telson. These are all given as mean values followed by the range (in parentheses). The parental female and larvae are deposited in the National Taiwan Ocean University (NTOU M02078).

## Results

### Larval descriptions

#### Zoea I (Fig. 1)

Period from hatching to end of instar: 1–5 days.

Size ( $N = 5$ ): CL, 0.44 mm (0.41–0.47 mm); BL, 2.24 mm (2.16–2.35 mm); TL, 2.63 mm (2.51–2.76 mm).

Carapace (Fig. 1A, B): Slightly dorsoventrally flattened; rostrum slightly curved downwards, slender, shorter than antennular peduncle; dorsal anterior and posterior processes present; anteroventral margin only bearing strong pterygostomial spine; eyes sessile.

Antennule (Fig. 1D): Peduncle unsegmented, slender and terminally bearing one long plumose seta and a small tubercle; outer flagellum with one spatulate seta, three long aesthetascs and one plumose seta.

Antenna (Fig. 1E): Peduncle unsegmented with single basal spine near endopod; endopod unsegmented, with single long terminal plumose seta, one sharp, slender spine; exopod (scaphocerite) 6-segmented, bearing inner tubercle and with nine plumose setae on the inner margin (2,1,1,1,1,3), two plumose setae on the outer margin and one simple seta on apex (1,1,0,0,0,1).

Mandible (Fig. 1F): Palp absent; incisor and molar processes developed; *lacinia mobilis* present.

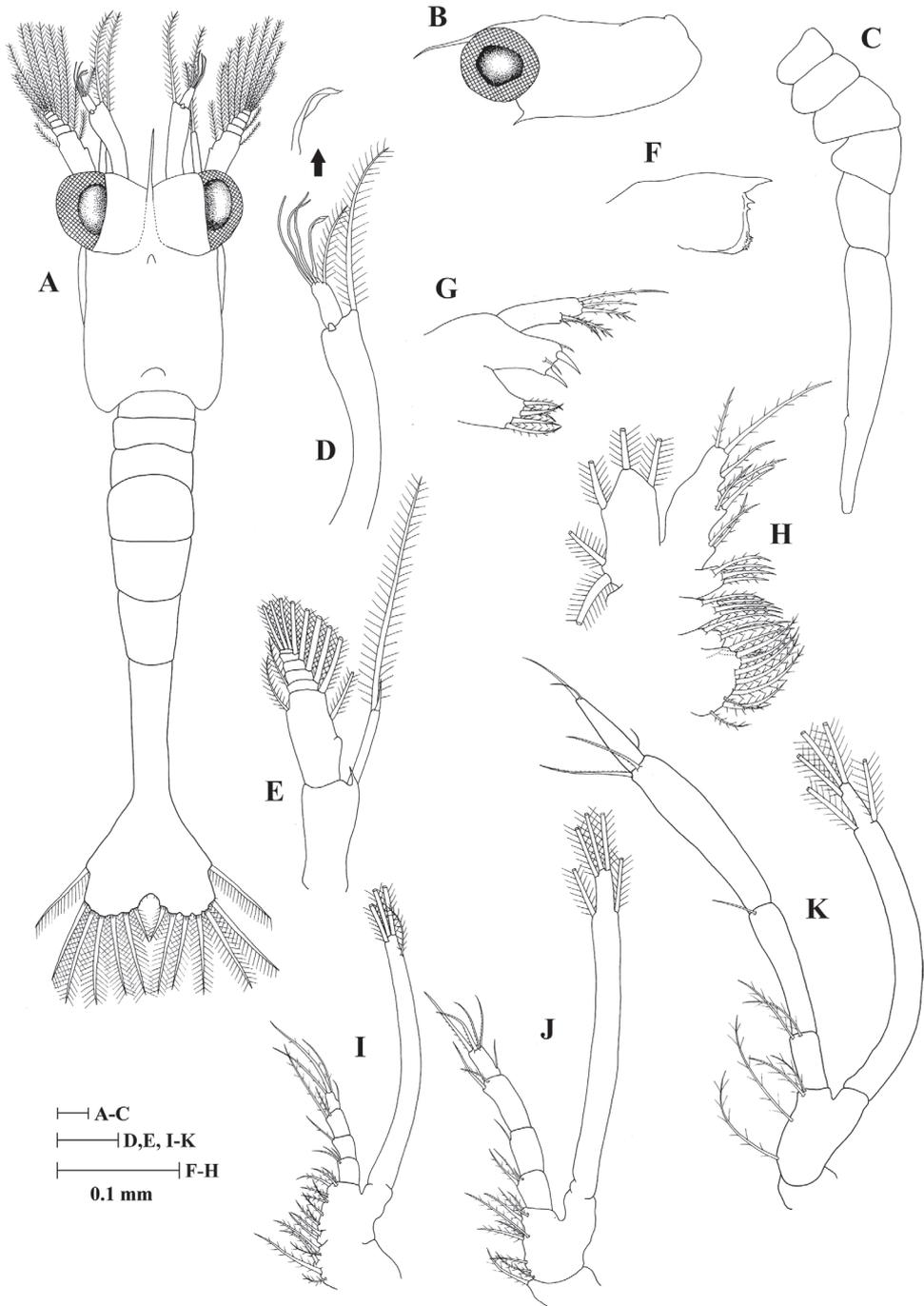
Maxillule (Fig. 1G): Coxal endite with five plumose setae; basal endite with two simple and two stout setae; endopod unsegmented with one small simple seta, one sparsely plumose seta subterminally, one sparsely hardy plumodenticulate seta and three terminal setae (one sparsely hardy plumodenticulate and two sparsely plumose); exopod absent.

Maxilla (Fig. 1H): Coxal endite bilobed with 9 + 4 setae (two papposerrate and eleven plumose); basal endite bilobed with 4 + 4 plumose setae; endopod 5-lobed, with nine (3 + 2 + 1 + 1 + 2) plumose setae; exopod (scaphognathite) margin with five plumose setae.

First maxilliped (Fig. 1I): Coxa with five setae (two papposerrate and three plumose); basis with eleven plumose setae; endopod 4-segmented, bearing 3 (simple), 1 (pappose), 2 (one papposerrate and one plumose), 4 (one median simple and three terminal sparsely plumose) setae; exopod unsegmented, armed distally with one subterminal and three plumose natatory setae.

Second maxilliped (Fig. 1J): Coxa with one plumose seta; basis with nine setae (one papposerrate and eight plumose); endopod 4-segmented, bearing 3 (one small simple, one pappose and one plumose), 1 (simple), 2 (one denticulate and one plumose), 5 (one subterminal simple and four terminal denticulate) setae; exopod unsegmented, armed distally with two subterminal and three plumose natatory setae.

Third maxilliped (Fig. 1K): Coxa without setae; basis with four plumose setae; endopod 4-segmented and slightly longer than exopod, with 2 (plumose), 1 (simple), 2 (denticulate), 3 (one subterminal simple and two terminal simple) setae; third segment



**Figure 1.** Zoa I of *Heterocarpus fascirostratus* **A** dorsal view **B** carapace lateral view **C** pleon lateral view **D** antennule **E** antenna **F** mandible **G** maxillule **H** maxilla **I** first maxilliped **J** second maxilliped **K** third maxilliped.

slightly swollen compared to second segment; exopod unsegmented, armed distally with two subterminal and three plumose natatory setae.

Pereiopods: Absent.

Pleon (Fig. 1A, C): With five pleonites, sixth pleonite fused with telson; lacking setae or spines.

Pleopods: Absent.

Uropod: Absent.

Telson (Fig. 1A): Subtriangular, posterior margin with 7 + 7 plumose setae, outermost two pairs only plumose on inner margin; bases of each seta except outermost one with row of minute spinules.

## Zoea II (Fig. 2)

Period from hatching to end of instar: 6–8 days.

Size ( $N = 2$ ): CL, 0.50 mm (0.48–0.51 mm); BL, 2.52 mm (2.37–2.66 mm); TL, 2.74 mm (2.62–2.86 mm).

Carapace (Fig. 2A, B): Rostrum shorter than in Zoea I and  $\sim 0.4 \times$  as long as CL; eyes stalked, funnel-shaped.

Antennule (Fig. 2D): Peduncle unsegmented, bearing a pair of terminal plumose setae and one long plumose seta; outer flagellum with one simple seta and five long aesthetascs.

Mandible (Fig. 2F): Incisor and molar processes developed.

Maxillule (Fig. 2G): Coxal endite with seven setae (one simple, one pappose subterminal and five terminal plumose); basal endite with three simple setae and four cuspidate setae.

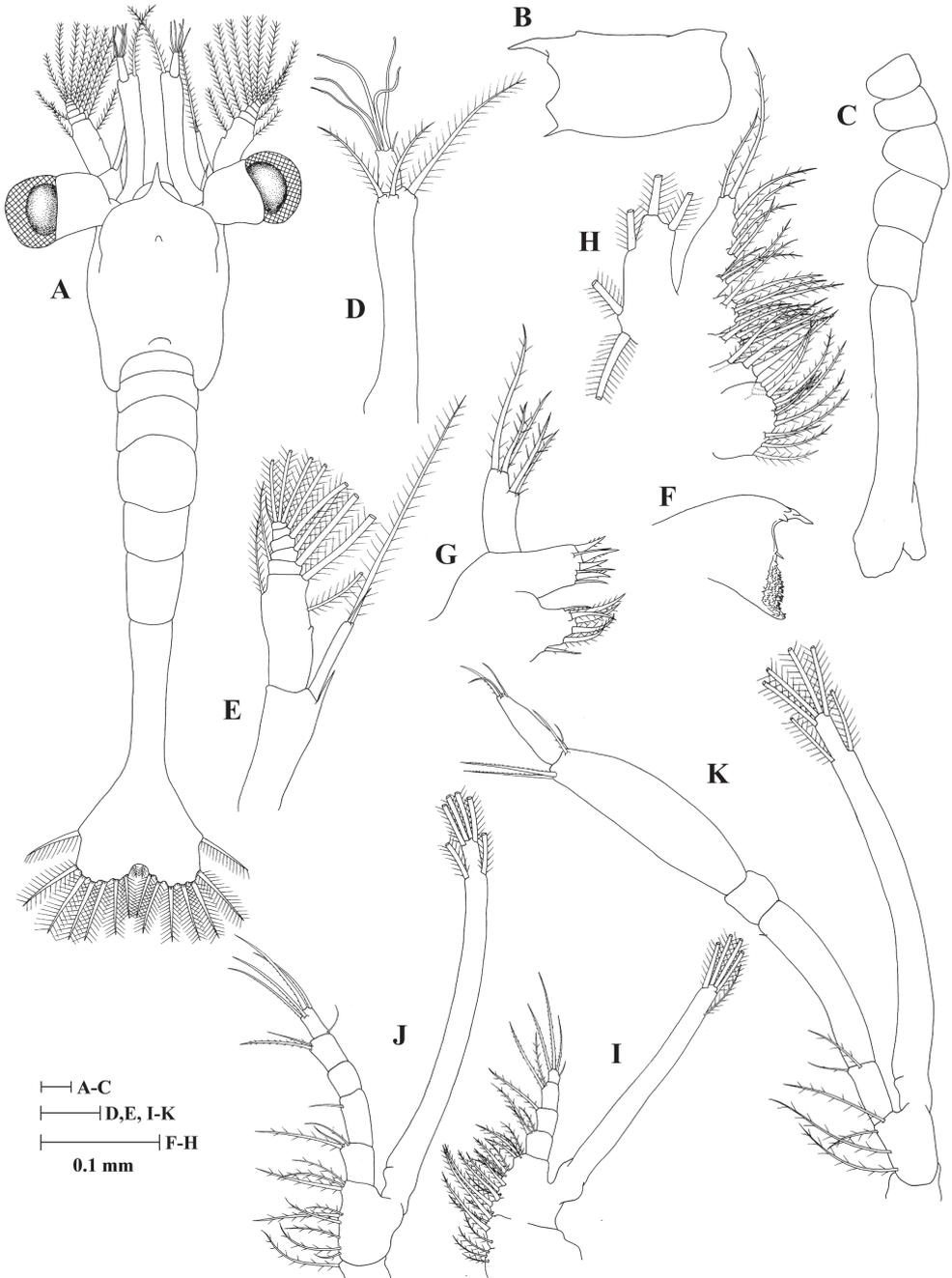
Maxilla (Fig. 2H): Coxal endite bilobed with 11 + 4 plumose setae; basal endite bilobed with 4 + 5 plumose setae.

First maxilliped (Fig. 2I): Coxa with seven plumose setae; basis with fourteen plumose setae; endopod 4-segmented, with 3 (one simple, one pappose and one plumose), 1 (plumose), 2 (one sparsely plumose and one plumose), 4 (one median simple and three terminal sparsely plumose) setae; exopod unsegmented, armed distally with one subterminal and four plumose natatory setae.

Second maxilliped (Fig. 2J): Endopod 5-segmented, with 3 (one simple, one pappose and one plumose), 1 (simple), 0, 2 (one denticulate and one plumose), 5 (one subterminal simple and four terminal denticulate) setae; exopod unsegmented, armed distally with two subterminal and four plumose natatory setae.

Third maxilliped (Fig. 2K): Endopod 5-segmented, with 2 (one pappose and one plumose), 1 (small simple), 0, 3 (one outer papposerrate and two inner denticulate), 4 (one subterminal simple and two terminal simple, one papposerrate) setae, third segment obvious swollen than second segment; exopod unsegmented, armed distally with two subterminal and four plumose natatory setae.

Telson (Fig. 2A): Posterior margin with 8 + 8 plumose setae.



**Figure 2.** Zoea II of *Heterocarpus fascirostratus* **A** dorsal view **B** carapace: lateral view **C** pleon: lateral view **D** antennule **E** antenna **F** mandible **G** maxillule **H** maxilla **I** first maxilliped **J** second maxilliped **K** third maxilliped.

**Zoea III (Fig. 3)**

Period from hatching: 9 days.

Size ( $N = 2$ ): CL, 0.62 mm (0.60–0.63 mm); BL, 2.77 mm (2.71–2.82 mm); TL, 2.93 mm (2.86–2.99 mm).

Carapace (Fig. 3A, B): Supraorbital spine present; rostrum short,  $\sim 0.35 \times$  as long as CL.

Antennule (Fig. 3D): Peduncle 2-segmented, with the proximal segment bearing a small process and six plumose setae, arranged like 1+5; distal segment bearing nine setae (two simple and seven plumose); outer flagellum with one long terminal aesthetasc, two long plumose, one small simple seta.

Antenna (Fig. 3E): Endopod spine-like and without seta; exopod distally 4-segmented, with eleven plumose setae on inner margin (6,1,1,3), three plumose setae on outer margin.

Maxillule (Fig. 3G): Basial endite with three simple setae and five cuspidate setae.

Maxilla (Fig. 3H): Exopod margin with seven plumose setae.

Third maxilliped (Fig. 3K): Endopod 5-segmented with 2 (one pappose and one plumose), 1 (simple), 2 (one outer small simple and one inner denticulate), 4 (one outer and three inner denticulate), 5 (one outer small simple and four terminal simple) setae.

Pereiopods (Fig. 3L): First pereiopod as biramous bud.

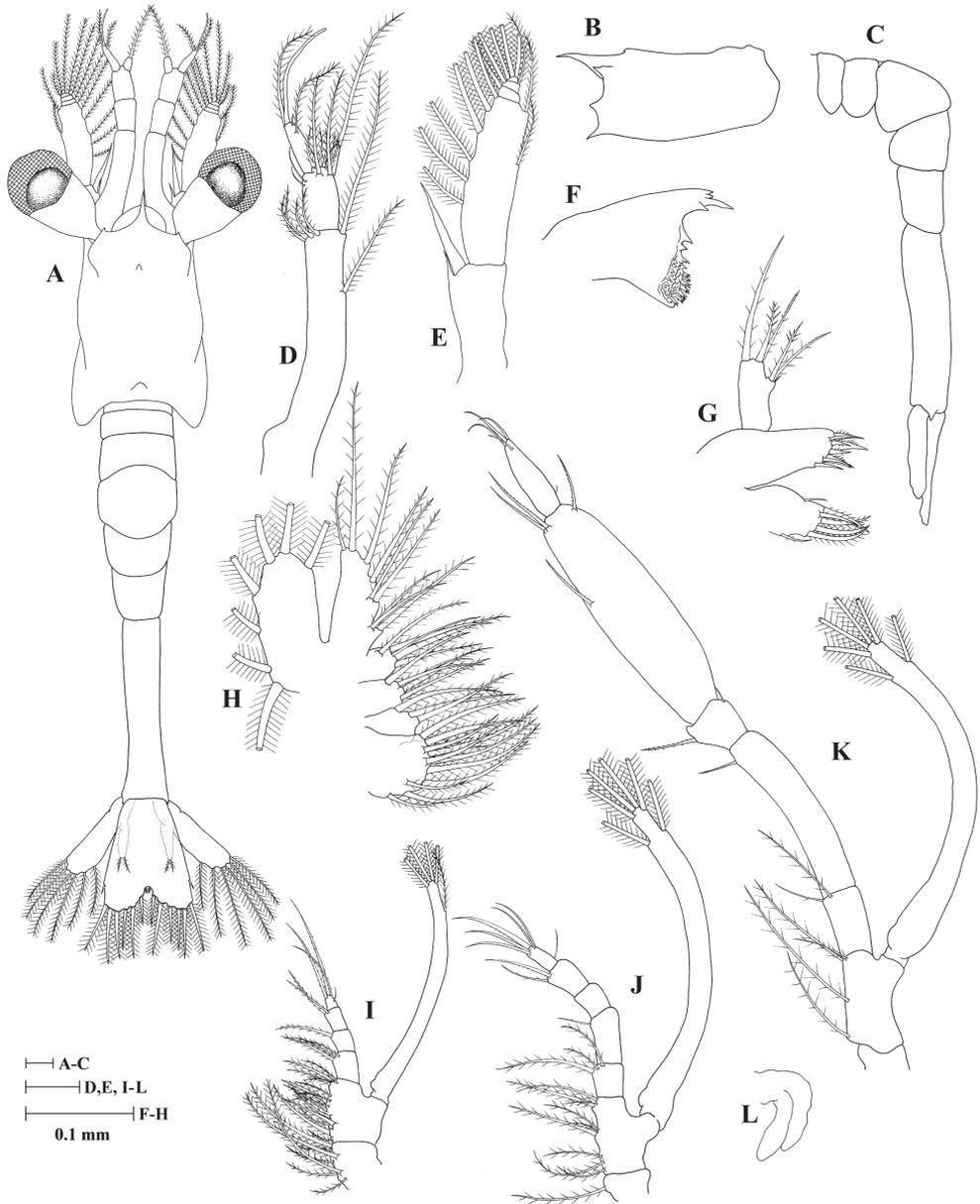
Pleon (Fig. 3A, C): With six pleonites.

Uropod (Fig. 3A): Biramous; endopods rudimentary with two plumose setae; exopods well developed with six plumose setae.

Telson (Fig. 3A): Posterior margin with 8 + 8 setae, comprising seven pairs of sparsely plumose setae with outermost seta on each side shorter, simple, subterminal in position.

**Discussion**

Previous studies together with the present work have shown the five species of *Heterocarpus* with known larval morphologies to belong to three different species groups: *H. abulbus* lacking spines on the pleon, *H. ensifer* / *H. hayashii* / *H. sibogae* bearing posterior spines on the pleonites III and IV, and *H. fascirostratus* only has pleonite III bearing an overhanging spine. Nevertheless, the general appearances of the early zoeal stages are rather similar amongst these five species. Thus, the early zoeal morphology of *H. fascirostratus* also has the common characters of pandalid larvae, such as the eye peduncle narrowed at the base, carapace with two dorsal protuberances and the anteroventral margin bearing spines, antennule with the peduncle strongly concave and exopod bearing spatulate seta, the antenna with a segmented exopod,



**Figure 3.** Zoea III of *Heterocarpus fascirostratus* **A** dorsal view **B** carapace lateral view **C** pleon lateral view **D** antennule **E** antenna **F** mandible **G** maxillule **H** maxilla **I** first maxilliped **J** second maxilliped **K** third maxilliped **L** first pereopod.

and the rostrum elongated in earlier stages (see Thatje and Bacardit 2000; Landeira et al. 2010; Jiang et al. 2014). On the other hand, the first zoea of *H. fascirostratus* differs from the other four congeneric species in body size, spinulation of the carapace, and setation of third maxilliped (see Table 1). Moreover, the third maxilliped

**Table 1.** Characteristics of the first zoeae in five species of *Heterocarpus*.

Characters	<i>H. abulbus</i> (see Jiang et al. 2014, 2016)	<i>H. ensifer</i> (see Landeira et al. 2010)	<i>H. fascirostratus</i> (present study)	<i>H. bayashii</i> (see Jiang et al. 2014)	<i>H. sibogae</i> (see Jiang et al. 2014)
<b>Carapace length (mm)</b>	0.53–0.58	~ 0.42	0.41–0.47	0.38–0.45	0.38–0.43
<b>Anterolateral spines</b>	2	2	0	2	1
<b>Antennule</b>					
Peduncle tubercle	1 small tubercle	2 small tubercles	1 small tubercle	1 small tubercle	1 small tubercle
<b>Maxillule</b>					
Endopod setation	5	6	6	5	5
<b>Maxilla</b>					
Coxal endite setation	9+4	9+4	9+4	8+3	9+4
Basial endite setation	4+4	5+5	4+4	4+4	3+4
<b>First maxilliped</b>					
Coxal setation	5	7	5	4	4
Basial setation	11	12	11	10	9
<b>Second maxilliped</b>					
Coxal setation	2	1	1	1	1
Basial setation	8	9	9	9	6
Endopod setation	3,1,2,5	3,1,2,4	3,1,2,5	3,1,2,5	2,1,2,4
<b>Third maxilliped</b>					
Endopod setation	2,1,2,4	2,1,2,4	2,1,2,3	2,1,2,4	2,1,2,4

endopod has the third segment slightly swollen in *H. fascirostratus* but rather slender in the other four species.

Although Iwata et al. (1986) reported on the ZI–ZV of *H. sibogae*, their description and illustrations are not detailed enough according to current standards for making comparisons (e.g., the presence of anteroventral spines on the carapace in ZI was not described; see Jiang et al. 2014). Therefore, the ZII and ZIII of *H. fascirostratus* can only be compared with those of *H. abulbus* and *H. ensifer*. They also differ in the number of spines on the anteroventral margin of carapace (none in *H. fascirostratus*, one in *H. abulbus*, two in *H. ensifer*), setation on the endopod of the third maxilliped (ZII and ZIII 2,1,0,3,4 and 2,1,2,4,5 setae, respectively for *H. fascirostratus*, vs. 2,1,0,2,4 and 2,1,1,2,5 respectively for the other two species), and the shape of the third maxilliped endopod (somewhat swollen in *H. fascirostratus*, vs. slender in the other two species). Moreover, in ZII the first segment of the endopod of the second maxilliped bears three setae in *H. fascirostratus* and *H. ensifer*, but four setae in *H. abulbus*.

Table 2 summarizes the characteristics of the three zoeal stages of *H. fascirostratus*. The major characters of each zoeal stage are:

- ZI- eyes sessile, three pairs of maxillipeds, slender rostrum slightly curved, antennule peduncle unsegmented and bearing one small tubercle, pleon with five somites.
- ZII- eyes stalked, rostrum shorter than in ZI and ~ 0.4 × as long as CL, antennule peduncle bearing two plumose setae.
- ZIII- antennule peduncle two segmented, pleon with six somites, first pereopod developed, uropods with exopods.

**Table 2.** Characteristics of the first three zoeal stages of *Heterocarpus fasciistratus*. Abbreviations: a, aesthetascs; b, basal spine; c, cuspidate seta; p, plumose seta; pa, pappose seta; pe, papposerrate seta; s, spatulate seta; sh, sparsely hardy plumodenticulate; sp, sparsely plumose seta; lob, lobed; t, stout seta; seg, segment/segmented; v, slender spine; x, simple seta.

Appendage	Stages		
	Zoea I	Zoea II	Zoea III
<b>Carapace length (mm)</b>	0.41–0.47	0.48–0.51	0.60–0.63
<b>Antennule</b>			
Peduncle	1 small tubercle+1p	3p	6p, 2x+7p
Primary flagellum setation	3a+1p+1s	5a+1x	1a+2p+1x
<b>Antenna</b>			
Peduncle	1b	1b	1b
Endopod	1p+1v	1p+1v	0
Exopod	6-seg, 11p+1x	6-seg, 11p+1x	4-seg, 14p
<b>Maxillule</b>			
Coxal endite setation	5p	7(1x+1pa+5p)	7(1x+1pa+5p)
Basial endite setation	2t+2x	4c+3x	5c+3x
Endopod setation	1x+1sp+1sh+3(1sh+2sp)	1x+1sp+1sh+3(1sh+2sp)	1x+1sp+1sh+3(1sh+2sp)
<b>Maxilla</b>			
Coxal endite setation	9p+4p (2pe+11p)	11p+4p	11p+4p
Basial endite setation	4p+4p	4p+5p	4p+5p
Endopod setation	5-lob, 3,2,1,1,2	5-lob, 3,2,1,1,2	5-lob, 3,2,1,1,2
Exopod setation	5p	5p	7p
<b>First maxilliped</b>			
Coxal setation	2pe+3p	7p	7p
Basial setation	11p	14p	14p
Endopod setation	4-seg, 3,1,2,4	4-seg, 3,1,2,4	4-seg, 3,1,2,4
Exopod setation	4p	5p	5p
<b>Second maxilliped</b>			
Coxal setation	1p	1p	1p
Basial setation	1pe+8p	1pe+8p	1pe+8p
Endopod setation	4-seg, 3,1,2,5	5-seg, 3,1,0,2,5	5-seg, 3,1,0,2,5
Exopod setation	5p	6p	6p
<b>Third maxilliped</b>			
Basial setation	4p	4p	4p
Endopod setation	4-seg, 2,1,2,3	5-seg, 2,1,0,3,4	5-seg, 2,1,2,4,5
Exopod setation	5p	6p	6p
<b>First pereopod</b>			
	Absent	Absent	Biramous bud
<b>Uropod</b>			
Protopod	–	–	0
Endopod	–	–	2p
Exopod	–	–	6p
<b>Telson</b>			
	7p+7p	8p+8p	(1x+7p)+(1x+7p)

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# A new, unusually dark, typhlocybinae leafhopper (Hemiptera, Cicadellidae, Typhlocybinae, Erythroneurini) from China

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## Abstract

An unusually dark typhlocybinae leafhopper (Cicadellidae, Typhlocybinae, Erythroneurini) from Guizhou Province, China, is described as a new genus and species, *Shibinga* **gen. nov.**, and *S. nigra* **sp. nov.** Detailed morphological descriptions and illustrations of the new species are provided.

## Keywords

Auchenorrhyncha, Homoptera, morphology, new taxa, taxonomy

## Introduction

Erythroneurini Young (1952) is the largest tribe in the subfamily Typhlocybinae. The tribe is distinguished by the hind wing without apical submarginal vein (Fig. 2N) and is particularly diverse in the Original region where many genera and species remain to be described. In the course of studying Chinese Erythroneurini, an unusually dark (almost black) colored species was collected from Guizhou Province (Southwest China) and found to belong to a new genus and species, described herein. Most other

Typhlocybinae are yellow or green, often with conspicuous markings. In addition to its unusual color, the new species is noteworthy for its short and robust subgenital plate (Fig. 2C) and greatly enlarged style preapical lobe (Fig. 2G, H).

## Materials and methods

Morphological terminology used in this work follows Dietrich (2005). Habitus photos were taken using a KEYENCE VHX-5000 digital microscope. Body length was measured from the apex of the vertex to the tip of the forewings. Abdomens were removed from specimens and cleared in cold 10% KOH solution overnight. The cleared material was rinsed with water and stored in glycerine. An Olympus SZX16 dissecting microscope was used for specimen study and Olympus BX53 stereoscopic microscopes were used for drawing of the dissected male genitalia and wings. All specimens examined are deposited in the collection of the School of Karst Science, Guizhou Normal University, China (GZNU).

## Results

**Hemiptera Linnaeus, 1758**

**Cicadellidae Latreille, 1825**

**Typhlocybinae Kirschbaum, 1868**

**Erythroneurini Young, 1952**

***Shibinga* gen. nov.**

<http://zoobank.org/C30CC595-A843-4509-A7F4-A50F690C2E5C>

**Type species.** *Shibinga nigra* sp. nov.

**Description.** Head, pronotum and mesonotum mainly blackish brown. Face brown marked with yellow. Forewings brownish hyaline. Legs yellow. Abdomen dark brown with margins of segments yellow.

Head narrower than pronotum, short; vertex with coronal suture long and distinct; face with frontoclypeus relatively slender, anteclypeus broad, nearly pentagonal. Pronotum broad, with pyramidal anterior margin; posterior margin slightly concave. Forewing with claval vein distinct; outer apical cell much more than twice as long as wide. Hind wing with RA vein present.

Male abdominal apodemes small, not exceeding 3<sup>rd</sup> sternite.

Male genitalia with pygofer lobe with posterior margin indented apically; with few fine setae and several microtrichia scattered on dorsal and ventral parts in caudal half; with elongate articulated dorsal appendage, extended to near pygofer apex. Subgenital plate short and robust, with few macrosetae laterally in apical half and numerous short stout setae along upper margin and on distal disc in lateral view; several micro-

trichia on outer surface medially. Style with foot-like apex, with preapical lobe greatly enlarged. Aedeagus relatively small and simple, preatrium and dorsal apodeme well developed, the latter with dorso-lateral corners greatly extended; gonopore subapical on ventral surface. Connective Y-shaped, with stem similar in length to arms, upturned apically; central lobe small.

**Etymology.** The genus is named after the locality of the type species, Shibing. The gender is feminine.

**Distribution.** China (Guizhou).

**Remarks.** The new genus belongs to Dworakowska's (2002) "Salka group" of genera in being almost entirely black in color with the head narrower than the pronotum. In particular it is near *Yakuza* Dworakowska, 2002, based on its short head, male pygofer with articulated dorsal appendage and without enlarged setae; subgenital plate with few macrosetae arranged obliquely; style apex footlike (with 2 points); connective with median anterior lobe and aedeagus short with dorsal apodeme enlarged and shaft lacking processes. However, it can be distinguished in the male genitalia by its short and robust subgenital plate and greatly enlarged style preapical lobe. In addition, the new genus is also similar to *Chujophila* Dworakowska, 1997 in its enlarged preapical lobe of the style and the shape of the aedeagus, but differs in having the connective central lobe present and lateral arms stronger; pygofer ventral appendages absent and dorsal appendages movably articulated basally, not fused to dorsal margin.

***Shibinga nigra* sp. nov.**

<http://zoobank.org/45DD05A4-BE4C-4F0B-9BAC-399320323F88>

Figs 1, 2

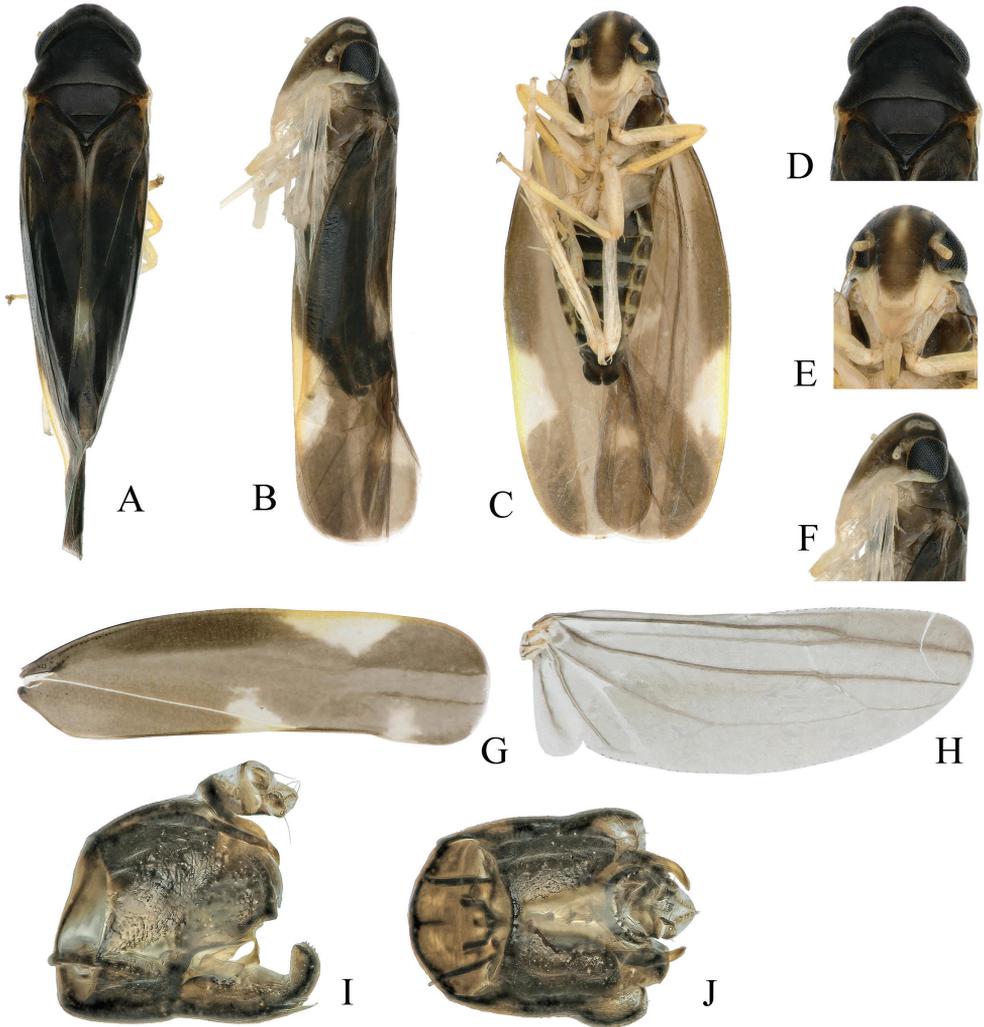
**Specimens examined.** *Holotype*: ♂, CHINA, Guizhou Prov., Shibing, Heichong, 24–28.v.2019, coll. Zhouwei Yuan & Chao Tan. *Paratypes*: CHINA, Guizhou Prov., Shibing: 1♂, same data as holotype; 1♂, Heichong, 22–24.x.2019, coll. Zhouwei Yuan & Xiao Yang; 2♂♂, Niejiayan, 24–28.v.2019, coll. Zhouwei Yuan & Chao Tan; 1♂, Wangjiazhuang, 24–28.v.2019, coll. Zhouwei Yuan & Chao Tan; 3♀♀, Lutianba, 24–28.v.2019, coll. Zhouwei Yuan & Chao Tan.

**Measurement.** Body length, males 2.6–2.7 mm, females 2.7–2.8 mm.

**Description.** Head, pronotum and mesonotum mainly blackish brown (Fig. 1A–F). Vertex with an irregular yellowish spot on each side at apex, extending onto face. Face dorsally brown, frontoclypeus with a longitudinal medial line in upper half, yellow; anteclypeus brownish yellow; genae yellow (Fig. 1C, E). Forewing dark brownish hyaline with three irregular yellowish white markings as in Fig. 1G. Legs yellow. Abdomen dark brown with margins of segments yellow.

Male abdominal sternal apodemes short, not extending to hind margin of 3<sup>rd</sup> segment (Fig. 2J); broad and expanded in lateral view (Fig. 2I).

Male genitalia as in generic description. Pygofer not extended to apex of subgenital plate, articulated dorsal appendage slightly curved distally (Fig. 2A). Subgenital plate

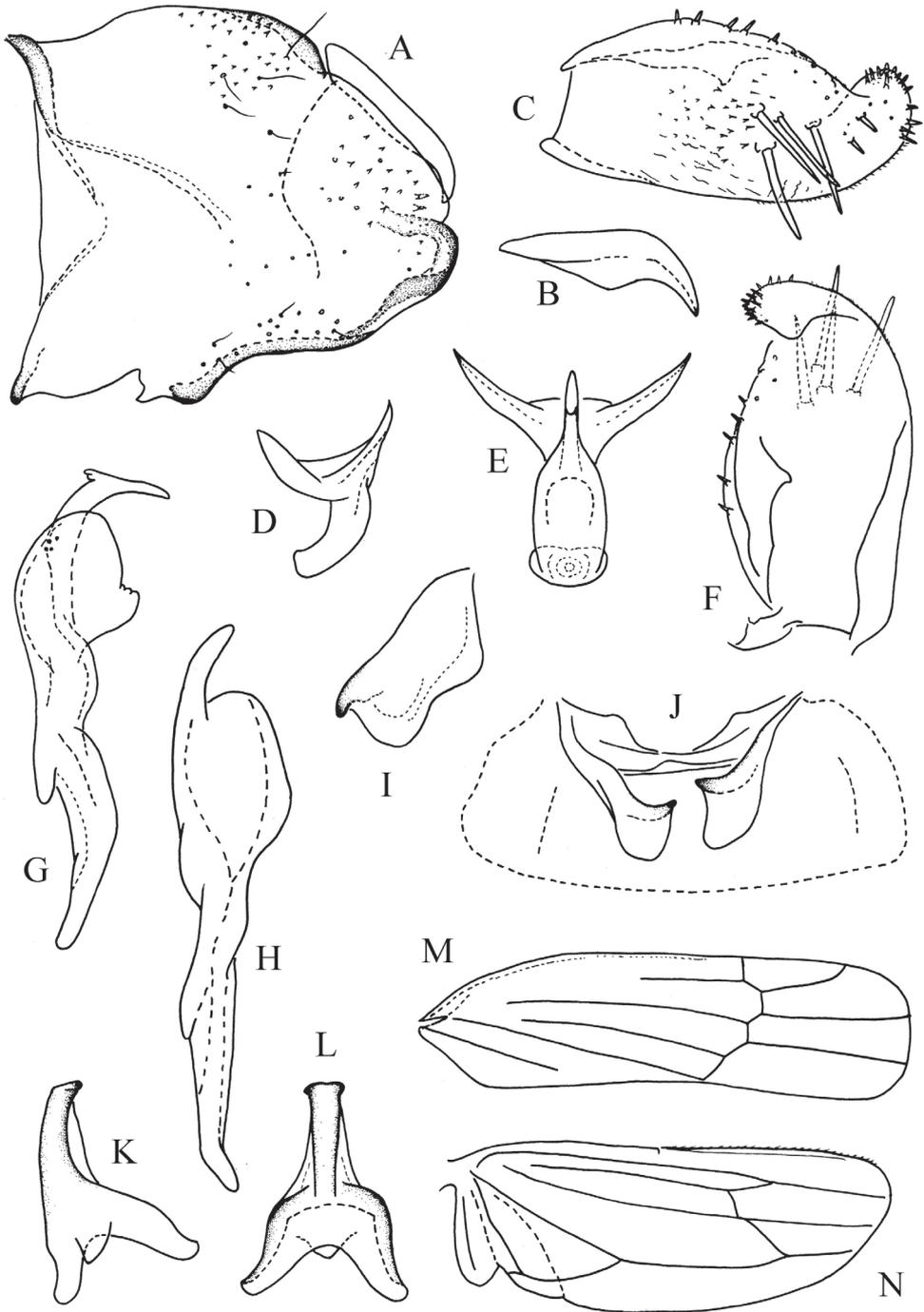


**Figure 1.** *Shibinga nigra* sp. nov. (♂) **A** habitus, dorsal view **B** habitus, lateral view **C** habitus, ventral view **D** head and thorax, dorsal view **E** face **F** face, lateral view **G** forewing **H** hind wing **I** genital capsule, lateral view **J** genital capsule, dorsal view.

with 4 macrosetae laterally in distal half (Fig. 2C, F). Style preapical lobe greatly enlarged (Fig. 2G, H). Aedeagal shaft short and slim (Fig. 2D); dorsal apodeme with dorsal lateral corners greatly extended and sharp apically (Fig. 2E); preatrium moderately long, little longer or equal to length of shaft (Fig. 2D, E); gonopore subapical on ventral surface (Fig. 2E). Connective Y-shaped (Fig. 2L).

**Etymology.** The species is named for its unusual dark color, from the Latin *niger*, black.

**Remarks.** This species can be distinguished by external and male genitalia characters (see generic remarks).



**Figure 2.** *Shibinga nigra* sp. nov. **A** male pygofer, lateral view **B** pygofer dorsal appendage **C** subgenital plate, ventrolateral view **D** aedeagus, lateral view **E** aedeagus, ventral view **F** subgenital plate, dorso-lateral view **G** style, ventral view **H** style, lateral view **I** left abdominal apodeme, lateral view **J** abdominal apodemes, ventral view **K** connective, dorso-lateral view **L** connective, ventral view **M** forewing **N** hind wing.

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# The true colours of the Formidable Pygmy Grasshopper (*Notocerus formidabilis* Günther, 1974) from the Sava region (Madagascar)

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## Abstract

The Formidable Pygmy Grasshopper, *Notocerus formidabilis* Günther, 1974 (Tetrigidae: ‘Malagasy Metrodorinae’), is certainly a stunning, extraordinary insect. Despite the fact that the species was described almost 50 years ago, its beauty had remained completely hidden until recently. The bright yellow colouration of the minute warts on its dorsal hump and even brighter purple-yellowish colouration of its abdomen have been, tragically, completely lost in museum specimens. Luckily, photographs of three live females taken in 2007, 2009 and 2015 were recently uploaded to the iNaturalist platform by the first author of this paper, where they were identified as *N. formidabilis* by the middle and last authors. Along with a male and a female discovered in the MNHN collections (Paris) and the holotype female, these are the only records of the species. All six records are presented and depicted in the present study, and the variation of the species is discussed for the first time. This rare species seems to be endemic to NE Madagascar, a region of truly wonderful diversity.

## Keywords

Anjanaharibe-Sud, Antohakalava, colouration, *Holocerus*, iNaturalist, Madagascar, Marojejy, orange, Tetrigidae

## Introduction

Most of the biota of Madagascar are endemic to the island, and new and interesting species are being discovered all the time, especially from the northern and north-eastern parts of the island (e.g., Glaw et al. 2021; Moravec et al. 2021). Pygmy grasshoppers are not an exception to this rule. More than 95% of all pygmy grasshopper species known from Madagascar are endemic (Devriese 1991, 1995; Cigliano et al. 2021). The lack of research on Malagasy Tetrigoidea (Günther 1959), combined with the severe deforestation that continuously occurs on the island (Harper et al. 2007; Arias-Ortiz et al. 2021), indicate the necessity of preserving all knowledge on Madagascar's biodiversity before it is lost. In this short communication, we present the first recent data on the Formidable Pygmy Grasshopper (*Notocerus formidabilis* Günther, 1974), a rare species that has not been observed since its description almost 50 years ago. To date, the only known preserved specimen of the species was the holotype female deposited in Paris. In the present study, we present records of five more specimens, two from the Paris Natural History Museum collection and three based on photographs of live specimens recently uploaded to the iNaturalist platform by the first author of this paper and identified by the middle and last authors. Platforms such as iNaturalist have significantly contributed to the study of biodiversity in recent years (Altrudi 2021; Aristeidou et al. 2021), and faunistic studies have never benefited more from such platforms (e.g., Hochmair et al. 2020; Winterton 2020).

## Materials and methods

All known specimens of *Notocerus formidabilis* were examined by the authors (museum specimens by J. Skejo, live specimens by É. Mathieu in the field and J. Skejo from the photographs). All information relating to these specimens is summarised in Table 1. The holotype of *N. formidabilis* as well as two additional specimens were examined in Paris, while photographs and associated data of three other specimens were uploaded on iNaturalist by É. Mathieu and identified by J. Skejo and M. Pavlović (Table 1). The photographs were taken in 2007, 2009 and 2015 by É. Mathieu during the walks in the mountainous parts of the Sambava district, NE Madagascar (including Antohakalava and Anjanaharibe-Sud). The first photographs were taken in the morning (at 9:12 and 11:04 a.m., respectively), while the third was taken in the afternoon (4:32 p.m.). The specimens were identified by comparison with the holotype and by consulting the original description of Günther (1974). Species mentioned in the discussion were identified using Bolívar (1887), Rehn (1929), Günther (1939, 1959, 1974), and Devriese (1991, 1995). The taxonomy follows the Orthoptera Species File (Cigliano et al. 2021). The common name of the species was introduced by IUCN (Danielczak et al. 2017). Morphological terminology follows Devriese (1991) and Storozhenko and Pushkar (2017). The abbreviation MNHN is used to indicate the Muséum national d'Histoire naturelle in Paris.

**Table 1.** All known records of *Notocerus formidabilis*, listed chronologically from the oldest to the newest. For records from the Muséum national d'Histoire naturelle (MNHN), coordinates were approximated.

Sex and number	Locality and coordinates	Date (time)	Collector or observer	Reference or link
1♀, holotype (MNHN)	Sambava district, Marojejy, Beondroka Mt., 1200 m a.s.l. (14.14S, 49.80E)	VI.1960	Pierre Soga	Günther (1974) (Fig. 1)
1♀, 1♂ (MNHN)	Belanono (= Belalona; 14.48S, 49.92E), between Sambava and Andapa	Probably between 1958 and 1970	André Peyriéras and Jean Vadon	This study (Fig. 2)
1♀	Sambava district, 800–1000 m a.s.l. (14.46S, 49.72E)	19.VIII.2007 (11:04 a.m.)	Éric Mathieu	This study <a href="https://inaturalist.org/observations/70243152">inaturalist.org/observations/70243152</a> (Fig. 5)
1♀	Sambava district, Antohakalava, 800–1000 m a.s.l. (14.77S, 49.73E)	02.IV.2009 (9:12 a.m.)	Éric Mathieu	This study <a href="https://inaturalist.org/observations/70139087">inaturalist.org/observations/70139087</a> (Fig. 3)
1♀	Sambava district, Anjanaharibe-Sud special reserve, 800–1000 m a.s.l. (14.73S, 49.56E)	06.V.2015 (4:32 p.m.)	Éric Mathieu	This study <a href="https://inaturalist.org/observations/69859528">inaturalist.org/observations/69859528</a> (Fig. 4)

### Observation and identification history of *Notocerus formidabilis*

- 1960 unidentified specimen collected by Soga (deposited in MNHN);
- 1958–1970 two unidentified specimens collected by Peyriéras and Vadon (deposited in MNHN);
- 1974 Soga's specimen described by Günther as a new species, *Notocerus formidabilis*;
- 2007 unidentified pygmy grasshopper photographed by Mathieu;
- 2009 second unidentified pygmy grasshopper photographed by Mathieu;
- 2015 third unidentified pygmy grasshopper photographed by Mathieu;
- 2016 Peyriéras and Vadon specimens identified as *N. formidabilis* by Skejo;
- 2021 specimen photographs uploaded to iNaturalist by Mathieu;
- 2021 Mathieu's specimens identified as *N. formidabilis* by Skejo and Pavlović.

## Results and discussion

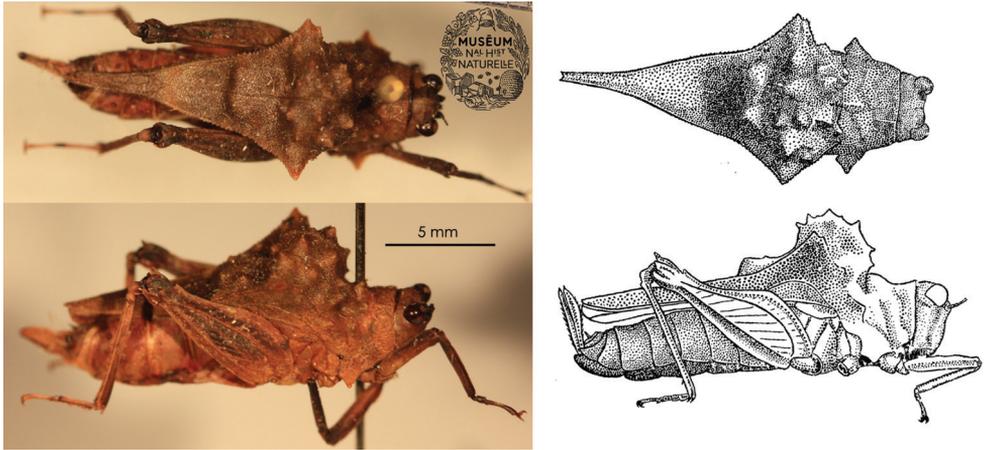
### Family Tetrigidae Rambur, 1838

#### Informal group 'Malagasy Metrodorinae'

#### Genus *Notocerus* Hancock, 1900

**Type species.** *Notocerus cornutus* Hancock, 1900, by monotypy.

**Composition and distribution.** This genus includes two species, *N. cornutus* Hancock, 1900 and *N. formidabilis*, both endemic to NE Madagascar.



**Figure 1.** Holotype of the Formidable Pygmy Grasshopper, *Notocerus formidabilis* Günther **A, B** in dorsal view **C, D** in lateral view. Female from NE Madagascar, Sambava-District, R.N. XII, Marojejy, Beondroka, 1200 m a.s.l., VI.1960, leg. P. Soga **A, C** Josip Skejo and Muséum national d'Histoire naturelle (Paris) **B, D** redrawn after Günther (1974).

### *Notocerus formidabilis* Günther, 1974

Common name: Formidable Pygmy Grasshopper.

**Type locality.** Sambava district: Marojejy NP: Beondroka Mt., 1200 m a.s.l.

### New records from iNaturalist show species colouration for the first time

Without iNaturalist, the collaboration between the authors of this paper would not have been possible, and the photographs may never have been identified to species level. The photos of live specimens of the Formidable Pygmy Grasshopper shown in Figs 3–5 witness how important it is to incorporate *in situ* data into modern biodiversity research. Loss of colouration is known to occur in museum specimens of pygmy grasshoppers (e.g., Mohagan et al. 2020), but it has never been observed to occur to such an extent. Everything we knew about this Malagasy endemic was based on a single known individual of the species, the female holotype (Fig. 1), collected in 1960 in the Sambava district, Marojejy, and deposited in MNHN (Günther 1974). The species was assessed as Near Threatened by the IUCN (Danielczak et al. 2017). Two more individuals (Fig. 2) from Belanono, between Sambava and Andapa, were discovered by the authors in the Orthoptera collections of the MNHN. These were collected between 1958 and 1970 by French naturalists André Peyriéras and Jean Vadon, both of whom worked and lived in Madagascar (Table 1).

### Intraspecific variation

The variation of the specimens reported to date is notable in the shape of the dorsal hump as well as in the shape of the minute warts on the dorsal hump. For example,



**Figure 2.** Museum specimens of *Notocerus formidabilis* **A–C** male (**A** in frontal view **B** in lateral view, and **C** in dorsal view) **D** labels (same on both specimens) **E–G** female (**E** in frontal view **F** in dorsal view, and **G** in lateral view). Photos by Josip Skejo, Karmela Adžić, Maks Deranja and Muséum national d’Histoire naturelle (Paris).

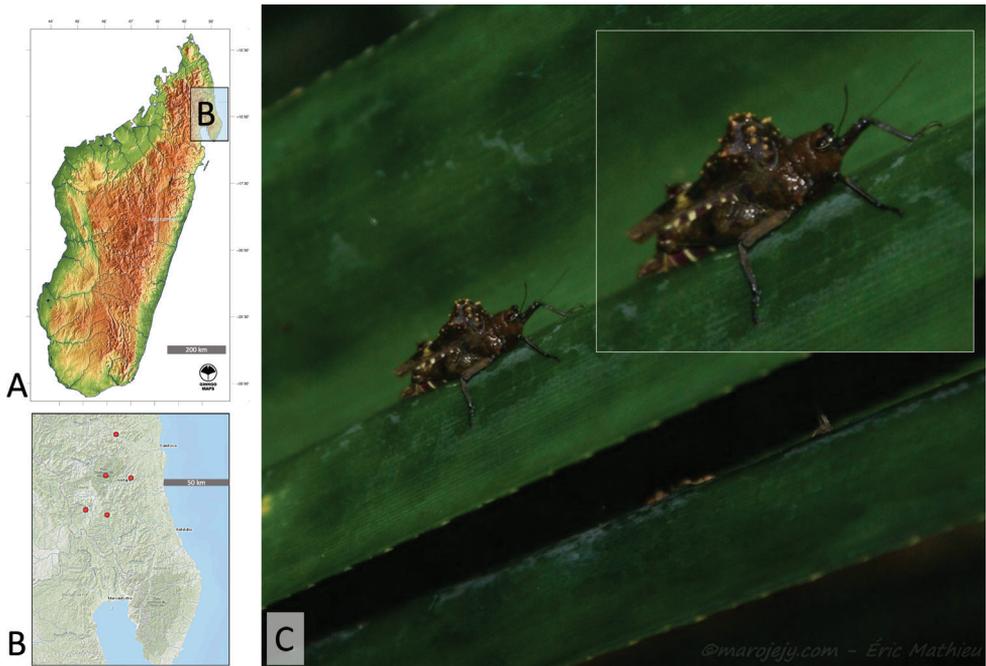
the holotype female (Fig. 1) has a rough pronotal hump with spine-shaped projections; the two additional specimens from MNHN (Fig. 2) have rather oblique and smooth dorsal humps with small warts; the three specimens reported from photographs (Figs 3–5) have large and rough humps with oblique warts. In the holotype and the other specimens from MNHN, a pale-yellow colouration was observed after careful examination under a stereomicroscope. Therefore, we concluded that the hump seems to be variable in *Notocerus formidabilis* – it can be smaller or larger, more or less smooth, but it is always directed cephalad, and the warts on the hump can be oblique or more or less projected. These differences cannot be attributed to sexual dimorphism, as only one male specimen is reported here (Fig. 2A–C). The variation in pronotal projections among Tetrigidae species has sometimes led to unwarranted new descriptions of the same species, for example in *Trachytettix* Stål, *Cladoramus* Hancock or *Misythus* Stål (Devriese 1999; Cigliano et al. 2021). The Formidable Pygmy Grasshopper is, interestingly, one of a few Tetrigidae species in which the metalateral projections (humeral angles or shoulders) reach more outwards than the apices of the lateral lobes. Examples of other species with very wide humeral projections are *Paragavialidium emeiense* Zheng & Cao (Deng et al. 2012) and *Eufalconius pendleburyi* Günther (Storozhenko and Pushkar 2017) from eastern Asia.



**Figure 3.** Live female of the Formidable Pygmy Grasshopper, *Notocerus formidabilis*, in dorsal view. Photo by Éric Mathieu.



**Figure 4.** Live female of the Formidable Pygmy Grasshopper, *Notocerus formidabilis*, in lateral view. Photo by Éric Mathieu.



**Figure 5. A, B** Distribution of the Formidable Pygmy Grasshopper and **C** a live female of the Formidable Pygmy Grasshopper, *Notocerus formidabilis*, in lateral view. Map in **A** generated using GinkgoMaps Free Digital Maps, map in **B** using Google maps, and **C** photo by Éric Mathieu.

Museum specimens of the Formidable Pygmy Grasshopper are almost uniformly brown (Figs 1, 2), making them so different from live specimens that when the photographs were uploaded by É. Mathieu to iNaturalist in 2021, J. Skejo concluded, at first glance, that they might have represented a new species. The bright orange colouration of the warts on the pronotal hump, together with the bright purple-yellowish abdomen and part of the pronotum, had not been published to date. Only after a careful comparison of the museum specimens and details on their pronotal surface did it become clear that the colour had completely faded. Because of that, for almost 50 years, we were completely deprived of seeing the species in all of its glory. There are still many questions about this species. For example, how did this morphology evolve? Do the yellow warts ‘mimic’ mites? Is the colouration cryptic or aposematic? With this short communication intending to shed some light on the species’ morphology and natural history, we would also like to encourage other researchers to investigate this interesting species if they happen to visit areas in the vicinity of Andapa and Sambava, i.e., the Sava region of NE Madagascar, where the species is endemic (Fig. 5A, B). Similarly to other *Holocerus* species, we expect that this species might be a good flier.

The Sava region, with Marojejy National Park, Anjanaharibe-Sud special reserve and Antohakalava private reserve as the most known reserves, is famous for many animal and plant endemics. For example, the Silky Sifaka (*Propithecus candidus* Grandi-

dier; Mammalia: Primates) (Patel 2014), the Helmet Vanga (*Euryceros prevostii* Lesson; Aves: Passeriformes) (Birdlife International 2018), and the dwarf palm (*Dypsis pumila* Beentje; Plantae: Arecaceae) (Dransfield and Beentje 1995). Now, this region will also be known for one of the morphologically most amazing pygmy grasshoppers.

### iNaturalist contributes to Tetrigidae studies in Madagascar

There are currently 66 iNaturalist records of Tetrigidae from Madagascar, among which 46 (i.e., 70%) are research-grade, altogether representing 16 taxa identified to genus or species level. This number represents around 20% of the known pygmy grasshopper fauna of the island (Cigliano et al. 2021). The Formidable Pygmy Grasshopper is not the only groundhopper species whose first record since its description has been contributed by the iNaturalist platform. Other examples include *Cryptotettix imerina* Rehn, 1929 (‘Malagasy Metrodorinae’) (18.92S, 48.49E, observed by Ehoarn Bidault on 16.IV.2010; [inaturalist.org/observations/37580891](https://inaturalist.org/observations/37580891); and 8.94S, 48.43E, observed by Micha Baum on 25.X.2014; [inaturalist.org/observations/53256082](https://inaturalist.org/observations/53256082)), *Eurybiades cerastes* Rehn, 1929 (‘Malagasy Metrodorinae’) (24.46S, 47.01E, observed by Andrianiaina Angelo on 17.XII.2020. [inaturalist.org/observations/67190643](https://inaturalist.org/observations/67190643)), *Pterotettix andrei* Bolívar, 1887 (‘Malagasy Metrodorinae’) (14.47S, 49.74E, observed by Éric Mathieu on 30.X.2016.; [inaturalist.org/observations/69807072](https://inaturalist.org/observations/69807072)); *Thymochares frontangulus* Günther, 1974 (Cladonotinae) (12.53S, 49.17E, observed by “c\_hutton” on 10.III.2019; [inaturalist.org/observations/68927516](https://inaturalist.org/observations/68927516)), and *Pseudosystolederus follvikae* Devriese, 1995 (not assigned to any subfamily) (21.26S, 47.43E, observed by Davorka Kitonić and Josip Skejo on 06.I.2019; [inaturalist.org/observations/39066871](https://inaturalist.org/observations/39066871)).

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# The complete mitochondrial genome of *Pentatoma rufipes* (Hemiptera, Pentatomidae) and its phylogenetic implications

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<http://zoobank.org/B80A1A95-A189-4CC1-9D5F-7F0C80CD9FF0>

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## Abstract

*Pentatoma rufipes* (Linnaeus, 1758) is an important agroforestry pest widely distributed in the Palaearctic region. In this study, we sequence and annotate the complete mitochondrial genome of *P. rufipes* and reconstruct the phylogenetic trees for Pentatomoidea using existing data for eight families published in the National Center for Biotechnology Information database. The mitogenome of *P. rufipes* is 15,887-bp-long, comprising 13 protein-coding genes, 22 transfer RNA genes, two ribosomal RNA genes, and a control region, with an A+T content of 77.7%. The genome structure, gene order, nucleotide composition, and codon usage of the mitogenome of *P. rufipes* were consistent with those of typical Hemiptera insects. Among the protein-coding genes of Pentatomoidea, the evolutionary rate of ATP8 was the fastest, and COX1 was found to be the most conservative gene in the superfamily. Substitution saturation assessment indicated that neither transition nor transversion substitutions were saturated in the analyzed datasets. Phylogenetic analysis using the Bayesian inference method showed that *P. rufipes* belonged to Pentatomidae. The node support values based on the dataset concatenated from protein-coding and RNA genes were the highest. Our results enrich the mitochondrial genome database of Pentatomoidea and provide a reference for further studies of phylogenetic systematics.

## Keywords

Mitogenome, Pentatomoidea, phylogenetic analysis

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\* These authors contributed equally to this work.

## Introduction

The mitochondrion is a semi-autonomous organelle with its own genetic material, known as the mitochondrial genome (mitogenome) (Nass and Nass 1963). The mitogenome is widely used in the fields of molecular evolution, phylogenetic analysis, molecular ecology, biogeography, and population genetics because of its advantages of small size, stable genetic composition, and maternal inheritance (Ballard and Whitlock 2004; Simon and Hadrys 2013; Cameron 2014; Yuan and Guo 2016). Insects, as the most diverse, numerous, and widely distributed animals on Earth, are hotspots in mitogenome research (Boore 1999). To date, mitochondrial genome research has been very extensive, covering all orders of insects (Cameron 2014). Insect mitogenomes are covalently closed, double-stranded, circular DNA molecules (14–20 k bp long), and usually contain a control region and 37 genes: 13 protein-coding genes (PCGs), 22 transfer RNA (tRNA) genes, and two ribosomal RNA (12S rRNA and 16S rRNA) genes (Boore 1999; Cameron and Whiting 2008; Cameron 2014). The structure of mitogenome in most known insects is stable, and the gene arrangement is relatively conservative, which are consistent with the genome composition and arrangement of the most typical insect mitochondrial genome, namely *Drosophila yakuba* Burla (Clary and Wolstenholme 1985).

Pentatomoidea, one of the most commonly encountered groups in Hemiptera, includes 1,410 genera and 8,042 species which are widely distributed worldwide (Rider et al. 2018). Pentatomoid insects have diverse feeding habits, although the majority are herbivorous. Some cause huge economic losses, such as *Dolycoris baccarum* (Linnaeus) and *Halyomorpha halys* Stål. In addition, some pentatomoid insects are predatory, including most of the species of Asopinae; and a few groups are suspected to be fungus feeders, such as members of the Canopidae and Megarididae (Rider et al. 2018; Zhao et al. 2018). Classification of the superfamily Pentatomoidea has long been contentious; and different scholars have distinct opinions. For example, Schaefer (1993) divided Pentatomoidea into 16 families, whereas Henry (1997) recognized 17 families, placing Eumenotidae and Thyreocoridae at the family level. Grazia et al. (2008) supported the monophyly of Pentatomoidea and most of the included families, which was based on morphological characters and molecular markers (16S rRNA, 18S rRNA, 28S rRNA and COI); Wu et al. (2016) reconstructed the phylogenetic relationships of 16 families within Pentatomoidea using 18S and 28S rDNAs sequences and showed that Cydnidae and Tessaratomidae might be polyphyletic; Lis et al. (2017) combined 28S+18S rDNA sequence, questioned the monophylicity of the “cydnoid” complex of pentatomoid families (Cydnidae, Parastrachiidae, Thaumastellidae, and Thyreocoridae), and demonstrated the polyphylicity of Cydnidae. Recently, many taxonomists reorganized the families, genera, and species of Pentatomoidea, and divided Pentatomoidea into 18 families (Rider et al. 2018). With the development of next-generation sequencing (NGS), an increasing number of pentatomoid mitogenome sequences have been obtained, which provide the possibility of resolving the phylogenetic relationships

among the superfamily at the genetic level (Yuan et al. 2015b; Bai et al. 2018; Zhao et al. 2018). Furthermore, Wu et al. (2017) confirmed the monophyly of Scutelleridae (based on 18S + 28S rDNAs + 13PCGs), and Liu et al. (2019) reconstructed the phylogeny of Pentatomomorpha and Pentatomoidea based on PCGRNA and PCG12RNA. However, despite the abundance of species in the superfamily, only 97 species have complete or nearly complete mitogenomes published in the National Center for Biotechnology Information (NCBI; <https://www.ncbi.nlm.nih.gov/2020.07>); these represent only eight families. Moreover, there has been no discussion about the phylogenetic position of *Pentatoma* species, except for the description of *Pentatoma semianulata* (Motschulsky) mitogenome by Wang et al. (2021). Therefore, it is necessary to determine more mitogenome sequences of *Pentatoma* species to better understand its phylogenetic relationships.

*Pentatoma rufipes* (Linnaeus, 1758) (Hemiptera, Heteroptera, Pentatomidae) is a medium-sized to large, dark brown insect with reddish-orange spots and bright orange legs (Hsiao 1977; Bantock and Botting 2013). These insects are widely distributed in the Palearctic region (Ling and Zheng 1987; Fan and Liu 2012). They can damage oak, poplar, elm, hawthorn, apricot, pear, and other trees, and they constitute an important agricultural and forestry pest (Hsiao et al. 1977; Powell 2020). There are also records of *P. rufipes* preying on *Zygaena filipendulae* L. (Lepidoptera, Zygaenidae) (Hamilton and Heath 1976). Previous studies on *P. rufipes* mostly focused on its physiological and morphological characteristics (Ling and Zheng 1987; Neupert et al. 2009), with limited molecular data on the mitochondrial COI and COII genes (Bu et al. 2005; Liang 2009), along with some studies identifying biological characteristics and potential control strategies (Peusens and Beliën 2012; Powell 2020).

In this study, we sequenced and annotated the mitogenome of *P. rufipes* and analyzed its mitogenome in detail, including the genome structure, nucleotide composition, and codon usage, and constructed RNA secondary structures. In addition, we combined the complete mitogenome of *P. rufipes* with the existing data for the eight families of Pentatomoidea to explore the phylogenetic position of *P. rufipes*.

## Materials and methods

### Sample collection

Adult *Pentatoma rufipes* specimens were collected in Baiji Hill (Tonghua City, Jilin Province, China; 41°58.14'N, 126°06.58'E) on 24 July 2015. All samples were immediately placed in absolute ethanol and stored in a freezer at -20 °C until DNA extraction. Specimen identification was performed by Qing Zhao. The voucher specimen is maintained at the Institute of Entomology of Shanxi Agricultural University (voucher number: SXAU 007; Taigu, China). The complete mitogenome of *P. rufipes* has been submitted to GenBank (accession number: MT861131).

## DNA extraction and sequencing

Whole-genome DNA was extracted from the thoracic muscle of adult samples using the Genomic DNA Extraction Kit (Sangon Biotech, Shanghai, China). The mitogenomes were sequenced using the whole-genome shotgun method on the Illumina Miseq platform (Personalbio, Shanghai, China), with 400-bp inserts and paired-end model. A5-miseq v. 20150522 (Coil et al. 2015) and SPAdes v. 3.9 (Bankevich et al. 2012) were used to assemble the data.

## Genome annotation and sequence analysis

After assembly, the complete mitogenome was manually annotated using Geneious v. 8.1.4 software (Kearse et al. 2012). A reference sequence of *Eurydema gebleri* Kolenati for annotation was obtained from the basic local alignment search tool (BLAST) in the NCBI database. The boundaries of the PCGs were determined using Open Reading Frame Finder (<http://www.ncbi.nlm.nih.gov/gorf/gorf.html>) on the NCBI website. MEGA v. 7.0 (Kumar et al. 2016) was used to translate the proteins to verify the start codons, stop codons, and amino acid sequences and to ensure the accuracy of the sequences. We annotated tRNA sequences using tRNAscan-SE (<http://lowelab.ucsc.edu/tRNAscan-SE/>) (Lowe and Eddy 1997) and MITOS (<http://mitos.bioinf.uni-leipzig.de/index.py/>) (Bernt et al. 2013) with the invertebrate mitochondrial code. The boundaries of rRNA genes were completed according to the positions of adjacent genes and published rRNA gene sequences from Pentatomidae insects in GenBank (Boore 2006). The codon usage, base composition, and amino acid composition of the mitogenome were analyzed using MEGA v. 7.0. The skew of the nucleotide composition was calculated with the formulas:  $AT\text{-skew} = (A - T) / (A + T)$  and  $GC\text{-skew} = (G - C) / (G + C)$  (Perna and Kocher 1995).

## Phylogenetic analyses

In this study, we selected the mitogenomes of *P. rufipes*, representative species from eight other Pentatomoidea families, and two Coreoidea species (outgroup) to analyze the phylogenetic position of *P. rufipes* and the phylogenetic relationships within Pentatomoidea. All species included in this analysis are listed in Table 1. The nucleic acid sequences of the 13 PCGs were extracted using Geneious v. 8.1.4. All PCGs were translated into their amino acid sequences and aligned using MUSCLE with default parameters in MEGA v. 7.0 (Edgar 2004). The tRNA and rRNA genes were also aligned using the MUSCLE algorithm in MEGA v. 7.0. The resulting alignments were concatenated into a combined matrix.

To determine if the sequences contained phylogenetic information, we tested nucleotide substitution saturation, and plotted transition and transversion substitutions against the TN93 distance for all datasets before reconstructing the phylogenetic trees using DAMBE v. 4.5.32 (Xia and Xie 2001; Xia and Lemey 2009). The optimal sub-

**Table 1.** List of species used to construct the phylogenetic tree.

Classificationstatus	Family	Species	Accession number
<b>Outgroup</b>			
Coreoidea	Coreidae	<i>Hydaropsis longirostris</i>	EU427337
		<i>Anoplocnemis curvipes</i>	NC_035509
<b>Ingroup</b>			
Pentatomoidea	Acanthosomatidae	<i>Acanthosoma labiduroides</i>	JQ743670
		<i>Sastragala edessoides</i>	JQ743676
		<i>Anaxandra taurina</i>	NC_042801
	Cydnidae	<i>Macrocytus gibbulus</i>	NC_012457
		<i>Adrisa magna</i>	NC_042429
		<i>Scoparipes salvazai</i>	NC_042800
	Dinidoridae	<i>Cyclopelta parva</i>	KY069962
		<i>Megymenum gracilicorne</i>	NC_042810
	Pentatomidae	<i>Halyomorpha halys</i>	NC_013272
		<i>Eurydema gebleri</i>	NC_027489
		<i>Graphosoma rubrolineatum</i>	NC_033875
		<i>Gonopsis affinis</i>	NC_036745
		<i>Dinorhynchus dybowskyi</i>	NC_037724
		<i>Plautia fimbriata</i>	NC_042813
		<b><i>Pentatoma rufipes</i></b>	<b>MT861131</b>
	Plataspidae	<i>Coptosoma bifaria</i>	EU427334
		<i>Megacopta cribraria</i>	NC_015342
	Scutelleridae	<i>Cantao ocellatus</i>	NC_042803
		<i>Eurygaster testudinaria</i>	NC_042808
	Tessaratomidae	<i>Dalcantha dilatata</i>	JQ910981
		<i>Eusthenes cupreus</i>	NC_022449
		<i>Tessaratoma papillosa</i>	NC_037742
	Urostylididae	<i>Urostylis flavoannulata</i>	NC_037747

stitution models for each dataset were calculated using PartitionFinder v. 1.1.1 (Lanfear et al. 2012). Phylogenetic analyses were conducted using the Bayesian inference method, in MrBayes v. 3.2.5 (Ronquist et al. 2012) under the GTR+G+I substitution model with four independent Markov chains run for 10,000,000 generations and stopped when the average standard deviation value was below 0.01. The first 25% of trees were discarded as burn-ins, and the remaining trees were used to construct a 50% majority-rule consensus tree (Zhao et al. 2018). The phylogenetic trees were constructed using three types of datasets: (1) all codon positions of the 13 PCGs; (2) the 13 PCGs, excluding the third codon position (PCG12); and (3) the PCGs, 22 tRNA genes, and two rRNA genes (PCGRNA).

## Results

### Genomic features

The mitochondrial genome of *Pentatoma rufipes* is 15,887-bp-long and contains a control region and 37 genes comprising 13 PCGs, 22 tRNA genes and two rRNA genes (Fig. 1; Table 2). Among these genes, 14 genes are located on the minority strand



**Table 2.** Organization of the mitochondrial genome of *Pentatoma rufipes*.

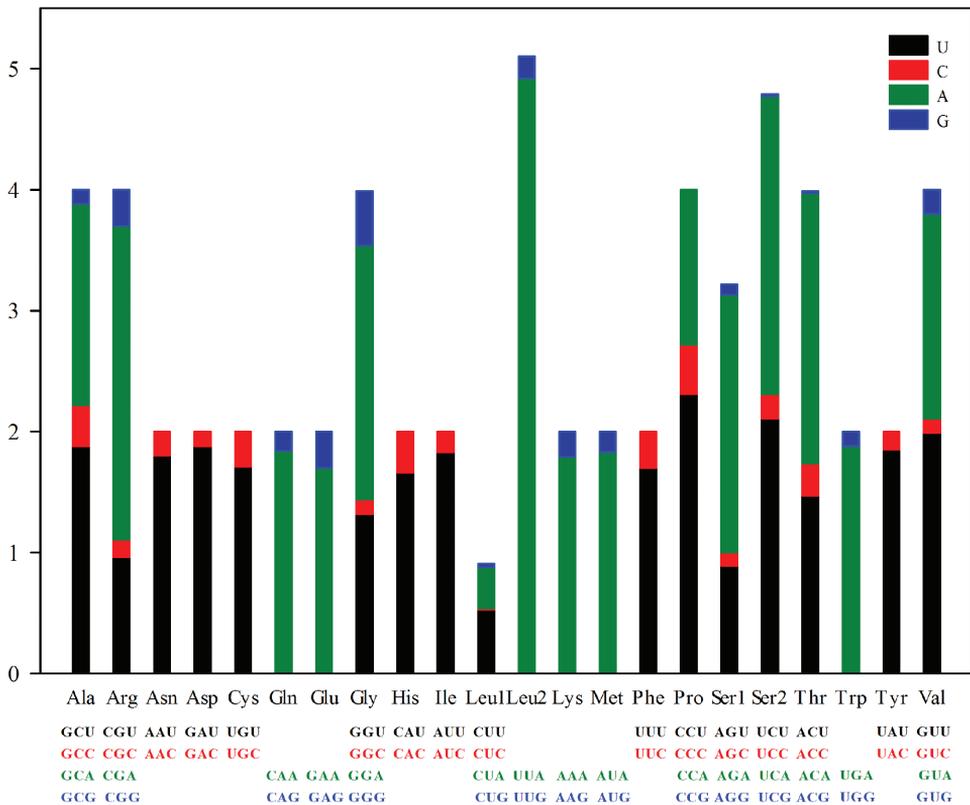
Gene	Strand	Position	Anticodon	Size(bp)	Start codon	Stop codon	Intergenic nucleotides*
trnI	J	1–67	GAT	67			
trnQ	N	65–134	TTG	70			–3
trnM	J	137–205	CAT	69			2
ND2	J	206–1189		984	ATT	TAA	0
trnW	J	1198–1265	TCA	68			8
trnC	N	1258–1321	GCA	64			–8
trnY	N	1331–1397	GTA	67			9
COX1	J	1407–2943		1537	TTG	T	9
trnL2 <sup>UUR</sup>	J	2944–3008	TAA	65			0
COX2	J	3009–3687		679	ATA	T	0
trnK	J	3688–3761	CTT	74			0
trnD	J	3761–3822	GTC	62			–1
ATP8	J	3823–3981		159	TTG	TAA	0
ATP6	J	3975–4649		675	ATG	TAA	–7
COX3	J	4652–5440		789	ATG	TAA	2
trnG	J	5446–5510	TCC	65			5
ND3	J	5511–5864		354	ATC	TAA	0
trnA	J	5873–5943	TGC	71			8
trnR	J	5960–6024	TCG	65			16
trnN	J	6033–6101	GTT	69			8
trnS1 <sup>AGN</sup>	J	6101–6170	ACT	70			–1
trnE	J	6171–6238	TTC	68			0
trnF	N	6237–6301	GAA	65			–2
ND5	N	6301–8007		1707	ATT	TAA	–1
trnH	N	8009–8076	GTG	68			1
ND4	N	8079–9410		1332	ATG	TAA	2
ND4L	N	9404–9691		288	ATT	TAA	–7
trnT	J	9694–9758	TGT	65			2
trnP	N	9759–9820	TGG	62			0
ND6	J	9823–10299		477	ATG	TAA	2
CYTB	J	10304–11440		1137	ATG	TAA	4
trnS2 <sup>UCN</sup>	J	11456–11524	TGA	69			15
ND1	N	11548–12477		930	ATA	TAA	23
trnL1 <sup>GLN</sup>	N	12472–12539	TAG	68			–6
16S rRNA	N	12540–13816		1277			0
trnV	N	13817–13886	TAC	70			0
12S rRNA	N	13887–14707		821			0
CR		14708–15887		1180			0

\*Numbers correspond to nucleotides separating a gene from an upstream one; negative numbers indicate that adjacent cent genes overlap.

The preference for nucleotide composition is also reflected in codon use. The relative synonymous codon usage values for the *P. rufipes* mitogenome are summarized in Figure 2 and Table 4. Figure 3 shows the amino acid composition of the *P. rufipes* mitogenome. The most common amino acids are Phe, Leu, Ile, and Met, and their most abundant codons (UUU for Phe, UUA for Leu2, AUU for Ile, and AUA for Met) are all composed of A and/or T. For each amino acid, the most commonly used coded codons are NNA and NNU, reflecting the skew of the nucleotide composition toward AT. In addition, the most frequently used codons do not strictly correspond to the tRNA anticodons for most amino acids.

**Table 3.** Nucleotide composition and skewness of the *Pentatoma rufipes* mitochondrial genome.

Feature	Length(bp)	A%	C%	G%	T%	A+T%	AT-skew	GC-skew
Whole genome	15737	42.0	12.4	9.9	35.7	77.7	0.08	-0.11
PCGs	11046	34.2	11.1	11.8	42.9	77.1	-0.11	0.03
PCG-J	6800	37.2	12.6	11.7	38.5	75.7	-0.02	-0.04
PCG-N	4246	29.4	8.8	11.9	49.9	79.3	-0.26	0.15
tRNA genes	1460	39.7	10.0	12.3	38.0	77.7	0.02	0.10
tRNA genes-J	936	40.6	11.0	11.1	37.3	77.9	0.04	0.01
tRNA genes-N	524	38.0	8.2	14.4	39.3	77.3	-0.02	0.27
rRNA genes	2053	35.6	7.6	12.6	44.2	79.8	-0.11	0.25
Control region	1142	38.3	13.6	7.6	40.4	78.7	-0.03	-0.28



**Figure 2.** The relative synonymous codon usage (RSCU) in the mitogenome of *Pentatoma rufipes*.

**PCG regions**

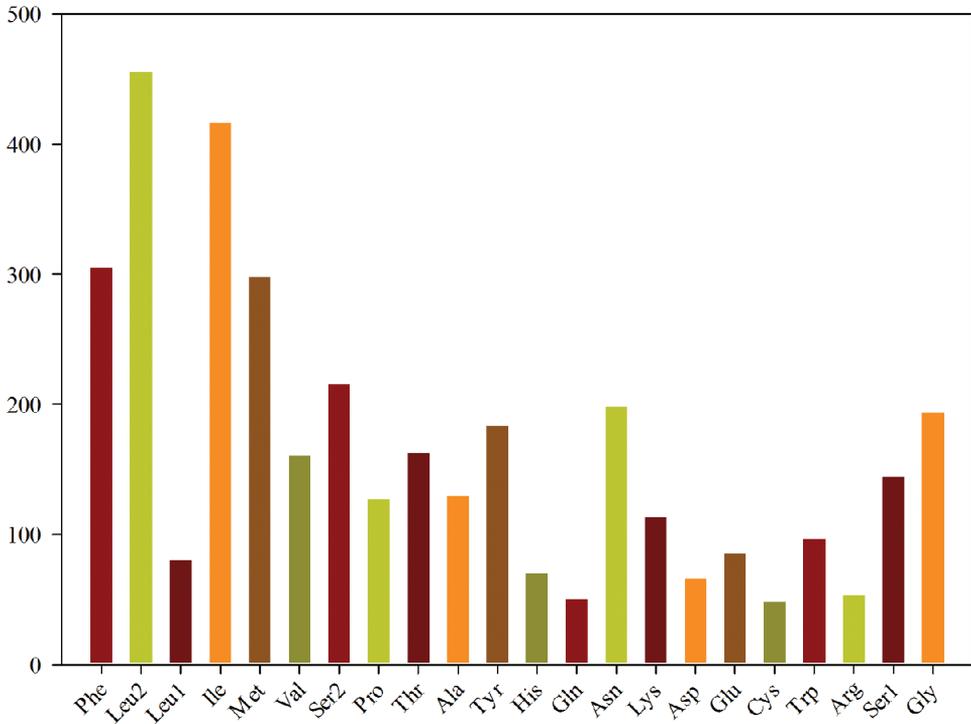
Most *P. rufipes* PCGs share the ATN start codon (five with ATG, three with ATT, two with ATA, and one with ATC), except for COX1 and ATP8, which start with TTG. COX1 and COX2 sequences terminate with a single T, and the stop codon for the remaining genes is TAA. The AT content (77.1%) of the 13 PCGs exceeded the GC content (22.9%), and the AT bias is moderately negative (absolute value: 0.1–0.2).

**Table 4.** Codon number and RSCU in the *Pentatoma rufipes* mitochondrial PCGs.

Amino acid	Codon	N	RSCU	N+	RSCU+	N-	RSCU-
Phe	UUU	<b>260</b>	1.7	118	1.49	<b>142</b>	1.92
	<u>UUC</u>	46	0.3	40	0.51	6	0.08
Leu2	<u>UUA</u>	<b>440</b>	4.92	<b>238</b>	4.89	202	4.95
	UUG	16	0.18	6	0.12	10	0.24
Leu1	CUU	47	0.53	19	0.39	28	0.69
	CUC	1	0.01	1	0.02	0	0
	<u>CUA</u>	30	0.34	26	0.53	4	0.1
	CUG	3	0.03	2	0.04	1	0.02
Ile	AUU	<b>382</b>	1.83	<b>255</b>	1.8	127	1.91
	<u>AUC</u>	35	0.17	29	0.2	6	0.09
Met	AUA	<b>274</b>	1.83	<b>179</b>	1.86	95	1.78
	<u>AUG</u>	25	0.17	13	0.14	12	0.22
Val	GUU	80	1.99	33	1.43	47	2.72
	GUC	5	0.12	1	0.04	4	0.23
	<u>GUA</u>	68	1.69	51	2.22	17	0.99
	GUG	8	0.2	7	0.3	1	0.06
Ser2	UCU	95	2.11	31	1.24	64	3.18
	UCC	9	0.2	6	0.24	3	0.15
	<u>UCA</u>	111	2.46	76	3.04	35	1.74
	UCG	1	0.02	0	0	1	0.05
Pro	CCU	74	2.31	48	2.04	26	3.06
	CCC	13	0.41	9	0.38	4	0.47
	<u>CCA</u>	41	1.28	37	1.57	4	0.47
	CCG	0	0	0	0	0	0
Thr	ACU	60	1.47	42	1.33	18	1.95
	ACC	11	0.27	5	0.16	6	0.65
	<u>ACA</u>	91	2.23	78	2.48	13	1.41
	ACG	1	0.02	1	0.03	0	0
Ala	GCU	61	1.88	42	1.77	19	2.17
	GCC	11	0.34	9	0.38	2	0.23
	<u>GCA</u>	54	1.66	44	1.85	10	1.14
	GCG	4	0.12	0	0	4	0.46
Tyr	UAU	170	1.85	67	1.7	103	1.96
	<u>UAC</u>	14	0.15	12	0.3	2	0.04
His	CAU	59	1.66	45	1.58	14	2
	<u>CAC</u>	12	0.34	12	0.42	0	0
Gln	<u>CAA</u>	47	1.84	35	2	12	1.5
	CAG	4	0.16	0	0	4	0.5
Asn	AAU	179	1.8	114	1.74	65	1.91
	<u>AAC</u>	20	0.2	17	0.26	3	0.09
Lys	AAA	102	1.79	73	1.9	29	1.57
	<u>AAG</u>	12	0.21	4	0.19	8	0.43
Asp	GAU	63	1.88	38	1.81	25	2
	<u>GAC</u>	4	0.12	4	0.19	0	0
Glu	<u>GAA</u>	73	1.7	56	1.9	17	1.26
	GAG	13	0.3	3	0.1	10	0.74
Cys	UGU	42	1.71	12	1.6	30	1.76
	<u>UGC</u>	7	0.29	3	0.4	4	0.24
Trp	<u>UGA</u>	91	1.88	68	1.97	23	1.64
	UGG	6	0.12	1	0.03	5	0.36

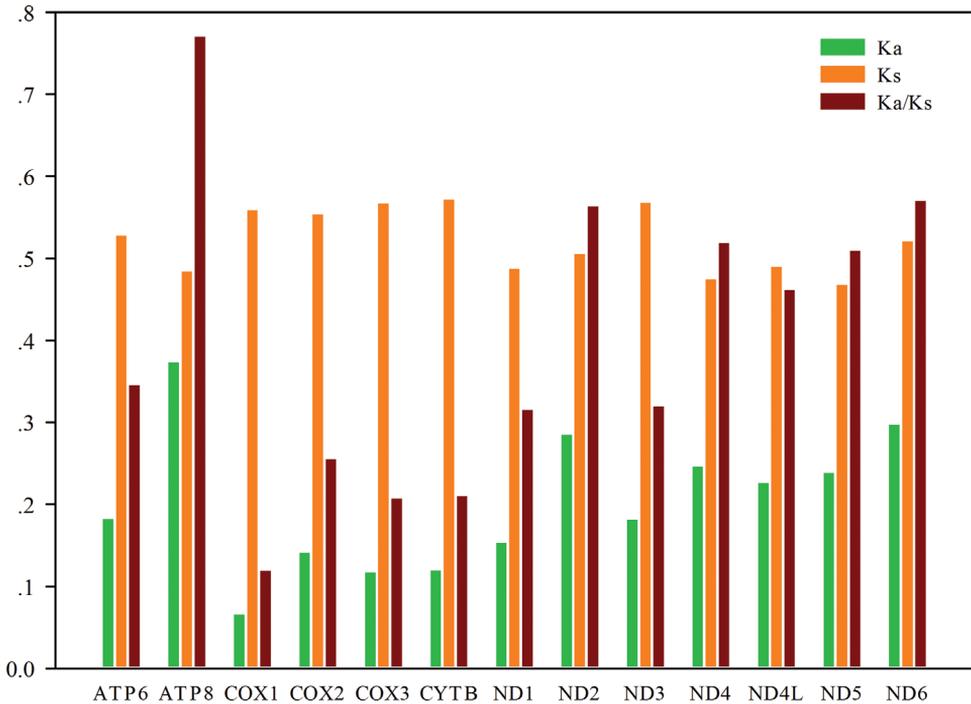
Amino acid	Codon	N	RSCU	N+	RSCU+	N-	RSCU-
Arg	CGU	13	0.96	2	0.23	11	2.32
	CGC	2	0.15	1	0.11	1	0.21
	<u>CGA</u>	35	2.59	30	3.43	5	1.05
	CGG	4	0.3	2	0.23	2	0.42
Ser1	AGU	40	0.89	14	0.56	26	1.29
	<u>AGC</u>	5	0.11	3	0.12	2	0.1
	AGA	96	2.13	69	2.76	27	1.34
	AGG	4	0.09	1	0.04	3	0.15
Gly	GGU	64	1.32	28	0.9	36	2.06
	GGC	6	0.12	2	0.06	4	0.23
	<u>GGA</u>	102	2.1	82	2.65	20	1.14
	GGG	22	0.45	12	0.39	10	0.57

N, N+, and N- are respectively the number of codons used in the total protein codon gene, the majority strand protein codon gene (J-strand), and the minority strand protein codon gene (N-strand). Values in bold type stand for most commonly used codon for the amino acid. Underlined codons stand for the cognate codon of tRNA for each amino acid.



**Figure 3.** Amino acid composition in the *Pentatoma rufipes* mitogenome. Codon families are provided on the x-axis. Numbers of codons of each amino acid are provided on the y-axis.

In addition, we calculated the synonymous substitutions (Ks), non-synonymous substitutions (Ka), and the Ka/Ks ratios of the 13 PCGs from Pentatomoid insects. We also compared the evolutionary rates of the 13 PCGs (Fig. 4). The evolutionary rate of ATP8 was the fastest, followed by that of ND6, and the COX1 gene was the most



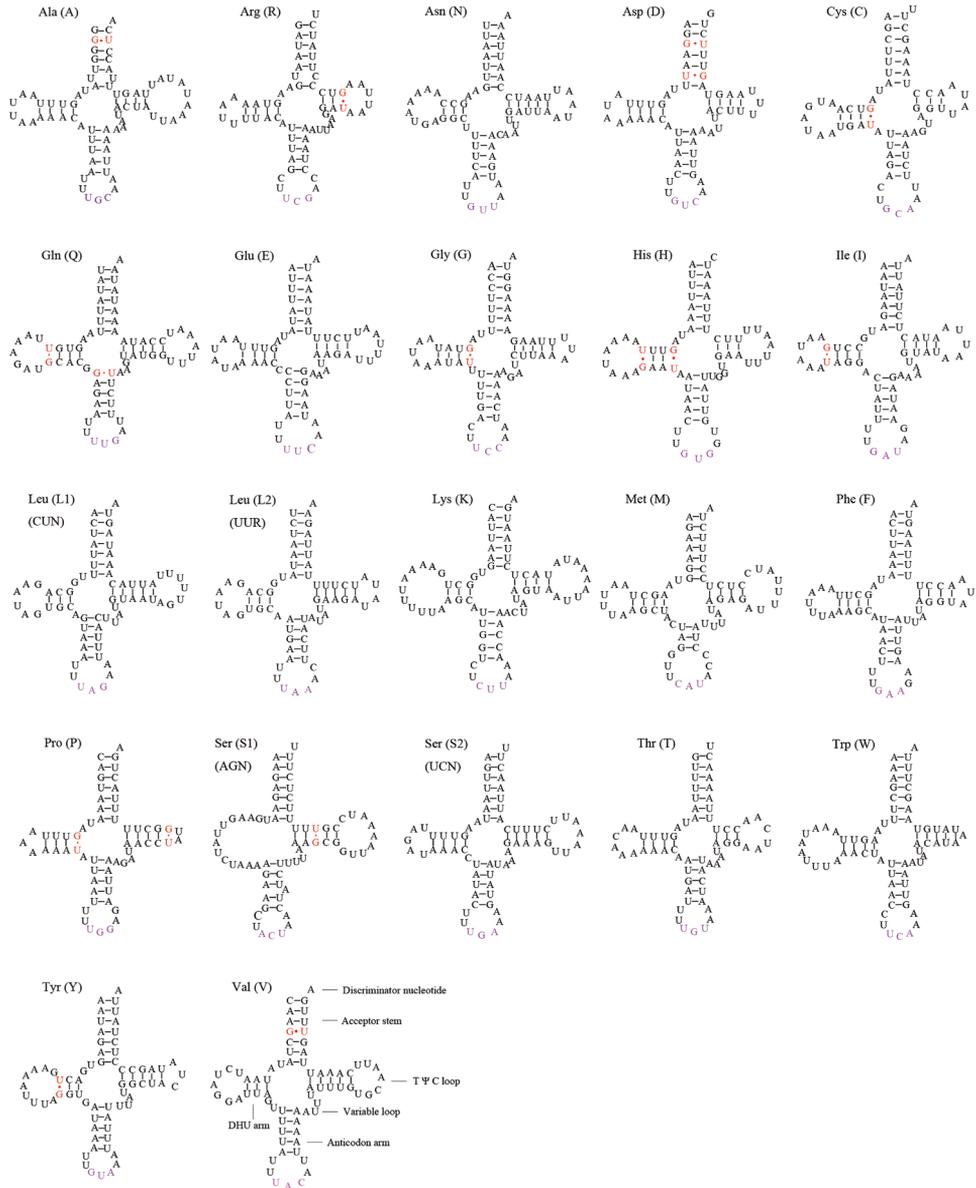
**Figure 4.** Evolutionary rates of 13 PCGs in Pentatomoidea. Rate of non-synonymous substitutions (Ka), rate of synonymous substitutions (Ks) and ratio of rate of non-synonymous substitutions to rate of synonymous substitutions (Ka/Ks) are calculated for each PCG.

conservative with the slowest rate. The evolutionary rates of the other genes were in the order of ND2 > ND4 > ND5 > ND4L > ATP6 > ND3 > ND1 > COX2 > COX3 > CYTB. Moreover, the Ks values of the 13 PCGs were all greater than the Ka values, and the Ka/Ks ratio was <1, which indicates that the genes are subject to purifying selection.

### tRNA genes, rRNA genes, and the control region

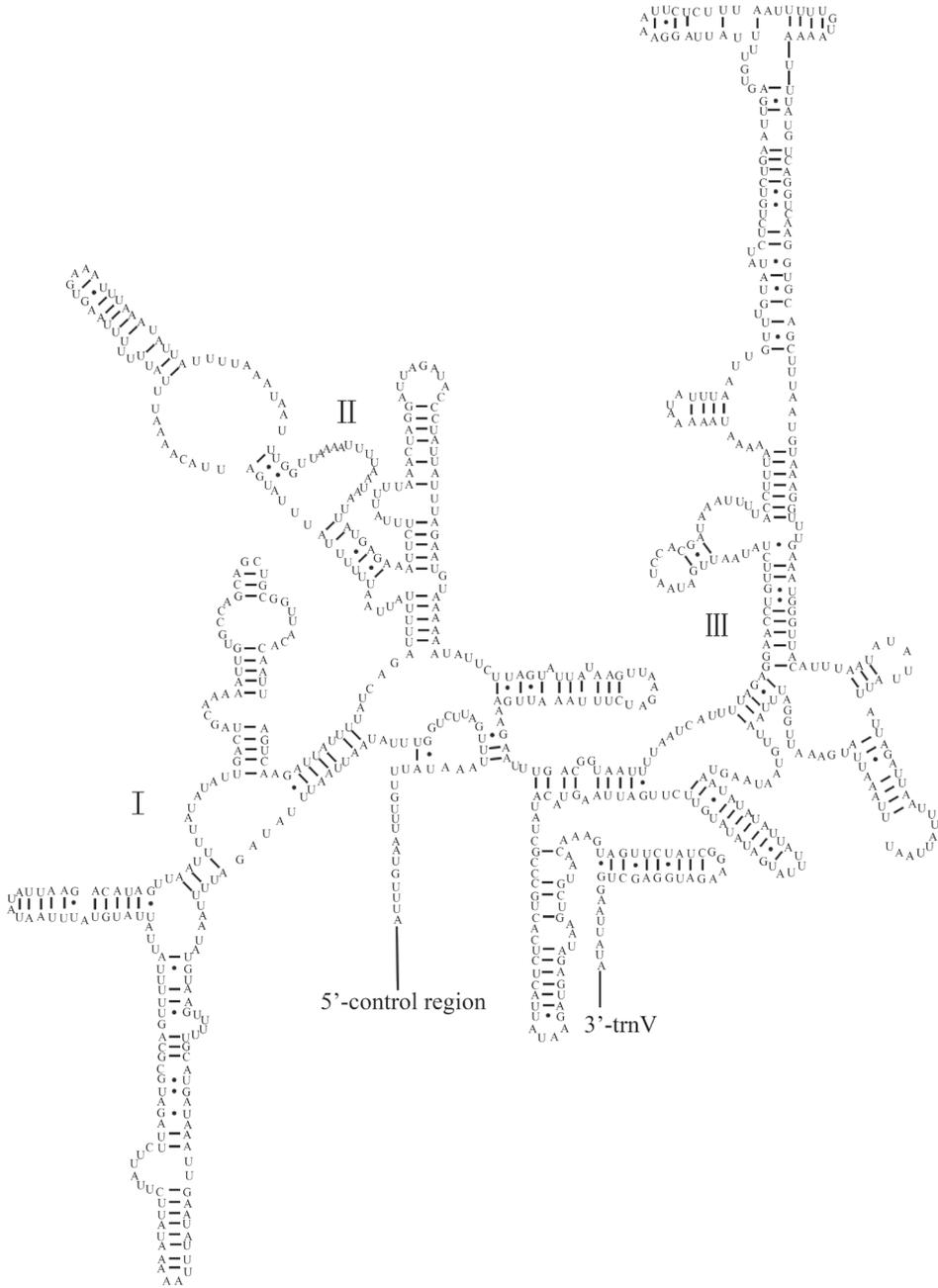
We detected 22 tRNA genes, which can transport all 20 amino acids, in the mitogenome of *P. rufipes*. There are two tRNAs each for leucine and serine: trnL1 (CUN) and trnL2 (UUR), and trnS1 (AGN) and trnS2 (UCN), respectively. The anticodons of trnL are TAA and TAG, and the anticodons of trnS are ACT and TGA. The 22 tRNA genes span 1,481 bp, between 62 and 74 bp in length. Although trnS1 lacks a dihydrouridine arm, the other tRNA genes all have the classic clover leaf secondary structure. In addition to the typical base pairs (A-U and G-C), some wobble G-U pairs appear in these secondary structures, which can form stable chemical bonds between G and U; In addition, atypical pairing of U-U and U-C is also found (Fig. 5).

The two *P. rufipes* rRNA genes (12S rRNA and 16S rRNA) are encoded on the N-strand. The 16S rRNA gene is located between trnL1 (CUN) and trnV, which is



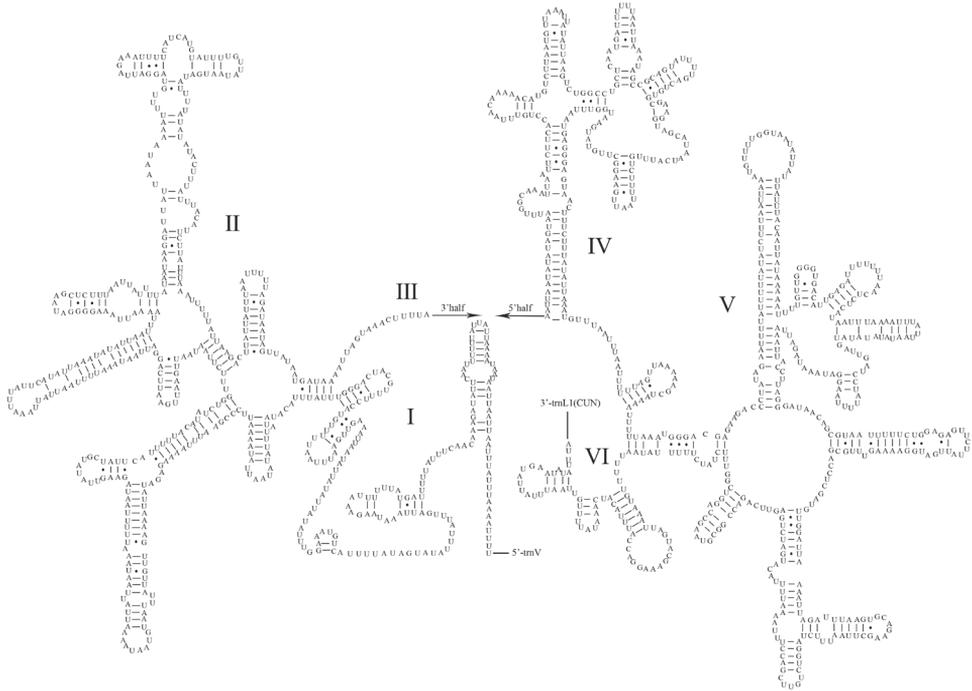
**Figure 5.** Predicted secondary structure of tRNA genes in the *Pentatoma rufipes* mitogenome.

1,277 bp in length, and there is no gene overlap between 16S rRNA and the two tRNA genes. The 12S rRNA gene (821 bp) is located between trnV and the control region, similar to the published pentatomid mitogenomes. The base content of the rRNA genes is in the order of T (44.2%) > A (35.6%) > G (12.6%) > C (7.6%). The AT-skews are negative, and the GC-skews are positive. The complete secondary structures of the 12S rRNA and 16S rRNA genes are shown in Figures 6, 7, respectively.



**Figure 6.** Predicted secondary structure of the 12S rRNA in the *Pentatoma rufipes* mitogenome.

The control region of the mitogenome of *P. rufipes* is located between the 12S rRNA gene and *trnI*. The control region is 1,180 bp long, making it the longest noncoding region in the mitogenome, and has an A + T content of 78.7%. The AT-



**Figure 7.** Predicted secondary structure of the 16S rRNA in the *Pentatoma rufipes* mitogenome.

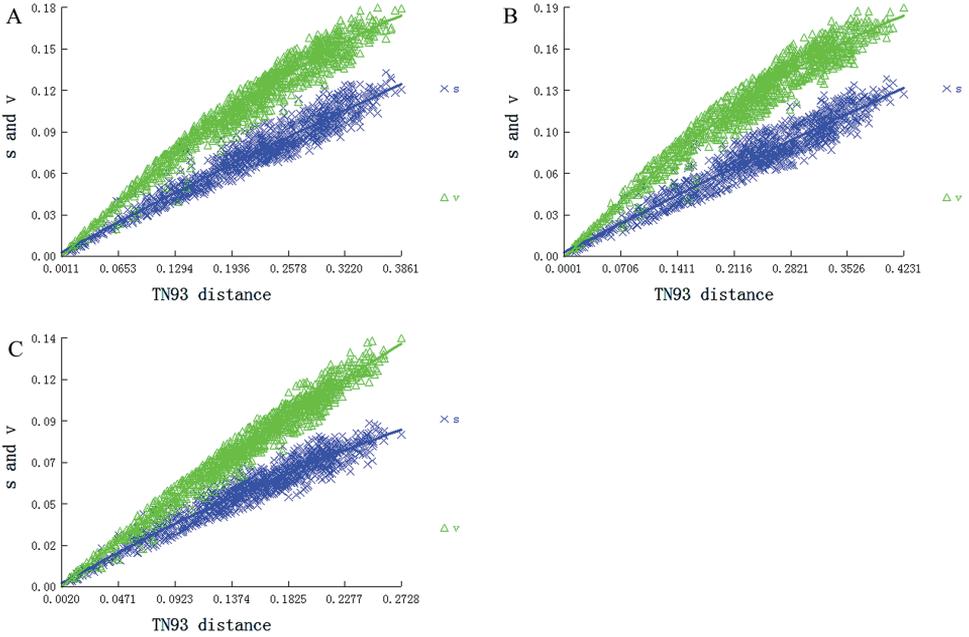
skew and GC-skew in the control area are  $-0.03$  and  $-0.28$ , respectively, indicating that the content of T is higher than that of A and the content of C is higher than that of G.

### Saturation test

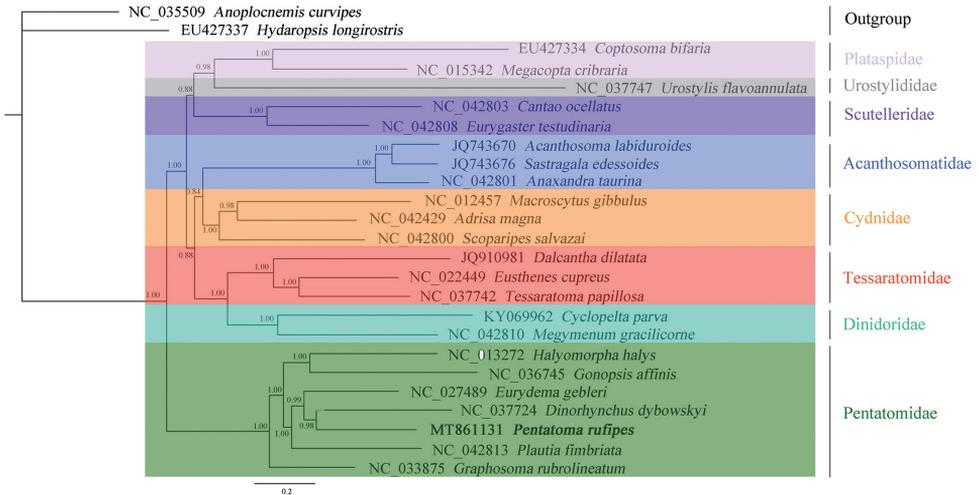
To eliminate the negative effect of the substitution saturation in the phylogenetic analysis, saturation tests on the three data sets were conducted. Nucleotide sequence substitution saturation is usually determined by analyzing the relationship between the transition and transversion values against the corresponding corrected genetic distance. In all tests, the Xia saturation index (Iss) was below the critical values for a symmetric (Iss.cSym) and asymmetric (Iss.cAsym) topology (Fig. 8). The values for base transition and transversion were linearly associated with the corrected genetic distance, indicating that the nucleotide sequences of these three datasets were not saturated, making them suitable for constructing phylogenetic trees.

### Phylogenetic analyses

We reconstructed the phylogenetic trees of eight families in Pentatomoidea from three datasets (PCGRNA, PCG, and PCG12) using Bayesian inference method. The

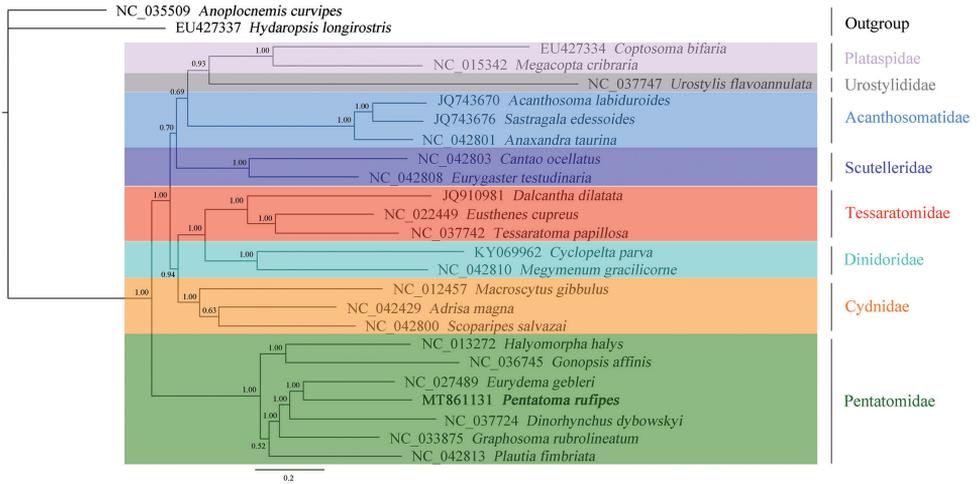


**Figure 8.** Substitution patterns of PCGRNA, PCG and PCG12 matrices. The graphs represent the increase in TN93 distance **A** PCGRNA saturation plot **B** PCG saturation plot **C** PCG12 saturation plot.

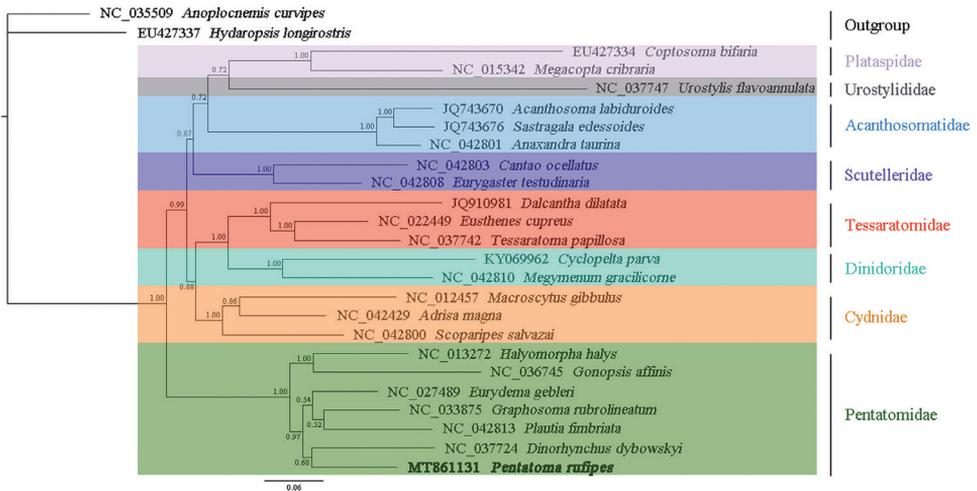


**Figure 9.** Phylogenetic tree inferred from PCGRNA constructed using BI analysis. The number on the branches indicates Bayesian posterior probabilities.

topological structures of the trees were similar, especially PCG and PCG12 showed similar family-level relationships (Figs 9–11). Among the three trees, the Bayesian posterior probability value of the phylogenetic tree based on the PCGRNA data-



**Figure 10.** Phylogenetic tree inferred from PCG constructed using BI analysis. The number on the branches indicates Bayesian posterior probabilities.



**Figure 11.** Phylogenetic tree inferred from PCG12 constructed using BI analysis. The number on the branches indicates Bayesian posterior probabilities.

set was the highest. Phylogenetic analysis based on PCGRNA data showed that *P. rufipes* and *Dinorhynchus dybowskyi* Jakovlev were closely related, these two species formed sister groups with *E. gebleri*, and *P. rufipes* and *Graphosoma rubrolineatum* (Westwood) had the farthest relationship. However, the results in the phylogenetic analysis based on PCG data were somewhat different from the above. In this analysis, *P. rufipes* and *E. gebleri* were the most closely related species, and they were sister groups with *D. dybowskyi*.

## Discussion and conclusions

In this study, we sequenced the complete mitogenome of *P. rufipes* using NGS technology, revealing a mitogenome that is 15,887-bp-long containing 37 genes. The order of the 37 genes is consistent with other published mitogenome of Hemiptera (Hua et al. 2009; Zhang et al. 2018; Zhao et al. 2019). There are three obvious overlapping regions in mitochondrial genome of *P. rufipes*. The longest overlap located between *trnW* and *trnC*, which is 8 bp in length, and the overlap bases are AAGCTTTA. This overlap also showed in most species of Pentatomidae (Yuan et al. 2015a and Zhao et al. 2019). The other two pairs of genes, namely ATP8/ATP6 and ND4/ND4L, overlap by 7 bp, and both overlap bases are ATGATAA, which is consistent with other hemipteran insects (Zhang et al. 2019; Zhao et al. 2020). The longest spacer region falls between *trnS2* and ND1, which is consistent with the findings of other studies (Hua et al. 2008; Zhao et al. 2019). The difference of mitogenome size between *P. rufipes* and other species of Hemiptera due to the length difference of the noncoding region.

The composition of the four bases in the *P. rufipes* mitogenome suggested highly unbalanced (A>T>C>G). The nucleotide composition shows an obvious AT preference, and the entire genome shows AT-skew and CG-skew. The above characteristics of mitogenome base composition of *P. rufipes* are ubiquitous to all sequenced species of Pentatomidae. The preference of bases composition is generally considered to be caused by asymmetric mutation and selection pressure of the four bases (Brown et al. 2005). Consistent with most species of Hemiptera, the PCGs of this species use the common triplet codon ATN as the start codon, TAA and a single T as the stop codon (Hua et al. 2008; Zhao et al. 2019).

The secondary structures of tRNAs for *P. rufipes* is conserved and *trnS1* lacks DHU arm, these features meet the character of metazoan mitochondrial genomes (Wolstenholme 1992). In addition to the typical Watson-Crick pairing (G-C and A-U), there are also some typical pairings such as U-G, U-C and U-U. Some scholars have proposed that those tRNAs with non-Watson-Crick matches can be transformed into fully functional proteins through post-transcriptional mechanisms (Chao et al. 2008; Pons et al. 2014). The rRNA secondary structure of this species is also conserved. The 12S rRNA sequence includes three domains and the 16S rRNA sequence includes six domains (domain III is absent), which is similar to pentatomoid insects.

The phylogenetic result suggested that there are some different topology compared to other studies, but we infer that the possible reasons are as follows: first, the number and taxon of samples selected are different. In this study, the phylogenetic relationship between *Pentatoma* and *Plautia* was relatively close, and they were far from *Graphosoma*. However, when the phylogenetic tree was constructed with *Pentatoma semiannulata*, the relationship between *Pentatoma* and *Graphosoma* was closer (Wang et al. 2021). Second, the selection of outgroup also affects the topological structure of phylogenetic tree. Comparing our results with Zhao et al. (2017) and Liu et al. (2019), because of the three studies choose different species as the outgroup, we got different phylogenies. Third, different molecular markers also might affect phylogenetic relationships. *Grazia*

et al. (2008) supported the monophyly of Pentatomoidea and most of the included families based on morphological characters and molecular markers (16S rRNA, 18S rRNA, 28S rRNA, and COI). Lis et al. (2012) constructed similar phylogenetic trees to our study using 12S and 16S rDNA datasets. Tian et al. (2011) (based on Hox genes), Liu et al. (2019) (based on PCGRNA and PCG12RNA) and Li et al. (2005) (based on 18S rDNA and COX1 sequence) also put forward their own opinions on the phylogenetic relationship of the superfamily. Our three topologies revealed that the Bayesian posterior probability of the tree based on PCGRNA sequences was significantly higher than that of the trees based on the PCG data, indicating that inclusion of rRNA and rRNA genes improves the accuracy of the analysis, which is consistent with the findings of the study conducted by Cameron et al. (2007, 2009).

In summary, the mitogenome of *P. rufipes* has typical sequence structures, and the gene content, nucleotide composition, codon usage, RNA structures, and rates of PCGs evolution are similar to those of other published pentatomid genomes. The mitochondrial genome of *P. rufipes* reveals the phylogenetic location of *Pentatoma*, indicating that the mitogenome can be used to reveal phylogenetic relationships among different taxonomic levels of insects. However, more insect mitogenomes should be sequenced, which would provide more insight into the phylogenetic relationships of species from different taxa.

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# An updated inventory of sea slugs from Koh Tao, Thailand, with notes on their ecology and a dramatic biodiversity increase for Thai waters

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## Abstract

Improved access to field survey infrastructure throughout South-East Asia has allowed for a greater intensity of biodiversity surveys than ever before. The rocky bottoms and coral reef habitats across the region have been shown to support some of the highest sea slug biodiversity on the planet, with ever increasing records. During the past ten years, intensive SCUBA surveys have been carried out at Koh Tao, in the Gulf of Thailand, which have yielded remarkable findings in sea slug biology and ecology. In this work a brief history of sea slug biodiversity research from Thailand is covered and a complete inventory of sea slugs from Koh Tao, Gulf of Thailand is provided. This inventory is based on surveys from 2012 to 2020, with previously unreported findings since 2016. Habitat specificity and species-specific ecology are reported where available with a focused comparison of coral reef habitats and deeper soft-sediment habitats. The findings contribute 90 new species records for Thai waters (92 for the Gulf of Thailand) and report a remarkable consistency in the proportional diversity found to be exclusive to one habitat type or another. Additionally, taxonomic remarks are provided for species documented from Koh Tao that have not been discussed in past literature from Thailand, and a summary of previous records in the Indo-West Pacific is given.

**Keywords**

Biodiversity exploration, coral reefs, Gulf of Thailand, Heterobranchia, soft sediment habitats

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## Introduction

Contemporary sea slug research is largely dominated by investigations into biochemistry, taxonomy, and systematics of the vast diversity of species currently known. Broader aspects remain largely understudied such as development, trophic ecology, and biogeography. Recent years have seen a dramatic increase in the abundance of biodiversity inventories, particularly from regions where much of this work had been sparse before. The importance of documenting local and regional species ranges and diversity is often overlooked despite such studies contributing to our understanding of large-scale environmental issues such as increasing ocean temperatures (Nimbs et al. 2016; Goddard et al. 2018; Ekimova et al. 2019). The problem of invasive species too relies heavily on understanding native and non-native species ranges (Zenetos et al. 2010; Nimbs and Smith 2018). It is thus vital that efforts be made to increase localised biodiversity monitoring, particularly at a time where the rate of change in terrestrial and marine environments is unprecedented and may drive significant biodiversity change and loss (Cowie et al. 2017). The documentation and understanding of baselines in localised species diversity allow for more accurate understanding of biodiversity change both spatially and across time (Nimbs and Smith 2018).

Among the earliest records of sea slugs from Thailand were provided by Bergh (1902) via the ‘Danish Expedition to Siam 1899–1900’ in which he provided records of 22 species (1 Sacoglossa, 3 Cephalaspidea, 4 Aplysiida, and 14 Nudibranchia), all from the Gulf of Thailand. Few additional records were made over the next century, notable inclusions being those of Jensen (1989, 1992), Brunckhorst (1993), and Swennen (1997). These were summarised with more records added in the first review of sea slugs from Thailand by Jensen (1998) and later numerous additional records were provided by Swennen et al. (2001). Thus, in the century since Bergh’s first documentation, the documented diversity in Thai waters reached 81 species, with 46 being recorded within the Gulf of Thailand. However, numerous species documented by Swennen et al. (2001) were only known from shells or remnants and therefore little ecological information could be gained. The waters of Thailand are extremely well suited for comparative investigations between the Indian Ocean and Western Pacific biodiversity and ecology. The Gulf of Thailand has, however, been consistently reported to host a lower diversity of marine life (i.e., Putchakarn and Sonchaeng 2004; Chanmethakul et al. 2010; Wallace et al. 2012), and is therefore often subject to less intensive sampling efforts and in fewer sampling sites. This trend extends to sea slugs with the most extensive review of nudibranch taxa in Thailand being conducted by Chavanich et al. (2013). Their work increased the known biodiversity and biogeography of sea slugs within Thai waters and documented a far greater diversity of taxa on the Andaman coast than the Gulf.

A dedicated survey effort was carried at the island of Koh Tao in the Gulf of Thailand which combined citizen science efforts with in-situ survey techniques and resulted in a dramatic increase in the documented diversity for the Gulf (Mehrotra and Scott 2016). Much of this increase was attributed to previously unexplored soft sediment habitats beyond the slope of fringing coral reefs, which appeared to host a high diversity of species that were not seen in shallower habitats nearer to coral reefs. Subsequent surveys in these habitats revealed a number of novel species descriptions and ecological features that had hitherto been overlooked (Mehrotra et al. 2017, 2019, 2020b). In the present work we summarise the findings of dedicated surveys subsequent to these studies and document a further expansion in sea slug biodiversity in Thai waters. In doing so and by providing a full inventory with known ecology of all species recorded at Koh Tao, we aim to provide a comprehensive baseline on the diversity and ecology of sea slugs in the region.

## Materials and methods

### Surveys and sampling

Benthic surveys were carried out using SCUBA at Koh Tao, Thailand, between January 2016 and February 2020. Roving-diver surveys were performed over both coral reef and soft sediment habitats. Belt transect surveys were also executed across both habitats following the Ecological Monitoring Protocol according to Scott (2012). The majority of surveys were done during the daytime, with a few night-time surveys achieved sporadically throughout the period. Survey intensity ranged from two to 16 people per survey and were carried out through most of the year. During the monsoon season (October–January), survey intensity was reduced to zero surveys per month in some months but were usually between ten to 20 surveys per month throughout the rest of the year. Surveys were carried out throughout the island coast and surrounding pinnacles (Fig. 1). Approximate coordinates for each site are provided in Table 1. As part of these documented surveys, approximately 9200 individual sea slug sightings were recorded across all habitats. Surveys were carried out in equal measure on the coral reef (dominated by scleractinian hard coral substrate) and soft sediment areas.

The soft sediment habitats, located outside coral reefs, had a surface substrate composition of > 90% sand or silt particles. These are typically large areas lacking natural solid substrates and are therefore deficient in rugosity and stability over longer periods (discussed below). Areas of sandy substrate within or in close proximity to coral-dominated areas were included as coral reef (Fig. 2). In the coral reef regions, the authors surveyed in particular among coral rubble, aforementioned sandy patches, and the underside of dead Fungiidae (Anthozoa: Hexacorallia: Scleractinia) corals. Previous surveys (Mehrotra and Scott 2016) had preliminarily suggested that closer examination of these areas could yield a host of cryptic taxa. Soft sediment areas with close proximity

**Table 1.** Surveyed sites with location codes given in each species after specimen size.

Location	Code	Coordinates
Leuk Bay	LB	10°4'11.65"N, 99°50'34.42"E
Suan Olan Artificial Reef	SO	10°4'6.70"N, 99°50'26.29"E
Coral-Aid Artificial Reef	CA	10°4'20.96"N, 99°50'31.84"E
Shark Island	SI	10°3'41.20"N, 99°50'40.54"E
Sai Daeng	SD	10°3'49.43"N, 99°50'23.80"E
Shark Bay	SB	10°3'39.75"N, 99°50'4.43"E
Chalok Bay	CB	10°3'44.77"N, 99°49'30.35"E
Tao Tong	TT	10°3'58.13"N, 99°49'4.76"E
Sai Nuan and Three Rocks	SN	10°4'45.02"N, 99°48'45.23"E
Mae Haad	MH	10°5'22.53"N, 99°49'14.07"E
Sairee Beach	SRB	10°6'0.99"N, 99°49'15.89"E
Hin Pee Wee	HPW	10°6'19.94"N, 99°48'47.73"E
Sattakut Wreck	SW	10°6'16.97"N, 99°48'47.52"E
White Rock	WR	10°6'27.94"N, 99°48'48.98"E
Hin Fai Artificial Reef	HF	10°6'43.42"N, 99°49'7.18"E
Twins	TW	10°7'1.93"N, 99°48'44.26"E
Green Rock	GR	10°7'31.24"N, 99°48'49.57"E
Red Rock	RR	10°7'19.92"N, 99°48'55.31"E
Mango Bay	MB	10°7'22.52"N, 99°50'5.06"E
Hin Wong Pinnacle	HWP	10°6'47.51"N, 99°51'1.95"E
Hin Wong Bay	HWB	10°6'12.30"N, 99°50'58.63"E
Mao Bay North	AMN	10°5'51.85"N, 99°51'7.69"E
Mao Bay	AM	10°5'32.95"N, 99°51'9.29"E
Laem Thien	LT	10°5'19.13"N, 99°51'17.64"E
Tanote Bay	TB	10°5'1.47"N, 99°50'57.50"E
King Kong Rocks	KKR	10°4'30.25"N, 99°50'46.46"E
Chumphon Pinnacle	CP	10°10'20.52"N, 99°46'44.49"E
Southwest Pinnacle	SWP	9°59'56.22"N, 99°46'44.28"E
Sail Rock	SR	9°56'42.47"N, 99°59'26.46"E

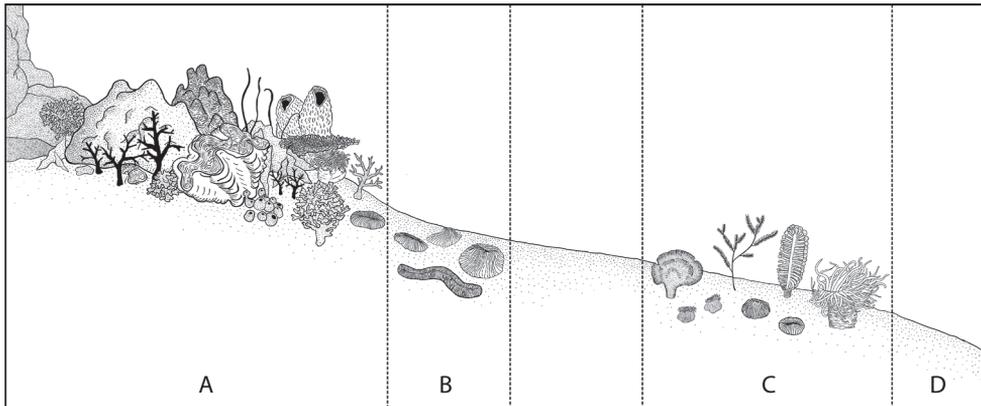
to coral reef habitats, and those with a substrate composition of > 10% hard substrate (particle sizes or corals > ca. 5 cm), were considered as coral reef or reef edge for the surveys and were assessed visually. Thus, there was always clear separation between habitats considered to be coral reef and the deeper soft sediment habitats (referred to here simply as soft sediments). Indicators for soft sediment habitats based on our definitions included organisms that have already been found to grow exclusively in these areas such as sea pens, specific macroalgal species, and specific free-living Scleractinia among others (Mehrotra et al. 2017, 2019).

For each documented species, a small number of specimens was examined closely for taxonomic purposes, with the vast majority of subsequent specimens recorded being noted for their ecology or simply their presence. Detailed specimen examination was carried out in-situ where possible or after sampling using high-magnification underwater photography. Ex-situ examination was carried externally on live specimens which were collected by hand and subsequently returned to their original habitats. All living specimens studied are here documented as 'material examined'. Specimens were externally identified by the authors aided by in-situ photographs based on relevant literature and contrasted with known species prevalence in Thai waters (see Table 2).



**Figure 1.** Map of Koh Tao showing surveyed locations in reference to material examined. The inset of the Gulf of Thailand shows the location of Koh Tao.

Additionally, taxon validity was confirmed with the most recent literature and assisted in part with the World Register of Marine Species (WoRMS 2021) and the references contained within.



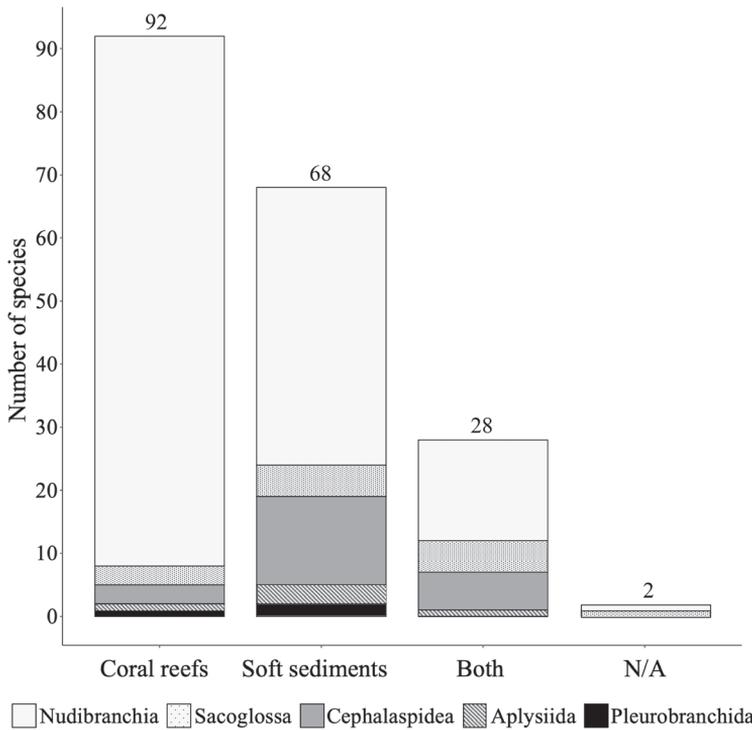
**Figure 2.** Schematic outline of benthic zones classified in the surveys conducted at Koh Tao **A** fringing reef slope, usually near-shore **B** reef edge as determined by drastic reduction in reef-building scleractinian abundance, leading to zone of no stable substrate nor any Scleractinia **C** soft sediment habitats characterised by sand/silt dominated substrates and colonised by organisms absent/extremely rare in zones **A** and **B**. **D** Deepening of soft sediment slope resulting in a drastic reduction but not absence of soft-sediment colonisers. Illustrated by Pau Urgell Plaza.

**Table 2.** List of published literature between 1989–2020 in which sea slug diversity and distribution records in Thai waters are contributed.

References	Gulf of Thailand diversity	Total Thailand diversity
Jensen 1989	19	20
Jensen 1992	19	24
Brunckhorst 1993	19	38
Gosliner and Johnson 1994	20	39
Jensen 1998; Swennen 1997	28	63
Swennen 2001; Swennen et al. 2001	46	81
Jensen 2007; Swennen 2007; Robba et al. 2007	49	88
Swennen and Buatip 2009	49	88
Nabhitabhata 2009	50	100
Swennen 2011	51	101
Swennen and Buatip 2012	52	102
Chavanich et al. 2013	111	203
Jensen et al. 2014a	111	204
Mehrotra and Scott 2016	154	239
Martynov et al. 2019; Korshunova et al. 2019	156	241
Mehrotra et al. 2020a, b; Wang et al. 2020	160	245
Present study	256	336

## Results

In total, 191 species of heterobranch sea slugs have been documented from Koh Tao to date across the orders Sacoglossa (14 species), Cephalaspidea (23 species), Aplysiida (5 species), Pleurobranchida (3 species), and Nudibranchia (146 species). These results



**Figure 3.** Habitat specificity of the major sea slug groups at Koh Tao. Number of species exclusively found at each habitat type at Koh Tao, compared with the number of species recorded from both habitat types. Two species without a confirmed benthic habitat type were recorded as N/A.

more than double the known taxa from Koh Tao (new records for Koh Tao identified below by an asterisk \*) and contribute a further 90 first records for Thai waters (96 for the Gulf of Thailand) from the island (not including the 32 species first documented in Mehrotra and Scott 2016). Approximately half of all recorded species ( $N = 92$ ) were found exclusively within coral reef habitats, with 68 species (36%) being exclusively recorded from the soft sediment habitats and 28 species recorded in both habitats. Two species could not be attributed to a particular benthic habitat type (see remarks for *Limapontiidae* sp. and *Scyllaea fulva*). A large number of species were found exclusively or in far greater abundance under the skeletons of dead Fungiidae corals (see discussion).

## Systematics

### Class Gastropoda Cuvier, 1795

#### Subclass Heterobranchia Burmeister, 1837

#### Superorder Panpulmonata Jörger, Stöger, Kano, Fukuda, Knebelberger & Schrödl, 2010

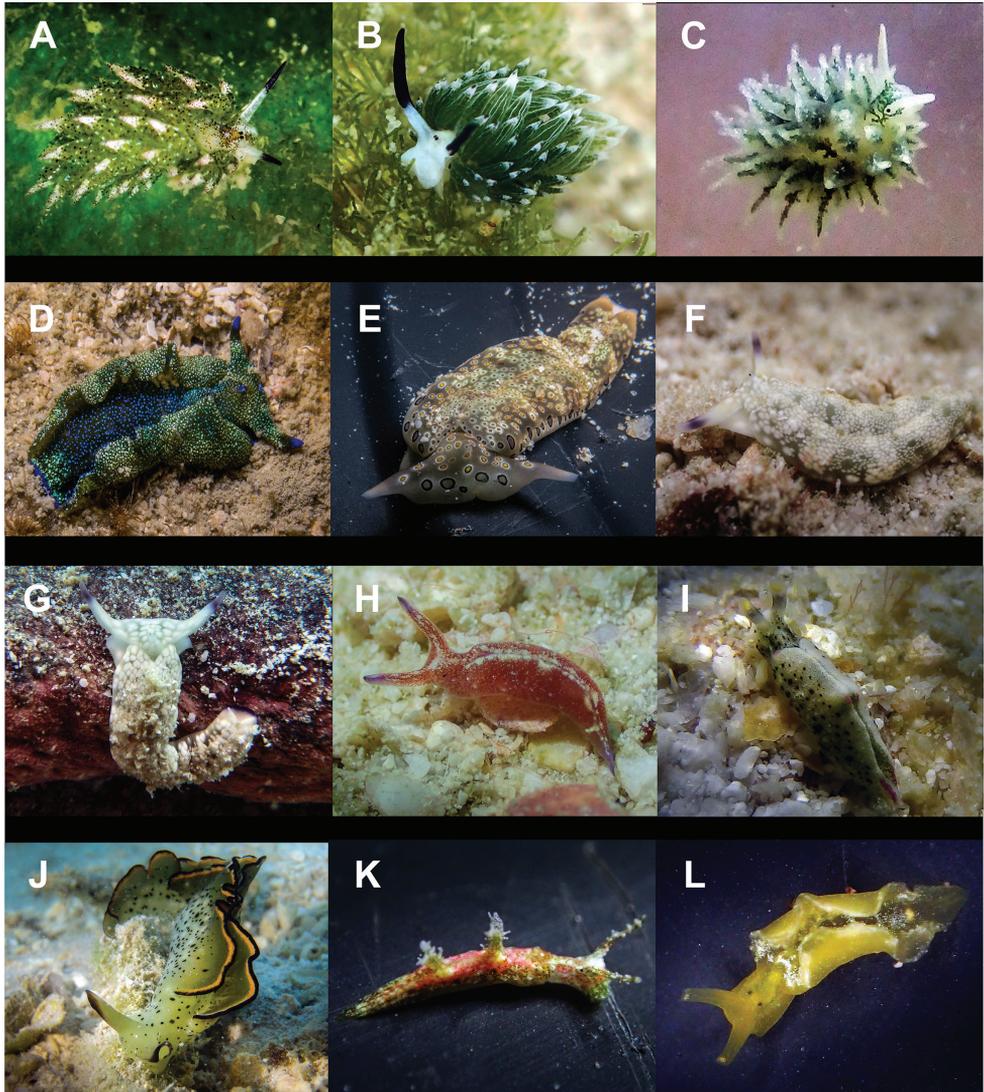
#### Order Sacoglossa Ihering, 1876

## Family Costasiellidae Clarke, 1984

Genus *Costasiella* Pruvot-Fol, 1951*Costasiella* cf. *kuroshimae* Ichikawa, 1993

## Figure 4A

**Material examined.** Two specimens 3–6 mm, LB; two specimens 4–6 mm, SN.



**Figure 4.** **A** *Costasiella* cf. *kuroshimae* 6 mm **B** *Costasiella usagi* 6 mm **C** Limapontiidae sp. 3 mm **D** *Plakobranchus noctistellatus* 21 mm (photograph by Pau Urgell Plaza) **E** *Plakobranchus ocellatus* 32 mm **F** *Plakobranchus papua* 27 mm **G** *Plakobranchus papua* 21 mm on *Holothuria edulis* **H** *Elysia aowthai* 12 mm **I** *Elysia asbecki* 15 mm **J** *Elysia* cf. *marginata* 70 mm **K** *Elysia mercieri* 12 mm **L** *Elysia obtusa* 9 mm.

**Ecology.** In soft sediment habitats, beyond the coral reef where it feeds predominantly on *Avrainvillea longicaulis* (Kützing) G. Murray & Boodle, 1889 and less commonly on *Vaucheria* sp. Depth 10–18 m.

**Distribution.** *Costasiella kuroshimae* is currently known from the Indo-Pacific including the Red Sea (Yonow 2015), Singapore (Jensen 2009), Indonesia (Eisenbarth et al. 2018), Japan (Ichikawa 1993), Guam (Jensen et al. 2014b), Madagascar, Tanzania, Malaysia, Papua New Guinea, Palau, and Australia (Gosliner et al. 2008). Known from the Gulf waters of Thailand (Mehrotra and Scott 2016).

**Remarks.** Due to the original description of the species being entirely based on external features, the identity of numerous similar species and the extent of the variability of the species has remained unclear for several years. Molecular work (Jensen et al. 2014b) has shown that specimens identified as *Costasiella kuroshimae* or *C. cf. kuroshimae* actually make up numerous distinct species that currently await description. Research carried out on specimens from Koh Tao (Mehrotra et al. 2019) indicates that this species is palatable to some scleractinian corals and, based on natural observations, may be viable prey for the free-living coral *Heteropsammia cochlea* (Spengler, 1781), in soft sediment habitats.

### *Costasiella usagi* Ichikawa, 1993

Figure 4B

**Material examined.** Three specimens 2–6 mm, LB.

**Ecology.** In soft sediment habitats beyond the coral reef where it feeds predominantly on *Avrainvillea longicaulis* and less commonly on *Vaucheria* sp. An individual of the species has been observed to be naturally captured and ingested by the free-living coral *Heteropsammia cochlea* with subsequent investigations suggesting the species may represent viable prey for the coral in soft sediment habitats (Mehrotra et al. 2019). Depth 10–18 m.

**Distribution.** Across the Indo-Pacific including India (Dixit et al. 2017), Singapore (Jensen 2009), Japan (Ichikawa 1993), Malaysia, the Philippines, Papua New Guinea, Australia, and Guam (Gosliner et al. 2008). Known from the Gulf waters of Thailand (Mehrotra and Scott 2016).

### Family Limapontiidae Gray, 1847

#### \* *Limapontiidae* sp.

Figure 4C

**Material examined.** One specimen 3 mm, location unknown.

**Ecology.** Local ecology is unknown.

**Distribution.** Unknown.

**Remarks.** Similar to *Ercolania translucens* Jensen, 1993 or *Stiliger* sp. 7 in Gosliner et al. (2018) in having cerata with elongated white apices and green pigment on the head not extending to the white rhinophores. The specimen was observed in a holding tank several days after a broad sampling effort of multiple algal species from Koh Tao. Algae were collected from several locations at the south of the island and although they had been checked carefully, the cryptic nature of the species allowed it to be overlooked. The species was recorded only once in April 2015 and has not been recorded since. The internal anatomy of the specimen was not studied and thus it could not be identified to genus level.

**Suborder Plakobranchea Gray, 1840**

**Superfamily Plakobranchoidea Gray, 1840**

**Family Plakobrancheidae Rang, 1829**

**Genus *Plakobrancheus* van Hasselt, 1824**

***Plakobrancheus noctisstellatus* Mehrotra, Caballer, Scott, Arnold, Monchanin & Chavanich, 2020**

Figure 4D

**Material examined.** One specimen 28 mm, SN; two specimens 26–31 mm, TT.

**Ecology.** From deeper soft sediments outside coral reef habitats. Depth 15–25 m.

**Distribution.** Vanuatu, Indonesia, Papua New Guinea (Gosliner et al. 2008, 2015) and the Gulf of Thailand (Mehrotra et al. 2020b).

***Plakobrancheus ocellatus* van Hasselt, 1824**

Figure 4E

**Material examined.** Three specimens 25–32 mm, CB.

**Ecology.** From shallow soft sediments to sandy areas along the reef edge. Rarely in deeper soft sediment habitats beyond the reef edge. Depth 0.5–11 m.

**Distribution.** *Plakobrancheus ocellatus* and *P.* cf. *ocellatus* are currently considered widespread across the Indo-Pacific including Kenya, Zanzibar, the Red Sea, Maldives, Seychelles, Réunion (Yonow 2012), India (Sheeja and Padma Kumar 2014), the Philippines (Christa et al. 2012), Indonesia (Eisenbarth et al. 2018; Yonow and Jensen 2018), Japan (Maeda et al. 2012), Australia, Papua New Guinea (Yonow and Jensen 2018), Guam (Wägele et al. 2011), Vanuatu (Krug et al. 2013), Hawaii (Wade and Sherwood 2016), Tanzania, Madagascar, Malaysia and Palau (Gosliner et al. 2008). Specimens considered as *P. ocellatus* have been previously recorded from the Andaman and Gulf waters of Thailand (Jensen 1992; Nabhitabhata 2009).

**Remarks.** Specimens from Koh Tao were recently reviewed by Mehrotra et al. (2020b).

***Plakobranthus papua* Meyers-Muñoz & van der Velde in Meyers-Muñoz et al., 2016**

Figure 4F, G

**Material examined.** Three specimens 19–30 mm, SN.

**Ecology.** Abundant in shallow soft sediment habitats and among the corals and soft sediments of the reef edge. Uncommon, but present in dense coral reef habitats. Rare in deeper soft sediment habitats outside the coral reef. Has been observed being ingested naturally by the scleractinian coral *Pleuractis paumotensis* (Stutchbury, 1833) but is mostly considered unpalatable by such corals (Mehrotra et al. 2015, 2019). During daytime surveys, a single observation was made of *P. papua* crawling upon the sea cucumber *Holothuria edulis* Lesson, 1830 (Fig. 4G), which may have been considered unremarkable were it not for the findings of Mercier and Hamel (2005). Depth 1–19 m.

**Distribution.** Known only from the Philippines, Malaysia, Indonesia, and Papua New Guinea (Meyers-Muñoz et al. 2016; Yonow and Jensen 2018). Known from Gulf waters of Thailand (Mehrotra et al. 2020b).

**Remarks.** Specimens from Koh Tao were recently reviewed (Mehrotra et al. 2020b).

***Elysia aowthai* Mehrotra, Caballer, Scott, Arnold, Monchanin & Chavanich, 2020**

Figure 4H

**Material examined.** One specimen 14 mm, LB; one specimen 16 mm, TT.

**Ecology.** From deeper soft sediments outside coral reef habitats. Depth 10–24 m.

**Distribution.** Guam, Australia, and the Gulf of Thailand (Mehrotra et al. 2020b).

**Genus *Elysia* Risso, 1818**

***Elysia asbecki* Wägele, Stemmer, Burghardt & Händeler, 2010**

Figure 4I

**Material examined.** One specimen 15 mm, HF; one specimen 23 mm, TW.

**Ecology.** In coral reef habitats throughout the island. Depth 3–18 m.

**Distribution.** Australia, Samoa (Wägele et al. 2010), the Philippines, Indonesia, Papua New Guinea, Japan, Guam, and Hawaii (Gosliner et al. 2008; Wägele et al. 2010). Known from the Gulf waters of Thailand (Mehrotra and Scott 2016).

**\**Elysia* cf. *marginata* (Pease, 1871)**

Figure 4J

**Material examined.** Three specimens 65–82 mm, CB.

**Ecology.** Mostly recorded from specimens inhabiting a shallow, isolated patch of *Halimeda macroloba* Decaisne, 1841 in soft sediment habits, although presumably feeding on other nearby algae. Also observed from shallow coral reef habitats, rarely. Depth 0.5–6 m.

**Distribution.** *Elysia marginata* is at present recorded from the Indo-Pacific including Myanmar (Sanpanich and Duangdee 2019), Vietnam (Martynov and Korshunova 2012), Indonesia (Yonow and Jensen 2018), Australia (Nimbs and Smith 2016), Japan, Guam, French Polynesia, Vanuatu, and Hawaii (Krug et al. 2013). Specimens from South Africa, Madagascar, and Réunion (Gosliner et al. 2008 as *Elysia ornata*) also are likely to correspond to this complex. Known from the Andaman waters of Thailand (Jensen 1992), here representing a first record for the Gulf of Thailand.

**Remarks.** Recent molecular investigations (Krug et al. 2013) have indicated up to four possible clades making up the species *Elysia marginata*, that was separated from its Caribbean counterpart *Elysia ornata* (Swainson, 1840), which was formerly considered circumtropical. Yonow and Jensen (2018) further discuss the challenges in assigning all specimens with the ‘characteristic’ orange and black marginal bands on the parapodia to *E. marginata* as similar species such as *E. faustula* Bergh, 1871 and *E. grandifolia* Kelaart, 1858 were described and illustrated with comparable features. Both aforementioned species differ in ground colour or the presence/absence of denticulation on radular teeth, and both of these features have been shown to be variable within a single species and often a single specimen (Mehrotra et al. 2020b). Therefore, all indications point to a need for a comprehensive analysis integrating morphology, ecology, and molecular data to delineate species in this complex.

**\**Elysia mercieri* (Pruvot-Fol, 1930)**

Figure 4K

**Material examined.** One specimen 12 mm, SO.

**Ecology.** Found upon concrete artificial reefs in soft sediment habitats that formed part of coral restoration efforts. Depth 11–14 m.

**Distribution.** Across the Indo-Pacific including the Red Sea (Yonow 2015), Indonesia (Eisenbarth et al. 2018), Japan (Trowbridge et al. 2011), Mariana Islands (Carlson and Hoff 2003), Malaysia, Papua New Guinea, New Caledonia, and Guam (Gosliner et al. 2008). Here representing a first record for Thai waters.

**Remarks.** *Elysia mercieri* is known to be predated upon by the nudibranch *Gymnodoris okinawae* Baba, 1936 (Nakano and Hirose 2011).

**\**Elysia obtusa* Baba, 1938**

Figure 4L

**Material examined.** One specimen 9 mm, CB; one specimen 12 mm, TW.

**Ecology.** Among rubble, particularly found underneath the skeletons of dead Fungiidae corals, in shallow coral reef habitats. No association with prey was observed but is known to be part of a group of species feeding on the alga *Bryopsis* (Krug et al. 2016). Depth 3–8 m.

**Distribution.** Across the Indo-Pacific including India (Apte et al. 2010), Taiwan (Huang et al. 2016), Hong Kong (Jensen 2003), Japan (Trowbridge et al. 2011), Australia (Nimbs and Smith 2016), Samoa (Wägele et al. 2010), Madagascar, Malaysia, Papua New Guinea, the Philippines, Korea, Guam, Marshall Islands, and Hawaii (Gosliner et al. 2008 as *Elysia flava* Verrill, 1901). Here representing a first record for Thai waters.

**Remarks.** Both individuals recorded were found adhering to the underside of dead fungiid skeletons. The species is locally rare and here included as a first record for the Gulf of Thailand and Thai waters in general.

**\**Elysia pusilla* (Bergh, 1871)**

Figure 6A

**Material examined.** Three specimens 3–7 mm, CB; one specimen 4 mm, SRB.

**Ecology.** Feeds on *Halimeda macroloba*, on which it is highly cryptic. Host and prey found in soft sediment habitats near coral reefs between 0.5 and 9 m depth. Multiple individuals may be found feeding on a single prey item. Populations of the host algae *H. macroloba* have been found at only two locations at the island, 6–9 m depth at SRB and a small intertidal patch at site CB at 0.5–1.5 m. The abundance of *E. pusilla* has been found to be greater at CB than on the larger but less dense population of *H. macroloba* at site SRB.

**Distribution.** Widespread across the Indo-Pacific including the Red Sea (Yonow 2008), Réunion (Bourjon et al. 2018), India (Sreeraj et al. 2012), Singapore (Jensen 2009), Vietnam (Martynov and Korshunova 2012), Indonesia (Eisenbarth et al. 2018), Australia (Nimbs and Smith 2016), Japan, Guam (Vendetti et al. 2012), Mexico (Goddard and Hermosillo 2008), Costa Rica (García-Méndez and Camacho-García 2016), South Africa, Tanzania, Madagascar, New Caledonia, and Hawaii (Gosliner et al. 2008). Known from the Andaman waters of Thailand (Jensen 1992), and here representing a first record for the Gulf of Thailand.

**Remarks.** The status of *Elysia pusilla* and its taxonomic implications for the genus needs closer investigation (Jensen 2009, 2015; Krug et al. 2016). Recent observations carried out by Mehrotra et al. (2019) indicate that *E. pusilla* specimens from Koh Tao are considered palatable to opportunistic scleractinian coral predators and are readily consumed by these reef building corals. However, to date, no instances of natural prey capture of *E. pusilla* by these corals has been documented.

**\**Elysia* cf. *tomentosa* Jensen, 1997**

Figure 6B

**Material examined.** One specimen 37 mm, CB.

**Ecology.** In soft sediment habitats outside the coral reef. Observed feeding on a pinnate form of *Caulerpa racemosa* (Forsskål) J. Agardh, 1873 which is found chiefly in soft sediment habitats beyond the coral reef. A more lenticular/globular form of the algae can be abundant in some shallow, degraded reef habitats; however, specimens from Koh Tao not been observed associated with this variety. Depth 12–20 m.

**Distribution.** At present *Elysia tomentosa* is considered widespread across the Indo-Pacific (but see remarks below) including Iran (Oladi et al. 2018), Madagascar, Malaysia (Gosliner et al. 2008), Australia (Jensen 1997), Réunion, India, Singapore, the Philippines, Indonesia, Japan, New Caledonia, and Hawaii (Jensen 2015). Likely introduced to the Mediterranean alongside the highly invasive *Caulerpa* spp. (Zenetos et al. 2010). Here representing a first record for Thai waters.

**Remarks.** Recent molecular investigations have found that specimens recognised as *Elysia tomentosa* likely correspond to a complex of at least six species (Krug et al. 2013). Discussions about the identity of specimens identifiable by black marginal lines along the parapodia and the similar species *Elysia expansa* (O'Donoghue, 1924) have yet to be resolved (Rudman 2009a; Krug et al. 2013). Additionally, Oladi et al. (2018) recently documented a species in this complex from Iran that matches a sequence of *E. cf. tomentosa* from the Andaman coast of Thailand, by Cornelius Swennen (GenBank accession number KC573755.1); however, no record of this species from the waters of Thailand has been found in the literature to date. Greater sampling efforts from more locations, with an assessment of internal characters, are needed to clarify this complex, including specimens from Koh Tao.

## Genus *Thuridilla* Bergh, 1872

### *Thuridilla cf. gracilis* (Risbec, 1928)

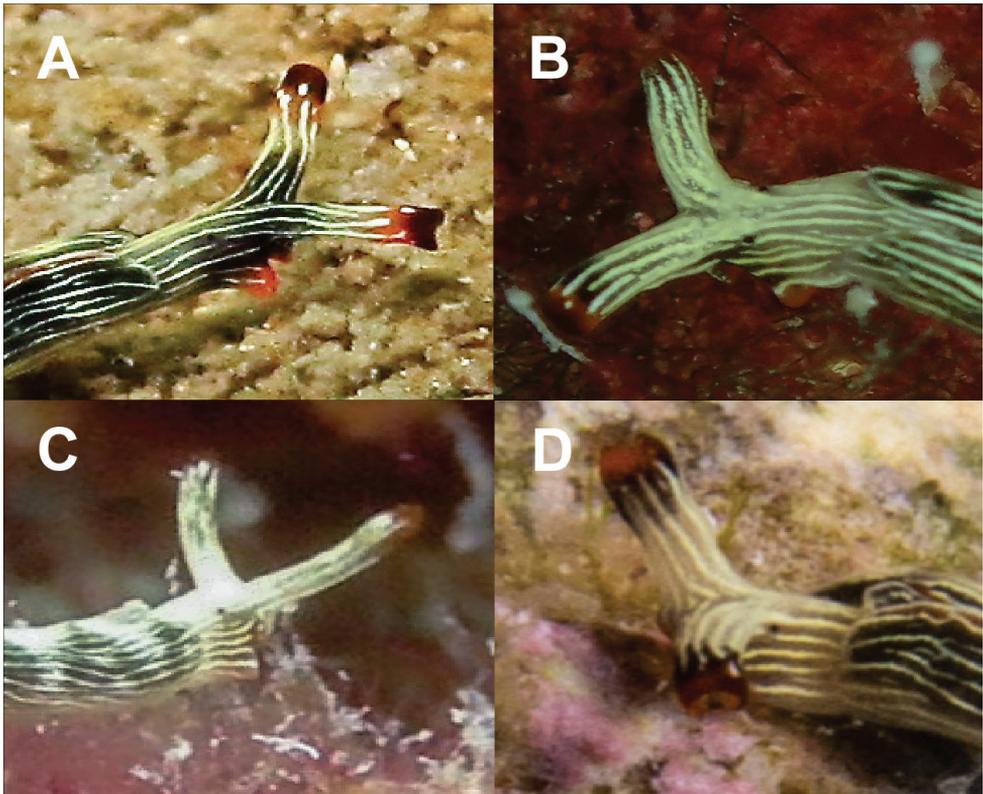
Figure 6C

**Material examined.** 1 specimen 18 mm, HWB; 2 specimens 8–15 mm, LB.

**Ecology.** Found in coral reef habitats throughout the island. Depth 2–25 m.

**Distribution.** *Thuridilla gracilis* sensu lato is known from Maldives, Seychelles (Yonow 2012), India (Apte 2009), Singapore (Jensen 2009), Myanmar (Sanpanich and Duangdee 2019), Indonesia (Yonow and Jensen 2018), Vietnam (Martynov and Korshunova 2012), Taiwan (Huang et al. 2016), Japan (Trowbridge et al. 2011), Australia (Nimbs and Smith 2016), Madagascar, Malaysia, the Philippines, Papua New Guinea, Palau, New Caledonia, Guam, and Fiji (Gosliner et al. 2008). Known from the Andaman and Gulf waters of Thailand (Jensen 1992; Nabhitabhata 2009).

**Remarks.** The taxonomic status of *Thuridilla gracilis* is at present unclear. Recent works (Yonow and Jensen 2018; Papu et al. 2020) have highlighted the significant variability of specimens ascribed to the species and questioned the synonymisation of multiple white-striped species of *Thuridilla* (Gosliner 1995; Rudman 2000b) under the single species *T. gracilis*. Indications suggest that the breadth of specimens currently considered as *T. gracilis* encompass a complex of species (Händeler and Wägele 2007; Yonow and Jensen 2018; Papu et al. 2020) that requires a comprehensive analysis utilising both morphological and



**Figure 5.** Variation in the heads of *Thuridilla* cf. *gracilis* at Koh Tao. Specimens 14 mm (A), 18 mm (B), 9 mm (C), 16 mm (D).

molecular means. Specimens from Koh Tao do not possess any blue markings, instead being closer to the original description and illustration of *T. gracilis* in possessing a thin orange-red marginal band along the parapodia that meets medially and having the white lines often extending to the tips of the rhinophores. Papu et al. (2020) provided photographs highlighting the external variability on the heads of specimens from Bangka, Indonesia suggesting possible diagnostic value. As such, we have emulated this and provided the range of variation visible in the heads of adult specimens from Koh Tao (Fig. 5).

### Order Cephalaspidea P. Fischer, 1883

#### Superfamily Cylichnoidea H. Adams & A. Adams, 1854

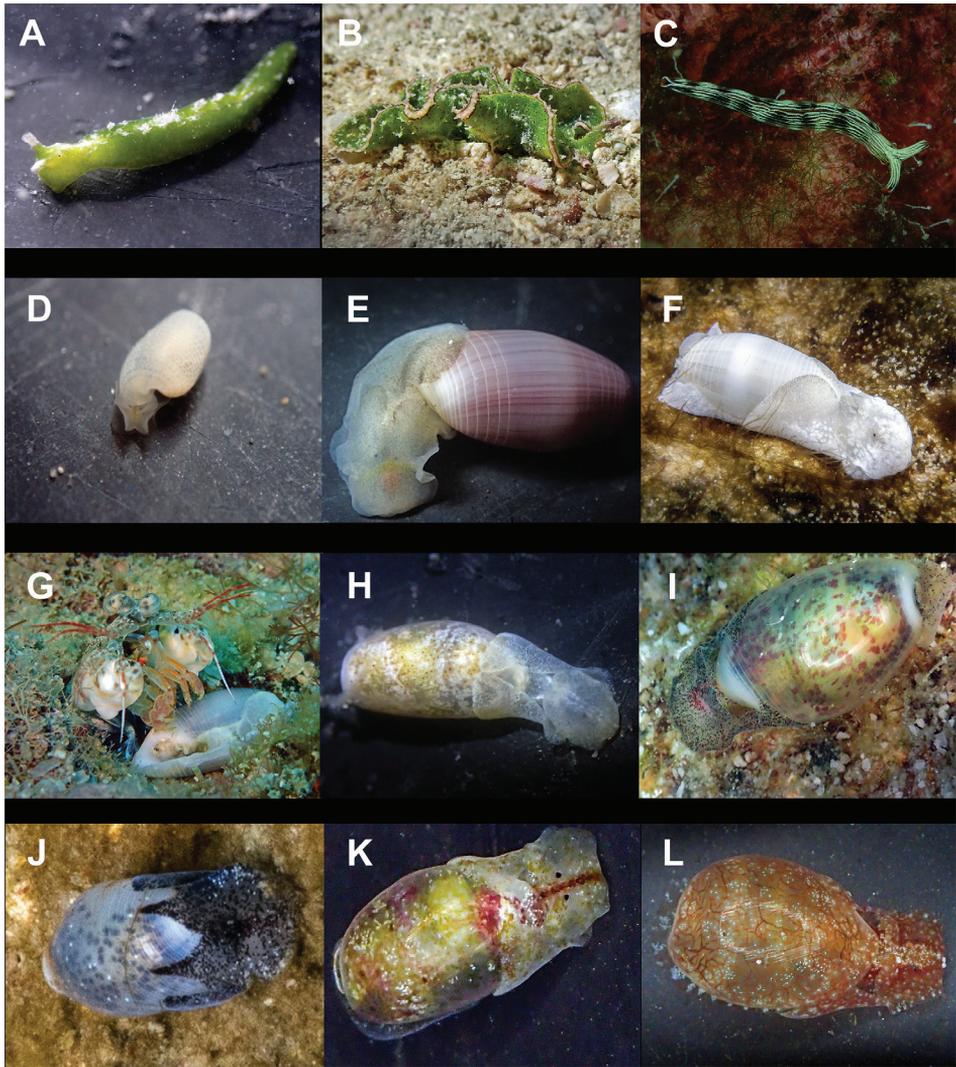
#### Family Colinatyidae Oskars, Bouchet & Malaquias, 2015

#### Genus *Colinatys* Ortea, Moro & Espinosa, 2013

#### \**Colinatys* sp.

Figure 6D

**Material examined.** One specimen 3 mm, CB.



**Figure 6.** **A** *Elysia pusilla* 7 mm **B** *Elysia* cf. *tomentosa* 37 mm **C** *Thuridilla* cf. *gracilis* 18 mm **D** *Colinatys* sp. 3 mm **E** *Aliculastrum cylindricum* 30 mm **F** *Aliculastrum debilis* 28 mm **G** *A. debilis* (shell 12 mm) captured alive and predated by *Haptosquilla* cf. *nefanda* **H** *Roxaniella multistriata* 9 mm **I** *Atys semistriatus* 8 mm **J** *Atys* sp. 11 mm **K** *Diniatys dentifer* 5 mm **L** *Diniatys dubius* 6 mm.

**Ecology.** Endobenthic in sand in coral reef habitats. Depth 3–11 m.

**Distribution.** The genus is currently recognised to be monospecific with *Colinatys alayoi* (Espinosa & Ortea Rato, 2004) known from the Bahamas, Cuba, Florida, and Martinique Island (Romani et al. 2015; Ortea Rato and Buske 2018). Indo-Pacific records are limited to specimens from Hawaii (Oskars et al. 2015) and Japan (SSW 2017) with species identity yet to be confirmed. Here representing a first record of the family from Thai waters.

**Superfamily Haminoeidea Pilsbry, 1895****Family Haminoeidae Pilsbry, 1895****Genus *Aliculastrum* Pilsbry, 1896****\**Aliculastrum cylindricum* (Helbling, 1779)**

Figure 6E

**Material examined.** Two specimens 25–30 mm, LB.

**Ecology.** In soft sediment habitats outside the coral reef where it is found associated with cyanobacterial mats on the benthos. May also be found near the reef edge when cyanobacteria abundances increase, indicating a possible seasonal influence in abundance. Often found together with other Haminoeidae species from Koh Tao, apart from *Atys* sp. It may be a probable prey species for the mantis shrimp *Haptosquilla* cf. *nefanda* (Kemp, 1911) (see ecology of *Aliculastrum debilis* below). Depth 8–18 m.

**Distribution.** Widespread across the Indo-Pacific including Mozambique (Macnae and Kalk 1958), Tanzania, Madagascar, the Philippines, Papua New Guinea, New Caledonia (Gosliner et al. 2008), South Africa, Seychelles, Mauritius, India, Japan, China, Fiji, and Tahiti (Too et al. 2014). Known from the Gulf waters of Thailand (Nabhitabhata 2009).

***Aliculastrum debilis* (Pease, 1860)**

Figure 6F, G

**Material examined.** Two specimens 30 mm, LB; one specimen 28 mm, TB.

**Ecology.** Extremely similar to *A. cylindricum* (see above). Often found together with other Haminoeidae species from Koh Tao, apart from *Atys* sp. As part of the present surveys, observations were made of hunting and capture of specimens of *A. debilis* by the stomatopod *Haptosquilla* cf. *nefanda* (Fig. 6G). Captured animals were taken into burrows made by the crustacean. While active feeding was not observed, it should be noted that shells of *A. debilis*, *A. cylindricum*, and rarely *Atys semistriatus* Pease, 1860 can be found in high abundance around the holes of *H. cf. nefanda* and other mantis shrimps in the soft sediment habitats. These shells are often broken, but not always, and are likely indications of predation by these crustaceans, which are abundant in these habitats. Depth 8–18 m.

**Distribution.** Across the western Pacific including the Philippines, Guam, Tahiti, Fiji, and Hawaii (Too et al. 2014). Known from the Gulf waters of Thailand (Mehrotra and Scott 2016).

**Genus *Roxaniella* Monterosato, 1884****\**Roxaniella multistriata* (Schepman, 1913)**

Figure 6H

**Material examined.** Two specimens 5–9 mm, LB.

**Ecology.** Very similar to those of *Aliculastrum* spp. though more regularly found immersed within/under cyanobacterial mats than on top. Often found together with other Haminoeidae species from Koh Tao, apart from *Atys* sp. Depth 8–18 m.

**Distribution.** Known across the Indo-Pacific including Tanzania, the Philippines, Fiji (Gosliner et al. 2008), Indonesia, Palau, Guam, Tahiti (Too et al. 2014), and Hawaii (Kay 1979). Here representing a first record from Thai waters.

### Genus *Atys* Montfort, 1810

#### \**Atys semistriatus* Pease, 1860

Figure 6I

**Material examined.** Two specimens 8–12 mm, LB.

**Ecology.** Very similar to *R. multistriata*, with which it is often found. A possible prey species for the mantis shrimp *Haptosquilla* cf. *nefanda* (see ecology of *Aliculastrum debilis*). Depth 8–18 m.

**Distribution.** Across the Indo-Pacific including Japan (Kuroda and Habe 1952), Madagascar, Malaysia, the Philippines, Papua New Guinea, Guam, Samoa (Gosliner et al. 2008), Indonesia, New Caledonia, Tahiti, Hawaii (Too et al. 2014), and the Red Sea (Heller and Thompson 1983; Yonow 2008). Here representing a first record for Thai waters.

#### \**Atys* sp.

Figure 6J

**Material examined.** One specimen 11 mm, AMB.

**Ecology.** In soft sediment habitats outside the coral reef. Depth 23 m.

**Distribution.** *Atys* sp. 6 (Gosliner et al. 2018) is currently known from the Philippines, Vanuatu, and Indonesia.

### *Diniatys* Iredale, 1936

#### \**Diniatys dentifer* (A. Adams, 1850)

Figure 6K

**Material examined.** Three individuals 2–5 mm, LB.

**Ecology.** Very similar to the other soft-sediment associated Haminoeidae such as *Aliculastrum* spp., *R. multistriata* etc., which are often found together. Depth 8–18 m.

**Distribution.** *Diniatys dentifer* is known from Madagascar, the Philippines, Japan, Indonesia, Papua New Guinea, Guam, Hawaii, French Polynesia (Too et al. 2014), and the Red Sea (Yonow 2008). Here documented as a first record for Thai waters.

**\**Diniatys dubius* (Schepman, 1913)**

Figure 6L

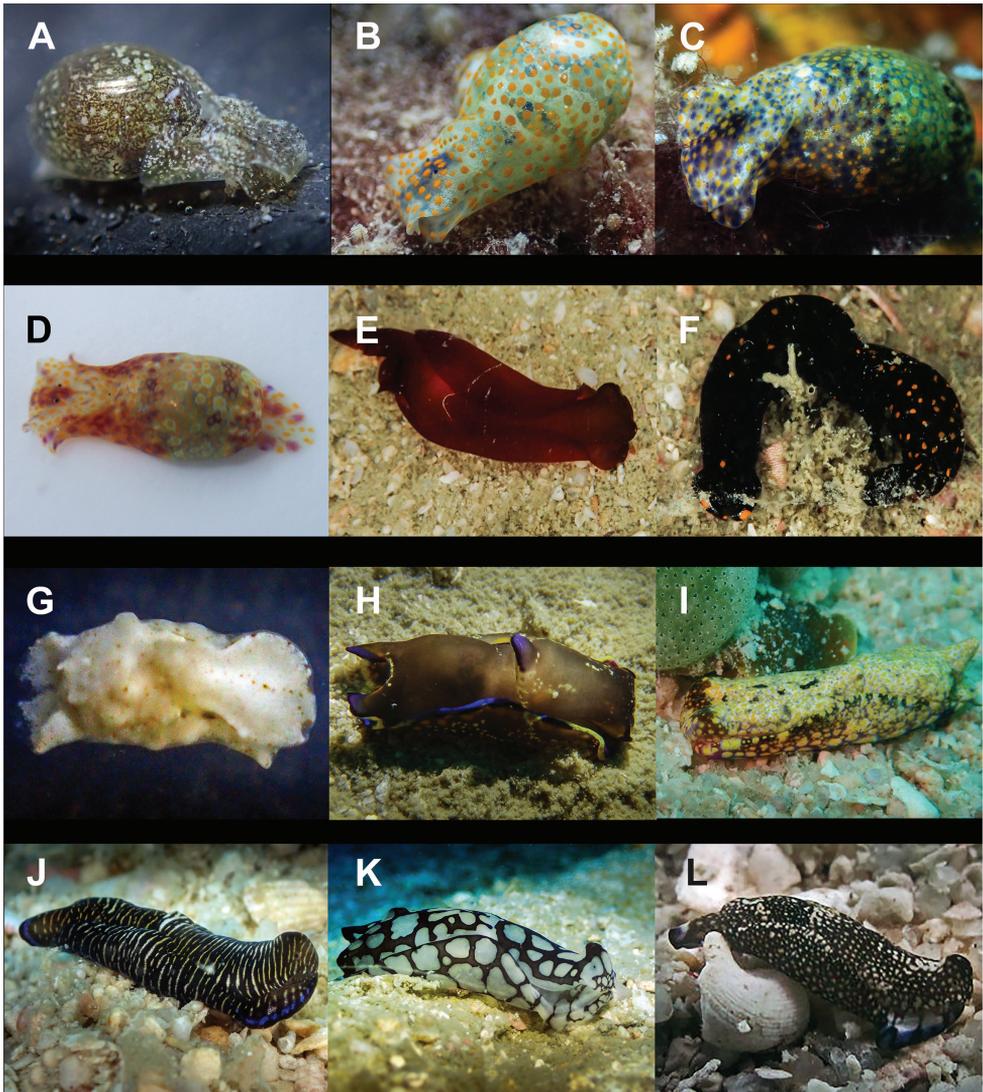
**Material examined.** Three individuals 3–6 mm, LB.**Ecology.** Very similar to *D. dentifer*. Depth 8–18 m.**Distribution.** *Diniatys dubius* is known from the Philippines, Indonesia, Papua New Guinea, Guam, Hawaii (Too et al. 2014), and the Red Sea (Yonow 2008). Here documented as a first record for Thai waters.***Haloa* Pilsbry, 1921****\**Haloa* sp.**

Figure 7A

**Material examined.** Three individuals 2–5 mm, LB.**Ecology.** While rarer than most other soft sediment associated Haminoeidae spp., from Koh Tao, the strong association with cyanobacterial mats is a shared feature across these species. Depth 8–18 m.**Distribution.** Unknown.***Lamprohaminoea* Habe, 1952****\**Lamprohaminoea ovalis* (Pease, 1868)**

Figure 7B, C, D

**Material examined.** Six individuals 9–35 mm, SB; eight individuals 6–21 mm; LB.**Ecology.** White morphs (Fig. 7B) among rubble in shallow coral reef habitats at depths 4–8 m. Purple/red morphs in soft sediment habitats outside the coral reef where it is found strongly associated with mats of cyanobacteria on the benthos. Purple/red morphs (Fig. 7C, D) may also be found near the reef edge when cyanobacteria abundances increase, indicating a possible seasonal influence in abundance. Often found together with other Haminoeidae species from Koh Tao, apart from *Atys* sp. White and purple/red morphs not found together suggesting a fundamental division in local ecology (i.e., diet), potentially contributing to the difference in colouration. Specimens from Koh Tao have been observed to be ingested, and sometimes rejected post-ingestion, by the wrasses *Cheilinus fasciatus* (Bloch, 1791) and *Thalassoma lunare* (Linnaeus, 1758). This method of prey rejection has been suggested as a vector for prey dispersal of sea slugs onto opportunistic predatory scleractinian corals (Mehrotra et al. 2019). Depth 8–18 m.**Distribution.** *Lamprohaminoea ovalis* known from the Red Sea, Oman, Philippines, Vanuatu, Guam, French Polynesia, Hawaii (Oskars and Malaquias 2020), Australia (Nimbs and Smith 2016), Mariana Islands (Carlson and Hoff 2003), Japan (Hori 2017), Marshall Islands (Marcus and Burch 1965), and invasive in the Mediter-



**Figure 7.** **A** *Haloa* sp. 5 mm **B** *Lamprohaminoea ovalis* 18 mm **C** *L. ovalis* 9 mm (photograph by Elouise Haskin) **D** *L. ovalis* 4 mm **E** *Chelidonura* cf. *castanea* 62 mm **F** *Chelidonura punctata* 32 and 34 mm **G** *Niparaya* sp. 4 mm **H** *Philinopsis speciosa* 18 mm **I** '*Philinopsis*' *coronata* 35 mm (photograph by Phannee Mccarthy) **J** *Tubulophilinopsis lineolata* 38 mm **K** *Tubulophilinopsis pilsbryi* 35 mm **L** *Tubulophilinopsis reticulata* 30 mm (photograph by Kirsty Magson).

ranean Sea (Fernández-Vilert et al. 2018). It is here recorded for the first time from Thai waters.

**Remarks.** With the recent comprehensive review of the genus *Lamprohaminoea* (Oskars and Malaquias 2020), specimens from Koh Tao were identified as *L. ovalis*. This identification was based on shell morphology and external colouration, the vari-

ability of both now being well documented. Despite specimens from Koh Tao being from the same species, the different morphs have been found to exhibit distinct ecological characteristics.

**Superfamily Philinoidea Gray, 1850 (1815)**

**Family Aglajidae Pilsbry, 1895 (1847)**

**Genus *Chelidonura* A. Adams, 1850**

**\**Chelidonura* cf. *castanea* Yonow, 1994**

Figure 7E

**Material examined.** Two specimens 62–74 mm, TT.

**Ecology.** In soft sediment habitats outside the coral reef. Depth 22–26 m.

**Distribution.** *Chelidonura castanea* is currently known only from the Maldives (Yonow 1994). Unconfirmed sightings have also been made from Mozambique and Myanmar (iNaturalist 2011; TSS 2020). Here representing a first record for Thai waters (but see below).

**Remarks.** Specimens from Koh Tao differ from those originally described by lacking orange spots across the dorsum, instead having only two tiny orange spots on the anterior portion of the head, on either side of the mouth. Additionally, the body is uniformly deep reddish brown with a thin white line on the upper margin of the cephalic shield. In the larger specimen (74 mm), both orange spots and the white line were markedly less distinct. The presence and absence of yellow/orange spots in such Aglajids has been shown to be an unreliable character for species delimitations (Turner and Wilson 2012). To date, *C. castanea* is only known from the Indian Ocean; however, a distribution from Thailand was recorded, without reference to any source, by Gosliner et al. (2008) but omitted in later versions (Gosliner et al. 2018). Therefore, we hereby provide details of a similar species from the Gulf of Thailand waters as a first record.

**\**Chelidonura punctata* Eliot, 1903**

Figure 7F

**Material examined.** Four specimens 32–39 mm, TT.

**Ecology.** In soft sediment habitats outside the coral reef. Depth 22–26 m.

**Distribution.** *Chelidonura punctata* is currently known from Kenya (Mangubhai 2007), Mozambique (Tibirićá and Malaquias 2016), Zanzibar, Mauritius, the Chagos Islands, the Maldives (Yonow 2012), India (Apte 2009), and Myanmar (Sanpanich and Duangdee 2019). *Chelidonura punctata* has been recorded from the Andaman sea of Thailand (Gosliner et al. 2008; Nabhitabhata 2009) and is here recorded for the first time from the Gulf of Thailand.

**Genus *Niparaya* Zamora-Silva & Malaquias, 2018****\**Niparaya* sp.**

Figure 7G

**Material examined.** Two specimens 4 mm, CB; one specimen 3 mm, TT.

**Ecology.** Among rubble in coral reef habitats and soft sediments near the reef edge. Depth 4–8 m.

**Distribution.** *Niparaya* sp. 3 is currently known only from eastern Malaysia (Gosliner et al. 2018).

**Genus *Philinopsis* Pease, 1860*****Philinopsis speciosa* Pease, 1860**

Figure 7H

**Material examined.** Two specimens 18–26 mm, SB; one specimen 14 mm, TT; one specimen 11 mm, SN.

**Ecology.** In soft sediment habitats outside the coral reef. Depth 14–26 m.

**Distribution.** Widespread across the Indo-Pacific including Mozambique (Tibiricá and Malaquias 2016), Maldives (Yonow 1994), Vietnam (Martynov and Korshunova 2012), Australia (Nimbs and Smith 2016), Guam, Hawaii, the Galapagos Islands (Zamora-Silva and Malaquias 2018), South Africa, Tanzania, the Philippines, Indonesia, Papua New Guinea, Japan, Panama (Gosliner et al. 2008), and Red Sea (Yonow 1990). Previously documented from Thai waters (Nabhitabhata 2009) but a specific location was not given. Here confirmed from the Gulf waters of Thailand.

**\**Philinopsis* *coronata* (Gosliner, 2011)**

Figure 7I

**Material examined.** One specimen 35 mm, SRB.

**Ecology.** In soft sediment habitats outside the coral reef. Depth 10 m.

**Distribution.** *Philinopsis* *coronata* is known from the Philippines (Gosliner 2011) and Indonesia (Gosliner et al. 2018). Here recorded for the first time from Thai waters.

**Remarks.** The taxonomic validity of this species name remains unresolved after it was designated the type species for the recently erected genus *Spinophallus* by Zamora-Silva and Malaquias (2018), which is a junior homonym of *Spinophallus* A. Riedel, 1962 [Gastropoda, Pristilomatidae] (MolluscaBase 2020). To date, no replacement name has been proposed leaving us to retain the use of the earlier but incorrect genus designation for this species.

**Genus *Tubulophilinopsis* Zamora-Silva & Malaquias, 2018*****Tubulophilinopsis lineolata* (H. Adams & A. Adams, 1854)**

Figure 7J

**Material examined.** One specimen 45 mm, LB; two specimens 32–38 mm, TT.

**Ecology.** In soft sediment habitats outside the coral reef. Depth 12–18 m.

**Distribution.** Currently known only from Australia (Nimbs and Smith 2016), Japan and the Philippines (Gosliner et al. 2018). Recorded from the Gulf waters of Thailand (Jensen 1998).

***Tubulophilinopsis pilsbryi* (Eliot, 1900)**

Figure 7K

**Material examined.** Two specimens 35–39 mm, SN; two specimens 25–42 mm, TT; one specimen 19 mm, MB.

**Ecology.** Abundant in soft sediment habitats outside the coral reef. A single individual of the species was observed being ingested by the scleractinian coral *Heteropsammia cochlea* (Mehrotra et al. 2019). Depth 12–28 m.

**Distribution.** Widespread across the Indo-Pacific including Mozambique (Tibiriçá and Malaquias 2016), Myanmar (Sanpanich and Duangdee 2019), Vietnam (Martynov and Korshunova 2012), Australia (Nimbs and Smith 2016), the Philippines, Vanuatu (Zamora-Silva and Malaquias 2018), Madagascar, Malaysia, Indonesia, Papua New Guinea, Palau, Guam, Marshall Islands, and Hawaii (Gosliner et al. 2008). Documented from the Gulf of Thailand (Mehrotra and Scott 2016).

**\**Tubulophilinopsis reticulata* (Eliot, 1903)**

Figure 7L

**Material examined.** One specimen 30 mm, SN.

**Ecology.** In soft sediment habitats outside the coral reef. Depth 14–16 m.

**Distribution.** Widespread across the Indo-Pacific including Mozambique (Tibiriçá and Malaquias 2016), Vietnam (Martynov and Korshunova 2012), Taiwan (Huang et al. 2016), Australia (Nimbs and Smith 2016), Marshall Islands (Zamora-Silva and Malaquias 2018), Tanzania, South Africa, Madagascar (Gosliner et al. 2008), and the Red Sea (Yonow 1990). Here documented as a first record for Thai waters.

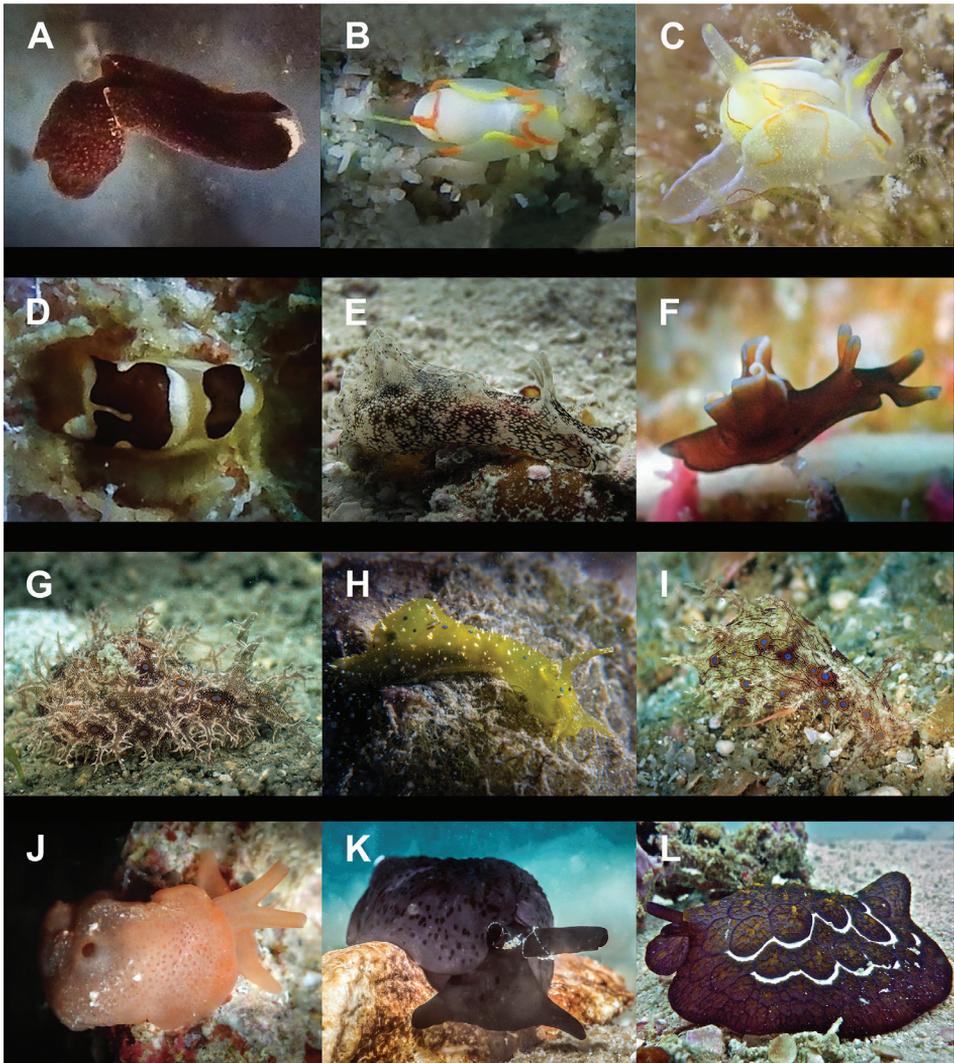
**Genus *Migaya* Ortea, Caballer & Espinosa, 2014****\**Migaya* sp.**

Figure 8A

**Material examined.** One specimen 3 mm, LB.**Ecology.** In soft sediment habitats outside the coral reef. Depth 24 m.**Distribution.** Currently known only from the Gulf of Thailand, documented here for the first time.**Remarks.** Ortea Rato et al. (2014) described the genus *Migaya* to hold all the Caribbean and Indo-Pacific cephalaspideans that were found to cluster (subclade B.2.) with *Aglaja felis* Er. Marcus & Ev. Marcus, 1970 in the molecular phylogeny inferred by Camacho-García et al. (2013). These authors transferred *A. felis* to the genus *Nakamigawaia* Kuroda & Habe, 1961 based on the apparently wide distribution of *A. felis* in the Indo-Pacific, assuming that they could only belong to the Japanese genus *Nakamigawaia* because of the similarities in their external morphology and colouration, but they did not include representatives of the type species of the genus, *N. spiralis* Kuroda & Habe, 1961, in their study, nor any other co-generic species coming from Japan. Ortea Rato et al. (2014) compared the shells *N. spiralis* with those of *A. felis* in the context of a wide-range shell comparison including all the Aglajidae, and concluded that both species belonged to different genera, consequently describing the genus *Migaya*. Afterwards, Zamora-Silva and Malaquias (2018) published a new molecular phylogeny based on a wider taxonomical sampling within the Aglajidae in which they synonymised the genus *Migaya* and transferred *A. felis* to the genus *Nakamigawaia*. Again, these authors did not include representatives of *N. spiralis* from Japan, but similar species from Australia and Papua New Guinea, without checking their internal anatomies. For these reasons, given the high rate of endemism of the Japanese sea slugs, and after the study of the shell of the specimen from Thailand (bearing a similar shell to that of *M. felis*), we prefer to maintain the genus *Migaya* until representatives of *N. spiralis* from Japan are sequenced and compared in a phylogenetic context.**Family Gastropteridae Swainson, 1840****Genus *Siphopteron* Gosliner, 1989****\**Siphopteron makisig* Ong & Gosliner, 2017**

Figure 8B

**Material examined.** One individual 3 mm, SO.**Ecology.** In soft sediment habitats outside the coral reef. Depth 12–16 m.**Distribution.** Currently known only from the Philippines, Indonesia, and Australia (Ong et al. 2017). Here documented as a first record for Thai waters.



**Figure 8.** **A** *Migaya* sp. 3 mm **B** *Siphopteron makisig* 3 mm **C** *Siphopteron* sp. 3 mm (photograph by Will Malsukum) **D** *Philine orca* 3 mm **E** *Aplysia kurodai* 30 mm (photograph by Geoffrey Chamayou) **F** *Aplysia nigrocincta* 9 mm **G** *Bursatella* cf. *ocelligera* 65 mm (photograph by Elouise Haskin) **H** *Stylocheilus longicauda* 45 mm (photograph by Kirsty Magson) **I** *Stylocheilus striatus* 29 mm **J** *Berthella* cf. *caledonica* 10 mm **K** *Berthella martensi* 60 mm (photograph by Paddy Steele) **L** *Pleurobranchus forskalii* 130 mm (photograph by Tine Kvamme).

**\**Siphopteron* sp.**

Figure 8C

**Material examined.** One individual 3 mm, RR.

**Ecology.** In soft sediment habitats outside the coral reef. Depth 20 m.

**Distribution.** Unknown

**Family Philinidae Gray, 1850 (1815)**

**Genus *Philine* Ascanius, 1772**

**\**Philine orca* (Pease, 1860)**

Figure 8D

**Material examined.** Two individuals 2–4 mm, CB; one individual 3 mm, SB.

**Ecology.** Observed exclusively under dead Fungiidae coral skeletons where it is extremely cryptic, although it may be abundant. The only cephalaspidean species recorded exclusively from the coral reef habitat at Koh Tao. Depth 3–8 m.

**Distribution.** Widespread across the Indo-Pacific including Japan (Baba 1990), Australia (Nimbs and Smith 2016), Madagascar, Malaysia, the Philippines, Indonesia, Papua New Guinea, Hawaii, and the Galapagos Islands (Gosliner et al. 2008). Here documented as a first record for Thai waters.

**Order Aplysiida**

**Superfamily Aplysioidea Lamarck, 1809**

**Family Aplysiidae Lamarck, 1809**

**Genus *Aplysia* Linnaeus, 1767**

***Aplysia kurodai* Baba, 1937**

Figure 8E

**Material examined.** Two specimens 60–81 mm, SN; one specimen 30 mm, MH.

**Ecology.** In soft sediment habitats, occasionally found in aggregations, although more often observed as solitary. Depth 8–22 m.

**Distribution.** Currently known only from China (Guang-Yu and Tchang 1965), Korea (Lee et al. 2014), and Japan (Baba 1937). Documented from the Gulf of Thailand (Mehrotra and Scott 2016).

**\**Aplysia nigrocincta* von Martens, 1880**

Figure 8F

**Material examined.** One specimen 9 mm, SB.

**Ecology.** Under a dead Fungiidae coral among rubble in shallow coral reef habitats. Depth 6 m.

**Distribution.** Across the Indo-Pacific including Mozambique, Mauritius, the Philippines, Indonesia, Papua New Guinea, Vanuatu (Golestani et al. 2019), Maldives (Yonow 1994 as *Aplysia fasciata*), and the Red Sea (Yonow 1990 as *Aplysia* cf. *parvula*). Here documented as a first record for Thai waters.

## Genus *Bursatella* Blainville, 1817

### \**Bursatella* cf. *ocelligera* (Bergh, 1902)

Figure 8G

**Material examined.** One specimen 65 mm, SB.

**Ecology.** In soft sediment habitats where it grazes on cyanobacterial mats on the benthos. Depth 18–25 m.

**Distribution.** *Bursatella ocelligera* is known only from the Philippines (Bazzicalupo et al. 2020) and the Gulf of Thailand (Bergh 1902). *Bursatella leachii* is circumtropical (Bazzicalupo et al. 2020) including Brazil (Galvão Filho et al. 2015), Guadeloupe (Ortea Rato et al. 2012), Spain (González-Wangüemert et al. 2014), Italy (Travaglini and Crocetta 2019), Tunisia (Zakhama-Sraieb 2009), Morocco (Selfati et al. 2017), Ghana (Bebbington 1969), Iran (Rezai et al. 2016), India (Sethi et al. 2015), Vietnam (Martynov and Korshunova 2012), Australia (Nimbs and Smith 2016), New Zealand (Appleton et al. 2002), South Africa, Madagascar, and Hawaii (Gosliner et al. 2008).

**Remarks.** Eales and Engel (1935) synonymised all species of *Bursatella* into the single circumtropical species *B. leachii*. Recent evidence (Bazzicalupo et al. 2020) has supported the presence of a second species, *B. ocelligera*, based on internal morphological differences such as an unarmed penis and supported by molecular data. This name was attributed to specimens described from the Gulf of Thailand by Bergh (1902), who was the first to describe specimens with an unarmed penis. At present, there is no reliable way of discerning between the two species based on external morphology alone, and no available molecular data for specimens from the Gulf of Thailand. The internal anatomy of specimens from Koh Tao could not be investigated as part of the present study; however, the proximity to the type locality (Koh Chang) supports the need for comprehensive analyses of specimens from the Gulf of Thailand in particular, given the wide geographical range of *B. leachii* and the recent separation of other ‘circumtropical’ aplysiids.

## Genus *Stylocheilus* Gould, 1852

### *Stylocheilus longicauda* (Quoy & Gaimard, 1825)

Figure 8H

**Material examined.** One specimen 45 mm, SRB; one specimen 30 mm, TT.

**Ecology.** In soft sediment habitats rarely and upon mooring ropes where it grazes on cyanobacteria. Far less common than *S. striatus*. The association with mooring ropes is believed to be driven by its pelagic lifestyle, as these ropes act as mid-water substrates for cyanobacterial growth. Depth 5–18 m.

**Distribution.** Circumtropical including Brazil (Galvão Filho et al. 2015), Gulf of Oman (Fatemi and Attaran 2015), Red Sea (Yonow 2008), India (Chinnadurai et al. 2014), Australia (Nimbs and Smith 2016), Tanzania, the Philippines, and

Hawaii (Gosliner et al. 2008). Documented from the Gulf of Thailand (Mehrotra and Scott 2016).

**Remarks.** Recent work (Yonow 2012; Bazzicalupo et al. 2020), has indicated the need for morphological and molecular examination of *S. longicauda* across their range with the taxonomic validity of the species being questioned. In the present work, *S. longicauda* is treated as distinct from *S. striatus* based on differences in external morphology (consistently shorter papillae and yellow/lime-green colouration in *S. longicauda*) and ecology. We here retain the use of the compound noun used in the original description of the species (see Nimbs et al. 2017).

### *Stylocheilus striatus* (Quoy & Gaimard, 1832)

Figure 8I

**Material examined.** One specimen 25 mm, SRB; one specimen 22 mm, CB; one specimen 29 mm, TT.

**Ecology.** From shallow and deep soft sediment habitats grazing of mats of cyanobacteria on the benthos. Depth 1–18 m.

**Distribution.** Circumtropical including Brazil (Galvão Filho et al. 2015), Mexico (Ortigosa et al. 2015), Guadeloupe (Ortea Rato et al. 2012), the Azores (Malaquias et al. 2009), Mozambique (Jochum and Favre 2017), India (Apte 2009), Vietnam (Martynov and Korshunova 2012), Indonesia (Eisenbarth et al. 2018), Australia (Nimbs and Smith 2016), French Polynesia (Horwitz et al. 2017), Fiji (Thaman et al. 2017), the Caribbean, Galapagos, South Africa, Red Sea, Hawaii and California (Gosliner et al. 2008). Documented from the Gulf of Thailand (Mehrotra and Scott 2016), and from Andaman Sea (as *S. longicauda*) by Jensen (1998).

### Clade Nudipleura Wägele & Willan, 2000

#### Order Pleurobranchida Deshayes, 1832

#### Superfamily Pleurobranchoidea Gray, 1827

#### Family Pleurobranchidae Gray, 1827

#### Genus *Berthella* Blainville, 1824

#### \**Berthella* cf. *caledonica* (Risbec, 1928)

Figure 8J

**Material examined.** Three specimens 10–15 mm, TW.

**Ecology.** Under coral rubble in shallow coral reef habitats. Depth 6–8 m.

**Distribution.** *Berthella caledonica* is known from New Caledonia (Risbec 1928), Mariana Islands (Carlson and Hoff 2003), Hawaii (Johnson 2002a), Marshall Islands (Johnson 2002b), Australia (Cobb 2009), and Japan (Bolland 2002).

**Remarks.** Overall colour variable from pink to light or dark brown, with numerous small, low tubercles across the dorsal surface, often surrounded by a brown ring, and with dark brown apices. A prominent brown mark surrounded by a diffuse ring of translucent white is located centrally on the dorsal surface. While specimens from Koh Tao resemble the description of *Berthella caledonica* (Risbec, 1928) rather well, records of *Berthella africana* (Pruvot-Fol, 1956) have also been made from Thailand, with an unclear locality (Nabhitabhata 2009). Both species share external similarities, in particular the presence of a brown spot or ‘hole’ found centrally on the dorsum, and the need for clarification between both species has been noted (Gosliner et al. 2008; Rudman 2009b). The present species is most similar to *Berthella* sp. 1 of Gosliner et al. (2018). With the Gulf of Thailand being distant from the type localities of both species (Morocco for *B. africana* and New Caledonia for *B. caledonica*), and the Pacific range currently known for *B. caledonica*, the present species is treated as potentially distinct until such a time as closer examinations can be made.

**\**Berthella martensi* (Pilsbry, 1896)**

Figure 8K

**Material examined.** One specimen 60 mm, LB.

**Ecology.** Exclusively recorded from soft sediment habitats outside coral reefs. Depth 11–21 m.

**Distribution.** Widespread throughout the Indo-Pacific including the Red Sea (Yonow 2015), Mozambique (Tibirićá et al. 2017), India (Sreeraj et al. 2012), Maldives (Yonow 1994), Tanzania, Mauritius, Indonesia, the Philippines, Taiwan, Australia, Papua New Guinea, Solomon Islands, Hawaii, and the Pacific coast of Mexico (Gosliner et al. 2008).

**Remarks.** Individuals from Koh Tao have a dark, almost black mantle with numerous inconspicuous black spots. *Berthella martensi* was recorded by Nabhitabhata (2009) based on a local record (in Thai), but the location(s) of this record is unknown. Therefore, while *B. martensi* is known from the Gulf of Thailand, its presence along the Andaman coast of Thailand is unconfirmed.

**Genus *Pleurobranchus* Cuvier, 1804**

***Pleurobranchus forskalii* Rüppell & Leuckart, 1828**

Figure 8L

**Material examined.** One specimen 265 mm, SN; one specimen 55 mm, TT.

**Ecology.** Exclusively recorded from soft sediment habitats outside coral reefs. Observed feeding on colonies of the tunicate *Didemnum molle* Herdmann, 1886. Depth 11–21 m.

**Distribution.** Widespread throughout the Indo-Pacific including Mozambique (Tibirićá et al. 2017), Gulf of Oman (Fatemi and Attaran 2015), India (Apte and

Bhave 2014), Tanzania, the Red Sea, the Philippines, Indonesia, Japan, Australia, Papua New Guinea, and Fiji (Gosliner et al. 2008). First documented from the Gulf of Thailand by Mehrotra and Scott (2016).

**Order Nudibranchia Cuvier, 1817**

**Suborder Doridina Odhner, 1934**

**Superfamily Doridoidea Rafinesque, 1815**

**Family Actinocyclidae O'Donoghue, 1929**

**Genus *Hallaxa* Eliot, 1909**

**\**Hallaxa iju* Gosliner & Johnson, 1994**

Figure 9A

**Material examined.** One specimen 10 mm, SO.

**Ecology.** Among rubble in coral reef and reef edge habitats. Associated with an unidentified pale/creamy white sponge. Depth 4–12 m.

**Distribution.** Across the Pacific including Australia (Nimbs and Smith 2016), the Philippines, Papua New Guinea, Japan, the Marshall Islands (Gosliner and Johnson 1994), Hong Kong, and Hawaii (Gosliner et al. 2008). Here representing a first record for Thai waters.

**\**Hallaxa indecora* (Bergh, 1905)**

Figure 9B

**Material examined.** One specimen 8 mm, SRB; one specimen 8 mm, CB.

**Ecology.** Among rubble and under dead fungiid coral skeletons in coral reef habitats. Occasionally near isolated unattached colonies of sponge in deeper soft sediment habitats. Associated with an unidentified pale/creamy white sponge. Depth 4–20 m.

**Distribution.** Red Sea (Yonow 2008) and across the Indo-Pacific including Australia (Nimbs and Smith 2016), the Gulf Aden, the Philippines, Indonesia, Japan, New Caledonia, and American Samoa (Gosliner et al. 2008). Here representing a first record for Thai waters.

**Family Chromodorididae Bergh, 1891**

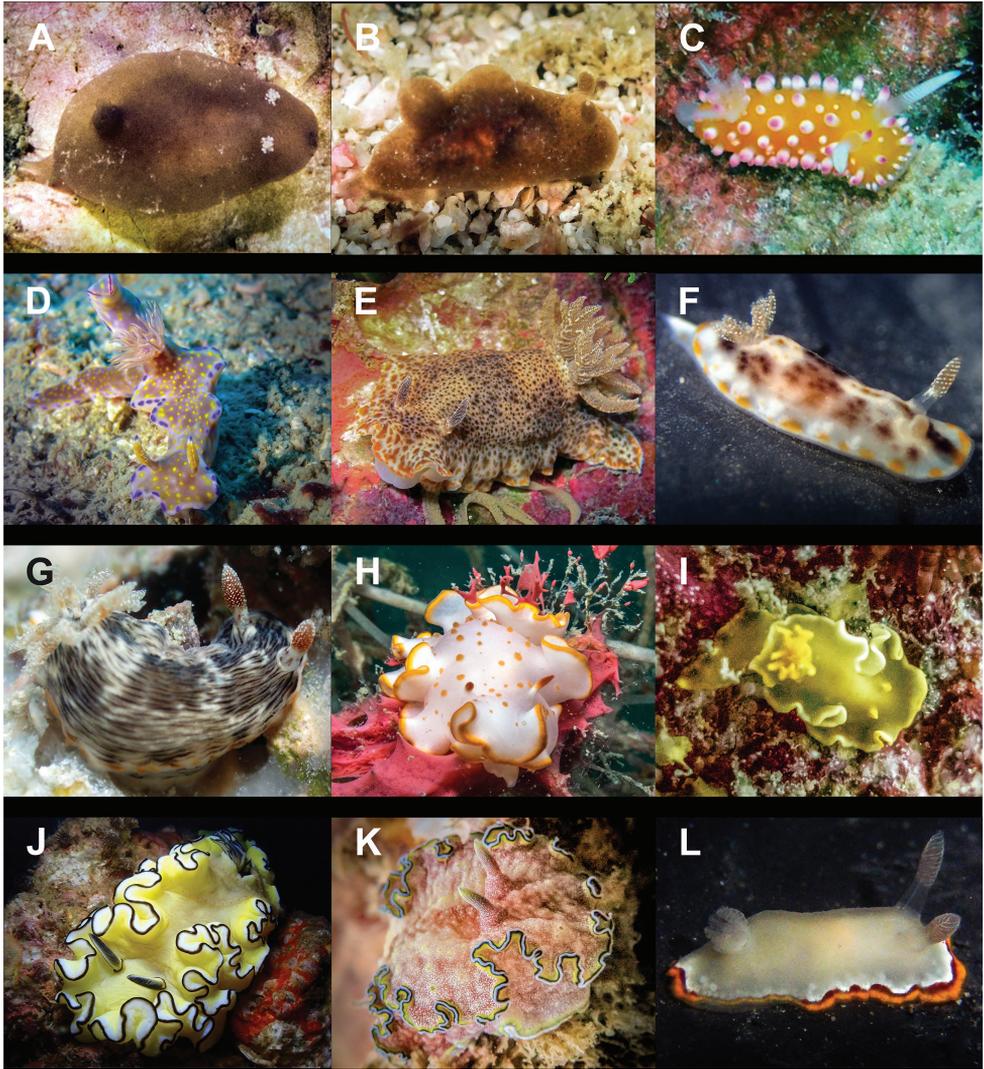
**Genus *Cadlinella* Thiele, 1931**

***Cadlinella ornatissima* (Risbec, 1928)**

Figure 9C

**Material examined.** Two specimens 12–30 mm, TT.

**Ecology.** On rocks and among corals at offshore pinnacles. Depth 8–25 m.



**Figure 9.** **A** *Hallaxa iju* 10 mm **B** *Hallaxa indecora* 8 mm **C** *Cadlinella ornatissima* 30 mm (photograph by Mati Pauner) **D** *Ceratosoma tenue* 85 mm **E** *Chromodoris mandapamensis* 50 mm (photograph by Tine Kvamme) **F** *Chromodoris* cf. *mandapamensis* 7 mm **G** *Chromodoris* cf. *balat* 25 mm (photograph by Elouise Haskin) **H** *Diversidoris aurantonodulosa* 30 mm **I** *Diversidoris crocea* 8 mm (photograph by Pau Urgell Plaza) **J** *Doriprismatica atromarginata* 60 mm **K** *Glossodoris* cf. *cincta* 40 mm **L** *Goniobranchus* cf. *albonares* 5 mm.

**Distribution.** Widespread in the Indo-Pacific including New Caledonia (Risbec 1928), Japan (Baba 1949), Mozambique (Tibirić et al. 2017), Chagos Islands (Yonow et al. 2002), India (Ramakrishna et al. 2010), Sri Lanka, Gulf of Oman, Réunion Island (Yonow 2012), Red Sea (Yonow 2008), Myanmar (Sanpanich and Duangdee

2019), Australia (Nimbs and Smith 2016), Taiwan, Hong Kong (Gosliner et al. 2008), Singapore (Lim and Chou 1970), the Gulf of Thailand, and the Andaman coast of Thailand (Chavanich et al. 2013).

### Genus *Ceratosoma* A. Adams & Reeve, 1850

#### \**Ceratosoma tenue* Abraham, 1876

Figure 9D

**Material examined.** One specimen 85 mm, AM.

**Ecology.** Soft sediment habitat. Depth 26 m.

**Distribution.** Widespread throughout the Indo-Pacific including Japan (Baba 1949), Indonesia (Yonow 2001), South Africa, Mozambique, Malaysia, Australia, New Caledonia, Hawaii (Gosliner et al. 2008), and the Red Sea (Yonow 2008). Here representing a first record for Thai waters.

### Genus *Chromodoris* Alder & Hancock, 1855

#### *Chromodoris mandapamensis* Valdés, Mollo & Ortea, 1999

Figure 9E

**Material examined.** One specimen 50 mm, CP.

**Ecology.** Among corals and coral rubble at offshore pinnacle sites. 9–20 m.

**Distribution.** Widespread throughout the Indo-Pacific including Mozambique (Tibiriçá et al. 2017), India (Valdés et al. 1999), South Africa, Solomon Islands, Papua New Guinea, Myanmar (Gosliner et al. 2008), and Gulf of Thailand (Chavanich et al. 2013).

**Remarks.** While externally matching the original description of the species completely, the internal anatomy was not analysed to verify this, the importance of which is particular to this and other similar species (Layton et al. 2018). See ‘Remarks’ for *Chromodoris* cf. *mandapamensis* below.

#### \**Chromodoris* cf. *mandapamensis* Valdés, Mollo & Ortea, 1999

Figure 9F

**Material examined.** Three specimens 5–10 mm, CB.

**Ecology.** Among reef rubble, in particular under dead fungiid coral skeletons, in shallow coral reef areas. Depth 2–8 m.

**Distribution.** *Goniobranchus pruna* (Gosliner, 1994) is known from Madagascar and South Africa (Gosliner 1994) and Mozambique (Tibiriçá et al. 2017). *Chromodoris* sp. 15 is known from Philippines and New Caledonia (Gosliner et al. 2018).

**Remarks.** Very similar to *Chromodoris* aff. *mandapamensis* (Layton et al. 2018; Bonomo and Gosliner 2020), *Chromodoris* sp. 15 (Gosliner et al. 2018), and *Goniobranchus pruna* (Gosliner 1994). While *C. mandapamensis* has been suggested as a possible synonym of *G. pruna* as discussed in Tibirićá et al. (2017), the present species is kept separate from *C. mandapamensis* due to difference in the local ecology of both species. *Chromodoris mandapamensis* is locally recorded only from sparse observations at offshore pinnacles, with no confirmed records for the past five years, whereas *C. cf. mandapamensis* is regularly found in surveys in shallow reef areas near the shore. While it is possible that this species undergoes its juvenile stages closer to shore before moving out towards the offshore pinnacles, no observations have been made of this species in the intervening deeper soft sediment habitats between the two. Additionally, no individuals larger than approximately 15 mm have been recorded and no individuals that externally match *C. mandapamensis* have yet been recorded near the island.

**\**Chromodoris* cf. *balat* Bonomo & Gosliner, 2020**

Figure 9G

**Material examined.** One specimen 25 mm, CB.

**Ecology.** Among reef rubble, in particular under dead fungiid coral skeletons, in shallow coral reef areas. Depth 4–8 m

**Distribution.** *Chromodoris balat* is known only from the Philippines (Bonomo and Gosliner 2020) and a similar species is recorded here for the first time from Thai waters.

**Remarks.** Similar to *Chromodoris balat* in having a striated dorsum with numerous large blotches and a broken yellow-orange marginal line. This species was differentiated from the similar *Chromodoris striatella* Bergh, 1877 based on these and other features (Layton et al. 2018; Bonomo and Gosliner 2020). Our specimen is differentiated from *C. balat* by lacking small yellow, orange, and red spots on the white parts of the dorsal surface, the pale tan-coloured gills with orange spots instead of red-brown as seen in *C. balat*, and by the blotches being pale grey-brown and indistinct instead of dark and pronounced. The indistinct blotches on the dorsum, the broken yellow-orange marginal band, and the colouration of rhinophores and gills do share a resemblance with *C. mandapamensis* and *C. cf. mandapamensis* (the latter of which may be found living alongside *C. cf. balat* at Koh Tao). Given the difficulties of relying on external features for species delineation in many of these striped and spotted species of *Chromodoris* (Layton et al. 2018; Bonomo and Gosliner 2020) we refrain from committing to a species identification until specimens from Koh Tao can be investigated further. Chavanich et al. (2013) recorded *C. striatella* from both Gulf and Andaman coasts of Thailand; however, in the absence of specimen details from both areas, this distribution record may be called into question in light of the recent findings regarding the complex surrounding

*C. striatella*. Further documentation of *Chromodoris* species from both coasts may clarify this.

### Genus *Diversidoris* Rudman, 1987

#### *\*Diversidoris aurantionodulosa* Rudman, 1987

Figure 9H

**Material examined.** One specimen 30 mm, SI.

**Ecology.** Found upon its pink host sponge, *Darwinella* sp., at deeper reef and pinnacle sites, and in muck habitats. Depth 12–30 m.

**Distribution.** Red Sea (Yonow 2015), South Africa, Tanzania, Australia, and Hong Kong (Gosliner et al. 2008). Here representing a first record for Thai waters

**Remarks.** This species was mistakenly identified as *Ardeadoris averni* (Rudman, 1985) by Mehrotra and Scott (2016) based on limited photographic data. Specimens found several years after initial second-hand observations have permitted reidentification, leaving *A. averni* remaining currently unrecorded in Thai waters.

#### *Diversidoris crocea* (Rudman, 1986)

Figure 9I

**Material examined.** One specimen 8 mm, TT.

**Ecology.** Coral reef habitats. Usually cryptic on its sponge, a yellow *Darwinella* sp. (Rudman 2005a).

**Distribution.** Widespread throughout the Indo-Pacific including Mozambique (Tibiriçá et al. 2017), Philippines, Indonesia, Japan, Papua New Guinea (Gosliner et al. 2008), Guam (Carlson and Hoff 2003), and Australia (Rudman 1986). First documented from the Gulf of Thailand by Mehrotra and Scott (2016).

### Genus *Doriprismatica* d'Orbigny, 1839

#### *Doriprismatica atromarginata* (Cuvier, 1804)

Figure 9J

**Material examined.** One specimen 60 mm, CP.

**Ecology.** On rocks and among corals at offshore pinnacles. Depth 8–25 m.

**Distribution.** Widespread throughout the Indo-Pacific including South Africa, Red Sea, French Polynesia, Solomon Islands, China, Philippines (Gosliner 1987), Papua New Guinea, Australia (Rudman 1986), Myanmar (Sanpanich and Duangdee 2019), Japan (Baba 1949), Indonesia (Yonow 2001), Gulf of Thailand (Jensen 1998), Mauritius (Yonow and Hayward 1991), and the Andaman coast of Thailand (Chavanich et al. 2013).

**Genus *Glossodoris* Ehrenberg, 1831*****Glossodoris* cf. *cincta* (Bergh, 1888)**

Figure 9K

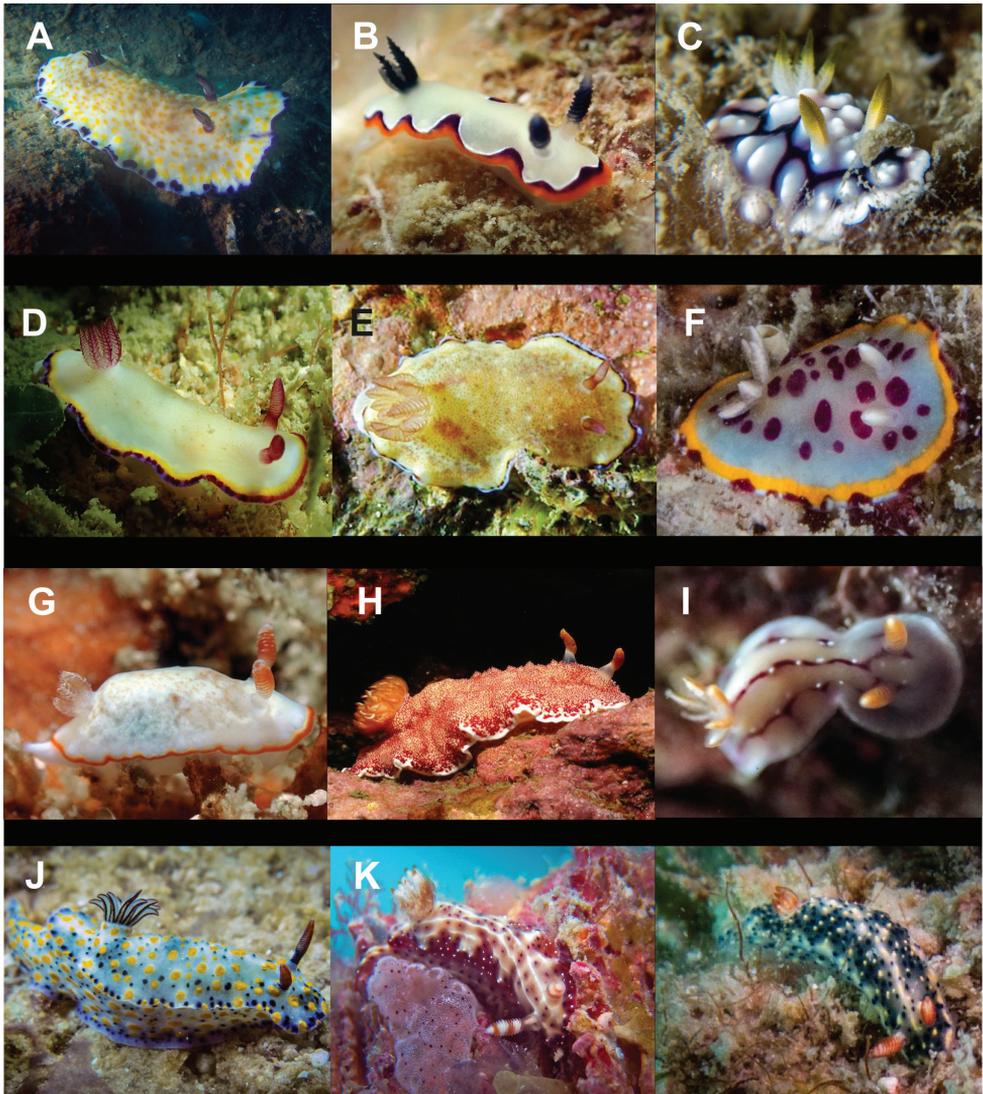
**Material examined.** One specimen 40 mm, HWB.**Ecology.** Coral reefs throughout the island. Depth 5–15 m.**Distribution.** Papua New Guinea, the Philippines and Madagascar (Matsuda and Gosliner 2018). First documented from the Gulf of Thailand by Mehrotra and Scott (2016).**Remarks.** Previously recorded as *Glossodoris cincta* (Bergh 1888), recent work by Matsuda and Gosliner (2018) has shown that Southeast Asian/western Pacific species may be distinct. However, this cannot be verified until specimens of *G. cincta* are analysed from the type locality of Mauritius. Therefore, the present species, which externally matches the description by Matsuda and Gosliner, is separated from the true Indian Ocean *Glossodoris cincta* for now.**Genus *Goniobranchus* Pease, 1866****\**Goniobranchus* cf. *albonares* (Rudman, 1990)**

Figure 9L

**Material examined.** Three specimens 4–6 mm, CB.**Ecology.** Observed under dead fungiid coral skeletons and occasionally among rubble in shallow coral reef. Depth 3–8 m**Distribution.** *Goniobranchus albonares* is known from Australia (Rudman 1990), Japan (Gosliner et al. 2008), Madagascar (Rassat 2016), and Mozambique (Tibirică et al. 2017).**Remarks.** Externally resembling both *Goniobranchus albonares* (Rudman, 1990) and *Goniobranchus rubrocornutus* (Rudman, 1985), the present species differs from the former by possessing a broken submarginal band of deep red and from the latter by the presence of completely white rhizophore clubs and gills as opposed to red. There is significant overlap in the range of both species, with *G. rubrocornutus* known from Australia, Hong Kong, and Japan (Rudman 1985). A comprehensive comparison of the three species is needed.***Goniobranchus aureopurpureus* (Collingwood, 1881)**

Figure 10A

**Material examined.** One specimen 45 mm, SN.**Ecology.** Locally rare, known only from soft sediment habitats outside the coral reef. Depth 12–16 m.



**Figure 10.** **A** *Goniobranchus aureopurpureus* 45 mm **B** *Goniobranchus fidelis* 12 mm **C** *Goniobranchus geometricus* 15 mm (photograph by Kirsty Magson) **D, E** *Goniobranchus sinensis* different morphs, 34 mm (**D**) and 55 mm (**E**) **F** *Goniobranchus tumuliferus* 10 mm **G** *Goniobranchus verrieri* 10 mm (photograph by Khumron Waipaka) **H** *Goniobranchus* sp. 55 mm (photograph by Phannee Mccarthy) **I** *Hypselodoris cerisae* 4 mm **J** *Hypselodoris confetti* 24 mm (photograph by Pau Urgell Plaza) **K** *Hypselodoris decorata* 18 mm **L** *Hypselodoris infucata* 12 mm.

**Distribution.** Across the Indo-Pacific including Myanmar (Sanpanich and Duangdee 2019), Australia (Nimbs and Smith 2016), the Philippines, Indonesia, China, Japan, Papua New Guinea, and New Caledonia (Gosliner et al. 2008). Known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

***Goniobranchus fidelis* (Kelaart, 1858)**

Figure 10B

**Material examined.** Two specimens 6–18 mm CB; one specimen 15 mm, SB; one specimen 12 mm, SD.

**Ecology.** Coral reef habitats throughout the region. Depth 2–25 m.

**Distribution.** Widespread throughout the Indo-Pacific including Mozambique (Tibirićá et al. 2017), Maldives (Yonow 1994), India (Ramakrishna et al. 2010), Myanmar (Sanpanich and Duangdee 2019), Madagascar, Red Sea, Philippines, Japan, Australia, New Caledonia (Gosliner et al. 2008), and Indonesia (Yonow 2001). Known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

***Goniobranchus geometricus* (Risbec, 1928)**

Figure 10C

**Material examined.** One specimen 15 mm, KKR.

**Ecology.** Locally rare, known only from the reef edge and soft sediment habitats outside the coral reef. Depth 12–25 m.

**Distribution.** Widespread throughout the Indo-Pacific including Myanmar (Sanpanich and Duangdee 2019), Tanzania, Madagascar, Guam, Japan, Papua New Guinea (Gosliner et al. 2008), Maldives (Yonow 1994), Indonesia (Yonow 2001), Philippines (Debelius 1996), and Australia (Nimbs and Smith 2016). Known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

***Goniobranchus preciosus* (Kelaart, 1858)**

**Material examined.** None found presently.

**Ecology.** Soft sediment habitats outside the coral reef. Depth 18–22 m.

**Distribution.** Across the Indo-Pacific including Indonesia (Scott 2005), Malaysia, the Philippines, Papua New Guinea, Australia, New Caledonia. Recorded from Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

**Remarks.** The species has historically been recorded from Koh Tao (Mehrotra and Scott 2016) based on a citizen science effort, but no material has been found in surveys to date.

**\**Goniobranchus sinensis* (Rudman, 1985)**

Figure 10D, E

**Material examined.** Three specimens 20–55 mm, CP.

**Ecology.** Among rocks and corals at offshore rocky pinnacles. Depth 9–22 m.

**Distribution.** Across the Indo-Pacific including the Gulf of Oman (Fatemi and Attaran 2015), India (Sreeraj et al. 2012), Malaysia, Indonesia, China, and Japan (Gosliner et al. 2008). Recorded from the Gulf waters of Thailand (Chavanich et al. 2013).

**Remarks.** Incorrectly identified as *Goniobranchus trimarginatus* (Winckworth, 1946) by Mehrotra and Scott (2016). Subsequent observations indicate that specimens from Koh Tao are *Goniobranchus sinensis*, with individuals being recorded with marginal and submarginal bands ranging from complete to broken.

***Goniobranchus tumuliferus* (Collingwood, 1881)**

Figure 10F

**Material examined.** Two specimens 10–15 mm, CP.

**Ecology.** Predominantly found among coral and rock at an offshore submerged pinnacle site. Also sparsely recorded from the deeper soft sediment habitats near the island. Depth 11–25 m.

**Distribution.** Across the western Pacific including Vietnam (Martynov and Korshunova 2012), the Philippines, Japan, Australia, and New Caledonia (Gosliner et al. 2008). Known from the Gulf of Thailand (Jensen 1998; Chavanich et al. 2013).

**\**Goniobranchus verrieri* (Crosse, 1875)**

Figure 10G

**Material examined.** One specimen 10 mm, GR.

**Ecology.** Coral reefs. Depth 5–10 m.

**Distribution.** Widespread throughout the Indo-Pacific including Mozambique (Tibirićá et al. 2017), Tanzania, New Caledonia (Rudman 1985), Australia (Nimbs and Smith 2016), South Africa, Madagascar, Indonesia, Philippines, Hawaii (Gosliner et al. 2008), and Red Sea (Yonow 1989). Here representing a first record for Thai waters.

**Remarks.** Locally known only from a single individual.

***Goniobranchus* sp.**

Figure 10H

**Material examined.** One specimen 55 mm, CP.

**Ecology.** Among rocks and corals at offshore rocky pinnacles. Depth 18 m.

**Distribution.** *Goniobranchus* sp. 5 (Soong et al. 2020) is known from the Philippines, Indonesia, Japan, and Australia. A similar species is known from the Gulf of Thailand, incorrectly recorded as *Goniobranchus reticulatus* by Mehrotra and Scott (2016).

**Remarks.** Red reticulated specimens of *Goniobranchus* have been known to represent a complex of species often attributed to *G. reticulatus* or *G. tinctorius*. Recent molecular work by Soong et al. (2020) concluded that none of the five distinct lineages identified corresponded exactly with the description of either of the aforementioned species. Due to the overlapping ranges and external variability of some of these, a further morphological investigation into these lineages is needed to define the species.

### Genus *Hypselodoris* Stimpson, 1855

#### \**Hypselodoris cerisae* Gosliner & Johnson, 2018

Figure 10I

**Material examined.** One specimen 4 mm, CB.

**Ecology.** Among reef rubble in shallow coral reef. Depth 4 m.

**Distribution.** Japan, Malaysia, and Taiwan (Epstein et al. 2018). Here representing a first record for Thai waters.

**Remarks.** Though a small individual, it is identified as *H. cerisae* based on pink and purple pigmentation and dark brown lines with white spots. An absence of orange/burnt orange pigmentation separates it from *H. krakatoa* Gosliner & Johnson, 1999.

#### \**Hypselodoris confetti* Gosliner & Johnson, 2018

Figure 10J

**Material examined.** Two specimens 12–24 mm, SB.

**Ecology.** Locally found exclusively from deeper soft sediment habitats of the island. Depth 14–25 m.

**Distribution.** Philippines, Papua New Guinea, probably Indonesia and Hong Kong (Epstein et al. 2018). Here representing a first record for Thai waters.

#### \**Hypselodoris decorata* (Risbec, 1928)

Figure 10K

**Material examined.** Two specimens 8–18 mm, CB.

**Ecology.** Abundant among reef rubble, in particular under dead fungiid coral skeletons, in shallow coral reef areas. Rare in other habitats. Depth 2–12 m.

**Distribution.** Widespread throughout the Indo-Pacific including Malaysia, Philippines, Indonesia, Papua New Guinea, New Caledonia, Vanuatu, and the Marshall Islands (Epstein et al. 2018). Here representing a first record for the Gulf of Thailand. *Hypselodoris decorata* was recorded as *Hypselodoris maculosa* (Pease, 1871) from the Andaman coast by Chavanich et al. (2013).

***Hypselodoris infucata* (Rüppell & Leuckart, 1830)**

Figure 10L

**Material examined.** One specimen 25 mm, SRB; one specimen 12 mm, CB; one specimen 8 mm, SB.

**Ecology.** Juveniles and smaller individuals common under dead fungiid corals and reef rubble in shallow coral reef areas, making up some of the most abundant nudibranch taxa in some areas. Larger individuals rarer. Throughout reef and deeper soft sediment habitats. Depth 2–25 m.

**Distribution.** Widespread and abundant in the Indo-Pacific including Mozambique (Tibirićá et al. 2017), Oman, South Africa, the Philippines, Australia (Debelius 1996), Red Sea (Yonow 1989), Madagascar, Mediterranean Sea, Indonesia, Japan, Papua New Guinea, and Hawaii (Gosliner et al. 2008). Distribution within Thailand currently unclear (see below), previously recorded from the Gulf of Thailand (Mehrotra and Scott 2016).

**Remarks.** Chavanich et al. (2013) recorded *Hypselodoris infucata* from Andaman and Gulf coasts, and *Hypselodoris obscura* from the Gulf of Thailand. While images were not presented alongside these records, review of the original data hints at a possible clarification. *Hypselodoris obscura* is known to be a sub-tropical species from eastern Australia (Epstein et al. 2018) while *H. infucata* is known to be widespread across the Indo-Pacific; therefore, records from the Gulf of Thailand by Chavanich et al. (2013) are likely to be *H. infucata*. Review of photographs used in the initial identifications supports this clarification, but also suggest that the species called *Hypselodoris infucata* found to be present on both coasts may or may not be the true *H. infucata*. A closer investigation on the distribution of *Hypselodoris* species across both coasts is needed to confirm its range in Thai waters.

**\**Hypselodoris* cf. *juniperae* Gosliner & Johnson, 2018**

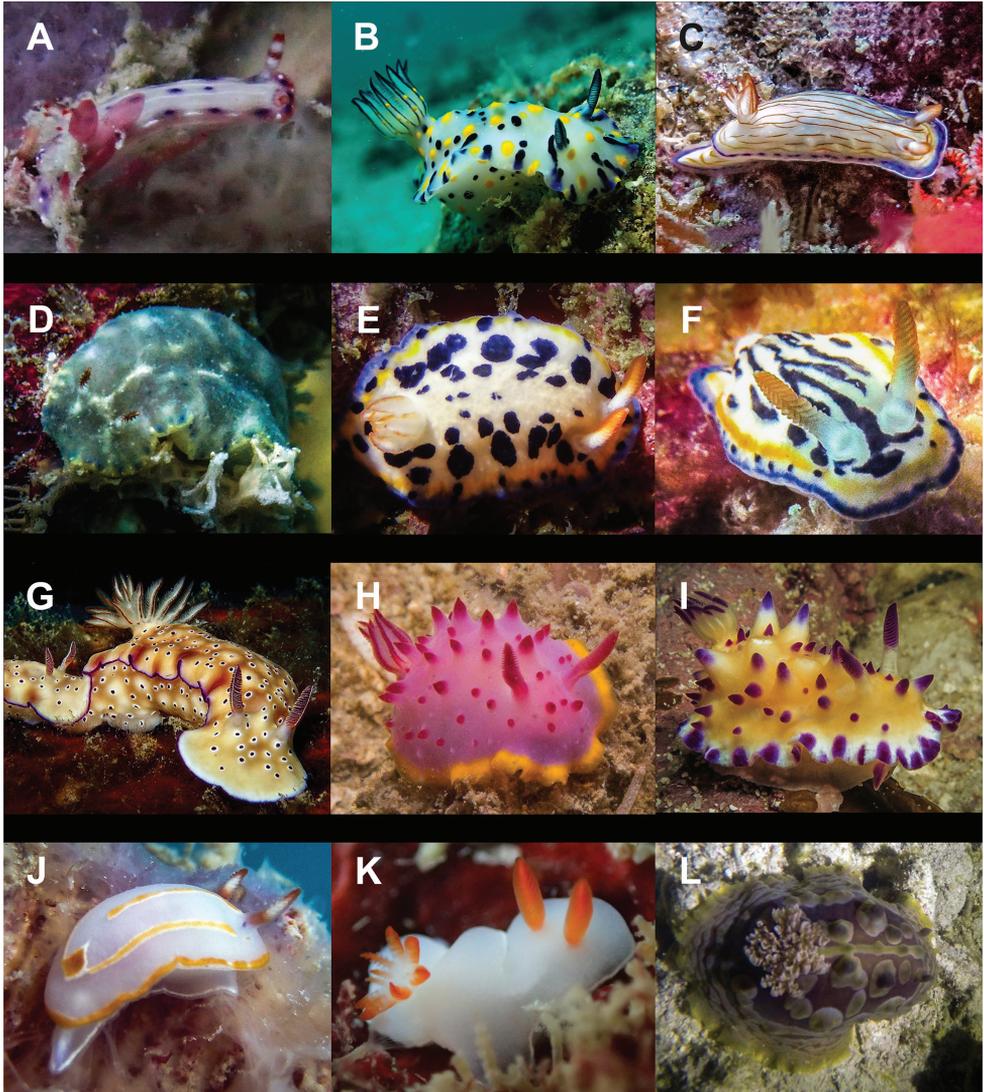
Figure 11A

**Material examined.** One specimen 6 mm, CB.

**Ecology.** Observed under a dead fungiid coral skeleton in shallow coral reef. Depth 6 m.

**Distribution.** *Hypselodoris juniperae* is currently known from Madagascar (Epstein et al. 2018) and potentially South Africa, Sri Lanka, and Réunion Island (Bidgrain 2005; Ogden 2005; Houben 2007). A similar species represents a first record for Thai waters.

**Remarks.** Externally similar to both *Hypselodoris maculosa* (Pease, 1871) and *Hypselodoris juniperae* Gosliner & Johnson, 2018 in bearing thin longitudinal white lines, dark purple spots, an opaque orange marginal band and white gills with red apices. Identified as the former species in Mehrotra and Scott (2016). Observed living



**Figure 11.** **A** *Hypselodoris* cf. *juniperiae* 6 mm **B** *Hypselodoris* cf. *kanga* 40 mm **C** *Hypselodoris katherinae* 15 mm **D** *Hypselodoris* cf. *lacuna* 10 mm **E, F** *Hypselodoris* cf. *maritima* 20 mm (**E**) and 25 mm (**F**) **G** *Hypselodoris tryoni*, right specimen 35 mm (photograph by Kirsty Magson) **H** *Mexichromis mariei* 15 mm (photograph by Pau Urgell Plaza) **I** *Mexichromis multituberculata* 30 mm (photograph by Pau Urgell Plaza) **J** *Mexichromis trilineata* 8 mm **K** *Verconia* cf. *hongkongiensis* 6 mm **L** *Asteronotus cespitosus* 120 mm (photograph by Emily Palmer).

sympatrically with *H. decorata*, readily distinguished by bearing two red rhinophoral rings and purple rather than reddish brown body colouration. Given the close relationship between all three species, a much closer study is required. Only a single individual has been observed in the area to date.

**\**Hypselodoris cf. kanga* Rudman, 1977**

Figure 11B

**Material examined.** One specimen 40 mm, TW; two specimens 10–25 mm, SB.

**Ecology.** Locally found exclusively from deeper soft sediment habitats of the island. Depth 14–25 m.

**Distribution.** Misidentified by Chavanich et al. (2013) as *H. kanga*, with a recorded distribution in both Andaman Sea and Gulf coasts of Thailand.

**Remarks.** *Hypselodoris kanga* bears blueish purple lines across its dorsum which are absent in this species, instead replaced by deep blue, almost black spots. These are more abundant towards the margin where they diffuse outwards turning into blue streaks closer to the edge. Given the historic confusion surrounding *H. kanga* (see Epstein et al. 2018), this difference in colouration merits the need for a closer investigation.

**\**Hypselodoris katherinae* Gosliner & Johnson, 2018**

Figure 11C

**Material examined.** Two specimens 5–15 mm, CB.

**Ecology.** Observed under dead fungiid coral skeletons and on rocks in shallow coral reef. Depth 3–15 m.

**Distribution.** Indonesia, Eastern Malaysia, and the Philippines (Gosliner et al. 2008). Here representing a first record for Thai waters.

**Remarks.** Recorded as undescribed from Koh Tao (Mehrotra and Scott 2016: fig. 2G) now identified as a first record for Thai waters.

**\**Hypselodoris cf. lacuna* Gosliner & Johnson, 2018**

Figure 11D

**Material examined.** One specimen 10 mm, CB.

**Ecology.** Observed under dead fungiid coral skeletons and on rocks in shallow coral reef. Depth 5 m.

**Distribution.** *Hypselodoris lacuna* is known from the Philippines, Indonesia, Japan, Papua New Guinea, Vanuatu, and Aldabra Atoll (Gosliner et al. 2008). Here representing a first record for Thai waters is a similar species.

**Remarks.** Dorsum centrally translucent grey with a network of opaque white lines. Gills grey with light grey apices, rhinophore stalks translucent, clubs white basally turning red with white tips. Mantle edge pale yellow areas with alternating blue spots. Differentiated from *H. lacuna* by having a mostly translucent grey dorsal surface rather than just isolated circles and by the pale yellow areas between the marginal ring of blue spots. Similar to *Hypselodoris* sp. 8 in Gosliner et al. (2018).

***Hypselodoris cf. maritima* (Baba, 1949)**

Figure 11E, F

**Material examined.** Three specimens 14–30 mm, TT; two specimens 15–25 mm, SWP; one specimen 20 mm, SR.

**Ecology.** On rocks and rubble within coral reef. Depth 5–25 m.

**Distribution.** *Hypselodoris maritima* is recorded from Japan (Baba 1949), Vietnam (Martynov and Korshunova 2012), Taiwan (Su et al. 2009), the Philippines, Indonesia, Hong Kong, Papua New Guinea, and Australia (Gosliner et al. 2008). The species is also recorded as being present in Thailand by Gosliner et al. (2008) but no confirmed records of this or similar species outside of Koh Tao have been found in the literature.

**Remarks.** Initially recorded as *H. maritima* from Koh Tao (Mehrotra and Scott 2016), further observations have shown variation in external morphology that diverges from the original description. In general, the dorsal surface is always white with scattered and slightly raised spots. While many individuals bear the deep blue to black ‘longitudinal streaks’ along the central dorsal surface, in others these are broken lines or even entirely disconnected spots of varying sizes. Rhinophore clubs range from entirely orange to white with orange apices, stalks always translucent white. The blue marginal band is always separated from the yellow submarginal band by the same white as the dorsum, and both bands are often broken or rows of pigmented spots, matching variation in the dark pigmentation. There are always deep blue-black spots between marginal and submarginal bands/rows, that may vary in size and often extend to the mantle edge. While closer examination may reveal individuals from Koh Tao and the nearby pinnacles to be more than one species, the population is here treated as a single variable species.

***Hypselodoris tryoni* (Garrett, 1873)**

Figure 11G

**Material examined.** Two specimens 30–35 mm, CB.

**Ecology.** On rocks and rubble within coral reef. Depth 1–30 m.

**Distribution.** Across the Indo-Pacific including Singapore (Toh 2016), Vietnam (Martynov and Korshunova 2012), Australia (Nimbs and Smith 2016), Malaysia, the Philippines, Indonesia, Japan, Palau, Papua New Guinea, Vanuatu, the Marshall Islands (Gosliner et al. 2008), and known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

**Genus *Mexichromis* Bertsch, 1977****\**Mexichromis mariei* (Crosse, 1872)**

Figure 11H

**Material examined.** One specimen 15 mm, SB.

**Ecology.** In deep soft sediment habitats. Depth 20 m. Feeding on *Dysidea* sp. sponge.

**Distribution.** Widespread throughout the Indo-Pacific including India (Patel and Apte 2014), Malaysia (Ho 1989), Australia (Nimbs and Smith 2016), South Africa, Madagascar, the Philippines, Indonesia, Japan, Papua New Guinea, and New Caledonia (Gosliner et al. 2008). Here representing a first record for Thai waters.

**Remarks.** Locally rare with only a single individual observed in the present surveys. Sharing the same habitat and prey preference as *M. multituberculata*.

### ***Mexichromis multituberculata* (Baba, 1953)**

Figure 11I

**Material examined.** One specimen 30 mm, SB, one specimen 8 mm, SN.

**Ecology.** Observed in deep soft sediment habitats throughout the island, though uncommon. Often found associated with or actively feeding on *Dysidea* sp. sponge which grows unattached on the benthos. Depth 14–25 m.

**Distribution.** Widespread throughout the Indo-Pacific including, India (Kumar et al. 2011), Myanmar (Sanpanich and Duangdee 2019), Vietnam (Martynov and Korshunova 2012), Taiwan (Huang et al. 2015), Hong Kong (Rudman and Darvell 1990), China (Lin 1990), the Philippines, Indonesia, and Japan (Gosliner et al. 2008). Recorded from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

### ***Mexichromis trilineata* (A. Adams & Reeve, 1850)**

Figure 11J

**Material examined.** Three specimens 5–8 mm, CB; two specimens 5 mm, TW.

**Ecology.** Usually found immersed in prey sponge *Dysidea* sp. under rubble and dead fungiid coral skeletons in shallow coral reef habitats. Uncommon, though multiple individuals may be observed together. Depth 3–8 m.

**Distribution.** Across the western Pacific including Indonesia (Yonow 2001; 2017), the Philippines, Palau, Papua New Guinea, and Australia (Gosliner et al. 2008). Recorded from the Gulf of Thailand (Mehrotra and Scott 2016). Very variable in pattern.

### **Genus *Verconia* Pruvot-Fol, 1931**

#### **\**Verconia* cf. *hongkongiensis* (Rudman, 1990)**

Figure 11K

**Material examined.** One specimen 6 mm, CB; one specimen 4 mm, TW.

**Ecology.** Observed under dead fungiid coral skeleton and rubble in shallow coral reef. Depth 3–8 m.

**Distribution.** *Verconia hongkongiensis* is known from Japan and Hong Kong (Gosliner et al. 2008, 2018). The present *Verconia* cf. *hongkongiensis* is a first record for Thai waters.

**Remarks.** Initially recorded as *Hypselodoris bullockii* (Collingwood, 1881) from a single small specimen by Mehrotra and Scott (2016), further observations have concluded that the species from Koh Tao is not *H. bullockii* but one superficially resembling *Verconia hongkongiensis* (Rudman 1990). Similarities between the two species are the thin marginal white line and pale variations in colour of the dorsum. However, rather than reddish tips, gills appear to be uniformly red (more orange in some specimens) and rhinophores appear pigmented throughout, basally red, sometimes with a paler median band, ending in red/orange tips, with all individuals recorded from Koh Tao being smaller than 6 mm.

### Family Discodorididae Bergh, 1891

#### Genus *Asteronotus* Ehrenberg, 1831

##### \**Asteronotus cespitosus* (van Hasselt, 1824)

Figure 11L

**Material examined.** One specimen 120 mm, CB.

**Ecology.** Locally found exclusively in soft sediment habitats. Depth 1–16 m.

**Distribution.** Widespread Indo-Pacific including Australia, Indonesia, Mauritius (Gosliner et al. 2008), Red Sea (Yonow 1990), Hawaii (Kay and Young 1969), Mozambique (Tibiriçá et al. 2017), and Gulf of Thailand (Chavanich et al. 2013).

#### Genus *Atagema* Gray, 1850

##### \**Atagema intecta* (Kelaart, 1859)

Figure 12A

**Material examined.** One specimen 25 mm, CB.

**Ecology.** Coral reefs. Depth 5–10 m.

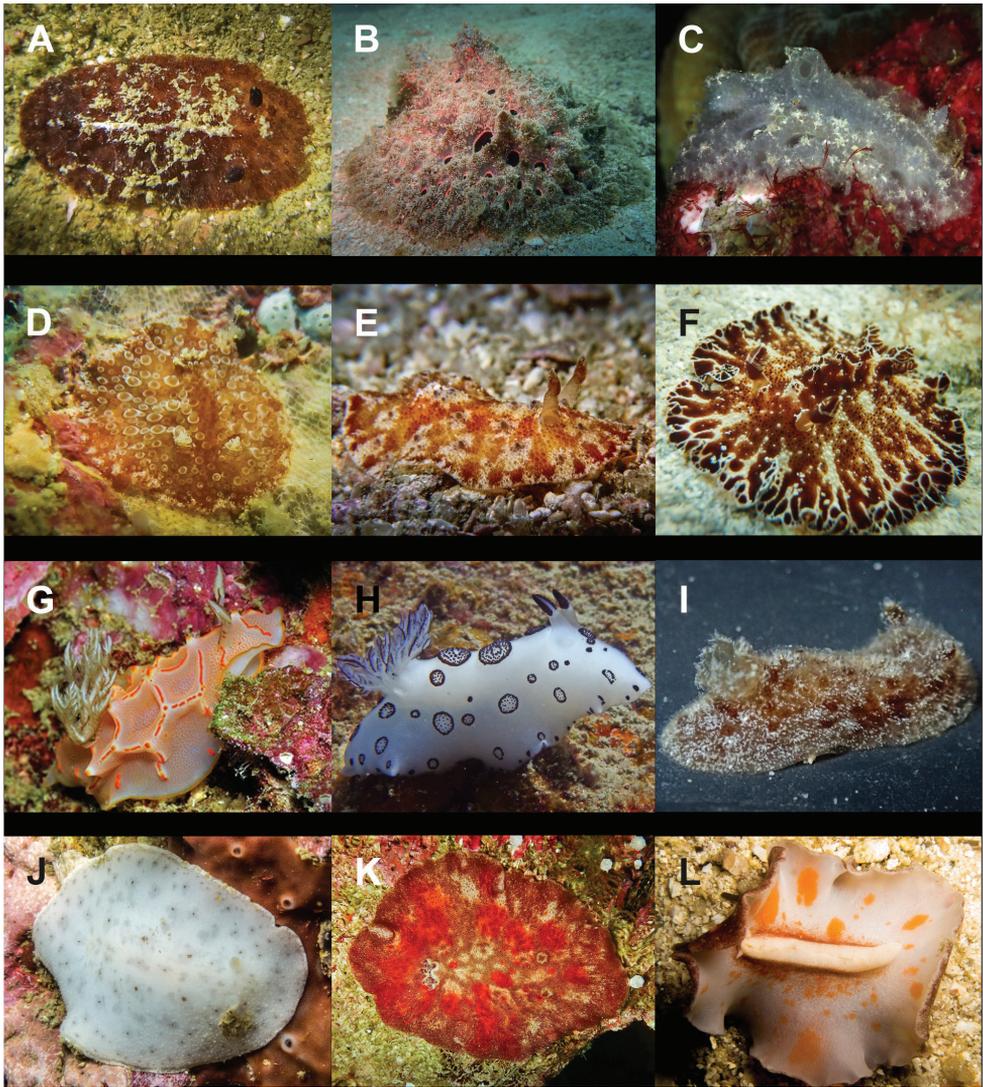
**Distribution.** Widespread Indo-Pacific including the Red Sea (Yonow 2008), Mozambique (Tibiriçá et al. 2017), Sri Lanka (Kelaart 1859), Indonesia (Debelius 1996), Australia (Nimbs and Smith 2016), Japan, Papua New Guinea, and Hawaii (Gosliner et al. 2008). Here representing a first record for Thai waters.

##### \**Atagema spongiosa* (Kelaart, 1858)

Figure 12B

**Material examined.** One specimen 95 mm, CB.

**Ecology.** Observed upon prey sponge *Dysidea* sp. in deeper soft sediment habitats. Depth 14–24 m.



**Figure 12.** **A** *Atagema intacta* 25 mm (photograph by Nick Tringham) **B** *Atagema spongiosa* 95 mm **C** *Atagema* sp. 32 mm **D** *Carminodoris* cf. *bifurcata* 9 mm **E** *Discodoris cebuensis* 30 mm (photograph by Kirsty Magson) **F** *Discodoris boholiensis* 55 mm **G** *Halgerda bacalusia* (unknown size, photograph by Stephan Pelletier) **H** *Jorunna funebris* 87 mm **I** *Jorunna* sp. 10 mm **J** *Peltodoris murrea* 30 mm **K, L** *Platydoris* cf. *formosa* 35 mm, dorsal and ventral views (photographs by Kirsty Magson).

**Distribution.** Gulf of Oman (Fatemi and Attaran 2015), Red Sea (Yonow 2008), India (Apte et al. 2010), Sri Lanka (Kelaart 1858), Australia (Nimbs and Smith 2016), Fiji (Brodie and Brodie 1990), Madagascar, Singapore, the Philippines, South Korea, and Papua New Guinea (Gosliner et al. 2008). Here representing a first record for Thai waters.

**\**Atagema* sp. (Kelaart, 1858)**

Figure 12C

**Material examined.** One specimen 32 mm, CB.

**Ecology.** Observed among rubble in shallow coral reef habitats at night with no observed association with prey. Depth 4–6 m.

**Distribution.** *Atagema* sp. 8 (Gosliner et al. 2018) is known only from the Philippines.

**Remarks.** Externally distinct from *Atagema spongiosa* (Kelaart, 1858) in being completely translucent pale grey, including the circular pits, separated by ridges, along the mantle. Similar to *Atagema* sp. 8 (Gosliner et al. 2018). Individuals from Koh Tao also differ from *A. spongiosa* in ecology, being observed in shallow reef environments instead of deeper soft sediment habitats.

**Genus *Carminodoris* Bergh, 1889****\**Carminodoris* cf. *bifurcata* Baba, 1993**

Figure 12D

**Material examined.** Two specimens 9–17 mm, HF.

**Ecology.** Among rubble in shallow coral reef habitats. Depth 3–8 m.

**Distribution.** *Carminodoris bifurcata* is recorded across the Indo-Pacific including from Mozambique (Tibirićá et al. 2017), the Red Sea (Yonow 2008), Korea (Koh 2006), the Philippines, Japan, and Hawaii (Gosliner and Fahey 2011) and *Carminodoris flammea* is recorded from Indonesia (Gosliner and Fahey 2011). Neither species has been previously recorded from Thai waters.

**Remarks.** Specimens from Koh Tao resemble both *Carminodoris bifurcata* Baba 1993 and *Carminodoris flammea* (Gosliner and Fahey 2011). They differ from the descriptions of the former by lacking any black spots on the dorsum and having a brown rather than grey ground colour and they differ from the latter in having brown rather than grey gill leaves, with white tips, and a tan median colouration instead of the bright red for which the species is named. A very similar looking specimen from Vietnam was identified as *Hoplodoris bifurcata* by Martynov and Korshunova (2012: pl. 31E). However, see discussions regarding *Carminodoris pustulata* (Abraham, 1877) by Jensen (1994), Yonow et al. (2002), and Yonow (2017) and indeed by Baba in the original description.

**Genus *Discodoris* Bergh, 1877****\**Discodoris cebuensis* Bergh, 1877**

Figure 12E

**Material examined.** One specimen 30 mm, SN.

**Ecology.** Locally found exclusively in soft sediment habitats. Depth 14–18 m.

**Distribution.** Across the Indo-Pacific including the Red Sea (Yonow 2008), South Africa (Gosliner 1987), Seychelles (Eliot 1910), Tanzania, the Philippines, Indonesia, Japan, Papua New Guinea, and Hawaii (Dayrat 2010). Here representing a first record for Thai waters.

***Discodoris boholiensis* Bergh, 1877**

Figure 12F

**Material examined.** One specimen 55 mm, SD.

**Ecology.** Found exclusively in soft sediment habitats. Depth 12–24 m.

**Distribution.** Widespread across the Indo-Pacific including India (Rao 1960), Vietnam (Risbec 1956), Singapore (Lim and Chou 1970), New Caledonia (Risbec 1928), Vanuatu (Coleman 2001), Madagascar, Indonesia, the Philippines, Palau, Papua New Guinea, Australia (Dayrat 2010), and the Gulf of Thailand (Chavanich et al. 2013).

**Genus *Halgerda* Bergh, 1880**

***Halgerda bacalusia* Fahey & Gosliner, 1999**

Figure 12G

**Material examined.** No specimen collected.

**Ecology.** Shallow coral reef habitats. Depth 5–10 m.

**Distribution.** The range of this species appears to be very limited thus far including only Myanmar (Gosliner et al. 2018) and Thailand, from both the Andaman coast (Fahey and Gosliner 1999) and Gulf of Thailand (Mehrotra and Scott 2016).

**Remarks.** Recorded at Koh Tao from a single individual in 2011 and not recorded since. The included figure (Fig. 12G) represents the only evidence of the species from the Gulf of Thailand. This largely agrees with the observations of the authors that specimens of the genus *Halgerda* are thus far exceptionally rare from within the Gulf of Thailand.

**Genus *Jorunna* Bergh, 1876**

***Jorunna funebris* (Kelaart, 1859)**

Figure 12H

**Material examined.** Two specimens 15–25 mm, LB; one specimen 30 mm, SI; one specimen 87 mm, CB.

**Ecology.** Abundant throughout corals and rubble in both nearshore reefs and offshore pinnacles. Rarely observed in soft sediment habitats. Depth 2–35 m; preys on blue *Xestospongia* sp. (Huang et al. 2016).

**Distribution.** Widespread in the Indo-Pacific including the Red Sea (Yonow 2008), India (Apte 2009), Sri Lanka (Kelaart 1859), Indonesia (Yonow 2011), Australia (Debelius 1996) Mauritius, Madagascar, Philippines, Japan, Palau, New Caledonia (Camacho-García and Gosliner 2008a), Malaysia (Ho 1989), Vietnam (Risbec 1956), and known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

**\**Jorunna* sp.**

Figure 12I

**Material examined.** Two specimens 10–15 mm, SB.

**Ecology.** Found exclusively in deeper soft sediment habitats. Depth 16–25 m.

**Distribution.** *Jorunna* sp. 7 recorded in the Philippines (Gosliner et al. 2018).

**Remarks.** An undescribed species covered in numerous long caryophyllidia, similar to *Jorunna* sp. 7 in Gosliner et al. (2018). Cream coloured dorsum with dark brown patches, white pigment on most caryophyllidia, dark brown rhizophore clubs with lamellae edged in white and white apices. Gills cream with some white. Here representing a first record for Thai waters.

**Genus *Peltodoris* Bergh, 1880**

**\**Peltodoris murrea* (Abraham, 1877)**

Figure 12J

**Material examined.** One specimen 30 mm, SR.

**Ecology.** Documented here from a single record found upon submerged concrete artificial substrate at an offshore pinnacle site. Depth 30 m.

**Distribution.** Widespread in the Indo-Pacific including the Red Sea (Yonow 2008), New Caledonia, Australia, Japan (Dayrat 2010), Indonesia, and Malaysia (Yonow 2017). Here representing a first record for Thai waters.

**Genus *Platydoris* Bergh, 1877**

**\**Platydoris* cf. *formosa* (Alder & Hancock, 1864)**

Figure 12K, L

**Material examined.** One specimen 20 mm, CA; two specimens 35–40 mm, SI.

**Ecology.** Among rubble at the coral reef edge. Depth 8–16 m.

**Distribution.** *Platydoris formosa* is known from Australia (Nimbs and Smith 2016), Tanzania, India, Indonesia, the Philippines, Samoa, New Caledonia, and Hawaii (Gosliner et al. 2008). *Platydoris cinereobranchiata* Dorgan et al., 2002 is known

from the Philippines, Australia, the Solomon Islands (Gosliner et al. 2008), and Indonesia (Yonow 2011). Neither species has yet been documented in Thai waters.

**Remarks.** Externally, the specimens bear similarity to *Platydoris formosa*, as detailed by Dorgan et al. (2002) although differ in numerous ways. The rhinophores of the present species are yellow to pale brown, sometimes with red spots near the apex, with no black spots between them. Rhinophores have 33–35 lamellae. The gills are grey with dark brownish red lines running along the rachises, with no black spots anterior to the gill sheath. A white ring is present around the rims of the rhinophore and gill sheaths. Most of the caryophyllidia covering the dorsum are a dark reddish colour with a few white patches randomly distributed. Larger bright red patches are more numerous and also randomly distributed across the dorsal surface. Ventrally white with large red spots which become more diffuse and concentrated towards the foot. Based on these characteristics, it appears that the specimens from Koh Tao bear characteristics of both *P. formosa* and *P. cinereobranchiata*.

### Genus *Rostanga* Bergh, 1879

#### \**Rostanga* sp.

Figure 13A

**Material examined.** Two specimens 6–18 mm, CB.

**Ecology.** Exclusively found under coral rubble and the skeletons of dead Fungiidae corals. Cryptic on its pink-red sponge. Depth 3–8 m.

**Distribution.** Unknown.

**Remarks.** The present species is only identified based on external morphology and as such has not been identified to species level. Chavanich et al. (2013) documented *Rostanga orientalis* Rudman & Avern, 1989 from the Gulf of Thailand, which bears some external similarities to the present specimens.

### Genus *Sebadoris* Er. Marcus & Ev. Marcus, 1960

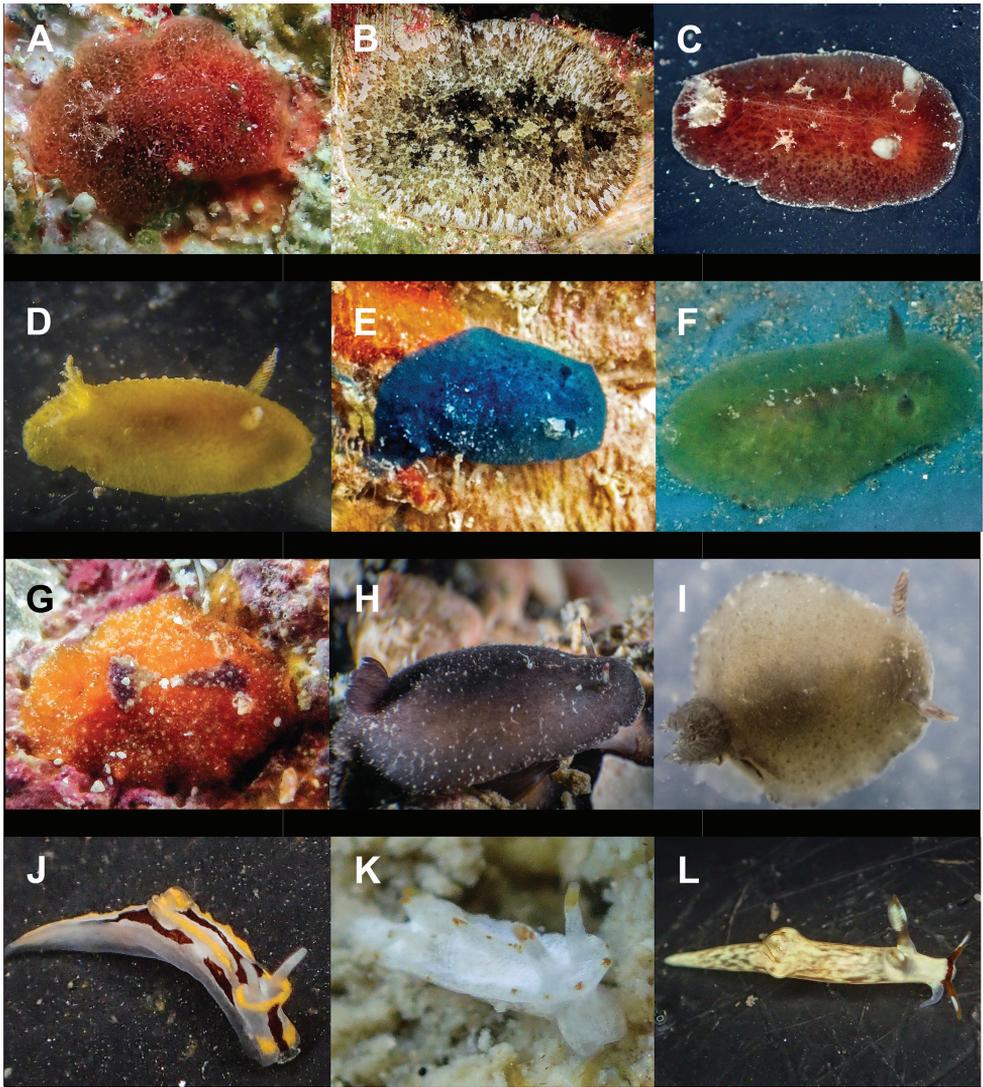
#### \**Sebadoris fragilis* (Alder & Hancock, 1864)

Figure 13B

**Material examined.** One specimen 70 mm, SB.

**Ecology.** Found under coral rubble and the skeletons of dead Fungiidae corals. Depth 3–8 m.

**Distribution.** Across the Indo-Pacific including Madagascar (Gosliner et al. 2008), Red Sea (Yonow 2008), Kuwait (Nithyanandan 2012), India (Bhave and Apte 2011), Indonesia, the Philippines, Papua New Guinea (Yonow 2017), and known from the Gulf of Thailand (Chavanich et al. 2013).



**Figure 13.** **A** *Rostanga* sp. 18 mm **B** *Sebadoris fragilis* 70 mm **C** *Thordisa* sp. 12 mm **D** *Doriopsis* cf. *granulosa* 7 mm **E** *Doriopsis pecten* 6 mm **F** *Doriopsis viridis* 4 mm **G** *Doris* cf. *immonda* 5 mm **H, I** Dorididae sp. 15 mm (**H** photograph by Jeremy Coz) and 8 mm (**I**) **J** *Goniodoridella* sp. 1.6 mm **K** *Goniodoridella* sp. 2.3 mm (photograph by Khumron Waipaka) **L** *Trapania* cf. *gibbera* 5 mm.

### Genus *Thordisa* Bergh, 1877

#### \**Thordisa* sp.

Figure 13C

**Material examined.** One specimen 12 mm, TT.

**Ecology.** Found in soft sediment habitats at 16 m depth.

**Distribution.** Unknown.

**Remarks.** Dorsal colour deep red, with white rhinophore clubs and gills. The most distinctive feature of the species appears to be a pair of distinct, elongated, white, conical papillae surrounded by 5–7 white extensions radiating out at the base of each papilla, on either side of the mid-dorsal ridge. Besides these are a few smaller but still elongated white papillae randomly distributed. Additionally, the base of the white gills and translucent red rhinophore stalks is surrounded by a thin white line which similarly can be found around the margin of the mantle. The most similar known species might be *T. sanguinea* Baba, 1955 which may be distinguished based on the ground colour, dorsal ornamentation (covered in papillae), and the colour of the rhinophores and gills.

### Family Dorididae Rafinesque, 1815

#### Genus *Doriopsis* Pease, 1860

##### \**Doriopsis* cf. *granulosa* (Pease, 1860)

Figure 13D

**Material examined.** One specimen 7 mm, HF.

**Ecology.** Under reef rubble and on rocks in coral reef habitats. Cryptic on its yellow prey sponge. Depth 6–12 m.

**Distribution.** *Doriopsis granulosa* is found across the Indo-Pacific including India (Apte and Bhawe 2014), Seychelles (Gosliner et al. 2008), Tanzania (Edmunds 1971), Japan (Baba and Hamatani 1961), Hong Kong (Orr 1981), Australia (Nimbs and Smith 2016), and Hawaii (Kay and Young 1969). Here representing a first record for Thai waters.

**Remarks.** While clearly resembling *Doriopsis granulosa* (Pease, 1860) by an overall yellow dorsum, six gill leaves arranged horizontally in an almost transverse line, and numerous low, rounded tubercles, it bears differences from other descriptions (see Baba and Hamatani 1961; Valdés 2002; Apte and Bhawe 2014). These include the absence of any brown spots along the dorsum and rhinophores that are not uniformly yellow-orange but instead have translucent stalks and abruptly transition from a yellow base to a white apex, separated by a thin brown median line. These subtle differences may be found to be within the variability of the species and cannot be confirmed without a closer investigation.

##### \**Doriopsis pecten* Collingwood, 1881

Figure 13E

**Material examined.** Two specimens 6 mm, CB.

**Ecology.** Among rubble in coral reef habitats. Depth 3–6 m.

**Distribution.** Across the Indo-Pacific including Taiwan (Collingwood 1881), Vietnam (Martynov and Korshunova 2012), the Philippines, Indonesia (Yonow 2017), New Caledonia (Risbec 1953), South Africa, Madagascar, and Hawaii (Gosliner et al. 2008). Previously documented from the Gulf of Thailand (Chavanich et al. 2013).

**\**Doriopsis viridis* (Pease, 1861)**

Figure 13F

**Material examined.** Two specimens 4–6 mm, CB.

**Ecology.** Among rubble in coral reef habitats. Depth: 3–6 m.

**Distribution.** Known from China (Lin 1990), Vietnam (Risbec 1956), Tahiti, Hawaii, and western Mexico (Gosliner et al. 2008). Here representing a first record for Thai waters.

**Genus *Doris* Linnaeus, 1758**

**\**Doris* cf. *immonda* Risbec, 1928**

Figure 13G

**Material examined.** One specimen 5 mm, HF.

**Ecology.** Under reef rubble and on rocks in coral reef habitats. Cryptic on its orange prey sponge. Depth 6–12 m.

**Distribution.** *Doris immonda* is known across the Indo-Pacific including Japan (Rudman 2000a), Australia (Nimbs and Smith 2016), Papua New Guinea, New Caledonia, Hawaii (Gosliner et al. 2008), and the Pacific coast of Costa Rica (Camacho-García and Gosliner 2008b). Here representing a first record for Thai waters.

**Remarks.** Broadly matches the description and variations highlighted by Valdés (2002); however, like specimens of *D. cf. granulosa*, specimens documented from Koh Tao differ in colouration from *Doris immonda*. The dorsal colour is a bright orange with numerous rounded or conical tubercles covering the surface, many capped in white. The Y-shaped marking between the rhinophores to in front of the gills is made up of purple tubercles and the rhinophore club is a pale brown with white edges of lamellae. As above, this variation in colouration may yet be considered to be within what can be found in *Doris immonda* Risbec, 1928.

**\*Dorididae sp.**

Figure 13H, I

**Material examined.** Three specimens 6–15 mm, SN.

**Ecology.** In soft sediment habitats beyond the coral reef.

**Distribution.** Unknown. Currently only documented from Koh Tao.

**Remarks.** A small dorid with a dark mantle ranging from grey to dark brown, covered in numerous small, clearly separated pustules. Gills arranged circularly, pinnate, dark brown. The lamellate rhinophores are basally dark brown with translucent white clubs and reddish brown apices with white tips. A much more in-depth analysis of this species is needed to ascertain its placement.

**Superfamily Onchidoridoidea Gray, 1827**

**Family Goniadorididae H. Adams & A. Adams, 1854**

**Genus *Goniadoridella* Pruvot-Fol, 1933**

***Goniadoridella* sp. 1**

Figure 13J

**Material examined.** One specimen 5 mm, TT; two specimens 6–8 mm, CA.

**Ecology.** Rare and cryptic within coral reef habitats. Depth 8–24 m.

**Distribution.** Similar to *Goniadoridella* sp. 2 (Gosliner et al. 2008) which is known only from the Philippines and Papua New Guinea. First documented from the Gulf of Thailand by Mehrotra and Scott (2016).

**\**Goniadoridella* sp. 2**

Figure 13K

**Material examined.** One specimen 3 mm, SI.

**Ecology.** Rare and cryptic within coral reef habitats. Depth 14 m.

**Distribution.** Similar to *Goniadoridella* sp. 10 (Gosliner et al. 2018) which is known only from the Indonesia. Here documented as a first record for Thai waters.

**Genus *Trapania* Pruvot-Fol, 1931**

**\**Trapania* cf. *gibbera* Gosliner & Fahey, 2008**

Figure 13L

**Material examined.** One specimen 5 mm, CB.

**Ecology.** Under rubble in shallow coral reefs. Depth 4–6 m.

**Distribution.** *Trapania gibbera* is known from Indonesia, Japan, and Papua New Guinea (Gosliner and Fahey 2008). Here representing a first record for Thai waters.

**Remarks.** Specimens from Koh Tao differ slightly from *Trapania gibbera* Gosliner and Fahey 2008 in colouration. The ‘hump’ located anterior to the gills, for which *T. gibbera* was named, is also seen in specimens from Koh Tao. The dorsal colouration is tan rather than white with numerous reddish brown patches spread over the body, sometimes giving animals a reticulated appearance. Rhinophore clubs

have nine lamellae that are mostly white with some edges being red, with translucent red stalks and red apices. A deep red mark can be seen at the anterior margin of the head that extends to the oral tentacles, which turn orange-brown and have a single distinctive white spot on the dorsal surface of each. Ventrally the oral tentacles are entirely orange.

**\**Trapania miltabranca* Gosliner & Fahey, 2008**

Figure 14A, B

**Material examined.** Three specimens 8–25 mm, LB.

**Ecology.** Among colonies of Didemnid tunicates in soft sediment habitats. Depth 12–15 m.

**Distribution.** Known only from Indonesia (Gosliner and Fahey 2008) and Japan (Uyeno and Nagasawa 2012). Here representing a first record for Thai waters

**Remarks.** While known to be predators of Entoprocta (Gosliner et al. 2018), the present individuals were all found directly upon *Didemnum molle* tunicate colonies in soft sediment habitats. While active feeding could not be confirmed, it is of interest to note that all 12 individuals recorded were initially found crawling upon the tunicates and not upon the benthos which may indicate the presence of a prey source associated with the tunicates but feeding investigations were not carried out.

**Superfamily Phyllidioidea Rafinesque, 1814**

**Family Dendrodorididae O’Donoghue, 1924 (1864)**

**Genus *Dendrodoris* Ehrenberg, 1831**

**\**Dendrodoris coronata* Kay & Young, 1969**

Figure 14C

**Material examined.** One specimen 30 mm, LT.

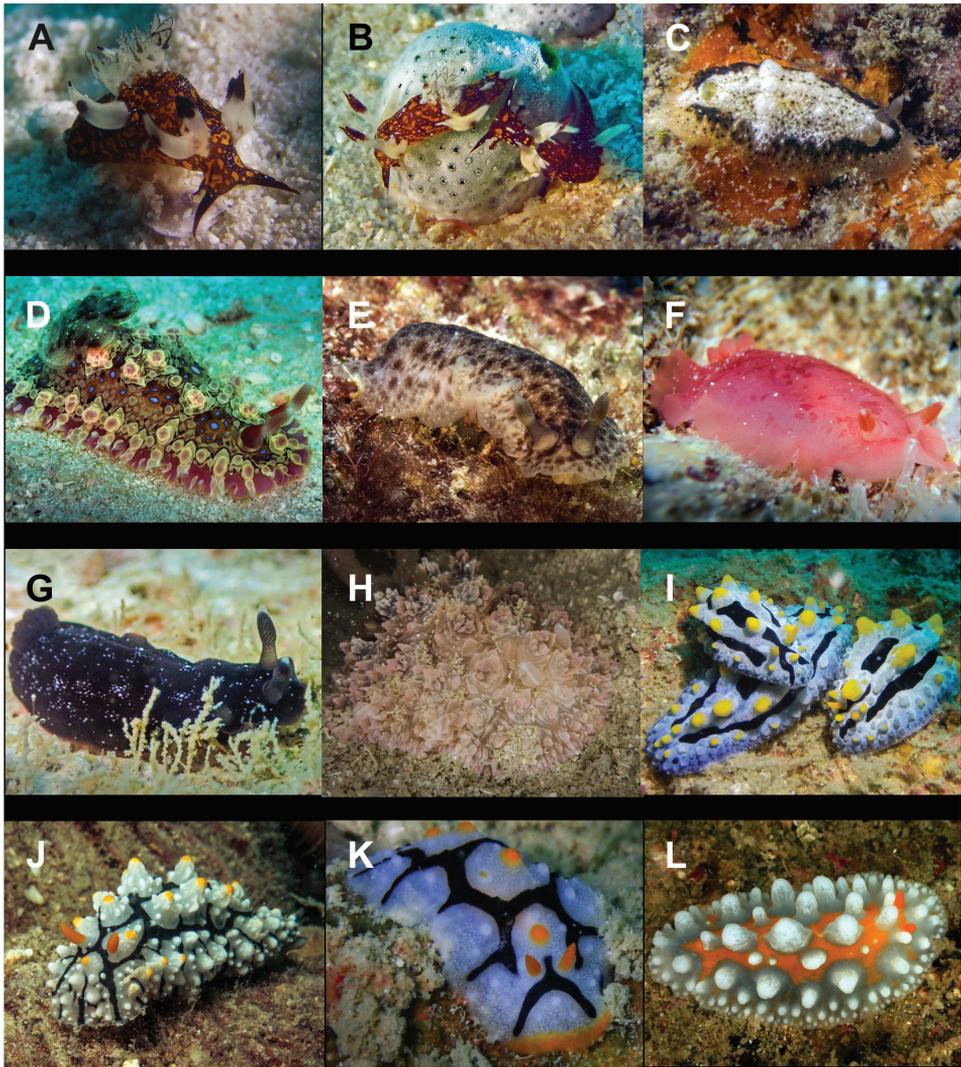
**Ecology.** On rocks and among corals in shallow reefs. Depth 2–6 m.

**Distribution.** Widespread in the Indo-Pacific including the Red Sea (Yonow 2008), Mozambique (Tibirićá et al. 2017), Japan, Australia, Palau, Papua New Guinea, New Caledonia, Marshall Islands (Gosliner et al. 2008), probably Indonesia (Yonow 2017), and Hawaii (Kay and Young 1969). Here representing a first record for Thai waters.

***Dendrodoris krusensternii* (Gray, 1850)**

Figure 14D

**Material examined.** Three specimens 8–45 mm, TT; one specimen 22 mm, SB.



**Figure 14.** **A, B** *Trapania miltabrancha* 25 mm (**A**) two specimens on *Didemnum molle* (**B**) **C** *Dendrodoris coronata* 30 mm (photograph by Kirsty Magson) **D** *Dendrodoris krusensternii* 45 mm **E** *Dendrodoris elongata* 29 mm **F** *Dendrodoris fumata* 55 mm **G** *Dendrodoris nigra* 16 mm **H** *Dendrodoris tuberculosa* 88 mm **I** *Phyllidia coelestis* specimens 25–35 mm **J** *Phyllidia elegans* 45 mm (photograph by Pau Urgell Plaza) **K** *Phyllidia exquisita* 30 mm **L** *Phyllidia ocellata* 60 mm.

**Ecology.** Exclusively recorded from soft sediment habitats beyond the fringing coral reef. Depth 14–26 m.

**Distribution.** Widespread in the Indo-Pacific including the Red Sea (Yonow 2015), Mozambique (Tibirić et al. 2017), South Africa, Hawaii (Gosliner 1987), Singapore, the Philippines, Indonesia, Korea, Papua New Guinea, New Caledonia, New

Zealand (Gosliner et al. 2008), Japan (Baba 1949), Australia (Angas 1864) and known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

**\**Dendrodoris elongata* Baba, 1936**

Figure 14E

**Material examined.** Three specimens 29–42 mm, CB.

**Ecology.** Found under coral rubble and the skeletons of dead Fungiidae corals. Depth 3–8 m.

**Distribution.** Across the Indo-Pacific including the Red Sea (Yonow 2008), India (Vadher and Kardani 2018), Vietnam (Risbec 1956), China (Lin 1990), Malaysia, the Philippines, Australia, New Caledonia, Fiji (Gosliner et al. 2008), and Indonesia (Yonow 2017). Here representing a first record for Thai waters.

**\**Dendrodoris fumata* (Rüppell & Leuckart, 1830)**

Figure 14F

**Material examined.** One specimen 7 mm, SB; one specimen 55 mm, CB.

**Ecology.** Found under coral rubble and the skeletons of dead fungiid corals. Depth 3–8 m

**Distribution.** Widespread in the Indo-Pacific including South Africa, Tanzania, Madagascar, Malaysia, Palau, Vanuatu, New Caledonia, Hawaii (Gosliner et al. 2008), Red Sea (Yonow 2008), Mauritius, Socotra, Persian Gulf, La Réunion (Yonow 2012), Hong Kong, Papua New Guinea, Fiji, Australia (Brodie et al. 1997), Indonesia (Yonow 2017), and known from the Gulf of Thailand (Chavanich et al. 2013).

***Dendrodoris nigra* (Stimpson, 1855)**

Figure 14G

**Material examined.** Two specimens 8–16 mm, LT; one specimen 25 mm, MH.

**Ecology.** Found under coral rubble and the skeletons of dead Fungiidae corals. More abundant towards the edge of the reef, less abundant but present in soft sediment habitats outside of the coral reef. Depth 2–25 m.

**Distribution.** Widespread in the Indo-Pacific including Mozambique (Tibirićá et al. 2017), Mauritius (Yonow and Hayward 1991), Red Sea (Yonow 1990), South Africa (Gosliner 1987), Socotra, Maldives, Zanzibar, Gulf of Oman, Seychelles, La Réunion, (Yonow 2012), India (Apte 2009), Gulf of Oman (Fatemi and Attaran 2015), Indonesia (Yonow 2017), Vietnam (Risbec 1956), Japan (Stimpson 1855), Australia (Burn 2006), Hawaii (Kay and Young 1969), and known from both Andaman and Gulf waters of Thailand (Jensen 1998; Chavanich et al. 2013).

***Dendrodoris tuberculosa* (Quoy & Gaimard, 1832)**

Figure 14H

**Material examined.** Two specimens 24–88 mm, TT.**Ecology.** Found in soft sediment habitats outside the coral reef alongside *D. kruse-nsternii*. Incorrectly classified as a coral reef-associated species from Koh Tao (Mehrotra and Scott 2016) based on a single observation in shallower waters nearer the coral reef.**Distribution.** Widespread in the Indo-Pacific including the Red Sea (Yonow 2008), Tanzania, South Africa, Maldives, Malaysia, Philippines, Korea, Papua New Guinea, Australia, Solomon Islands, Marshall Islands (Gosliner et al. 2008), Mozambique (Tibiriçá et al. 2017), India (Apte 2009), Chagos (Yonow et al. 2002), Vietnam (Risbec 1956), Japan (Baba 1949), Hawaii (Kay and Young 1969), and known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013; Mehrotra and Scott 2016).**Family Phyllidiidae Rafinesque, 1814****Genus *Phyllidia* Cuvier, 1797*****Phyllidia coelestis* Bergh, 1905**

Figure 14I

**Material examined.** Three specimens 25–35 mm, GR.**Ecology.** Abundant in coral reef habitats. Depth 3–30 m**Distribution.** Widespread in the Indo-Pacific including Mozambique (Tibiriçá et al. 2017), South Africa (Brunckhorst 1993), Madagascar, Seychelles (Yonow 2012), Tanzania (Edmunds 1972), Sri Lanka (Yonow 1984), Chagos Islands (Yonow et al. 2002), India (Apte 2009), the Philippines, Japan, Papua New Guinea (Gosliner et al. 2008), Australia (Nimbs and Smith 2016), China (Lin 1990), Indonesia (Yonow 2011), and known from both Andaman and Gulf waters of Thailand (Brunckhorst 1993; Chavanich et al. 2013).***Phyllidia elegans* Bergh, 1869**

Figure 14J

**Material examined.** One specimen 45 mm, LT; one specimen 30 mm, RR; one specimen 45 mm, SP.**Ecology.** Abundant in coral reef habitats. Depth 3–30 m**Distribution.** Widespread in the western Pacific including), Indonesia, Taiwan, Australia, Guam, Solomon Islands (Brunckhorst 1993), Myanmar, Malaysia, the Philippines, Japan, Fiji, Papua New Guinea, Vanuatu (Gosliner et al. 2008), Vietnam (Risbec 1956), China (Lin 1990), Singapore (Lim and Chou 1970) and known from both Andaman and Gulf waters of Thailand (Brunckhorst 1993; Chavanich et al. 2013).

**\**Phyllidia exquisita* Brunckhorst, 1993**

Figure 14K

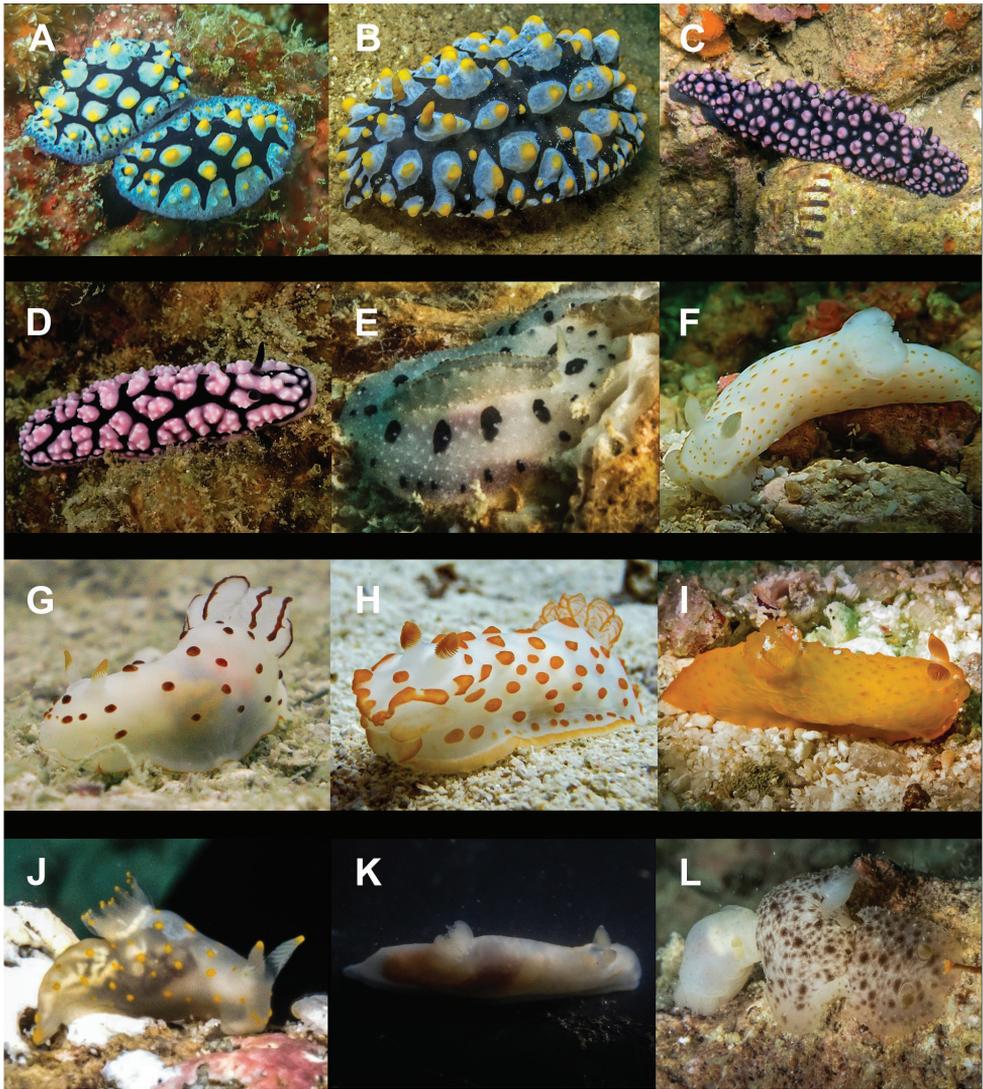
**Material examined.** One specimen 30 mm, SI.**Ecology.** Rare, found in coral reef habitats, Depth 15 m.**Distribution.** Known from the Maldives (Yonow 2012), Vietnam (Martynov and Korshunova 2012), Hong Kong (Orr 1981), Malaysia, Indonesia, Philippines, Palau, Japan (Gosliner et al. 2008), Australia, Papua New Guinea, Fiji, the Marshall Islands, and the Andaman sea of Thailand (Brunckhorst 1993). Here representing a first record for the Gulf of Thailand.***Phyllidia ocellata* Cuvier, 1804**

Figure 14L

**Material examined.** One specimen 30 mm, AMN; one specimen 65 mm, SP; three specimens 45–60 mm, HF.**Ecology.** Abundant in coral reef, reef edge, and soft sediment habitats. Depth 3–30 m.**Distribution.** Widespread in the Indo-Pacific including Mozambique (Tibirić et al. 2017), Oman, Sri Lanka, the Philippines (Debelius 1996), India (Ramakrishna et al. 2010), Myanmar (Sanpanich and Duangdee 2019), Indonesia (Yonow 1996), South Africa, Mauritius, Madagascar, Tanzania, Japan, Papua New Guinea, Australia, Guam, Fiji, Vanuatu (Gosliner et al. 2008) and known from both Andaman and Gulf waters of Thailand (Brunckhorst 1993; Chavanich et al. 2013).***Phyllidia picta* Pruvot-Fol, 1957**

Figure 15A

**Material examined.** Two specimens 28 mm, CB; one specimen 33 mm, TB.**Ecology.** Abundant in coral reef habitats. Depth 3–30 m**Distribution.** Known mostly from South-East Asia and the western Pacific including Malaysia, the Philippines, Indonesia, Hong Kong, Papua New Guinea, Australia, Japan, Fiji, Vanuatu, the Solomon Islands (Gosliner et al. 2008) and known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013). Indian Ocean records are limited but include Socotra Island and Christmas Island (Yonow 1996, 2012).**Remarks.** External identification of some specimens yielded the incorrect inclusion of *Phyllidia marindica* (Yonow & Hayward, 1991) by Mehrotra and Scott (2016) from Koh Tao. More intensive surveys have yielded no specimens that externally match *P. marindica*, which appears to be limited to the Indian Ocean. Brunckhorst (1993) recorded this species from the Andaman coast of Thailand and later Chavanich et al.



**Figure 15.** **A** *Phyllidia picta* specimens 28 mm **B** *Phyllidia varicosa* 55 mm (photograph by Pau Urgell Plaza) **C** *Phyllidiella nigra* 50 mm **D** *Phyllidiella* cf. *pustulosa* 35 mm **E** *Phyllidiopsis loricata* 28 mm **F** *Gymnodoris* cf. *alba* 25 mm (photograph by Tine Kvamme) **G** *Gymnodoris ceylonica* 35 mm **H** *Gymnodoris impudica* 60 mm **I** *Gymnodoris inornata* 28 mm (photograph by Pau Urgell Plaza) **J** *Gymnodoris* sp. 1 25 mm (photograph by Pim Bontenbal) **K, L** *Gymnodoris* sp. 2 14 mm, same specimen feeding on *Dendrodoris elongata*.

(2013) included the species from the Gulf of Thailand. Collections of *P. marindica* from the Gulf of Thailand are needed to firmly establish its presence within the Gulf and therefore indicating its range as one not exclusive to the Indian Ocean.

***Phyllidia varicosa* Lamarck, 1801**

Figure 15B

**Material examined.** One specimen 32 mm, HWB; one specimen 55 mm, SR.

**Ecology.** Abundant in coral reef habitats. Depth 3–30 m.

**Distribution.** Widespread in the Indo-Pacific including the Red Sea (Yonow 1996), South Africa (Gosliner 1987), Tanzania (Edmunds 1971), Mozambique (Tibiriçá et al. 2017), Madagascar (Risbec 1928), Socotra, Kenya, Mauritius, Zanzibar, Seychelles, Maldives (Yonow 2012), Chagos Islands (Yonow et al. 2002), Sri Lanka, Hawaii (Debelius 1996), India (Apte 2009), Myanmar (Sanpanich and Duangdee 2019), Philippines, Vietnam (Brunckhorst 1993), Indonesia (Yonow 2011), Australia (Nimbs and Smith 2016), Palau, Japan, Papua New Guinea (Gosliner et al. 2008), and known from both Andaman and Gulf waters of Thailand (Brunckhorst 1993; Chavanich et al. 2013).

**Genus *Phyllidiella* Bergh, 1869*****Phyllidiella nigra* (van Hasselt, 1824)**

Figure 15C

**Material examined.** One specimen 50 mm, AMN; one specimen 50 mm, TB.

**Ecology.** Abundant in coral reef habitats. Depth 3–30 m.

**Distribution.** Widespread in the Indo-Pacific including the Philippines, Australia, Papua New Guinea (Brunckhorst 1993), Myanmar (Sanpanich and Duangdee 2019), Malaysia, Vietnam, Indonesia, Japan, Palau, Guam (Gosliner et al. 2008), and known from both Andaman and Gulf waters of Thailand (Swennen et al. 2001; Chavanich et al. 2013).

***Phyllidiella* cf. *pustulosa* (Cuvier, 1804)**

Figure 15D

**Material examined.** Two specimens 35–40 mm, TT; one specimen 35 mm, CB.

**Ecology.** Abundant in coral reef habitats. Depth 3–30 m.

**Distribution.** '*Phyllidiella pustulosa*' is known from India (Apte 2009), the Red Sea, Indonesia, the Philippines, Japan, Papua New Guinea, Australia, Fiji (Brunckhorst 1993), Hawaii (Gosliner et al. 2008), both Andaman and Gulf waters of Thailand (Brunckhorst 1993; Chavanich et al. 2013), and an externally different morphotype referred to as '*Phyllidiella* cf. *pustulosa*' is known from Mozambique (Tibiriçá et al. 2017).

**Remarks.** Morphological and molecular work (Chang and Willan 2015; Stoffels et al. 2016) has indicated that *P. pustulosa* is composed of a number of cryptic species. Specimens recorded from Koh Tao externally look similar to those

illustrated in Brunckhorst (1993: pl. 5E, F) and Stoffels et al. (2016: figs 11I, J, 12F, 13B) but dissimilar from specimens in Mozambique (Tibiriçá et al. 2017: figs 20C, D).

### Genus *Phyllidiopsis* Bergh, 1876

#### *Phyllidiopsis loricata* (Bergh, 1873)

Figure 15E

**Material examined.** One specimen 28 mm, SB; one specimen 15 mm, CP.

**Ecology.** Under and among rocks and coral rubble. Depth 3–30 m.

**Distribution.** Across the Indo-Pacific including Australia, Guam, Marshall Islands, Tahiti (Brunckhorst 1993), western Indian Ocean of Réunion, Papua New Guinea, Hawaii (Gosliner et al. 2008) and Singapore (Lim and Chou 1970). First documented from the Gulf of Thailand by Mehrotra and Scott (2016).

### Superfamily Polyceroidea Alder & Hancock, 1845

#### Family Polyceridae Alder & Hancock, 1845

#### Genus *Gymnodoris* Stimpson, 1855

#### *Gymnodoris* cf. *alba* (Bergh, 1877)

Figure 15F

**Material examined.** One specimen 25 mm, SI.

**Ecology.** Among coral and rubble in coral reef habitats. Depth 4–18 m.

**Distribution.** *Gymnodoris alba* is currently believed to be found across the Indo-Pacific, from the Red Sea (Yonow 2008), Australia (Nimbs and Smith 2016), South Africa, the Philippines, Japan, Papua New Guinea, and Hawaii (Gosliner et al. 2008). *Gymnodoris alba* is also known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

**Remarks.** Similar to *Gymnodoris alba* (Bergh, 1877) but more observations and material are needed to confidently ascertain an identification. A clarification of the *G. alba* species complex and indeed a revision of the genus is sorely needed to provide a biogeographical and taxonomic understanding of *Gymnodoris* in the Indo-Pacific. This species was first recorded as *Gymnodoris* sp. by Mehrotra and Scott (2016: fig. 2E) and is distinct from specimens of *G. alba* as recorded in both Andaman and Gulf waters by Chavanich et al. (2013).

#### *Gymnodoris ceylonica* (Kelaart, 1858)

Figure 15G

**Material examined.** Two specimen 35 mm, TB.

**Ecology.** Exclusively recorded from soft sediment habitats beyond the fringing coral reef. Depth 14 m.

**Distribution.** Widespread in the Indo-Pacific including Mozambique (Tibirićá et al. 2017), the Red Sea (Yonow 1990), Indonesia (Debelius 1996), India (Apte 2009), Taiwan (Huang et al. 2015), Singapore (Lim and Chou 1970), Réunion Island, Seychelles, Sri Lanka, the Philippines, Japan, Papua New Guinea, Australia, Guam, Marshall Islands (Gosliner et al. 2008), and known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013; Mehrotra and Scott 2016).

### *Gymnodoris impudica* (Rüppell & Leuckart, 1830)

Figure 15H

**Material examined.** One specimen 45 mm, TT; two specimens 65 mm, HF; one specimen 60 mm, TW.

**Ecology.** In coral reef, rubble and soft sediment habitats throughout the island and nearby offshore pinnacles. Depth 5–25 m.

**Distribution.** Widespread in the Indo-Pacific including the Red Sea (Yonow 2008), Mozambique (Tibirićá et al. 2017), India (Ramakrishna et al. 2010), Singapore (Lim and Chou 1970), Japan (Baba 1949), South Africa, Tanzania, the Philippines, Indonesia, New Caledonia, Hawaii (Gosliner et al. 2008) and known from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

### \**Gymnodoris inornata* (Bergh, 1880)

Figure 15I

**Material examined.** One specimen 28 mm, HF.

**Ecology.** Among coral and rubble in coral reef habitats. Depth 6–12 m.

**Distribution.** Widespread in the Indo-Pacific including Mozambique (Tibirićá et al. 2017), China (Lin 1990), Hong Kong (Orr 1981), Japan (Baba 1949), Australia (Nimbs and Smith 2016), South Africa, Tanzania, Red Sea, Indonesia, Philippines, New Caledonia, and Hawaii (Gosliner et al. 2008). Here representing a first record for Thai waters.

### *Gymnodoris* sp. 1

Figure 15J

**Material examined.** One specimen 25 mm, TT.

**Ecology.** On rocks and among coral and rubble in coral reef habitats. Depth 4–18 m.

**Distribution.** First documented as *Gymnodoris* sp. from the Gulf of Thailand by Mehrotra and Scott (2016: fig. 2D). Similar *Gymnodoris* species (Gosliner et al. 2008: sp. 5; Gosliner et al. 2018: sp. 21) known from Japan and Papua New Guinea only.

**\**Gymnodoris* sp. 2**

Figure 15K, L

**Material examined.** One specimen 14 mm, CB.**Ecology.** Among rubble in shallow coral reef habitats, observed feeding on *Dendrodoris elongata* by progressively feeding on the extended mantle around the animal. Depth 6 m.**Distribution.** Unknown.**Remarks.** Resembling multiple species considered undescribed according to Gosliner et al. (2008, 2018). Gills white, pinnate, overall body relatively cylindrical, translucent white with numerous very small yellow-orange spots throughout the dorsum, internal viscera visible throughout. Rhinophores triangular, pale yellow.**\**Gymnodoris* sp. 3**

Figure 16A

**Material examined.** One specimen 12 mm, HF.**Ecology.** Among rubble in coral reef habitats. Depth 6–12 m.**Distribution.** *Gymnodoris* sp. 36 (Gosliner et al. 2018) is known from the Philippines and Papua New Guinea.**Remarks.** Smooth, translucent white dorsum with club shaped gill leaves. Observed feeding on an unknown nudibranch species (Fig. 16A).**\**Gymnodoris nigricolor* Baba, 1960**

Figure 16B

**Material examined.** Two specimens 5–7 mm, SN.**Ecology.** Recorded exclusively from deeper soft sediment habitats, crawling on the substrate. Depth 19–27 m.**Distribution.** *Gymnodoris nigricolor* is known from the Philippines, Japan, New Caledonia, and the Solomon Islands (Gosliner et al. 2008). Here recorded as a first for Thai waters.**Remarks.** The present species closely resembles externally the description by Baba (1960) possessing a black (sometimes translucent black) dorsum and rhinophores, and a translucent foot. The gills match the description in being black, small, and club-shaped and arranged in a semi-circle. It should also be noted that the plate supplementing the original description of the species shows gills in a circular arrangement and seemingly plumose rather than reduced and club shaped. While the species is known to be parasite of gobies (Osumi and Yamasu 1994), all observations from Koh Tao were not in the vicinity of any demersal fish, including any in the family Gobiidae. Ongoing searches of gobies from both soft sediment and coral reef habitats have thus far revealed no observations of parasitic nudibranchs.



**Figure 16.** **A** *Gymnodoris* sp. 3 12 mm **B** *Gymnodoris nigricolor* 5 mm **C** *Gymnodoris* cf. *nigricolor* 6 mm **D** *Gymnodoris* sp. 4 9 mm **E** *Plocamopherus tilesii* 90 mm **F** *Polycera* sp. 12 mm **G** *Tambja amakusana* 6 mm (photograph by Richard Brinke) **H** *Tambja pulcherrima* 40 mm (photograph by Liam Kelly) **I** *Tambja* sp. 4 mm (photo by Kaitlyn Harris) **J** *Thecacera* sp. 6 mm **K** *Antaeaeolidiella* sp. 15 mm **L** *Aeolidiopsis harrietae* 17 mm.

**\**Gymnodoris* cf. *nigricolor* Baba, 1960**

Figure 16C

**Material examined.** One specimen 6 mm, SB; one specimen 7 mm, LB.

**Ecology.** Recorded exclusively from deeper soft sediment habitats, crawling on the substrate. Depth 19–27 m.

**Distribution.** Unknown

**Remarks.** Strikingly similar to *Gymnodoris nigricolor* from Koh Tao in sharing habitat, size, and much of their external morphology except the arc of gills. Both observed specimens, several months and kilometres apart, were found to possess white club-shaped gills instead of black. As such we treat this species as likely distinct.

**\**Gymnodoris* sp. 4**

Figure 16D

**Material examined.** One specimen 9 mm, TW.

**Ecology.** In soft sediment habitats beyond fringing coral reefs. Depth 12–16 m.

**Distribution.** So far only recorded in the Gulf of Thailand.

**Remarks.** Incorrectly identified as *Gymnodoris bicolor* (Alder & Hancock, 1864) by Mehrotra and Scott (2016) due to low quality images, additional material has shown several unique differences, including translucent club-shaped gills with yellow tips in an arc and a prominently raised area between the eyes, behind the rhinophores.

**Genus *Plocamopherus* Rüppell & Leuckart, 1828**

**\**Plocamopherus tilesii* Bergh, 1877**

Figure 16E

**Material examined.** Two specimens 102 mm, TT.

**Ecology.** Exclusively recorded from soft sediment habitats beyond the fringing coral reef. Depth 18–25 m.

**Distribution.** *Plocamopherus tilesii* is known from Turkey (Yokeş et al. 2012), Vietnam (Martynov and Korshunova 2012), the Philippines (Gosliner et al. 2008), Hong Kong (Jensen 2000), Japan (Nakano 2017), China (Gosliner and Vallès 2006), Australia (Nimbs and Smith 2016), and Korea (Song et al. 2017). Here documented as a first record for Thai waters.

**Genus *Polycera* Cuvier, 1816**

**\**Polycera* sp.**

Figure 16F

**Material examined.** One specimen 12 mm, SN.

**Ecology.** Exclusively recorded from soft sediment habitats beyond the fringing coral reef where it feeds on Bugulidae spp. arborescent bryozoans. Depth 12–25 m.

**Distribution.** *Polycera* sp. 1 (Gosliner et al. 2008, 2018) is known from Indonesia only. Here representing a first record for Thai waters.

**Genus *Tambja* Burn, 1962*****Tambja amakusana* Baba, 1987**

Figure 16G

**Material examined.** One specimen 6 mm, CP.**Ecology.** Among rocks and corals on offshore pinnacle sites.**Distribution.** Widespread in the Indo-Pacific including Mozambique (Tibirićá et al. 2017), Maldives (Yonow 2012), Japan (Baba 1987), Australia (Marshall and Willan 1999), Papua New Guinea (Pola et al. 2006), Vanuatu and Hawaii (Gosliner et al. 2008). First documented from the Gulf of Thailand by Mehrotra and Scott (2016).***Tambja pulcherrima* Willan & Chang, 2017**

Figure 16H

**Material examined.** One specimen 40 mm, SWP.**Ecology.** Locally recorded exclusively in deep soft sediment habitats at an offshore pinnacle. Depth 25–30 m.**Distribution.** Known from South Korea, Japan, Taiwan, Malaysia, Papua New Guinea Australia, and New Zealand (Willan and Chang 2017). First documented from the Gulf of Thailand by Mehrotra and Scott (2016).**Remarks.** Externally, the present species matches the species recently described by Willan and Chang (2017) and was initially documented as an unidentified species of *Tambja* by Mehrotra and Scott (2016: fig. 2H).**\**Tambja* sp.**

Figure 16I

**Material examined.** One specimen 4 mm, TT.**Ecology.** Recorded from soft sediment habitats beyond the fringing coral reef where it was found on Bugulidae spp. Depth 12–25 m.**Distribution.** *Tambja* sp. 2 (Gosliner et al. 2018) is known from the Philippines and Indonesia. Here representing a first record for Thai waters. All available photographs show this species on the arborescent bryozoans of the family Bugulidae.**Genus *Thecacera* J. Fleming, 1828*****Thecacera* sp.**

Figure 16J

**Material examined.** Two specimens 6–16 mm, SB; one specimen 12 mm, KKR.

**Ecology.** Exclusively recorded from soft sediment habitats beyond the fringing coral reef where it feeds on Bugulidae spp. arborescent bryozoans. Depth 12–25 m.

**Distribution.** Similar species are known from Mozambique (Tibirićá et al. 2017), Maldives (Yonow 1994), Malaysia, Indonesia, and Japan (Gosliner et al. 2008).

**Remarks.** While similar to *Thecacera* cf. *picta* Baba, 1972 from Mozambique (Tibirićá et al. 2017) our preliminary investigations indicate that this species is distinct from both *Thecacera picta* Baba, 1972, *Thecacera vittata* Yonow, 1994, and the supposedly pan-tropical/sub-tropical species *Thecacera pennigera* (Montagu, 1813) which was incorrectly documented from Koh Tao by Mehrotra and Scott (2016). This species is also distinct from *Thecacera pennigera* previously recorded from both Andaman and Gulf waters of Thailand by Chavanich et al. (2013).

### Suborder Cladobranchia Willan & Morton, 1984

#### Superfamily Aeolidioidea Gray, 1827

#### Family Aeolidiidae Gray, 1827

#### Genus *Anteaeolidiella* Miller, 2001

#### \**Anteaeolidiella* sp.

Figure 16K

**Material examined.** One specimen 15 mm, CA.

**Ecology.** Among corals and rubble in coral reef habitats. Depth 6–10 m.

**Distribution.** *Anteaeolidiella cacaotica* (Stimpson, 1855) is known from Australia and Japan (Carmona et al. 2014b) and *Anteaeolidiella* sp. 2 (Gosliner et al. 2018) is known from Indonesia. Here representing a first record for Thai waters.

#### Genus *Aeolidiopsis* Pruvot-Fol, 1956

#### *Aeolidiopsis harrietae* Rudman, 1982

Figure 16L

**Material examined.** Two specimens 21–29 mm, LB; one specimen 17 mm, SRB.

**Ecology.** Cryptic on their prey, *Palythoa* sp. which has thus far only been recorded growing on isolated pieces of rubble or artificial substrate (i.e., discarded plastic) in deeper soft sediment habitats outside the coral reef.

**Distribution.** Known from Japan (Ono 2004), Australia (Rudman 1982), the Philippines and Papua New Guinea (Gosliner et al. 2008). Previously recorded from the Gulf of Thailand (Mehrotra and Scott 2016).

**Remarks.** Specimens from Koh Tao have papillate rhinophores (similar to Carmona et al. 2014a: fig. 3D) with distinctly white tips, have between 4–6 cerata per row which are the same brown colour as the dorsum with distinctive yellowish to pale brown cnidosacs.

**\**Aeolidiopsis ransoni* Pruvot-Fol, 1956**

Figure 17A, B

**Material examined.** Two specimens 25–30 mm, SB; one specimen 23 mm, CB.

**Ecology.** Exclusively recorded on its prey species, the zoanthid *Palythoa tuberculosa* (Esper, 1805), on which it is extremely cryptic. Depth 1–18 m.

**Distribution.** Across the Pacific including Japan (Ono 2004), French Polynesia (Pruvot-Fol 1956), Hawaii (Carmona et al. 2014a), the Philippines, Australia, and Papua New Guinea (Gosliner et al. 2008). Here representing a first record for Thai waters.

**Remarks.** Separated from *Aeolidiopsis harrietae* and *A. palythoae* (Gosliner, 1985) by the presence of smooth rhinophores and highly elongate body with between 17–23 pairs of cerata. Unlike specimens described by Carmona et al. (2014b) but similar to those described by Rudman (1982), specimens from Koh Tao have rhinophores that lack white tips.

**Genus *Baeolidia* Bergh, 1888****\**Baeolidia salaamica* (Rudman, 1982)**

Figure 17C

**Material examined.** One specimen 10 mm, CA.

**Ecology.** Among corals and rubble in coral reef habitats. Depth 6–10 m.

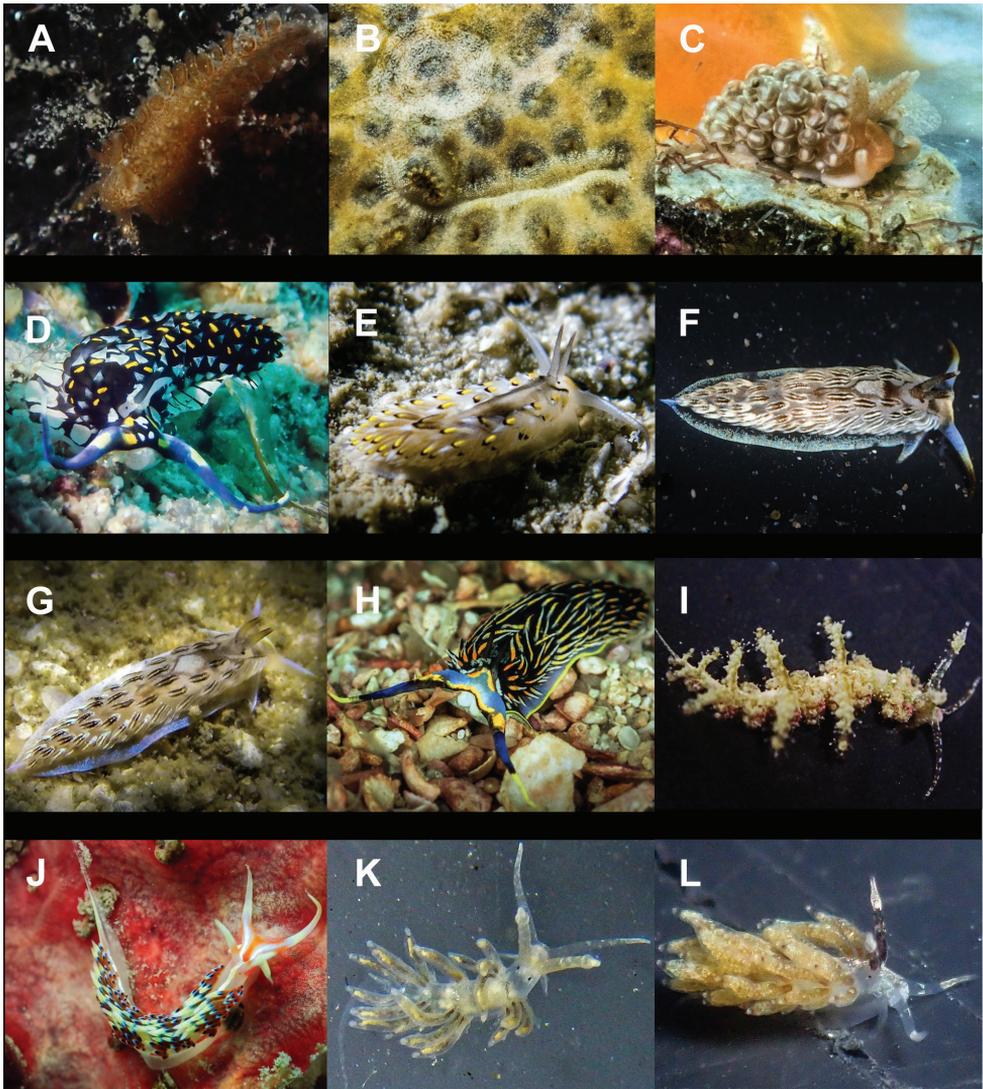
**Distribution.** Across the Indo-Pacific including Tanzania (Rudman 1982), Japan (Ono 2004), Korea (Koh 2006), Hawaii (Carmona et al. 2014a), Philippines, and Papua New Guinea (Gosliner et al. 2008). Here representing a first record for Thai waters.

**Remarks.** Rhinophores with numerous small white knobs leading to white apices, a faint white ring visible on the head, anterior to the rhinophores. Foot white and wide. Oral tentacles basally translucent with white tips, often held curled closer to the head (Fig. 17C) but longer than rhinophores when extended. Cerata moderately long, brown with white speckles with very distinctive white cnidosacs. A similar brown colour (though often more orange) is the main colouration of the dorsum, head, and rhinophores, under the aforementioned white pigmentation, with some faint white pigmentation anterior and posterior to the pericardium. This brownish orange colouration appears to be the main externally obvious difference between the specimens from Koh Tao and those described by Carmona et al. (2014b), but orange pigmentation was described in the original description of the species, particularly in relation to the rhinophores.

**Genus *Cerberilla* Bergh, 1873*****Cerberilla ambonensis* Bergh, 1905**

Figure 17D

**Material examined.** One specimen 10 mm, TT; one specimen 20 mm, SN.



**Figure 17.** **A, B** *Aeolidiopsis ransoni* 23 mm (**A**) and 25 mm (**B**) **C** *Baeolidia salaamica* 10 mm **D** *Cerberilla ambonensis* 20 mm **E** *Cerberilla asamusiensis* 8 mm (photograph by Pau Urgell Plaza) **F, G** *Cerberilla* cf. *incola* variants 12 mm (**F**) and 7 mm (**G**) **H** *Cerberilla* sp. 22 mm **I** *Limenandra confusa* 12 mm **J** *Caloria indica* 26 mm **K** *Favorinus* sp. 1.5 mm **L** *Favorinus* sp. 2.5 mm

**Ecology.** Exclusively found in deeper soft sediment habitats outside coral reef habitats, where it exhibits an endo-benthic substrate preference. Depth 14–20 m.

**Distribution.** Across the Indo-Pacific including Mozambique (Tibiricá et al. 2017), India (Ramakrishna et al. 2010), Indonesia, Australia, and the Solomon Islands (Gosliner et al. 2008). First documented from the Gulf of Thailand by Mehrotra and Scott (2016).

***Cerberilla asamusiensis* Baba, 1940**

Figure 17E

**Material examined.** One specimen 8 mm, TT.**Ecology.** Exclusively found in deeper soft sediment habitats outside coral reef habitats, where it exhibits an endo-benthic substrate preference. Depth 14–20 m.**Distribution.** Across the Indo-Pacific including Australia (Nimbs and Smith 2016), China (Lin 1990), South Korea (Koh 2006), Japan (Baba 1957), and Indonesia (Gosliner et al. 2018). First documented from the Gulf of Thailand by Mehrotra and Scott (2016).**\**Cerberilla* cf. *incola* Burn, 1974**

Figure 17F, G

**Material examined.** Two specimens 7–12 mm, TT.**Ecology.** Exclusively found in deeper soft sediment habitats outside coral reef habitats, where it exhibits an endo-benthic substrate preference. Depth 14–20 m.**Distribution.** *Cerberilla incola* is known from Australia (Burn 1974) and Réunion Island (Bachel 2010). First documented from the Gulf of Thailand by Chavanich et al. (2013).**Remarks.** *Cerberilla incola* as described by Burn (1974) represents a largely brown animal with dark brown rhinophores, dark brown lines across oral tentacles and along lateral and central lines of the dorsum with central cerata tipped with dark arrow-shaped marks. A later observation from near the type locality of South-East Australia (Cobb 2010) highlighted a light brown to nearly white specimen with pale blue lines along oral tentacles, a distinctive yellow-orange band along the anterior portion of the head, and with most cerata bearing parallel lines ranging from light to dark brown. A further observation from Réunion Island in the Indian Ocean (Bachel 2010) was also considered to be *C. incola* by Rudman (2010) bearing the same parallel lines along the cerata but lacking in the yellow-orange band of the earlier observation. All animals appear to have dark brown-grey rhinophores and the same dark colour anterior to the pericardium. Specimens from Koh Tao have been observed to show external variability (Fig. 17F, G) and further investigation is required.**\**Cerberilla* sp.**

Figure 17H

**Material examined.** One specimen 22 mm, SN.**Ecology.** Exclusively found in deeper soft sediment habitats outside coral reef habitats, where it exhibits an endo-benthic substrate preference. Depth 14–20 m.**Distribution.** *Cerberilla* sp. 4 (Gosliner et al. 2018) is currently known from Indonesia.

**Genus *Limenandra* Haefelfinger & Stamm, 1958****\**Limenandra confusa* Carmona, Pola, Gosliner & Cervera, 2014**

Figure 17I

**Material examined.** One specimen 4 mm, LT; one specimen 7 mm, LB; two specimens 6–12 mm, CB.

**Ecology.** On rocks and under rubble, including skeletons of dead fungiid corals, in coral reef habitats. Depth 2–14 m.

**Distribution.** Until recently, known only from the Pacific including Costa Rica (Camacho-García et al. 2005), Gulf of California (Bertsch 1972), Hawaii (Kay 1979), Australia (Nimbs and Smith 2016), Mexico, and the Philippines (Gosliner et al. 2008). Recorded in the Indian Ocean from Mozambique (Tibiriçá et al. 2017) and the Red Sea (Yonow 2015). Here documented as a first record for Thai waters.

**Family Facelinidae Bergh, 1889****Genus *Caloria* Trinchese, 1888*****Caloria indica* (Bergh, 1896)**

Figure 17J

**Material examined.** One specimen 26 mm, TW; two specimens 31–39 mm, SWP; two specimens 18–25 mm, HF.

**Ecology.** Abundant in coral reef habitats, particularly at the numerous coral reef restoration sites at Koh Tao and at rocky pinnacle sites nearshore and offshore. Depth 2–30 m.

**Distribution.** Widespread across the Indo-Pacific including Mozambique (Tibiriçá et al. 2017), India (Sreeraj et al. 2012), Maldives (Yonow 1994), Myanmar (Sanpanich and Duangdee 2019), Papua New Guinea (Baine and Harasti 2007), South Africa, Tanzania, Indonesia, Australia, Japan, Hawaii (Gosliner 1987), Oman, Seychelles, New Caledonia, Solomon Islands, Fiji (Gosliner et al. 2008) and documented from both Andaman and Gulf waters of Thailand by Chavanich et al. (2013).

**Genus *Favorinus* Gray, 1850****\**Favorinus* sp. 1**

Figure 17K

**Material examined.** One specimen 5 mm, CB; one specimen 5 mm, MH.

**Ecology.** Documented in habitats ranging from shallow reef rubble and soft sediments to deeper soft sediment habitats. Depth 5–18 m.

**Distribution.** *Favorinus* sp. 8 (Gosliner et al. 2018) is known from Papua New Guinea and Palau. Here documented as a first record for Thai waters.

**Remarks.** Similar to *Favorinus* sp. 8 in Gosliner et al. (2018) which they record as feeding on the eggs of *Stylocheilus striatus* under ex-situ conditions. While the prey of the present species has yet to be documented, its range almost directly overlaps with the range of *S. striatus* from Koh Tao, which grazes on cyanobacteria in shallow and deeper soft sediment habitats at sites CB and SRB.

**\**Favorinus* sp. 2**

Figure 17L

**Material examined.** Two specimens SB, 5 mm.

**Ecology.** Documented from deeper soft sediment habitats only. Depth 18–25 m.

**Distribution.** *Favorinus* sp. 4 and *Favorinus* sp. 12 (Gosliner et al. 2018) are known from the Philippines. Here documented as a first record for Thai waters.

**\**Myja* cf. *longicornis* Bergh, 1896**

Figure 18A

**Material examined.** One specimen GR, 9 mm.

**Ecology.** Found exclusively on its prey hydroid *Pennaria disticha* (Goldfuss, 1820) uncommonly found in both coral reef and deeper soft sediment habitats. Depth 8–25 m.

**Distribution.** *Myja longicornis* is known from Indonesia (Bergh 1896), Australia (Nimbs and Smith 2016), Japan, and Papua New Guinea (Gosliner et al. 2008). A similar species *Myja* cf. *longicornis* was recently documented from the Gulf of Thailand (Martynov et al. 2019).

**Remarks.** This genus was recently reviewed and expanded based on specimens from Japan and the Gulf of Thailand (Martynov et al. 2019). In that study, authors concluded that the studied specimens from the Gulf of Thailand have a close resemblance to the description of *M. longicornis* by Bergh, with some internal and external differences that would require examination of specimens from the type locality of Ambon. The single specimen found at Koh Tao closely resembles other specimens found in the Gulf of Thailand, and thus its species designation remains unresolved in the absence of contemporary studies of the genus from closer to the type locality.

**Genus *Noumeaella* Risbec, 1937**

**\**Noumeaella* sp. 1**

Figure 18B, C

**Material examined.** One specimen 5 mm, CB.

**Ecology.** Found under rocks and coral rubble in shallow coral reef habitats. Depth 4–8 m.

**Distribution.** *Noumeaella* sp. 4 is known from the Philippines (Gosliner et al. 2018). *Noumeaella rehderi* Er. Marcus, 1965 is known from Madagascar, Tanzania, Australia, Papua New Guinea, Philippines, Palau, Marshall Islands, and Hawaii (Gosliner et al. 2008). Here documented as a first record for Thai waters.

**\**Noumeaella* sp. 2**

Figure 18D, E

**Material examined.** One specimen 5 mm, SN.

**Ecology.** Recorded from soft sediment habitats beyond the fringing coral reef. Depth 15–20 m.

**Distribution.** Unknown. Here documented as a first record for Thai waters.

**Remarks.** Generally translucent throughout with some patches of white or light grey, and cerata edged in white with white apices. Bears resemblance to a number of species within the genus and requires a larger sampling effort to identify further.

**Genus *Phidiana* Gray, 1850**

***Phidiana militaris* (Alder & Hancock, 1864)**

Figure 18F

**Material examined.** Two specimens 30–35 mm, SO; two specimens 30–40 mm, HF.

**Ecology.** Occasionally found among rubble and corals in reef habitats. Most abundant at some artificial reef sites at the island, which were initially constructed from steel rebar or concrete to support coral restoration efforts. It is likely that these substrates, while promoting scleractinian conservation, also support different potential prey items than might be found in coral reef or soft sediment habitats. Depth 8–25 m.

**Distribution.** Across the Indo-Pacific including the Gulf of Oman (Fatemi and Attaran 2015), Red Sea (Yonow 2008), Malaysia (Ho 1989), United Arab Emirates, India, Singapore, and the Philippines (Gosliner et al. 2008). Known to have been introduced into the Mediterranean from the Red Sea (Rothman et al. 2017). Known from Andaman and Gulf waters of Thailand (Gosliner et al. 2008; Mehrotra and Scott 2016).

**\**Phidiana* sp.**

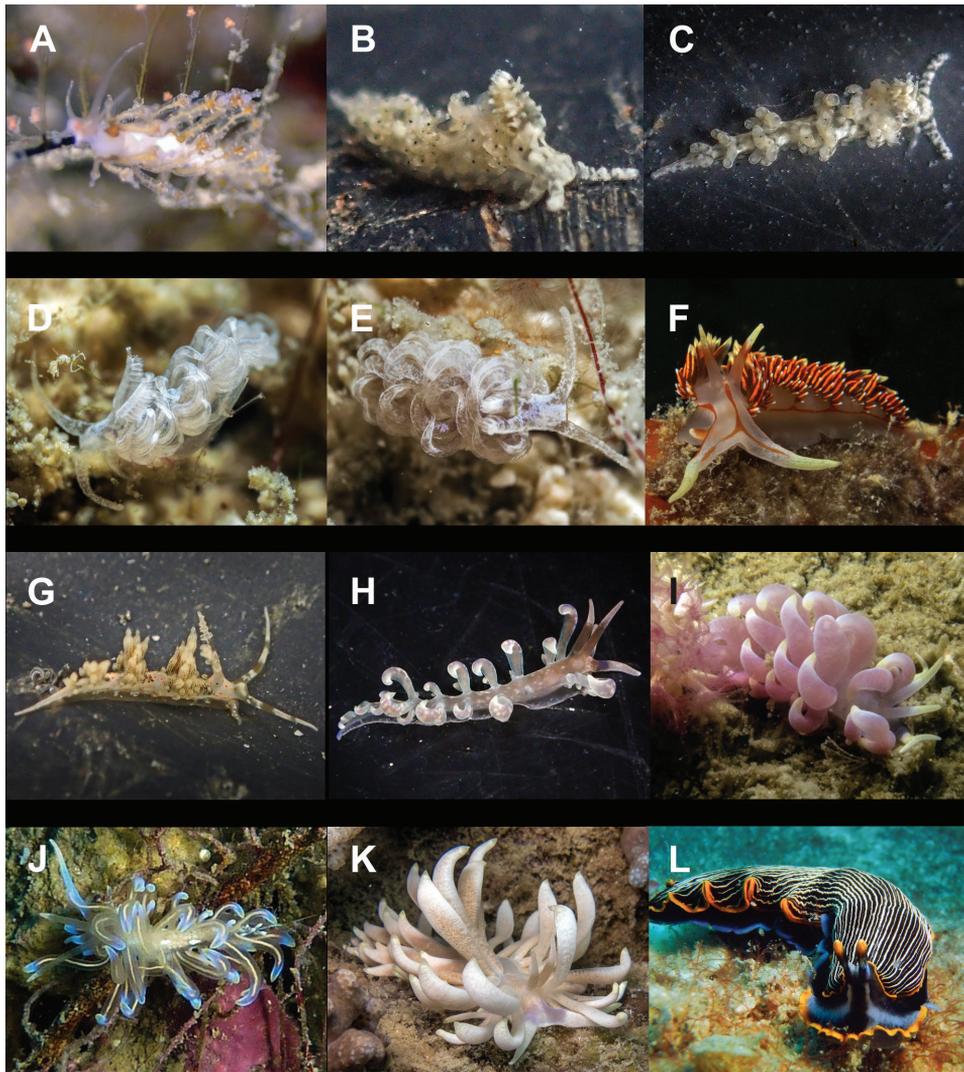
Figure 18G

**Material examined.** One specimen 7 mm, HWP.

**Ecology.** Among rocks and coral rubble. Depth 5–16 m.

**Distribution.** Unknown.

**Remarks.** Bearing some similarities to *Phidiana anulifera* (Baba, 1949) and *Phidiana semidecora* (Pease, 1860).



**Figure 18.** **A** *Myja* cf. *longicornis* 9 mm (photograph by Phannee Mccarthy) **B, C** *Noumeaella* sp. 1.5 mm **D, E** *Noumeaella* sp. 2.5 mm (photographs by Tony Myshlyayev) **F** *Phidiana militaris* 35 mm (photograph by Pau Urgell Plaza) **G** *Phidiana* sp. 7 mm **H** *Phyllodesmium magnum* 30 mm **I** *Phyllodesmium* cf. *magnum* 35 mm (photograph by Pau Urgell Plaza) **J** *Phyllodesmium opalescens* 35 mm, (photograph by Guillaume Gandoin) **K** *Phyllodesmium* sp. 55 mm (photograph by Pau Urgell Plaza) **L** *Armina occulta* 65 mm.

### Family Myrrhinidae Bergh, 1905

#### Genus *Phyllodesmium* Ehrenberg, 1831

#### *Phyllodesmium magnum* Rudman, 1991

Figure 18H

**Material examined.** Two specimens 30–40 mm, TT.

**Ecology.** In coral reef habitats where it feeds on the octocoral *Sinularia* sp. Depth 5–18 m.

**Distribution.** Widespread across the Indo-Pacific including Mozambique (Tibirić et al. 2017), South Africa (Fraser 2001), the Red Sea (Koretz 2005), Hong Kong, New Caledonia, Australia, Marshall Islands (Rudman 1991), Japan (Ono 2004), Tanzania, Philippines, Indonesia, and Papua New Guinea (Gosliner et al. 2008). Documented from both Andaman and Gulf waters of Thailand by Chavanich et al. (2013).

***Phyllodesmium* cf. *magnum* Rudman, 1991**

Figure 18I

**Material examined.** One specimen 15 mm, TT; one specimen 35 mm, SB.

**Ecology.** In soft sediment habitats outside coral reef habitats, found regularly on or in the immediate vicinity of *Dendronephthya* octocorals, though active feeding has not yet been confirmed. Depth 16–28 m.

**Distribution.** Unknown

**Remarks.** The present species externally appears to match *Phyllodesmium magnum* Rudman, 1991, though smaller with relatively short cerata and no brown pigment on the animal, having pale yellow tips to rhinophores and oral tentacles. All individuals recorded to date were separately found on or very close to *Dendronephthya* spp., distant from any colonies of *Sinularia* which at Koh Tao grow only on rocks in shallower coral reef habitats. While it is possible that some animals recorded at Koh Tao are indeed *P. magnum* with differences in external colouration reflecting a drastically different diet from that known for *P. magnum*, the present species is provisionally treated as distinct due to its unique ecology.

**\**Phyllodesmium opalescens* Rudman, 1991**

Figure 18J

**Material examined.** One specimen 35 mm, CP.

**Ecology.** Among coral, rocks, and discarded fishing equipment at an offshore pinnacle site. Depth 16 m.

**Distribution.** Known from the Philippines, Hong Kong, Korea, and Japan (Gosliner et al. 2008). Here documented as a first record for Thai waters.

**\**Phyllodesmium* sp.**

Figure 18K

**Material examined.** Two specimens 40–55 mm, HWB.

**Ecology.** In shallow coral reef habitats where it observed feeding on a different species of *Sinularia* than *P. magnum*. Depth 2–8 m.

**Distribution.** *Phyllodesmium* sp. 2 (Gosliner et al. 2018) is known from Indonesia.

**Remarks.** Similar to *Phyllodesmium* sp. 2 by Gosliner et al. (2018) which in turn is similar to *P. magnum*. External differences here are pale cerata that are less curved and held more upright than those of *P. magnum*, with digestive glands clearly visible and lacking any blueish purple pigment. Some purple-grey pigment is seen on the head.

### **Superfamily Arminoidea Iredale & O’Donoghue, 1923 (1841)**

#### **Family Arminidae Iredale & O’Donoghue, 1923 (1841)**

#### **Genus *Armina* Rafinesque, 1814**

#### ***Armina occulta* Mehrotra, Caballer & Chavanich, 2017**

Figure 18L

**Material examined.** Two specimens 65–72 mm, SN.

**Ecology.** Exclusively known from soft sediment habitats outside the coral reef where it feeds on the sea pen *Virgularia* sp. Depth 14–22 m.

**Distribution.** Known from the western Pacific including Indonesia (Yonow 2017), the Philippines (Koehler 2002), Australia (Hatton 2019), Papua New Guinea (Adams 2000), and Palau (Gosliner et al. 2008). Known from the Gulf of Thailand (Mehrotra et al. 2017). Koh Tao is the type locality of this species.

#### ***Armina scotti* Mehrotra, Caballer & Chavanich, 2017**

Figure 19A

**Material examined.** Two specimens 35–49 mm, SB; one specimen 41 mm, TT.

**Ecology.** Exclusively known from soft sediment habitats outside the coral reef where it feeds on the sea pen *Virgularia* sp. One individual observed feeding on partially decomposed *Pteroeides* sp. (Octocorallia: Pennatulidae). Depth 12–29 m.

**Distribution.** Known from the western Pacific including Japan (Okutani 2000), Singapore, the Philippines, and Indonesia (Gosliner et al. 2008). Known from the Andaman and Gulf waters of Thailand (Chavanich et al. 2013; Mehrotra et al. 2017). Koh Tao is the type locality of this species.

**Remarks.** Specimens identified as *Armina semperi* (Bergh, 1866) from coasts of Thailand correspond to this species (Mehrotra et al. 2017).

#### **Genus *Dermatobranchus* van Hasselt, 1824**

#### **\**Dermatobranchus caeruleomaculatus* Gosliner & Fahey, 2011**

Figure 19B

**Material examined.** Two specimens 55–67 mm, SN.

**Ecology.** Exclusive to the soft sediment habitats outside the coral reef. Depth 14–24 m.

**Distribution.** Known from the western Pacific including Malaysia, Indonesia, and the Philippines (Gosliner et al. 2008), Papua New Guinea (Coleman 2008), and Japan (Nakano and Fujii 2014). Here documented as a first record for Thai waters.

**\**Dermatobranchus dendronephthyphagus* Gosliner & Fahey, 2011**

Figure 19C

**Material examined.** Two specimens 40–50 mm, SB.

**Ecology.** Exclusive to the soft sediment habitats outside the coral reef where it may be found feeding on *Dendronephthya* sp. or partially buried in the nearby silt/sand. Depth 14–24 m.

**Distribution.** Known from the West Pacific including Japan and Australia (Rudman 2005b; Nimbs and Smith 2016). Here documented as a first record for Thai waters.

**Remarks.** Recorded as *Dermatobranchus* sp. by Mehrotra and Scott (2016: fig. 3C).

***Dermatobranchus fortunatus* (Bergh, 1888)**

Figure 19D

**Material examined.** Two specimens 7–11 mm, CB; one specimen 9 mm, SB.

**Ecology.** On rocks and under rubble, in particular under skeletons of dead Fungiidae corals, in shallow coral reef habitats. Depth 1–18 m.

**Distribution.** Across the Indo-Pacific including the Indian Ocean of Java (Bergh 1888), India (Dixit et al. 2017), Japan (Bolland 2003), Australia (Marshall and Willan 1999), the Seychelles, the Philippines, Malaysia, Indonesia, and Papua New Guinea (Gosliner and Fahey 2011). Documented from the Gulf waters of Thailand by Mehrotra and Scott (2016).

**\**Dermatobranchus semilunus* Gosliner & Fahey, 2011**

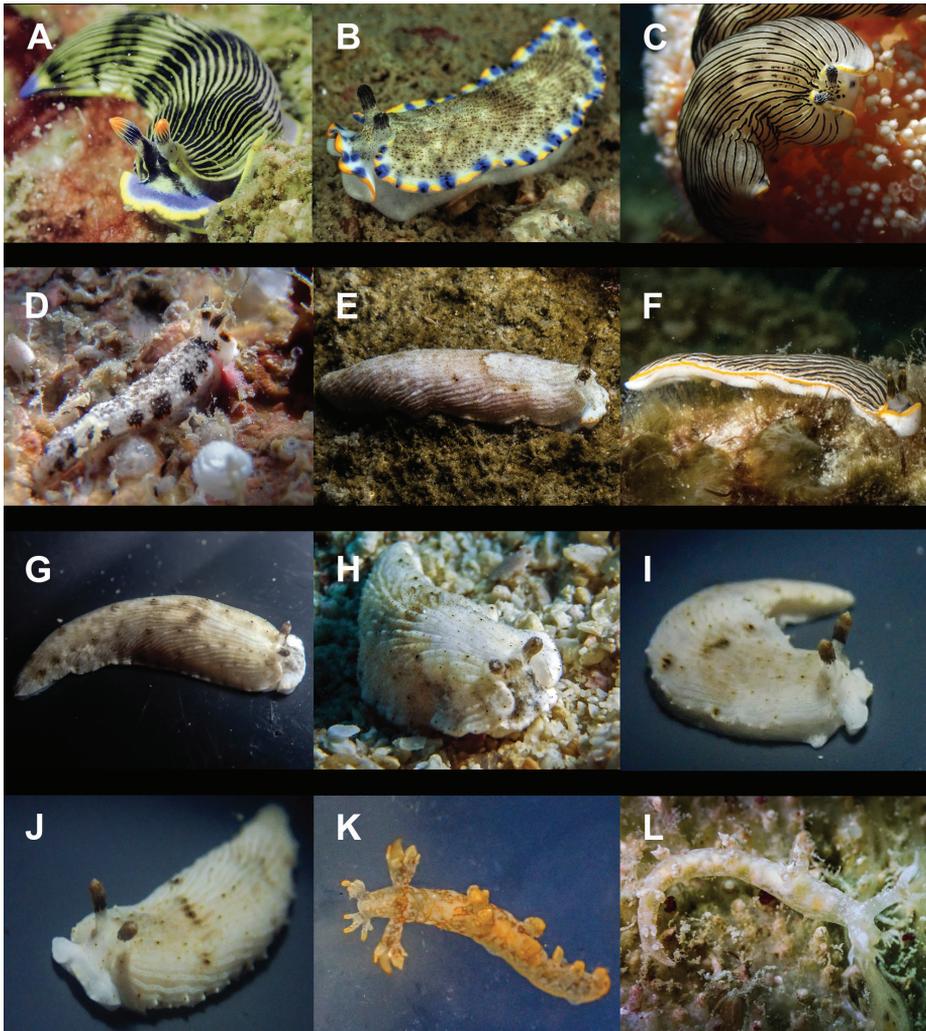
Figure 19E

**Material examined.** One specimen 33 mm, TB.

**Ecology.** Exclusive to the soft sediment habitats outside the coral reef. Observed on *Dendronephthya* sp. octocoral, though active feeding was not observed. Depth 14–24 m.

**Distribution.** Known from the West Pacific including Malaysia, the Philippines, Indonesia, and Papua New Guinea (Gosliner and Fahey 2011). Here documented as a first record for Thai waters.

**Remarks.** Specimens from Koh Tao are sometimes found with a pale yellow-pink margin to the oral veil. A similar trait is known from the closely related *Dermatobranchus fasciatus* Gosliner and Fahey 2011; however, the present specimens externally match *D. semilunus* based on other characteristics. Additionally, similar pigment



**Figure 19.** **A** *Armina scotti* 41 mm **B** *Dermatobranchus caeruleomaculatus* 55 mm **C** *Dermatobranchus dendronephthyphagus* 40 mm **D** *Dermatobranchus fortunatus* 11 mm **E** *Dermatobranchus semilunus* 33 mm (photograph by Pau Urgell Plaza) **F** *Dermatobranchus* cf. *striatus* 14 mm **G,H** *Dermatobranchus* sp. 1 32 mm (**G**) and 28 mm (**H**) **I,J** *Dermatobranchus* sp. 2 27 mm **K** *Bornella hermanni* 12 mm **L** *Bornella johnsonorum* 35 mm.

appears to be visible in a photograph of a specimen in the original description of the species (Gosliner and Fahey 2011: fig. 74C).

#### *Dermatobranchus* cf. *striatus* van Hasselt, 1824

Figure 19F

**Material examined.** Two specimens 9–12 mm, SI; two specimens 11 mm, HPW; one specimen 14 mm, SW.

**Ecology.** On rocks in coral reef habitats where it feeds on the octocoral *Briareum stechei* (Kükenthal, 1908). Occasionally observed among colonies of *B. stechei* growing on artificial substrates (i.e., discarded fishing nets) in deeper soft sediment habitats. Depth 6–22 m.

**Distribution.** *Dermatobranchus striatus* is known from Indonesia, Papua New Guinea, and Japan (see Gosliner and Fahey 2011).

**Remarks.** This species was recorded as *Dermatobranchus striatus* van Hasselt, 1824 by Mehrotra and Scott (2016). Due to taxonomic uncertainty between this and similar species (see Gosliner and Fahey 2011), and with *D. striatus* being the type species for the genus, we refer to this species as *D. cf. striatus*.

### \**Dermatobranchus* sp. 1

Figure 19G, H

**Material examined.** Three specimens 28–40 mm, SB.

**Ecology.** Exclusive to the soft sediment habitats outside the coral reef where it feeds on colonies of the octocoral *Dendronephthya* sp. Depth 14–24 m.

**Distribution.** Unknown.

**Remarks.** A species that vaguely resembles but is distinct from *Dermatobranchus semilunus* is regularly recorded from the same habitats and locations as other soft-sediment dwelling members of the genus. Specimens of *Dermatobranchus* sp. 1 externally appear to have characteristics of *D. fasciatus* and *D. semilunus*. All specimens have prominent longitudinal ridges on a generally white dorsum, with numerous black spots of varying sizes distributed along the ridges and margin of the oral veil. The oral veil always has patches of grey and the margin is sometimes pigmented with a yellow-pink band which is often pale or completely absent in some specimens. The dorsal surface usually has a single horizontal diffuse band approximately one third of the total animal length. The foot is pale pink to white, sometimes with numerous small black spots. The rhinophores have white tips, dark clubs with white lines along the lamellae, and white stalks with dark grey pigment along the inner edge of the stalks often forming a dark grey band in between and anterior to the rhinophores.

### \**Dermatobranchus* sp. 2

Figure 19I, J

**Material examined.** One specimen 27 mm, TT.

**Ecology.** Exclusive to the soft sediment habitats outside the coral reef. Depth 21 m.

**Distribution.** Unknown.

**Remarks.** *Dermatobranchus* sp. 2 is characterised by prominent pale yellow marginal sacs that are very visible as conical papillae. The dorsal longitudinal ridges and grooves are white to pale brown and scattered sparsely with small brown spots of

varying sizes. These spots extend to the oral veil, which is noticeably whiter than the dorsum. The rhinophore stalks are translucent white followed by a sharp black band at the base of the rhinophore club. This fades into brown, becoming paler apically with a translucent white apex. The anterior foot corners are blunt and short, with the foot being white. This species resembles *D. fasciatus* but differs in lacking any marginal pigmentation on either mantle or foot, and possessing prominent marginal papillae that are not seen in *D. fasciatus*.

### **Superfamily Dendronotoidea Allman, 1845**

#### **Family Bornellidae Bergh, 1874**

#### **Genus *Bornella* Gray, 1850**

#### ***Bornella hermanni* Angas, 1864**

Figure 19K

**Material examined.** Two specimens 12–18 mm, HWB.

**Ecology.** Among corals, rocks and under rubble in shallow coral reef habitats. Depth 2–12 m.

**Distribution.** Across the Indo-Pacific including Christmas Island in the Indian Ocean, Malaysia, the Marshall Islands (Pola et al. 2009), Korea (Koh 2006), Japan (Baba 1949), and Australia (Angas 1864). First recorded from the Gulf of Thailand by Mehrotra and Scott (2016).

#### **\**Bornella johnsonorum* Pola, Rudman & Gosliner, 2009**

Figure 19L

**Material examined.** One specimen 35 mm, CB.

**Ecology.** On rocks and under rubble, in particular under skeletons of dead fungiid corals, in shallow coral reef habitats. Depth 2–8 m.

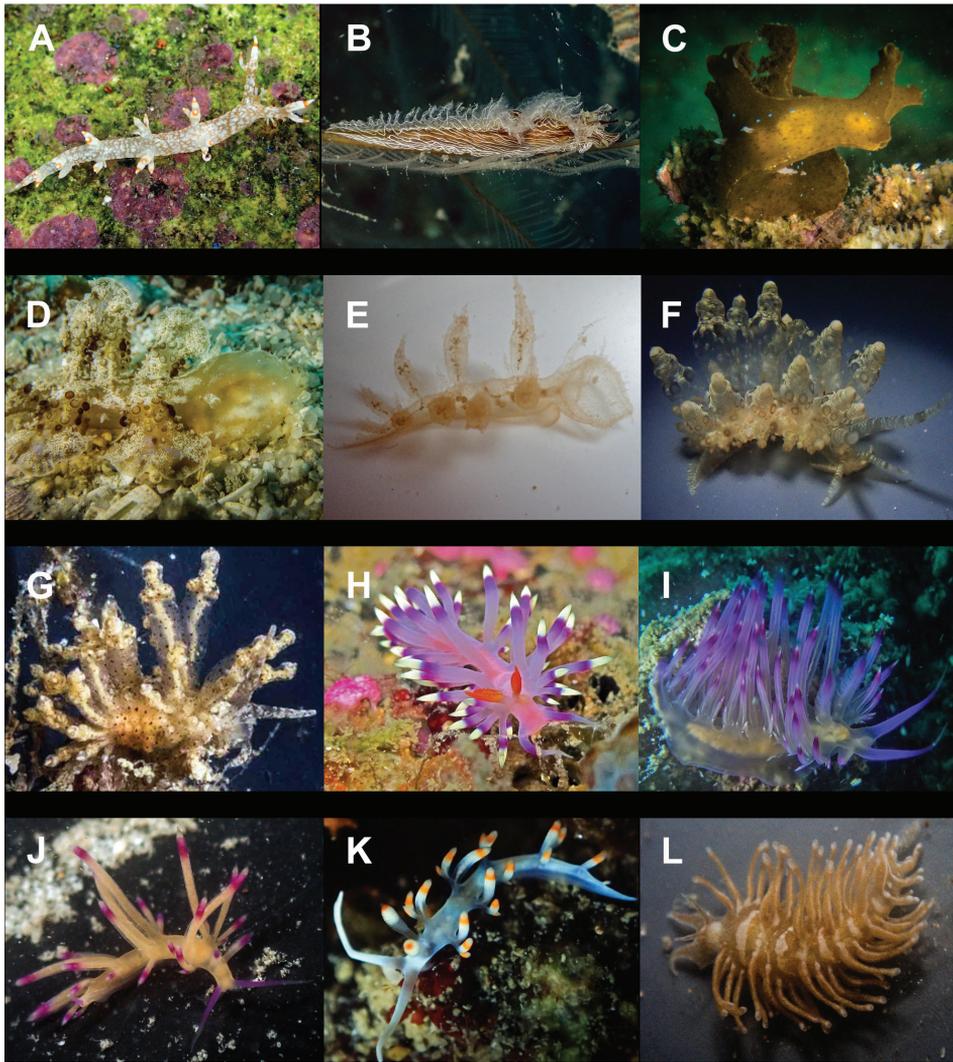
**Distribution.** *Bornella johnsonorum* is known from the Marshall Islands in the Pacific (Pola et al. 2009) and maybe from Réunion Island and the Red Sea and in the western Indian Ocean (Bidgrain 2009; Yonow 2015). Here documented as a first record for Thai waters.

**Remarks.** The present species matches the external description of the species (Pola et al. 2009) very closely, although lacking any signs of orange reticulation. Specimens from Koh Tao have six paired dorsal processes and a single, extremely small, unpaired dorsal process near the tip of the tail.

#### ***Bornella stellifera* (A. Adams & Reeve in A. Adams, 1848)**

Figure 20A

**Material examined.** One specimen 31 mm, CB.



**Figure 20.** **A** *Bornella stellifera* 31 mm **B** *Lomanotus vermiformis* 25 mm **C** *Scyllaea fulva* 45 mm **D** *Melibe viridis* 97 mm **E** *Melibe* sp. 22 mm **F** *Eubranchus ocellatus* 22 mm **G** *Eubranchus* sp. 7 mm **H** *Coryphellina exoptata* 15 mm (photograph by Tine Kvamme) **I, J** *Coryphellina* cf. *lotos* variants 40 mm (**I**) and 35 mm (**J**) **K** *Samla bicolor* 12 mm **L** *Phestilla fuscostrata* 15 mm.

**Ecology.** On rocks and under rubble, in particular under skeletons of dead Fungiid corals, in shallow coral reef habitats. Depth 2–8 m.

**Distribution.** Widespread across the Indo-Pacific including the Red Sea (Vayssi re 1912), Mozambique (Tibiri a et al. 2017), South Africa (Gosliner 1987), Japan (Baba 1949), Singapore, Madagascar, India, Malaysia, the Philippines, Australia, Papua New Guinea, Fiji, Hawaii (Pola et al. 2009), Indonesia, Taiwan and New Caledonia (Gosliner et al. 2008). Recorded from the Andaman and Gulf waters of Thailand (Jensen 1998; Pola et al. 2009).

**Family Lomanotidae Bergh, 1890****Genus *Lomanotus* Vérany, 1844*****Lomanotus vermiformis* Eliot, 1908**

Figure 20B

**Material examined.** Two specimens 15–25 mm, SN; one specimen 17 mm, TW; one specimen 30 mm, SI.

**Ecology.** Cryptic on its host hydroid *Macrorhynchia* sp., colonies of which are found exclusively in soft sediment habitats outside the coral reef. Depth 12–34 m.

**Distribution.** Circumtropical, recorded from Florida, the Bahamas (Valdés et al. 2006), Panama (Collin et al. 2005), the Red Sea (Vayssière 1912), India (Dixit et al. 2017), Malaysia (Mayes 2008), the Philippines (Koehler 2005), Australia (Nimbs and Smith 2016), Indonesia, and Papua New Guinea (Gosliner et al. 2008). Recorded from the Andaman and Gulf waters of Thailand (Koehler 1999; Mehrotra and Scott 2016).

**Family Scyllaeidae Alder & Hancock, 1855****Genus *Scyllaea* Linnaeus, 1758****\**Scyllaea fulva* Quoy & Gaimard, 1824**

Figure 20C

**Material examined.** One specimen 45 mm, CB.

**Ecology.** Recorded from a single individual on floating algae *Sargassum oligocystum* (Montagne, 1845).

**Distribution.** Across the Indo-Pacific including Mozambique (Tibirićá et al. 2017), Réunion Island (Cadet 2012), Japan (Baba 1949), the Philippines, Papua New Guinea (Pola et al. 2012), and maybe the Mediterranean (Yokes 2002; Pola et al. 2012). Here documented as a first record for Thai waters.

**Family Tethydidae Rafinesque, 1815****Genus *Melibe* Rang, 1829*****Melibe viridis* (Kelaart, 1858)**

Figure 20D

**Material examined.** One specimen 12 mm, TT; one specimen 122 mm, SB; one specimen 97 mm, SN.

**Ecology.** Recorded from the soft sediment habitats outside the coral reef; however, individuals have rarely been observed swimming near the surface closer to shore. It is likely that these individuals were disturbed as no individuals have been recorded in shallower reef or sandy habitats after five years of survey. Depth 14–24 m.

**Distribution.** Across the Indo-Pacific including Mozambique (Tibirićá et al. 2017), Tanzania (Eliot 1904), the Red Sea (Yonow 2015), India (Parasharya and Patel 2014), Vietnam, the Philippines, Japan, and Australia (Gosliner et al. 2008). It has also recently moved into the waters of the Mediterranean (Mastrototaro et al. 2004). Recorded from the Gulf waters of Thailand (Mehrotra and Scott 2016).

***Melibe* sp.**

Figure 20E

**Material examined.** Two specimens 15–22 mm, TT.

**Ecology.** In soft sediment habitats beyond the coral reef, grazing upon the substrate. Depth 17–22 m.

**Distribution.** *Melibe engeli* Risbec, 1937 is known across the Indo-Pacific including Mozambique (Tibirićá et al. 2017), the Red Sea (Burghardt and Wägele 2014), the Philippines, Indonesia, Japan, New Caledonia, and Hawaii (Gosliner et al. 2008). *Melibe* sp. 1 (Gosliner et al. 2008) is known from Indonesia only. Recorded from Koh Tao as *Melibe* sp. 1 by Mehrotra and Scott (2016: fig. 3D, E).

**Remarks.** Externally similar to *Melibe engeli* and *Melibe* sp. 1 (Gosliner et al. 2008, 2018) in shape and some morphology, with similarities between the two also being noted by Yonow (2017). Specimens recorded from Koh Tao range in colour from near colourless to strongly golden brown, although always at least slightly transparent. The body is covered in numerous small papillae, the oral hood is able to stretch to at least half of the length of the remaining body, which have four or five pairs of cerata. Cerata are mostly ovoid to cylindrical in shape, terminating in numerous large pointed white papillae. In smaller individuals, two papillae may dominate the apex of each ceras giving them a bifurcate appearance. Most intriguingly and substantially different from the morphology of *M. engeli* are the rhinophore sheaths which lack the ‘sail-like’ appendage but instead have a single long and thin almost ‘whip-like’ extension. While the overall body shape of *M. engeli* has been shown to go through numerous changes during development (Burghardt and Wägele 2014), the specimens from Koh Tao do not entirely match *M. engeli*.

**Superfamily Fionoidea Gray, 1857**

**Family Eubranchidae Odhner, 1934**

**Genus *Eubranchus* Forbes, 1838**

**\**Eubranchus ocellatus* (Alder & Hancock, 1864)**

Figure 20F

**Material examined.** One specimen 22 mm, SN.

**Ecology.** On its prey hydroid *Idiellana pristis* Lamouroux, 1816 rare in soft sediment habitats and absent from the coral reefs of Koh Tao. Depth 12–24 m.

**Distribution.** *Eubranchnus ocellatus* is known from the Red Sea (Yonow 2008), Australia (Nimbs and Smith 2016), Tanzania, Philippines, Indonesia, and New Caledonia (Gosliner et al. 2008). Here representing a first record for Thai waters and a first record for the genus in the Gulf of Thailand.

**Remarks.** It necessary here to clarify the brief historical records of Eubranchnidae in Thai waters. Chavanich et al. (2013) recorded *Baeolidia japonica* Baba, 1933 from the Gulf of Thailand as a member of the Eubranchnidae, which in fact belongs to the Aeolidiidae, as a representation of the first record of the family from Thai waters. Not mentioned in the same review, however, was the observation of *Eubranchnus rubropunctatus* Edmunds, 1969 from the Andaman coast of Thailand (Neal 2010) which is believed to represent the first record of the family from Thai waters.

**\**Eubranchnus* sp.**

Figure 20G

**Material examined.** One specimen 7 mm, HF.

**Ecology.** From an artificial reef structure at a reef restoration site in coral reef habitats. Depth 8–11 m.

**Distribution.** *Eubranchnus* sp. 2 (Gosliner et al. 2008) is known from Indonesia only. A similar species was also documented in India (Bhave and Apte 2011: fig. 13). Here representing a first record for Thai waters.

**Remarks.** The present species bears numerous dark brown to black spots throughout its body with bulbous transparent cerata with the digestive gland clearly visible. The dorsal colour and that of ceratal tips is a pale yellow-brown. The rhinophores, oral tentacles, and head are colourless with numerous small white patches spread throughout.

**Family Flabellinidae Bergh, 1889**

**Genus *Coryphellina* O'Donoghue, 1929**

***Coryphellina exoptata* (Gosliner & Willan, 1991)**

Figure 20H

**Material examined.** One specimen 15 mm, GR.

**Ecology.** Among rocks and corals in coral reef habitats. Depth 5–15 m.

**Distribution.** Widespread across the Indo-Pacific including Mozambique (Tibirică et al. 2017), India (Ramakrishna et al. 2010), South Africa, Réunion Island, Malaysia, the Philippines, Indonesia, Japan, Australia, Papua New Guinea, and Hawaii (Gosliner et al. 2008). Recorded from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

**Remarks.** This species was recently transferred to the genus *Coryphellina* in an extensive revision of the family Flabellinidae (Korshunova et al. 2017a).

***Coryphellina cf. lotos* Korshunova et al., 2017**

Figure 20I, J

**Material examined.** Two specimens 35–40 mm, HWP; two specimens 35 mm, KKR.

**Ecology.** Often feeding on hydroids growing among rocks and corals in deeper coral reef habitats and on stable substrates such as discarded nets and the remains of large terrestrial plant matter in soft sediment habitats. It is likely that the currently unknown prey hydroid of this species is able to grow in greater abundance away from shallow coral reef habitats. Depth 10–35 m.

**Distribution.** *Coryphellina lotos* is currently known only from Japan (Korshunova et al. 2017a). A similar species is here recorded for the first time from Thai waters.

**Remarks.** Specimens from Koh Tao strongly resemble *Coryphellina lotos*; however, a few differences may indicate a possible cryptic species. While *C. lotos* is described as light violet with parts of the rhinophores, oral tentacles, and cerata apices as lilac to reddish lilac (Korshunova et al. 2017a: fig. 38A–E), specimens from Koh Tao appear have a background colour ranging from almost colourless to pale blue-violet, with rhinophore apices and subterminal bands on oral tentacles and cerata being a much deeper purple than the reddish violet of *C. lotos*. Most distinctive, however, is the presence of a mid-dorsal deep purple line which remains continuous in some specimens, entirely broken or limited to the oral surface in others, and completely absent in yet other specimens. The same pattern seen (if present) in the dorsal line is often mimicked laterally on both sides of some specimens. While no mention of dorsal or lateral linear pigmentation was made in the description of the species, these lines are visible in images provided supplementing the description (Korshunova et al. 2017a: fig. 38A–C). Erroneously identified as *Flabellina rubrolineata* by Mehrotra and Scott (2016), the true identity of which has recently been shown to be restricted to its type locality in the Red Sea (Ekimova et al. 2020; Yonow 2020).

**Family Samlidae Korshunova et al., 2017****Genus *Samla* Bergh, 1900*****Samla bicolor* (Kelaart, 1858)**

Figure 20K

**Material examined.** Two specimens 9–12 mm, CB; one specimen 18 mm, SI; one specimen 16 mm, SN.

**Ecology.** On rocks and under rubble, including skeletons of dead Fungiidae corals, in coral reef habitats. Depth 2–14 m.

**Distribution.** Widespread across the Indo-Pacific including the Red Sea (Yonow 2000), Mozambique (Tibirićá et al. 2017), India (Apte 2009), Chagos Islands (Yonow et al. 2002), Myanmar (Sanpanich and Duangdee 2019), Indonesia (Eisenbarth et al. 2018), South Africa, Madagascar, Tanzania, Seychelles, Malaysia, Philippines, Hong Kong, Japan, Korea, Papua New Guinea, Australia and Hawaii (Gosliner et al. 2008). Recorded from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

**Family Trinchesiidae F. Nordsieck, 1972****Genus *Phestilla* Bergh, 1874****\**Phestilla fuscostriata* Hu, Zhang, Xie & Qiu, 2020**

Figure 20L

**Material examined.** Two specimens 11–15 mm, SRB; one specimen 12 mm, HF; one specimen 18 mm, LT.

**Ecology.** Exclusively on its prey, the scleractinian coral *Pavona decussata* Dana, 1846, which is abundant throughout the depth range of coral reefs around Koh Tao. Depth 1–19 m.

**Distribution.** *Phestilla fuscostriata* was previously known only from Hong Kong (Hu et al. 2020). Here we record it for the first time from Thai waters.

***Phestilla lugubris* (Bergh, 1870)**

Figure 21A

**Material examined.** One specimen 30 mm, HWB; two specimens 25–30 mm, SO.

**Ecology.** Exclusively on or in the immediate vicinity of its prey, the scleractinian coral *Porites* in coral reef habitats. Locally observed to be predated colonies of *Porites lobata* Dana, 1846, *Porites lutea* Milne Edwards, 1860, and *Porites* sp., all of which have been observed hosting the distinctive egg ribbons of the species. Depth 1–16 m.

**Distribution.** Widespread across the Indo-Pacific including the Red Sea (Yonow 2000), Mozambique (Tibirićá et al. 2017), India (Apte 2009), Vietnam (Risbec 1956), Indonesia (Burghardt et al. 2006), Tanzania, Madagascar, Seychelles, the Philippines, Japan, Papua New Guinea, Australia, New Caledonia, Hawaii, and the Pacific coast of North America (Gosliner et al. 2008). Recorded from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).

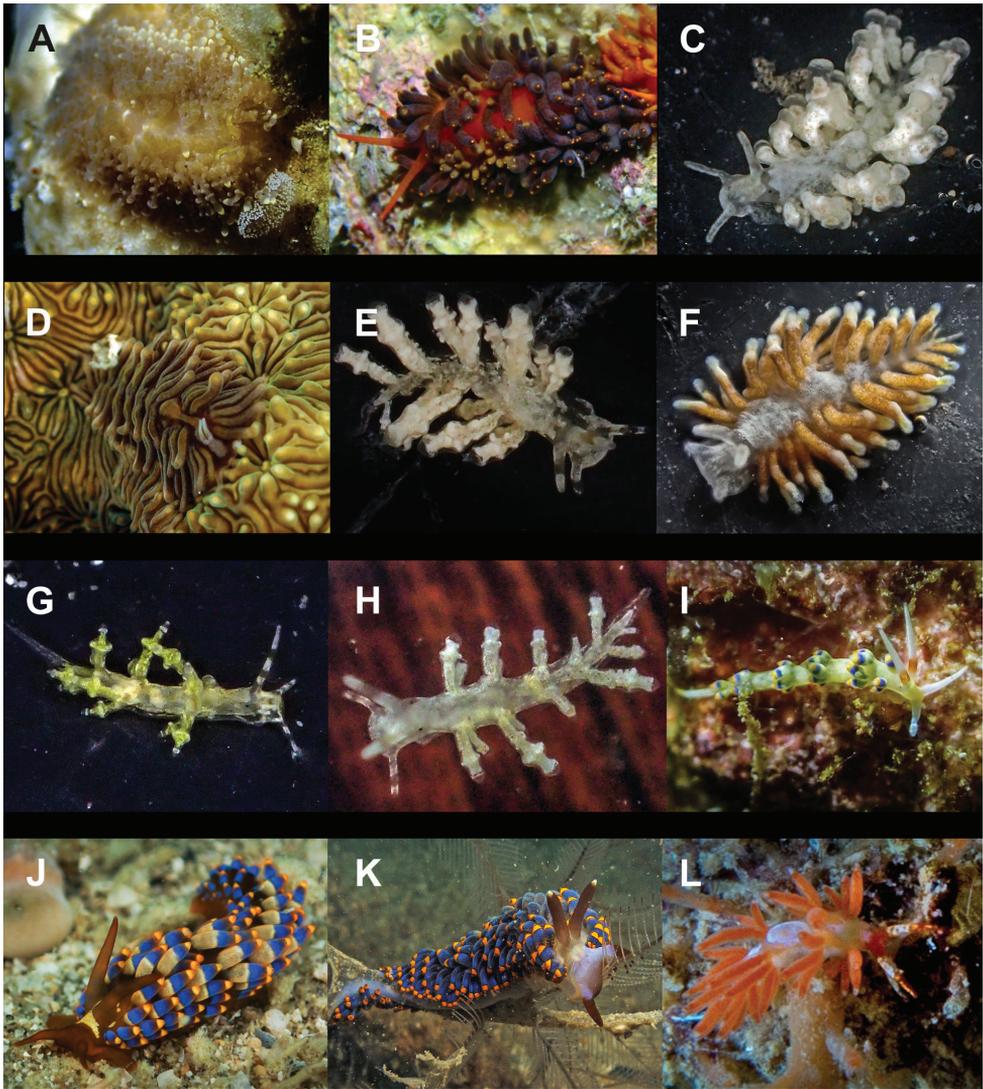
***Phestilla melanobranchia* Bergh, 1874**

Figure 21B

**Material examined.** Two specimens 15–30 mm, SI.

**Ecology.** Exclusively on or in the immediate vicinity of its prey, the scleractinian corals *Tubastraea* spp., in coral reef habitats. Depth 6–32 m.

**Distribution.** Widespread across the Indo-Pacific including Red Sea (Yonow 2000), Mozambique (Tibirićá et al. 2017), Chagos Islands (Yonow et al. 2002), Maldives (Yonow 1994), Myanmar (Sanpanich and Duangdee 2019), Hong Kong (Scott 1984), South Africa, Réunion Island, Malaysia, the Philippines, Indonesia, Japan, Papua New Guinea, Australia, Hawaii, and Mexico (Gosliner et al. 2008). Recorded from both Andaman and Gulf waters of Thailand (Chavanich et al. 2013).



**Figure 21.** **A** *Phestilla lugubris* 30 mm **B** *Phestilla melanobrachia* 30 mm (photograph by Tom Jang) **C** *Phestilla* cf. *minor* 18 mm **D** *Phestilla viei* 20 mm **E** *Phestilla subodiosa* 2 mm **F** *Phestilla* sp. 1 8 mm **G** *Phestilla* sp. 2 4 mm **H** *Phestilla* sp. 3 3 mm **I** *Trinchesia* sp. 1 10 mm (photograph by Wanraya Kraikruan) **J** *Trinchesia* sp. 2 40 mm **K** *Trinchesia* sp. 3 45 mm (photograph by Pau Urgell Plaza) **L** *Trinchesiidae* sp. 6 mm.

**\**Phestilla* cf. *minor* Rudman, 1981**

Figure 21C

**Material examined.** Four specimens 15–25 mm, CA.

**Ecology.** Exclusively on or in the immediate vicinity of its prey, the scleractinian coral *Porites* in coral reef habitats. Locally observed to be predated colonies of *Porites lobata* and *Porites lutea*. Depth 6–14 m.

**Distribution.** Across the Indo-Pacific including Tanzania, Australia, Hawaii (Rudman 1981), Indonesia (Burghardt et al. 2006), Madagascar, Seychelles, Philippines, Japan, Papua New Guinea, and New Caledonia (Gosliner et al. 2008). Recorded from the Gulf waters of Thailand (Chavanich et al. 2013).

**Remarks.** Recent molecular analyses have revealed *Phestilla minor* to be a complex of up to six distinct species (Mehrotra et al. 2020a).

### *Phestilla viei* Mehrotra, Caballer & Chavanich, 2020

Figure 21D

**Material examined.** Two specimens 20–25 mm, AMN; one specimen 25 mm, TT; one specimen 33 mm, SB.

**Ecology.** Exclusively on its prey, the scleractinian coral *Pavona* in coral reef habitats. Locally observed to be predated colonies of *Pavona explanulata* Lamarck, 1816. Depth 4–22 m.

**Distribution.** *Phestilla viei* is known from Madagascar, Thailand, Philippines, Indonesia, and Papua New Guinea (Mehrotra et al. 2020a).

### *Phestilla subodiosa* Wang, Conti-Jerpe, Richards & Baker, 2020

Figure 21E

**Material examined.** One specimen 2 mm, SB.

**Ecology.** Exclusively on its prey coral *Montipora*, in coral reef habitats. Depth 2–8 m.

**Distribution.** *Phestilla subodiosa* is currently known from Thailand (type locality Koh Tao) and South Korea, and possibly Singapore (Wang et al. 2020).

### \**Phestilla* sp. 1

Figure 21F

**Material examined.** Two specimens 8–14 mm, CB.

**Ecology.** Exclusively on its prey, the scleractinian coral *Goniopora* in coral reef habitats. Locally observed to be predated colonies of *Goniopora fruticosa* Saville-Kent, 1891. Depth 2–8 m.

**Distribution.** *Phestilla* sp. 3 (Gosliner et al. 2008) is recorded from Tanzania, the Philippines, Indonesia, Japan, Hong Kong, Papua New Guinea, Australia, and the Marshall Islands. Here representing a first record for Thai waters.

**\**Phestilla* sp. 2**

Figure 21G

**Material examined.** Two specimens 4–7 mm, SB.**Ecology.** Exclusively on its prey, the scleractinian coral *Acropora* sp. in coral reef habitats. Depth 2–8 m.**Distribution.** Unknown. Here representing a first record for Thai waters.**\**Phestilla* sp. 3**

Figure 21H

**Material examined.** One specimen 3 mm, HWB.**Ecology.** Recorded from a single individual found during sampling of the rare octocoral *Nanipora* (Urgell Plaza et al. 2018). The individual was recorded from the skeleton, among polyps of the coral itself. Depth 7 m.**Distribution.** Unknown.**Remarks.** Very similar to *Phestilla subodiosa*, which is considered an obligate feeder of *Montipora* sp. corals. While *Montipora* corals were observed in the vicinity, the present sample was observed upon *Nanipora*, although no feeding or egg masses were observed. The specimen has smooth rhinophores and oral tentacles with clear indications of a darker band approximately halfway on both. Cerata with clearly visible digestive glands and a distinct bulge followed by a subterminal black band (broken up into black spots in some cerata), terminating in translucent rounded apices.**Genus *Trinchesia* Ihering, 1879*****Trinchesia* sp. 1**

Figure 21I

**Material examined.** One specimen 10 mm, TW.**Ecology.** Among rocks and corals in coral reef habitats. Depth 5–10 m.**Distribution.** *Cuthona* sp. 2 (Gosliner et al. 2008) is known from Tanzania, the Philippines, Papua New Guinea, Japan, Australia, and Guam. Known from the Gulf of Thailand (Mehrotra and Scott 2016).**Remarks.** Incorrectly identified as *Cuthona ornata* Baba, 1937 by Mehrotra and Scott (2016), the present species is similar to *Cuthona* sp. 2 (Gosliner et al. 2008). The status of numerous taxa historically described under multiple families and genera such as *Cuthona*, *Trinchesia*, *Tenellia*, etc. is currently in dire need of clarification with recent attempts being made at extensive lumping of groups (Cella et al. 2016). The most recent evidence provided involved the family Trinchesiidae and genus *Trinchesia* being re-instated by Korshunova et al. (2017b). We therefore follow this (likely temporary) state of affairs until this group of taxa is stabilised.

***Trinchesia* sp. 2**

Figure 21J

**Material examined.** Two specimens 35–40 mm, TT; one specimen 45 mm, TW.

**Ecology.** Cryptic on its host hydroid *Macrorhynchia* sp., colonies of which are found exclusively in soft sediment habitats outside the coral reef. Depth 12–24 m.

**Distribution.** *Tenellia* sp. 17 is known only from the United Arab Emirates (Gosliner et al. 2018) and *Tenellia* sp. (Tibiriçá et al. 2017) is known from Mozambique. Known from the Gulf of Thailand (Mehrotra and Scott 2016).

**Remarks.** Mistakenly identified as *Cuthona yamasui* Hamatani, 1993 by Mehrotra and Scott (2016). Very similar also to *Trinchesia* sp. 3, with which it shares a prey species (alongside *Lomanotus vermiformis*).

**\**Trinchesia* sp. 3**

Figure 21K

**Material examined.** Three specimens 12–45 mm, SN.

**Ecology.** Cryptic on its host hydroid *Macrorhynchia* sp., colonies of which are found exclusively in soft sediment habitats outside the coral reef. Depth 12–24 m.

**Distribution.** ‘*Cuthona yamasui*’ (Gosliner et al. 2008) is known from Tanzania, Oman, Malaysia, the Philippines, Indonesia, Japan, and Australia. Here representing a first record for Thai waters.

**Remarks.** Very similar to *Trinchesia* sp. 2, with which it shares a prey species (alongside *Lomanotus vermiformis*). Distinguished by the presence of a white body with brown rhinophores and oral tentacles, unlike the brown body with white markings around the rhinophores as seen in *Trinchesia* sp. 2. Cerata in the present species are basally transparent (with the blue digestive glands clearly visible) turning blue with a thin black band, a thick yellow band, and another thin black subapical band below translucent apices. The cerata of *Trinchesia* sp. 2 on the other hand are basally opaque white followed by a distinct large blue band and yellow apices with colourless tips. The present species is similar to *Tenellia* sp. 15 and *Tenellia* sp. 16 of Gosliner et al. (2018). See above comments regarding genus and family instability.

***Trinchesiidae* sp.**

Figure 21L

**Material examined.** One specimen 6 mm, HF.

**Ecology.** On artificial reef structures feeding on the same orange *Corydendrium* sp. hydroid as *Unidentia aliciae*, on which it is cryptic. Depth 8–12 m.

**Distribution.** *Cuthona* sp. 19 (Gosliner et al. 2008) is known from the Philippines and Papua New Guinea. Known from the Gulf of Thailand (Mehrotra and Scott 2016: fig. 2A).

**Family Unidentiidae Millen & Hermosillo, 2012****Genus *Unidentia* Millen & Hermosillo, 2012*****Unidentia aliciae* Korshunova, Mehrotra, Arnold, Lundin, Picton & Martynov, 2019**

Figure 22A

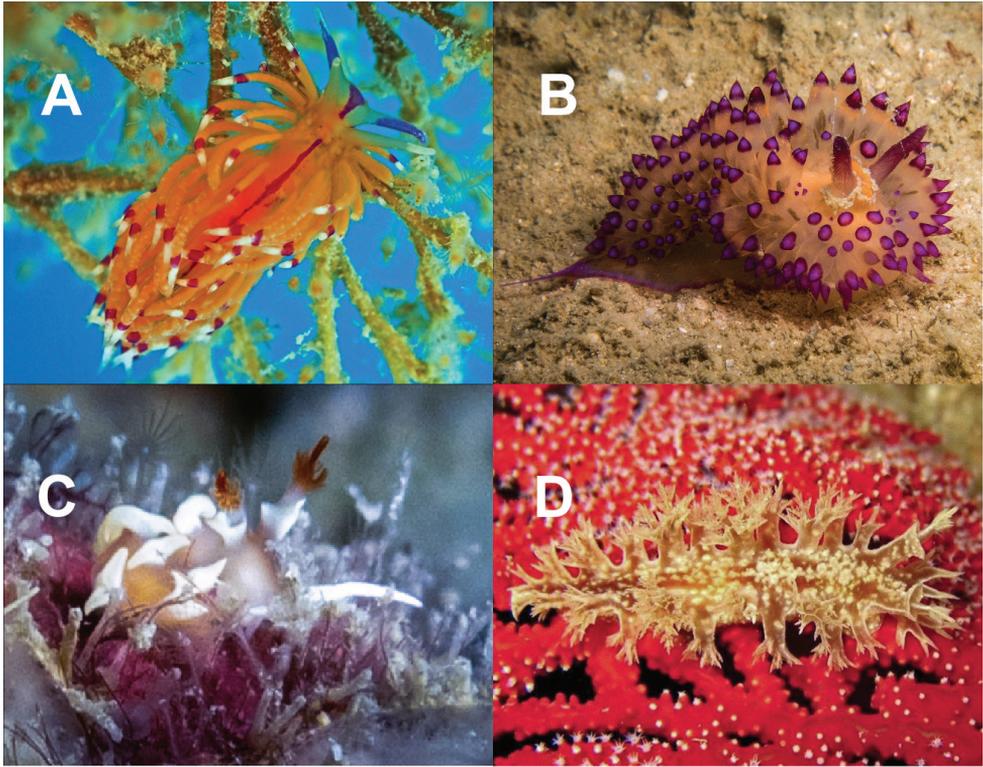
**Material examined.** Three specimens 19–24 mm, HF.**Ecology.** On artificial reef structures feeding on the same orange hydroid *Corydendrium* sp. as Trinchesiidae sp. This hydroid is predominantly known from artificial reef structures at Koh Tao (see Korshunova et al. 2019). Depth 5–18 m.**Distribution.** Currently known only from the Gulf of Thailand (Korshunova et al. 2019).**Superfamily Proctonotoidea Gray, 1853****Family Janolidae Pruvot-Fol, 1933****Genus *Janolus* Bergh, 1884*****Janolus savinkini* Martynov & Korshunova, 2012**

Figure 22B

**Material examined.** Two specimens 55–70 mm, LB; one specimen 38 mm, SW.**Ecology.** In soft sediment habitats outside the coral reef. Depth 18–28 m.**Distribution.** Across the Indo-Pacific including the Red Sea (Yonow 2015), Australia (Nimbs and Smith 2016), Vietnam (Martynov and Korshunova 2012), the Philippines, Indonesia, and Japan (Gosliner et al. 2008). Known from the Gulf of Thailand (Mehrotra and Scott 2016).**Superfamily Tritonioidea Lamarck, 1809****Family Tritoniidae Lamarck, 1809****Genus *Marianina* Pruvot-Fol, 1931****\**Marianina rosea* (Pruvot-Fol, 1930)**

Figure 22C

**Material examined.** One specimen 10 mm, CB.**Ecology.** Under rubble, among small hydroids, in coral reef habitats. Depth 5–8 m.**Distribution.** Across the Indo-Pacific including India (Apte 2009), Australia (Burn 1978), South Africa, Madagascar, the Philippines, Papua New Guinea, and New Caledonia (Gosliner et al. 2008). Here representing a first record for Thai waters.**Remarks.** The single specimen observed from Koh Tao appears paler than is typical for the species, though such colour differences are not unheard of (see Fraser 2000). It is clearly recognised by its cerata and rhinophoral morphology, unique among the Tritoniidae.



**Figure 22.** **A** *Unidentia aliciae* 24 mm **B** *Janolus savinkini* 55 mm (photograph by Pau Urgell Plaza) **C** *Marianina rosea* 10 mm **D** *Tritonia* sp. 35 mm (photograph by Khumron Waipaka).

### Genus *Tritonia* Cuvier, 1798

#### *Tritonia* sp.

Figure 22D

**Material examined.** One specimen 35 mm, GR.

**Ecology.** Known from a single specimen observed on the octocoral *Echinogorgia* sp. Depth 14 m.

**Distribution.** *Tritonia* sp. 7 (Gosliner et al. 2008) is known only from Indonesia. Known from the Gulf of Thailand (Mehrotra and Scott 2016).

### Discussion

Prior to studies from Koh Tao, the documented diversity of sea slug taxa from the Gulf of Thailand numbered 111 species, with 204 species in total recorded for Thailand (Table 2). Surveys by Mehrotra and Scott (2016) increased these numbers to 154 for

the Gulf specifically and 235 for Thai waters overall. The present findings further increase the documented diversity of sea slug taxa from the Gulf and Thai waters to 256 and 336 respectively. In general, species were recorded from coral reef habitats or soft sediment habitats exclusively, with only 28 species being found across both (Fig. 3). Of those found in coral-dominated habitats, numerous species were documented to have one of two further specialist habitat types that have thus far remained unexplained.

The first of these are those species that are documented preferentially from artificial substrates such as artificial reefs and debris. Nudibranch species such as *Phidiana militaris*, Trinchesiidae sp., and *Unidentia aliciae* were found in abundance over the years and were mostly or exclusively documented associated with prey growing on such substrates, with *U. aliciae* being described associated from these substrates (Korshunova et al. 2019). The role of artificial substrates in the benthic ecology of reef environments requires further exploration, in particular the association of sea slugs with regards to the role of synthetic materials as substrates for colonial organisms and vectors for their dispersal (Hoeksema et al. 2012; McCuller et al. 2018). Such trends may reveal unexpected ecological impacts from habitat manipulation such as coral restoration or marine debris, if they are found to promote certain organisms over others (i.e., hydroids or sponges as prey to nudibranch taxa).

The second specialist habitat type within the hard substrate habitats was the ventral surface of the skeletons of dead Fungiidae corals. These corals are known to be in high abundance around Koh Tao (Hoeksema et al. 2013; Scott et al. 2017). Benthic surveys among rubble and reef substrate environments revealed that taxa that were rarer or more cryptic due to size or camouflage were recorded in noticeably greater abundances adhering to the underside of the skeletons of dead mushroom corals than other rubble or living coral substrates in reef habitats. In particular, the species *Elysia obtusa*, *Philine orca*, *Goniobranchus* cf. *albonares*, *Mexichromis trilineata*, and *Dermatobranchus fortunatus* were all recorded almost exclusively from under these skeletons. The rugosity and proportionally larger surface area of these skeletons, in combination with the shelter from light and wave action likely provide attractive conditions for the high diversity of poriferan, algal, cnidarian, and bryozoan taxa observed under these corals. A closer investigation into the dynamics of species composition across different benthic substrate types in more coral reef areas may yield greater information on species traditionally considered ecologically cryptic.

Mehrotra and Scott (2016) found that 37% of species documented were not observed in hard substrate habitats such as fringing reefs and offshore pinnacles but were instead exclusive to deeper soft sediment habitats beyond the reef slope. Remarkably, the present findings document only 36% of all species being exclusive to these habitats, despite a more than doubling of documented taxa. These habitats support a diverse community of organisms not observed in hard substrate areas such as the fringing reef and offshore pinnacles. These include cnidarians such as pennatulacean and *Dendronephthya* sp. octocorals (Mehrotra et al. 2017), *Heteropsammia* spp. and *Heterocyathus* spp. scleractinian corals (Hoeksema and Matthews 2015; Mehrotra et al. 2016, 2019), and diverse assemblages of cerianthids and benthic hydrozoans (Martynov et al. 2019).

Additionally, algae such as *Avrainvillea longicaulis* and *Vaucheria* sp. are often abundant in these areas (Mehrotra et al. 2019) as well as bryozoans of the family Bugulidae and other known prey items of sea slugs (McDonald and Nybakken 1997), most of which are either rare or entirely absent from hard substrate habitats around Koh Tao. Indeed, such ecological aspects have already been suggested as key drivers in the description of four new species from the soft sediments of Koh Tao (Mehrotra et al. 2017, 2020b).

It is possible that many of these specialised organisms can colonise much of the benthic environment in the Gulf due to its particular characteristics. Apart from being among the western-most ecological regions attributed to the Pacific, the Gulf of Thailand differs greatly from the Andaman coast of Thailand, being a region inundated by heavy sedimentation due to the many rivers that flow into it and remained entirely frozen until the glacial retreat into the Holocene (Sathiamurthy and Voris 2006). The Gulf of Thailand today has a maximum depth of 84 m (Cheevaporn and Menasveta 2003) although the vast majority of the Gulf is shallower than 75 m with only the central region exhibiting a depth of greater than this (Voris 2000; Sojisuporn et al. 2010). Therefore, the Gulf of Thailand is a 320,000 km<sup>2</sup> sediment-rich basin entirely in the photic zone. It is at present challenging to draw sweeping conclusions on the comparative sea slug diversity between the Gulf of Thailand and other West-Pacific regions, as it is extremely unlikely that the majority of taxa present within either the Gulf or the surrounding seas have been documented. Nonetheless, recent years have seen attempts being made to quantitatively compare diversity estimates between West-Pacific regions (i.e., Eisenbarth et al. 2018; Undap et al. 2019). However, despite an increase in the numbers of sea slug biodiversity inventories in the past decade, there remains a paucity of in-depth ecological information for most species.

Beyond the habitat preferences, the present study further expands on the trophic dynamics of different sea slugs allowing insights into their place in the food webs of Koh Tao.

For example, predation upon sea slugs were documented from both habitat types, with predation upon Haminoeidae spp. in particular observed numerous times in the present study. In soft sediment habitats, predation by crustaceans (both decapod and stomatopod) appeared prominent (Fig. 6G), and in coral reef habitats, predation by Labriidae fish was abundant, in both cases agreeing with growing evidence of sea slugs as viable prey items to non-heterobranchs in the Indo-Pacific tropics (Mehrotra et al. 2019; Anker and Ivanov 2020). Furthermore, habitat-specifics of various prey items were distinctly visible, with certain groups (i.e., hydroids) having a much more complex habitat distribution across coral reef and soft sediment habitats than others such as major anthozoan groups. A deeper exploration of these observations is needed to investigate ecological drivers for such habitat distribution.

## Conclusions

The findings presented here highlight the need for a greater documentation and understanding of sea slug ecology in the Indo-Pacific as many questions remain regarding the habitat

and prey preferences of the majority of species documented from the Gulf of Thailand and elsewhere. It is apparent that the diversity of sea slug taxa in the Gulf of Thailand has been greatly under-reported and that the marine habitats in the region support a high diversity of benthic species. With the increasing availability of SCUBA infrastructure around the Gulf, it is likely that a greater area within the region will be made accessible for the study of marine benthic environments. In conjunction, the expansion of surveys into deeper soft sediment habitats will likely further expand on the known diversity of a great number of species in these areas. Very little has been documented on the distinct biological and ecological characteristics of marine soft sediment habitats (Wilson 1991), yet it has been shown that they are able to support a USD\$150 million tourism industry in South-East Asia alone (De Brauwier et al. 2017). A combination of increased efforts on surveying unexplored benthic habitats and the growing utility of citizen science efforts will yield much needed advancements in the understanding of benthic ecology in the Gulf of Thailand.

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