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Redescription of *Streptaxis mouhoti* Pfeiffer, 1863 and *Streptaxis strangulatus* Möllendorff, 1894 (Eupulmonata: Streptaxidae) from Peninsular Thailand and Their Assignment to a New Genus

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ABSTRACT.– Two species of the family Streptaxidae found in Peninsular Thailand are redescribed and assigned to a new genus, *Panhartemis* **gen. nov.** The new genus has two distinctive species, *Panhartemis strangulatus* **comb. nov.** and *Panhartemis mouhoti* **comb. nov.**, from isolated limestone karsts in western Thailand. *Panhartemis* Siriboon, **gen. nov.** exhibits an oblique-cylindrical shell shape, elevated conical spire, last whorl slightly axially deflected, and penial hooks separated by elevated reticulated folds; none of these characteristics occur in other streptaxids. Details of the genital anatomy and the radula of the two species are provided for the first time. The current study advances knowledge of the streptaxid land snail species in Peninsular Thailand and emphasizes the value of limestone habitats for preserving biodiversity.

KEYWORDS: carnivorous snail, endemic species, genitalia, limestone, systematics

INTRODUCTION

Members of the carnivorous snail superfamily Streptaxoidea Gray, 1860 have a small to medium shell size but much diversity in shell shape, ranging from regularly coiled to extremely eccentric to bearing a distorted last whorl, from discoidal to elongate conic, and with none to numerous apertural dentitions (Zilch, 1960; Bruggen, 1967; Schileyko, 2000). A small fraction of these diverse forms, those with small size (height about 5 mm), cylindrical or pupoid shell shape with axially detached last whorl were recently reclassified into the distinct family Diapheridae Panha & Naggs, 2010, based on both morphological and molecular evidence (Sutcharit et al., 2010). Subsequently, the status of some genera was revised and they were transferred to this newly erected family based mainly on shell characters (Páll-Gergely et al., 2020). The remaining members with larger shells (height about 5–20 mm) and ovate to eccentric shapes are classified into the Streptaxidae, which comprises five to six subfamilies distributed worldwide (Richardson, 1988; Schileyko, 2000; Rowson et al., 2010; Sutcharit et al., 2010; Bouchet et al., 2017). In mainland Southeast Asia, the streptaxids are currently classified into ten genera: *Carinartemis* Siriboon & Panha, 2014; *Discartemon* Pfeiffer, 1856; *Elma* Adams, 1866; *Haploptychius* Möllendorff, 1906; *Indoartemon* Forcart, 1946; *Oophana* Ancey, 1884; *Pallgergelyia* Thach, 2017; *Perrottetia* Kobelt, 1905; *Stremmatopsis* Mabille, 1887; and *Thachia* Huber, 2018 (Bruggen, 1972; Richardson, 1988; Schileyko, 2000; Siriboon et al., 2013, 2014a; Do and Do, 2015; Páll-Gergely et al., 2015; Thach, 2017, 2018). Although shell shape and apertural dentition are the main distinguishing characteristics for this group, the genital anatomy is believed to be more taxonomically informative and reliable in classification; however, studies providing descriptions of genitalia are still scarce in this family (Schileyko, 2000; Rowson and Tattersfield, 2013; Siriboon et al., 2014b). Moreover, the first overview of the molecular phylogeny of the major Thai streptaxid genera has shown high diversity and interesting biogeographic patterns. At least 10 clades with distinct geographic distributions were found, according to the data. In particular, *Oophana* and *Haploptychius* were revealed to be polyphyletic and represented polytomy in several clades, and each clade could possibly be recognized as a distinct genus (Siriboon et al., 2020).

Focusing on *Oophana*, the genus is traditionally recognized as having an oblique heliciform shell, the last whorl being axially distorted from the columellar axis, and by having one parietal and three or more additional lamellae (Kobelt, 1906; Richardson, 1988; Schileyko, 2000). Moreover, the distribution of the genus is restricted to Indochina and Peninsular Malaysia, and about twenty nominal species have been previously reported (Richardson, 1988). According to the recent molecular relationship analysis that covered mostly taxa from Thailand, at least three distinct clades could be recognized, namely the *O. expansilabris* clade, the *O. subbulbulus–O. siamensis* clade, and the *O. mouhoti–O. strangulatus* clade (see Siriboon et al.,

2020: fig. 2). Interestingly, one clade, containing only two species that display a regularly coiled and cylindrical shape, shows discordance with traditional classification based on the shell morphology of the *Oophana*. '*Streptaxis strangulatus* Möllendorff, 1894' and '*Streptaxis mouhoti* Pfeiffer, 1863' are cylindrical-shelled species with *Oophana*-type apertural dentition, and they seem to be narrowly distributed in Peninsular Thailand. Based on their high genetic divergence, Siriboon et al. (2020) suggested this cylindrical shell is an apparently distinguishing character from the other clades, even without the genitalia information of these species.

A large number of specimens of these two cylindrical-form '*Oophana* s.l.' species were collected from the eastern slope of the Tenasserim Range in Peninsular Thailand during field surveys. Therefore, the main purpose of this research is to revise and redescribe the species based on the newly collected materials, living organisms, genitalia, and radula morphology in accordance with the suggestion by Siriboon et al. (2020). Furthermore, the new genus *Panhartemis* gen. nov. is proposed to accommodate these two species, which will be referred to as *Panhartemis mouhoti* comb. nov. and *Panhartemis strangulatus* comb. nov.

MATERIALS AND METHODS

The specimens were collected from Peninsular Thailand from the 1990s until recently by Animal Systematics Research Unit members, Department of Biology, Faculty of Science, Chulalongkorn University, Thailand. These field surveys focused mainly on limestone areas on the east slope of the Tenasserim Range, particularly in Phetchaburi and Prachuap Khiri Khan provinces. The coordinates were recorded using GPS and approximate collection localities are presented in Figure 1.

Living specimens were photographed, euthanized following guidelines by the American Veterinary Medical Association (2020), and then preserved in 70% ethanol (v/v) for anatomical studies. The identifycations were made based on Pfeiffer (1863), Möllendorff (1894), Kobelt (1905–1906) and Blanford and Godwin-Austen (1908). Shell height, shell width and whorl count were measured, and the height/width ratio was calculated following Siriboon et al. (2013). The shells were examined and photographed. One to five adult specimens in ethanol were dissected, and the genitalia were examined under a stereomicroscope. A representative specimen was illustrated with the aid of a camera lucida. The buccal masses were removed, and the radulae were soaked in 10% NaOH, then cleaned in distilled water. Radula and internal wall sculpture of genitalia (hooks) were examined and photographed under SEM (JEOL, JSM-5410 LV).

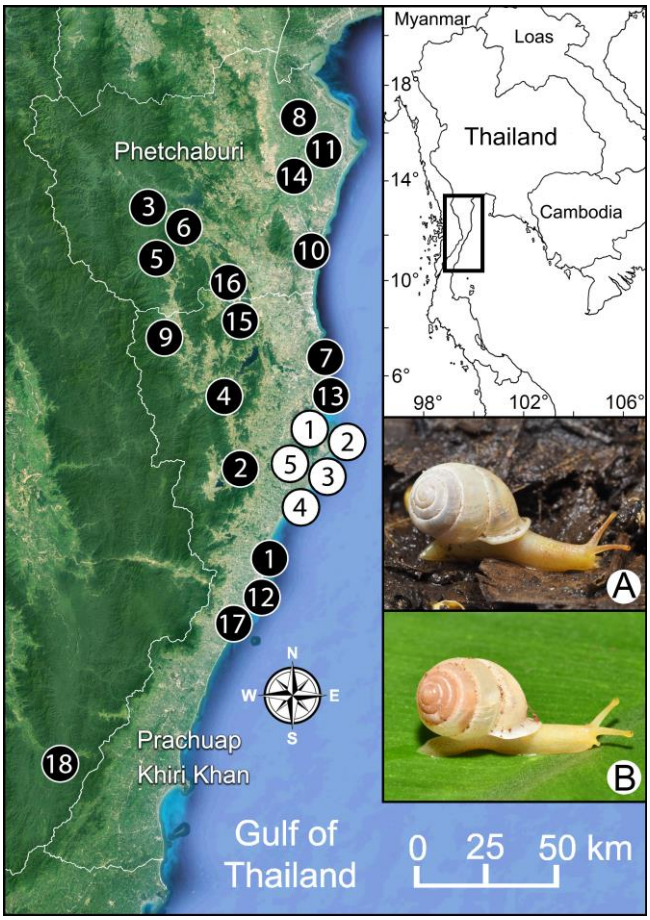

FIGURE 1. Approximate collection localities for surveys in this study. Location names are indicated in Table 1. Dark circles indicate *Panhartemis mouhoti*, and **A.** specimen from Wat Khao Krachiu, Tha Yang, Phetchaburi (shell width about 10 mm); open circles indicate *Panhartemis strangulatus*, and **B.** specimen from Sam Roi Yot, Prachuap Khiri Khan (shell width about 8 mm).

The nominal genus name described as new to science in this work is attributed to the last author (T. Siriboon). Thus, a complete citation of the authors is Siriboon in Chunkhajorn et al.

Anatomical abbreviations.– ag, albumen gland; at, atrium; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hd, hermaphroditic duct; ov, ovary; p, penis; pr, penial retractor muscle; ps, penial sheath; psr, penial sheath retractor muscle; sv, seminal vesicle; ta, talon; v, vagina; vd, vas deferens (Sutcharit et al., 2010; Siriboon et al., 2013, 2014a, b).

Institutional abbreviations.– Materials examined in this study were deposited in the following institutions:

CUMZ: Chulalongkorn University Museum of Zoology, Bangkok, Thailand

NHMUK: The Natural History Museum, London, United Kingdom
SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany
SWUMZ: Srinakharinwirot University Museum of Zoology, Bangkok, Thailand

RESULTS

Systematics

Family Streptaxidae Gray, 1860

Genus *Panhartemis* Siriboon gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:8197BC0D-52D4-4A00-BF31-CD4540A2D1E5

Type species.– *Streptaxis strangulatus* Möllendorff, 1894.

Etymology.– The generic name *Panhartemis* gen. nov. is derived from the last name of Professor Somsak Panha from Chulalongkorn University and the Greek word '*artemis*' meaning 'goddess of chase'. This name is proposed to commemorate Prof. Dr. Panha's 65th birthday anniversary in 2023.

Diagnosis.– Shell translucent, oblique-cylindrical, spire elevated and conical, and rounded periphery. Last whorl almost descends axially below preceding whorl. Aperture subcircular and expanded. Apertural dentition consists of one parietal lamella, and with weak to strong additional lamellae. Umbilicus opened and deep. Genitalia with thin penial sheath extending more than half of penis length; penial hooks located on conical papillae and separated by elevated reticulated folds; vaginal wall with longitudinal vaginal folds, vaginal hook absent.

Remarks.– In terms of shell morphology and apertural dentition, *Panhartemis* gen. nov. is superficially similar to *Haploptychius* and *Oophana*. However, this new genus can be distinguished from the latter two genera by having cylindrical to oblique-cylindrical shell, elevated conical spire, with one parietal lamella and weak to strong lamellae on palatal wall. In comparison, *Haploptychius* and *Oophana* are generally similar in having oblique-heliciform to oblique-ovate shell, convex to conical spire, and last whorl much deviated from the columellar axis. However, *Haploptychius* has only one parietal lamella, while *Oophana* has one parietal and always additional multiple lamellae on the palatal wall (Man et al., 2022). In comparison with the currently available genital morphology data for *Haploptychius* and *Oophana* (Schileyko, 2000), this new genus has conical penial hooks located on papillae that are separated by reticulated folds, and absent vaginal hooks. In contrast, *Haploptychius* has long and slender penial hooks and vaginal hooks; and *Oophana* has shorter and stouter penial hooks, more elevated reticulated hooks located on papillae that are separated by higher reticulated folds, and vaginal hooks may be present.

For further comparison, *Carinartemis* distinctly differs from this new genus by its sub-oblique heliciform shell, last whorl much deviated from the columellar axis, strong peripheral keel along nearly the entire penultimate whorl, with or without parietal lamella (Siriboon et al., 2014b; Man et al., 2022). In addition, *Indoartemon* can be distinguished from the new genus by having oblique-heliciform shell, aperture semi-ovate, apertural dentition with one parietal and one palatal lamella (Siriboon et al., 2014b). In terms of the genitalia, *Carinartemis* has a thin to very thickened penial sheath and vaginal hooks may be present, while *Indoartemon* has vas deferens attached to the distal end of the penial sheath by a narrow band of connective tissue (Siriboon et al., 2014a).

This new genus is noticeably distinct from *Discartemon* by having an oblique-cylindrical shell, regularly expanded, more axially deflected last whorl, and narrower umbilicus. Regarding the genitalia, this new genus possesses a long penis with brownish penial hooks located on conical papillae and separated by elevated reticulated folds. Penial appendix is absent. In contrast, *Discartemon* has a flattened to subglobose-heliciform shell, regularly to rapidly expanded, not axially deflected last whorl, and umbilicus wide to very wide. Additionally, the genitalia of *Discartemon* possesses a short to long penis, with or without penial appendix and sometimes with transparent penial hooks (Siriboon et al., 2014b).

Perrotettia can be distinguished from the new genus by having a sub-oblique heliciform to oblique-heliciform shell, with longitudinal furrows behind the apertural lip and usually with two parietal lamellae. In contrast, *Panhartemis* gen. nov. exhibits an oblique-cylindrical shell without longitudinal furrows behind the apertural lip, and one parietal lamella. In genitalia, *Perrottetia* sometimes has penial hooks located on conical papillae without elevated reticulated folds, and vaginal hooks are present. In contrast, the new genus has penial hooks located on conical papillae and separated by elevated reticulated folds without vaginal hooks (Siriboon et al., 2013).

Currently the new genus consists of two species, *P. mouhoti* comb. nov. and *P. strangulatus* comb. nov., previously referred to as *Oophana* (Richardson, 1988;

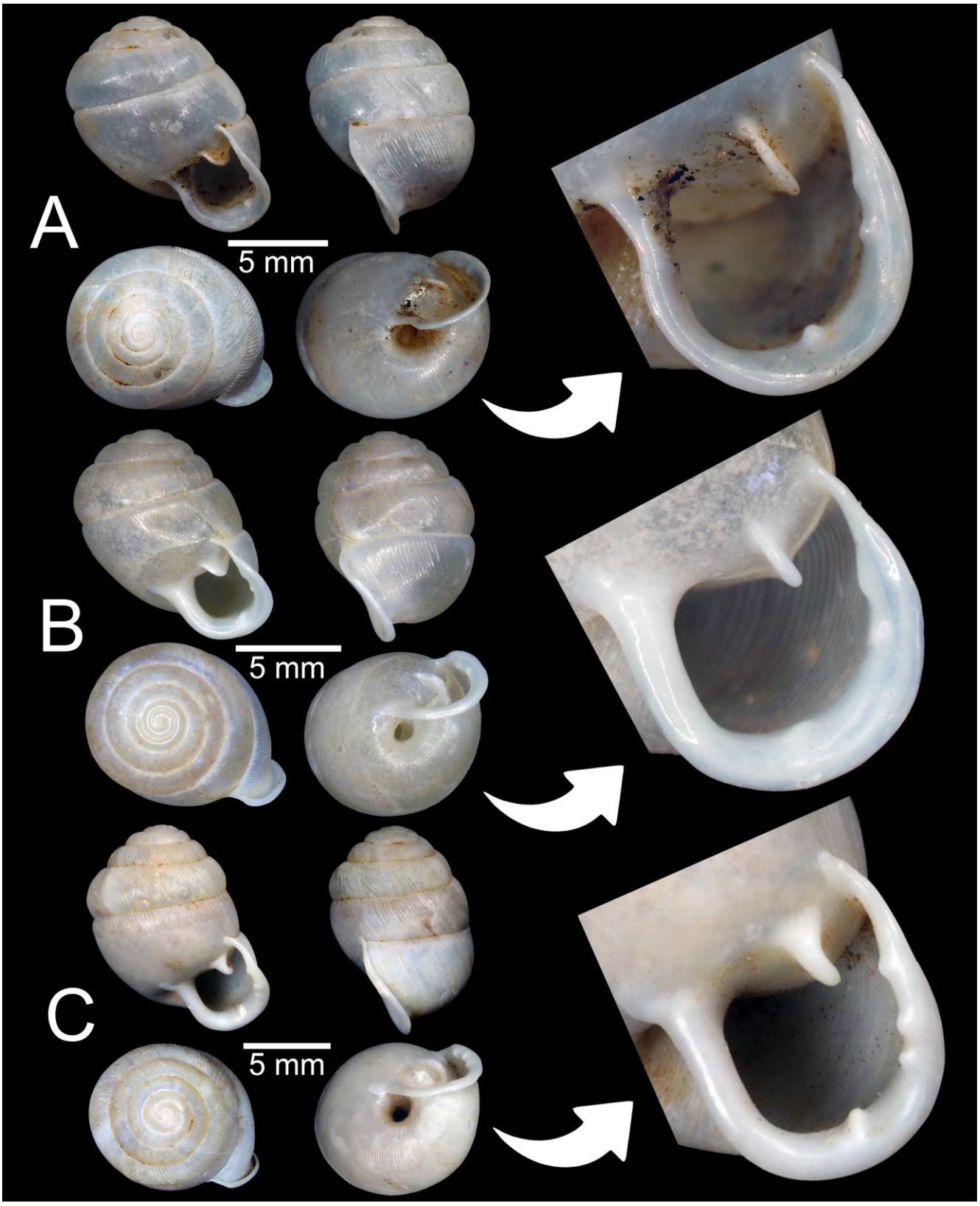

FIGURE 2. *Panhartemis mouhoti*. **A.** possible syntype NHMUK ex. Cuming collection from Camboja with apertural dentition. **B.** specimen CUMZ 6137 from Ban Lat, Phetchaburi with apertural dentition. **C.** specimen CUMZ 3688 from Kaeng Krachan, Phetchaburi with apertural dentition.

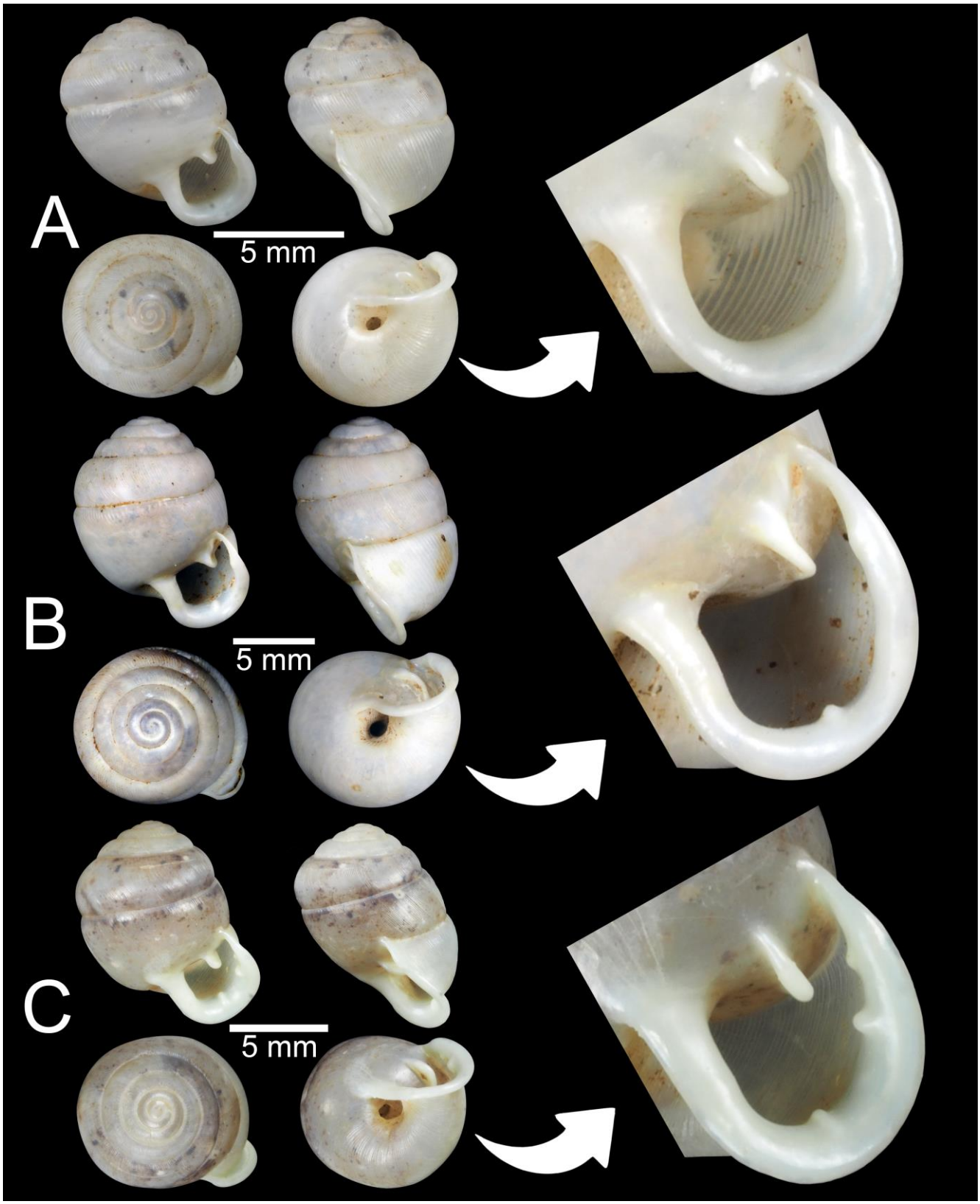

FIGURE 3. *Panhartemis mouhoti*. **A.** specimen CUMZ 6139 from Khao Kalok, Pran Buri, Prachuap Khiri Khan with apertural dentition**. B.** specimen CUMZ 8006 from Kui Buri, Prachuap Khiri Khan with apertural dentition. **C.** specimen CUMZ 4229 from Khao Lom Muak, Mueang, Prachuap Khiri Khan with apertural dentition.

Man et al., 2022). They are endemic to Peninsular Thailand and tend to have narrow distributions in Phetchaburi and Prachuap Khiri Khan provinces, with a single record from Myanmar (Man et al., 2022). Living animals are found under leaf litter on the ground in limestone forests. The soft body is typical of streptaxids, having bright yellowish reticulated skin, and brownish digestive gland and kidney that are slightly visible through the translucent shell. Anterior body has upper tentacles which are longer than the lower pair, with a dark eye spot on the tip of the fully extended tentacle; yellowish to reddish retractor muscles show through the translucent skin, and the posterior body has a short, narrow and undivided foot (Fig. 1A, B).

***Panhartemis mouhoti* (Pfeiffer, 1863) comb. nov.**
(Figs 1, 2A–C, 3A–C, 5A, B, 6A–G; Table 1)

Streptaxis mouhoti Pfeiffer, 1863 [1862]: 273. Type locality: Siam [Thailand]. Martens, 1867: 84, pl. 22, fig. 22. Pfeiffer, 1868: 446. Nevill, 1878: 4. Tryon, 1885: 80, pl. 15, fig. 46. Bourguignat, 1889: 133. Gude, 1903: 225. Panha, 1996: 33.

Streptaxis johswichi Martens, 1864: 528. Type locality: Siam, bei Petchaburi [Petchaburi Province, Thailand]. Richardson, 1988: 236

Gonaxis mouhoti—Bourguignat, 1889: 133.

Odontartemon (Oophana) mouhoti—Kobelt, 1906: 104, 105, pl. 55, fig. 23.

Oophana mouhoti—Benthem Jutting, 1954: 96. Richardson, 1988: 235, 236. Hemmen and Hemmen, 2001: 43. Sutcharit et al., 2018: 197, 198. Siriboon et al., 2020: fig. 14, 15; Table 1. Man et al., 2022: 54–56, fig. 7a, b.

Type material.– Possible syntypes NHMUK ex. Cuming collection (3 shells; Fig. 3A) from ‘Camboja’ [very likely in error; see below].

Other material examined.– **MYANMAR:** Phra (Buddha) Cave, Tanintharyi Region, Myanmar: CUMZ 13005 (1 shell). **THAILAND:** Siam: NHMUK ex. Cuming collection (2 shells) labeled as ‘*johswichi*’. **Phetchaburi Province:** Tam Khao Rong, Ban Lat District (13°01'31.3"N, 99°55'01.9"E): CUMZ 6135 (15 specimens in ethanol; Figs 5A, B, 6A–G), CUMZ 6137 (117 shells; Fig. 2B), Tam Khao Hua Chang, Kaeng Krachan District (12°42'25.0"N, 99°31'36.9"E): CUMZ 3741 (4 shells). Kaeng Krachan District (12°53'28.9"N, 99°38'10.9"E): CUMZ 3688 (2 shells; Fig. 2C), 3723 (12 shells), 6123 (5 shells). Khao Nang Phanthurat, Cha-am District (12°50'21.8"N, 99°57' 10.4"E): CUMZ 3745 (3 shells), 6133 (13 shells). Khao Wang, Mueang District (13°06'24.7"N, 99°56'18.2"E): CUMZ 3755 (9 shells). Ban Yang Chum, Kaeng Krachan District (12°46'20.9"N,99°40'31.6"E): SWUMZ 1025 (4 shells). Ban Krang, Kaeng Krachan District (12°47'55.7"N, 99°27'15.0"E): SWUMZ 1026 (2 shells). Wat Khao Krachiu, Tha Yang District (12°57' 41.7"N, 99°54'48.6"E): SWUMZ 1027 (13 specimens in ethanol; Fig. 1B). **Prachuap Khiri Khan Province:** Khao Lom Muak, Mueang District (11°47'07.3"N, 99° 48'50.5"E): CUMZ 4229 (10 shells; Fig. 3C), SWUMZ 1019 (9 shells). Ao Manao, Mueang District (11°45' 53.0"N, 99°48'03.6"E): CUMZ 3767 (26 shells). Nam Tok Pala-U, Hua Hin District (12°32'17.4"N, 99°27' 48.7"E): CUMZ 3684 (14 shells), 3768 (5 shells). Khao Kalok, Pran Buri District (12°20'21.6"N, 99°59' 54.8"E): CUMZ 6139 (34 shells; Fig. 3A), CUMZ 3698 (4 specimens in ethanol), 6143 (16 shells), SWUMZ 1018 (30 shells). Kui Buri District (12°16' 09.2"N, 99°56'27.2"E): CUMZ 8006 (34 shells; Fig. 3B). Tam Dao, Hua Hin District (12°35'28.1"N, 99°43'44.5"E): SWUMZ 1015 (8 shells). Tam Kai Lon, Hua Hin District (12°36'47.5"N, 99°42'37.0"E): SWUMZ 1016 (3 shells). Ban Nong Bua, Pran Buri District (12°21'10.5"N, 99°59'10.8"E): SWUMZ 1017 (6 shells). Kong Bin Hospital, Ao Manao, Mueang District (11°45'51.4"N, 99°47'50.6"E): SWUMZ 1020 (3 shells).

Differential diagnosis.– *Panhartemis mouhoti* can be distinguished from *P. strangulatus* by having strong ridges on the shell, penultimate whorl slightly extended, last whorl slightly axially deflected, with weak palatal and basal lamellae, and without columellar lamella. In contrast, *P. strangulatus* has fine radial ridges over the entire shell, penultimate whorl not extended, lip expanded, with strong lamellae and columellar lamella present. In terms of the genitalia, *P. mouhoti* has a short penial sheath (about half of penis length) and a short vagina (about a quarter of penis length), while *P. strangulatus* has a long penial sheath (about two-thirds of penis length) and a long vagina (about one-third of penis length).

This species also differs from *Haploptychius heliakosus* Man & Panha, 2022 from Myanmar by having a subcircular aperture, with one to four weak lamellae on the palatal wall; genitalia with thin penial sheath, penial hooks located on conical penial papillae, and long vagina. Meanwhile, *H. heliakosus* has subquadrangular aperture, without palatal lamella, genitalia with muscular penial sheath, penial hooks located on trapezoidal papillae, and a short vagina (Man et al., 2022).

In addition, *P. mouhoti* superficially resembles *Haploptychius pellucens* (Pfeiffer, 1863) from Laos, but the latter species has a more axially deflected last

TABLE 1. Shell measurements of the *Panhartemis* species recognized in this study. Numbers listed with collection locality correspond to the map in Figure 1.

Species, locality and CUMZ/ SWUMZ no.	No. of specimens	Range, mean ± S.D. in mm. of			Number of whorls
		Shell Hight	Shell Width	H/W ratio	
Panhartemis mouhoti					
1. Ao Manow, Mueang, Prachuap Khiri Khan (CUMZ 3767)	26	9.8–13.3 11.48±1.02	8.8–13.4 10.68±1.39	0.96–1.27 1.08±0.10	6½
2. Ban Yang Chum, Kaeng Krachan, Pethchaburi (SWUMZ 1025)	4	11.3–12.6 11.86±0.57	10.1–10.9 10.56±0.33	1.04–1.19 1.12±0.07	6½
3. Ban Krang, Kaeng Krachan, Phetchaburi (SWUMZ 1026)	2	11.2–11.9 11.54±0.54	9.3–10.9 10.11±1.12	1.02–1.28 1.15±0.18	6½
4. Kui Buri, Prachuap Khiri Khan (CUMZ 8006)	34	10.1–13.4 11.97±0.70	8.79–11.2 10.18±0.50	1.02–1.44 1.18±0.10	6½
5. Tam Khao Hua Chang, Kaeng Krachan, Phetchaburi (CUMZ 3741)	4	9.8–12.5 11.26±1.17	9.4–10.3 9.90±0.40	0.99–1.21 1.14±0.10	6½
6. Kaeng Krachan, Phetchaburi (CUMZ 3688, 3723, 6132)	19	9.9–12.72 11.47±0.63	9.2–11.6 10.58±0.60	0.85–1.26 1.09±0.09	6½
7. Khao Kalok, Pran Buri, Prachuap Khiri Khan (CUMZ 6139, CUMZ 3698, 6143, SWUMZ 1018)	84	9.77–11.48 10.74±0.44	6.96–8.00 7.51±0.27	1.36–1.51 1.43±0.04	6½
8. Khao Wang, Mueang, Phetchaburi (CUMZ 3755)	9	9.2–13.1 11.51±1.25	8.8–12.3 10.21±10.07	0.96–1.21 1.13±0.13	6½
9. Nam Tok Pala-U, Kaeng Krachan, Phetchaburi (CUMZ 3684, 3768)	19	10.0–11.7 11.12±0.49	9.0–11.2 9.92±0.64	0.95–1.24 1.12±0.07	6½
10. Khao Nang Phanthurat, Cha–am, Phetchaburi (CUMZ 3745, 6133)	16	10.5–13.1 11.69±0.77	9.9–12.6 11.38±0.72	0.92–1.23 1.03±0.10	6½
11. Tam Khao Rong, Ban Lat, Phetchaburi (CUMZ 6135, 6137)	132	9.4–11.7 10.43±0.64	8.9–10.3 9.41±0.51	1.00–1.23 1.11±0.07	6½
12. Khao Lom Muak, Ao Manao, Mueang, Prachuap Khiri Khan (CUMZ 4229, SWUMZ 1019)	19	11.6–12.8 12.13±0.55	10.7–12.6 11.70±0.61	0.96–1.06 1.04±0.40	6½
13. Ban Nong Bua, Pranburi, Prachuap Khiri Khan (SWUMZ 1017)	6	11.1–12.8 11.87±0.63	7.2–8.6 7.96±0.48	1.40–1.58 1.49±0.06	6½
14. Wat Khao Krachiu, Tha Yang, Phetchaburi (SWUMZ 1027)	13	8.7–11.4 10.19±0.87	8.8–11.0 9.82±0.78	0.89–1.16 1.04±0.09	6½
15. Tam Dao, Hua Hin, Prachuap Khiri Khan (SWUMZ 1015)	8	12.7–14.6 13.54±0.62	8.8–9.8 9.16±0.38	1.45–1.50 1.48±0.02	6½
16. Tam Kai Lon, Hua Hin, Prachuap Khiri Khan (SWUMZ 1016).	7	11.9–13.4 12.87±0.56	8.5–9.5 9.00±0.30	1.39–1.47 1.43±0.04	6½
17. Kong Bin Hospital, Ao Manao, Mueang, Prachuap Khiri Khan (SWUMZ 1020).	3	12.0–13.2 12.69±0.66	9.0–9.2 9.15±0.10	1.30–1.46 1.39±0.08	6½
18. Phra (Buddha) Cave, Tanintharyi, Myanmar (CUMZ 13005)	1	11.2	10	0.6	6½
Panhartemis strangulatus					
1. Wat Bang Pu, Sam Roi Yot, Prachuap Khiri Khan: (CUMZ 3747, SWUMZ 1024)	16	10.6–11.2 10.82±0.30	8.0–8.7 8.34±0.22	1.25–1.35 1.30±0.04	6½–7
2. Tam Phraya Nakhon, Sam Roi Yot, Prachuap Khiri Khan (CUMZ 3738)	11	9.5–11.3 10.55±0.92	7.2–8.4 7.90±0.67	1.29–1.39 1.34±0.05	6½–7
3. Khoa Daeng, Kui Buri, Prachuap Khiri Khan: (SWUMZ 1021)	4	10.6–11.7 11.26±0.49	6.8–7.4 7.14±0.26	1.53–1.64 1.58±0.05	6½–7
4. Had Sam Phraya, Sam Roi Yot, Prachuap Khiri Khan (CUMZ 3751, 6141, SWUMZ 1022, 1023)	39	8.2–10.7 9.38±1.30	7.5–8.1 7.78±0.28	1.08–1.32 1.20±0.12	6½–7
5. Samnakphut Bueng Bua, Sam Roi Yot, Prachuap Khiri Khan (CUMZ 14128, 14129)	8	9.82–11.75 10.92±0.76	7.98–8.87 8.57±0.36	1.14–1.39 1.28±0.08	6½–7

whorl, only one parietal lamella, proximal penis stout, vas deferens passes through about one-third of the penial sheath, and penial hooks located on lower conical penial papillae (Inkhavilay et al., 2016).

Description.– Shell oblique-cylindrical, white, and translucent; whorls 6½; spire conical with distinct suture. Shell surface with radial ridges which diminish below periphery. Embryonic shell about 2½ whorls with smooth surface; following whorls regularly coiled. Shell periphery rounded; last whorl axially deflected. Aperture subcircular; peristome discontinuous, thickened, expanded, and reflected. Apertural dentition usually with one strong parietal, one weak upper palatal, one weak palatal (rarely inconspicuous) and one weak basal lamella; sometimes one weak lower palatal lamella may be present. Umbilicus opened and deep. Live specimens exhibit pale yellowish reticulated skin, and orange tentacular retractor muscles are visible through the semi-transparent body (Figs 1A, 2A–C, 3A– C).

Genital organs.– Atrium (at) short and stout. Penis (p) long, slender and then tapering to smaller diameter distally. Penial sheath (ps) thin and extending about half of penis length; penial sheath retractor muscle (psr) thin, originating near genital orifice and attached to atrium with thin connective tissue, and inserting distally on penial sheath (Fig. 5A). Vas deferens (vd) passes through about one-sixth of penial sheath length before entering penis distally (Fig. 5B). Penial retractor muscle (pr) thin, very long, and inserting at penis and vas deferens junction.

Internal wall of atrium with corrugated surface and sparse atrial pores (Fig. 6A). Penial wall with scattered pale brownish penial hooks, about 4 hooks/200 μm^2; hooks located on conical penial papillae that are separated by elevated reticulated folds (Fig. 6B, C). Penial hook small (< 0.02 mm in length), expanded at base, tip pointed and curved towards genital orifice (Fig. 6D, E).

Vagina (v) long, about quarter of penis length. Gametolytic duct (gd) a long tube, as long as albumin gland; gametolytic sac (gs) ovate. Proximal free oviduct (fo) enlarged then tapering to smaller diameter distally. Oviduct (ov) enlarged and folded; prostate gland inconspicuous and bound to oviduct. Talon (ta) small, short and club shaped. Hermaphroditic duct (hd) bearing long seminal vesicle (sv) about one and a half times longer than the length from talon to branching point of seminal vesicle (Fig. 5A). Inner wall of vagina with prominent longitudinal folds and vaginal hook absent (Fig. 6F).

Radula.– Each row contains 49–55 teeth with formula (24–27)–1–(24–27). Central tooth small with pointed cusp. Latero-marginal teeth gradually reducing in size, with outer teeth much smaller and shorter than inner teeth (Fig. 6G).

Distribution.– This species is commonly recorded from the limestone karst forests of Peninsular Thailand in Phetchaburi and Prachuap Khiri Khan provinces (Fig. 1). It is also known from the southeastern part of the Tenasserim Range, Tanintharyi Region of Myanmar (Fig. 1; Man et al., 2022). The location noted for the historical collection from ‘Camboja [Cambodia]’ may be erroneous, since no specimens for this species were found during an intensive survey in southern Cambodia (Sutcharit et al., 2020).

Remarks.– The taxonomic history, comments on the status of the type specimens, and type locality of this species have been recently provided (Man et al., 2022). The authors also suggested that perhaps a more precise type locality may be from Peninsular Thailand in Phetchaburi and Prachuap Khiri Khan provinces.

In our surveys, nearly 400 specimens were recorded from numerous populations. All the collected specimens were examined, and some morphological variation between populations in terms of shell shape and apertural dentition was observed.

The number of lamellae on the palatal wall tended to have high variability, ranging from one or inconspicuous lamella (Fig. 3A, B), two lamellae (Fig. 2A, B, 3C), to three lamellae (Fig. 2C). The specimens from Ban Lat, Phetchaburi (Fig. 2B) had the last whorl more deviated from the columellar axis than the typical forms (Fig. 2A). In addition, the specimens from Kui Buri, Prachuap Khiri Khan (Fig. 3B) had a cylindrical shell and last whorl less deviated from the columellar axis, which is very similar to the shell form of *P. strangulatus*; however, the weak lamellae on palatal wall and without columellar lamella suggest it is closer to *P. mouhoti*. However, we considered the different number, development, and position of lamellae to be variations, and currently all of them are treated as the same species. Additional genitalia studies and molecular analysis will reveal whether these forms are not conspecific.

Panhartemis strangulatus (Möllendorff, 1894) comb. nov.

(Figs 1, 4A–C, 5C, D, 7A–G; Table 1)

Streptaxis (Oophana) strangulatus Möllendorff, 1894: 148, pl. 16, fig. 5. Type locality: Samui Islands, Gulf of Siam.

Streptaxis strangulatus—Gude, 1903: 225.

Odontartemon (Oophana) strangulatus—Kobelt, 1906: 105, pl. 55, fig. 24.

Oophana strangulatus—Benthem Jutting, 1954: 96. Zilch, 1961: 85, pl. 5, fig. 18. Richardson, 1988: 237. Panha, 1996: 33. Hemmen and Hemmen, 2001: 43. Sutcharit et al., 2018: 197, 198.

Type material.– Lectotype (designation in Zilch (1961)) SMF 108522/1 (Fig. 4A) from Siam: Ko Samui. Paralectotypes SMF 108523/4 (3 adults + 1 juvenile), SMF 108524/1 (1 shell), SMF 108525/1 (1 shell), all from the same locality as the lectotype.

Other material examined.– **THAILAND:** Golf von Siam: SMF 169063/2 (2 shells). **Prachuap Khiri Khan Province:** Had Sam Phraya, Kui Buri District (12° 09'06.9"N, 99°58'59.2"E): CUMZ 3751 (26 shells), 6141 (1 specimen in ethanol), SWUMZ 1022 (3 shells), SWUMZ 1023 (9 shells; Fig. 4C). Tam Phraya

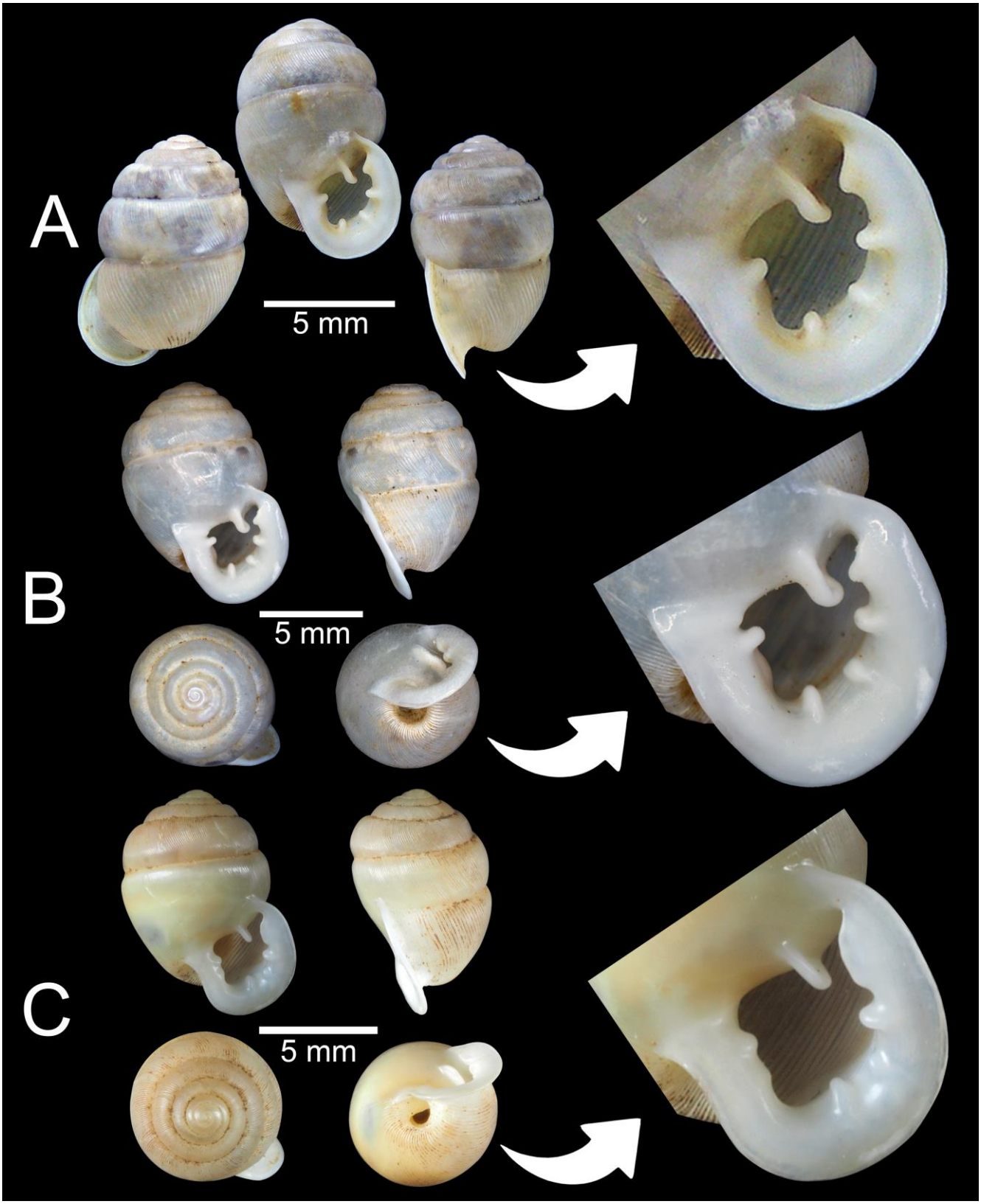

FIGURE 4. *Panhartemis strangulatus*. **A.** lectotype SMF 108522/1 from type locality with apertural dentition. **B.** specimen SWUMZ 1023 from Had Sam Phraya, Kui Buri, Prachuap Khiri Khan with apertural dentition. **C.** specimen CUMZ 14128 from Samnakphut Bueng Bua, Sam Roi Yot, Prachuap Khiri Khan with apertural dentition.

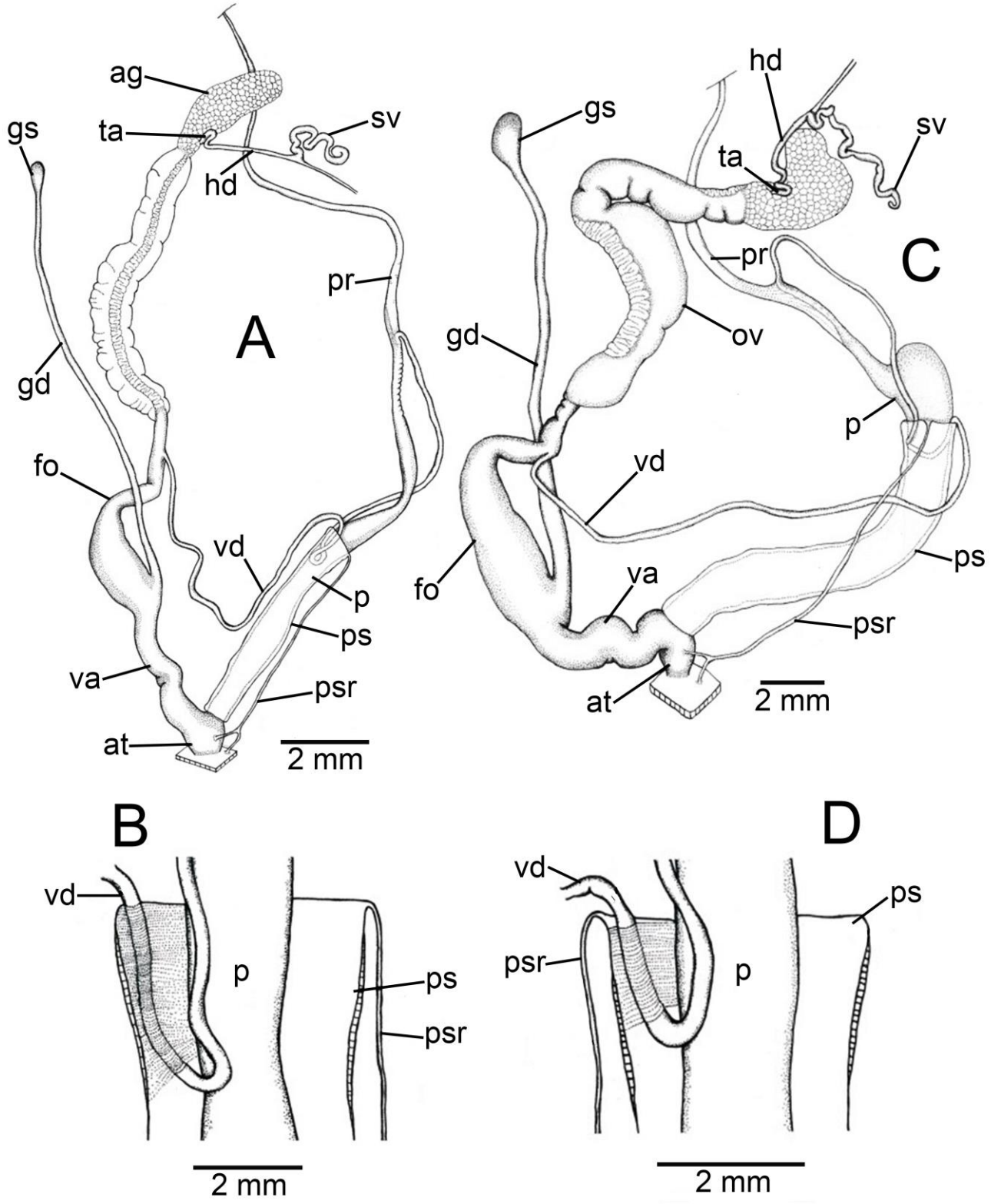

FIGURE 5. Genital anatomy of **A, B.** *Panhartemis mouhoti*, specimen CUMZ 6135 from Ban Lat, Phetchaburi. **A.** reproductive system and **B**. insertion of vas deferens into penial sheath. **C, D.** *Panhartemis strangulatus* CUMZ 3738 from Tam Phraya Nakhon, Sam Roi Yot, Prachuap Khiri Khan **C.** reproductive system and **D.** insertion of vas deferens into penial sheath.

Nakhon, Sam Roi Yot District (12°12'20.8"N, 100°00' 37.3"E): CUMZ 3738 (11 specimens in ethanol; Figs 4B, 5C, D, 7A–G). Wat Bang Pu, Sam Roi Yot District (12°12'16.9"N, 100°00'30.8"E): CUMZ 3747 (7 shells), SWUMZ 1024 (9 shells). Khoa Daeng, Kui Buri District (12°08'03.5"N, 99°57'43.8"E): SWUMZ 1021 (4 shells) Samnakphut Bueng Bua, Sam Roi Yot, Prachuap Khiri Khan (12°14'14.79"N, 99°55'55.10"E), CUMZ 14128 (4 specimens in ethanol), CUMZ 14129 (4 shells).

Differential diagnosis.– *Panhartemis strangulatus* differs from all other known *Oophana* species recorded from Thailand, Myanmar and Peninsular Malaysia in having a nearly cylindrical shell shape, whereas all other species have an oblique-ovate to oblique-heliciform shell (Benthem Jutting, 1954; Clements, 2006; Inkhavilay et al., 2016; Man et al., 2022). This species can also be distinguished from *Haploptychius pellucens*, *H. heliakosus* and *Indoartemon medius* by having an oblique-cylindrical shell, elevated spire, broadly expanded peristome, one parietal, three lamellae on the palatal wall, one basal and one columellar lamella. And in the genitalia, *P. strangulatus* has a cylindrical penis, conical penial hooks, and a vaginal wall with thickened and longitudinal vaginal folds. In contrast, *H. pellucens* and *H. heliakosus* have an oblique-ovate shell, lower spire, last whorl more axially deflected, less expanded lip and only one parietal lamella. Additionally, *H. pellucens* has an enlarged proximal penis, elongated and slender penial hooks, and vaginal wall with transverse and undulated vaginal folds (Inkhavilay et al., 2016); *H. heliakosus* has muscularly thickened penial sheath, penial hooks located on irregular trapezoidal penial papillae (Man et al., 2022). In addition, *I. medius* from central Thailand differs by possessing an oblique-heliciform shell, keeled periphery, vas deferens attached to the distal end of penial sheath, penial hook retracted into penial papillae, and vaginal wall with oblique parallel vaginal folds (Siriboon et al., 2014b).

Description.– Shell oblique-cylindrical, white, translucent; whorls 6½–7; spire conical with distinct suture. Embryonic shell about 2½ whorls with smooth surface; following whorls regularly coiled. Shell surface glossy with fine radial ridge across entire shell. Shell periphery rounded; last whorl very slightly axially deflected. Aperture subcircular; peristome discontinuous; lip thickened, broadly expanded, and little reflected. Apertural dentition with one strong parietal, one upper palatal with expanded base, one palatal, one lower palatal, one basal and one columellar lamella. Umbilicus open and deep, Live specimens exhibit bright yellowish reticulated skin, and bright orange tentacular retractor muscles are visible through the semi-transparent body (Figs 1B, 4A–C).

Genital organs.– Atrium (at) short and stout. Penis (p) long and slender proximally, then tapering to smaller diameter distally. Penial sheath (ps) thin and extending about two-thirds of penis length; penial sheath retractor muscle (psr) thin, originating near genital orifice and attached to atrium with short and thin connective tissue, and inserting distally on penial sheath (Fig. 5C). Vas deferens (vd) passes through about one-twelfth of penial sheath length before entering penis distally (Fig. 5D). Penial retractor muscle (pr) thin and very long, inserting at penis and vas deferens junction.

Internal wall of atrium with corrugated surface with sparse atrial pores (Fig. 7A). Penial wall with scattered pale brownish penial hooks, about 8 hooks/200 μm^2; hooks located on conical penial papillae that are separated by elevated reticulated folds (Fig. 7B–D). Penial hook small (< 0.07 mm in length), expanded at base, tip pointed and curved towards genital orifice (Fig. 7D, E).

Vagina (v) short, about one-thirds of penis length. Gametolytic duct (gd) a long tube, as long as albumin gland; gametolytic sac (gs) ovate. Proximal free oviduct (fo) enlarged then tapering to smaller diameter distally. Oviduct (ov) enlarged and folded; prostate gland inconspicuous and bound to oviduct. Talon (ta) small, short and club shaped. Hermaphroditic duct (hd) bearing long seminal vesicle (sv) about twice as long as the length from talon to branching point of seminal vesicle (Fig. 5C). Inner wall of vaginal with thickened longitudinal folds and vaginal hook absent (Fig. 7F).

Radula.– Each row contains 33–37 teeth with formula (16–18)–1–(16–18). Central tooth small with pointed cusp. Latero-marginal teeth gradually reducing in size, with outer teeth much smaller and shorter than inner teeth (Fig. 7G).

Distribution.– *Panhartemis strangulatus* is currently known from the limestone karsts in Sam Roi Yot District, Prachuap Khiri Khan Province, western Thailand.

Remarks.– Although the type locality of this nominal species was not precisely stated in the original description, it was roughly inferred from the title of the work as ‘Samui Islands, Gulf of Siam’. Additionally, in the preamble of this article Möllendorff (1894) mentioned specimens that were received from the orchid collector, Carl Roebelen (1855–1927). Kerr (1927), an Irish botanist, stated that, like other ‘…plant hunters, Roebelen did not give away the exact localities of his finds…’,

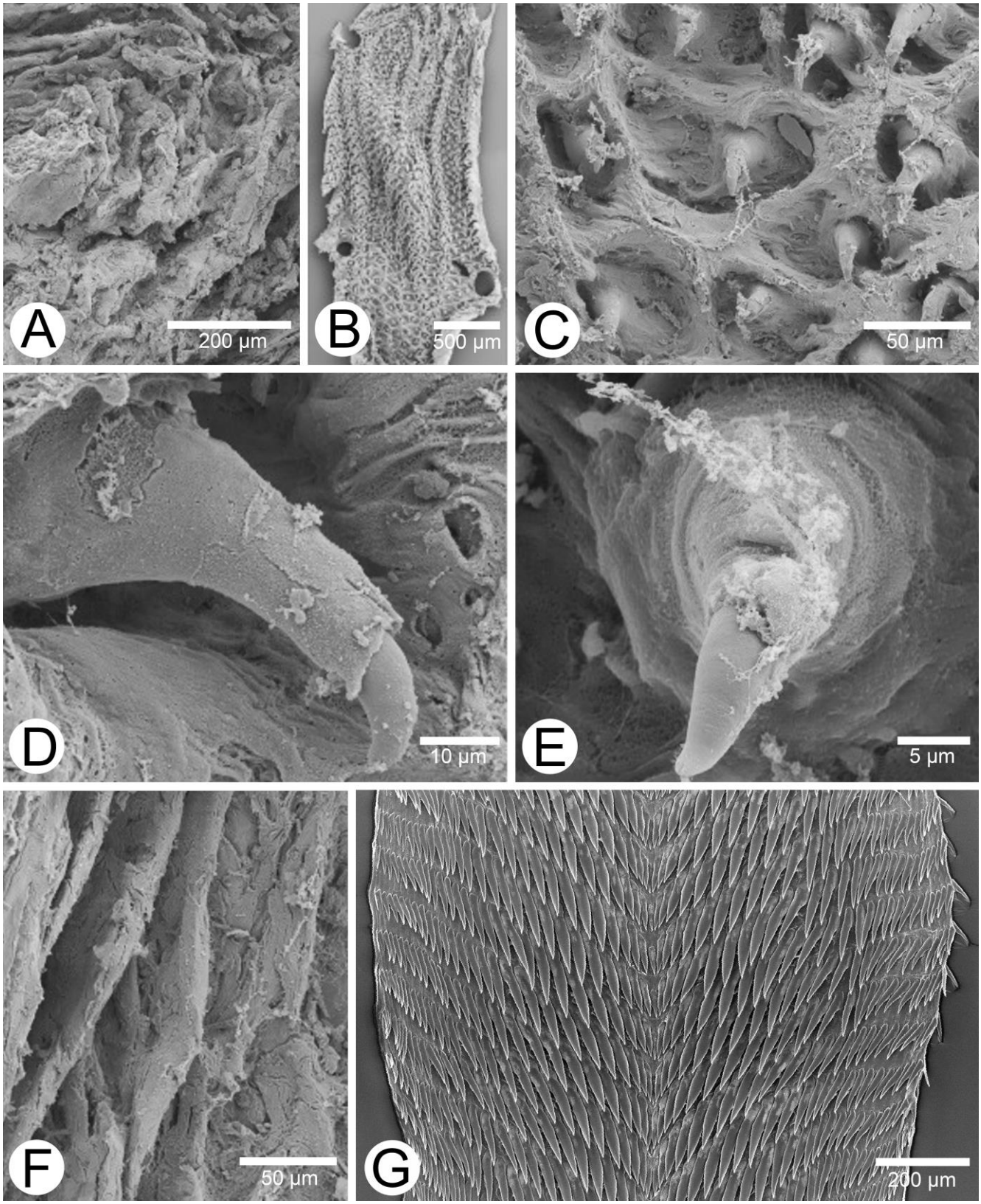

FIGURE 6. Internal sculpture of genitalia and radula morphology of *P. mouhoti*, specimen CUMZ 6135. **A.** atrium surface. **B.** overview of internal penial wall. **C.** low magnification view of arrangement of penial hooks. **D.** lateral view of penial hooks. **E**. top view of penial hooks. **F.** arrangement of longitudinal vaginal folds. **G.** radula morphology.

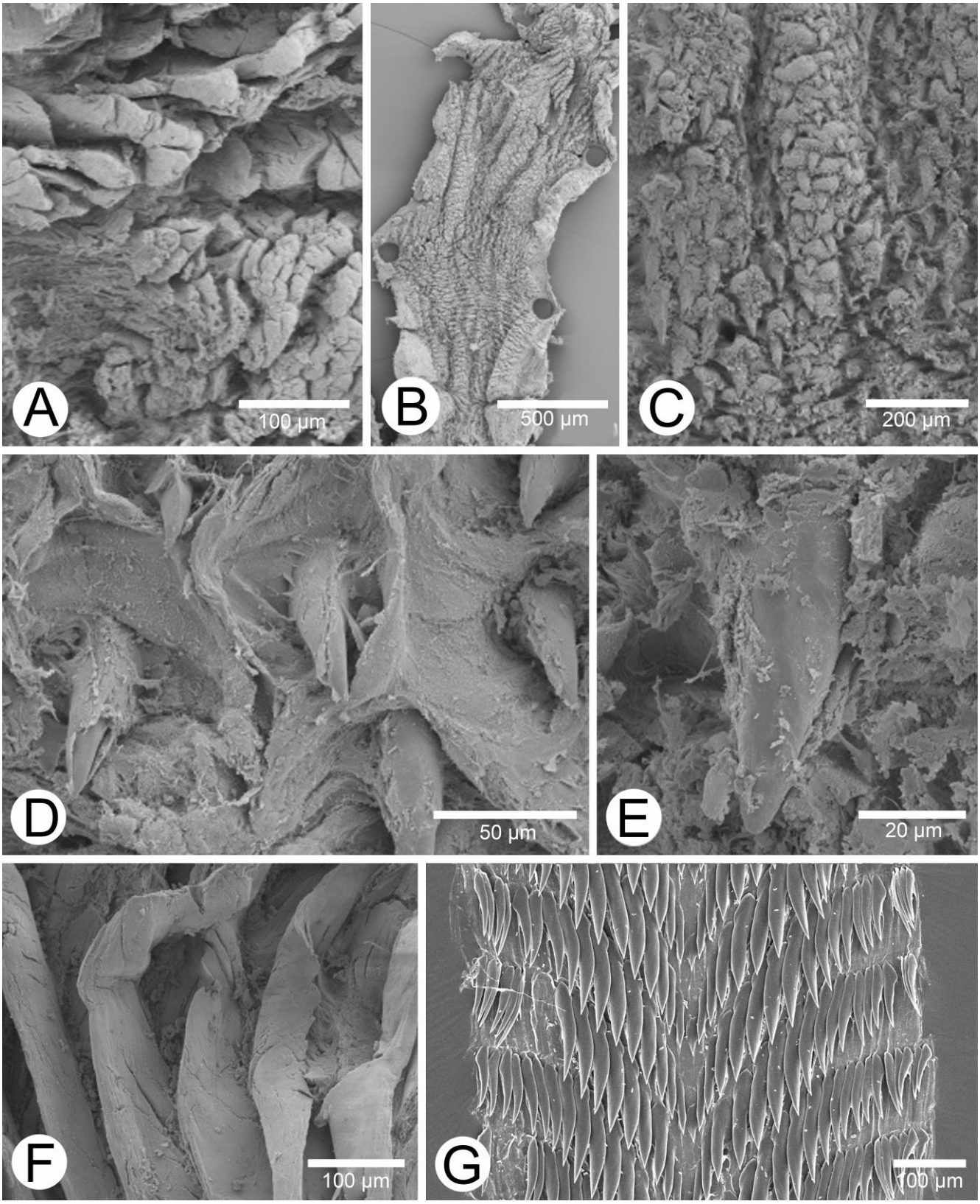

FIGURE 7. Internal sculpture of genitalia and radula morphology of *P. strangulatus*, CUMZ 3738. **A.** atrium surface. **B.** overview of internal penial wall. **C.** low magnification view of arrangement of penial hooks. **D.** high magnification view of arrangement of penial hooks. **E.** lateral view of penial hooks. **F.** arrangement of longitudinal vaginal folds. **G.** radula morphology.

which implied that the specimens described by Möllendorff (1894) could be very approximate and perhaps inaccurate.

This collection locality, 'Samui Islands', encompasses the present-day Koh Samui (island) and its satellite islands, and the limestone islands 'Kwangtong' referred to as Mu Koh Ang Thong (islands) situated about 25 km east of Koh Samui. Therefore, these two island groups are most likely the type locality of this species (sensu Möllendorff, 1894). However, we did not find any specimens of *P. strangulatus* on either of the island groups during our survey. We did find *Discartemon roebeleni* (Möllendorff, 1894), which commonly occurs in these areas (Siriboon et al., 2014a). All the specimens examined herein were collected from the coastal limestone outcrops in Prachuap Khiri Khan Province. These specimens match well with the type series, which we examined in detail and have redescribed herein.

Moreover, the specimens from Samnakphut Bueng Bua in the western part of the Sam Roi Yot mountain chain, Sam Roi Yot District, Prachuap Khiri Khan tend to have a more expanded upper palatal lamella (Fig. 4C) than those from other localities in the eastern part of the mountains.

DISCUSSION

The genus *Panhartemis* gen. nov. is distributed in western Thailand from Phetchaburi to Prachuap Khiri Khan province, between latitudes 10°–13º. Only one specimen of *P. mouhoti* was found in Myanmar, in the southern province of Tanintharyi. In Thailand, *P. mouhoti* was found throughout the southern peninsula. However, *P. strangulatus* has an endemic distribution range limited to Prachuap Khiri Khan Province, and was only found in Sam Roi Yot, an isolated limestone mountain chain in Sam Roi Yot and Kui Buri districts.

According to Siriboon et al. (2020), the phylogenetic study of Thai streptaxids revealed a well-supported 'Western-II' clade. It included one specimen of *P. strangulatus*, which was placed as sister taxon to all specimens identified as *P. mouhoti*, which were retrieved as a strongly supported monophyletic group. Members of the Western-II clade, comprising *P. mouhoti* and *P. strangulatus* from the western region exhibit an oblique-cylindrical shell shape, elevated conical spire, and last whorl slightly axially deflected; penial hook stout, expanded at base, located on conical penial papilla, and separated by elevated reticulated folds; vaginal wall with longitudinal vaginal folds and vaginal hooks are absent. These characteristics can be used to distinguish these two species from the other *Oophana* species. Our additional field surveys, and intensive examination of the specimen collection, shell morphology, genitalia, and radula in this current study suggest the reevaluation of the generic status of the western regional streptaxid fauna in Peninsular Thailand.

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