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Revision of the carnivorous snail genus *Indoartemon* Forcart, 1946 and a new genus *Carinartemis* from Thailand (Pulmonata: Streptaxidae)

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Abstract. Carnivorous land snails attributed to the genera *Indoartemon* Forcart, 1946 and *Carinartemis*, new genus, are recorded from Thailand for the first time. *Indoartemon eburneus* (Pfeiffer, 1861), *I. prestoni* (Gude, 1903) and *I. medius*, new species, were collected from central and northeastern Thailand. These two genera are easily distinguished: *Carinartemis*, new genus, possesses a distinctive sharp and wide peripheral keel that does not occur in *Indoartemon*. We provide the first description of the internal anatomy of *Indoartemon* and *Carinartemis*, new genus, and establish the presence of several distinctive characters. The new genus has two new distinctive species, *Carinartemis vesperus*, new species, and *Carinartemis striatus*, new species, from isolated limestone hills in western Thailand.

Key words. systematics, biodiversity, genitalia, predator, Streptaxidae, Thailand

INTRODUCTION

Carnivorous snails in the family Streptaxidae Gray, 1860 are remarkable predators. They exhibit distinctive shell characteristics and adaptations for a carnivorous diet include lanceolate radula teeth, strong buccal mass retractor muscles, a protrudable proboscis, and a long anterior body that accommodates these enlarged and specialised organs (Berry, 1963). They hunt various soil invertebrates, and are considered to play a major role in limestone ecosystems (Gray, 1860; Blanford & Godwin-Austen, 1908; Benthem Jutting, 1954; Berry, 1963). Streptaxids have a wide distribution from South America to Africa and Asia (Bruggen, 1967; Schileyko, 2000; Sutcharit et al., 2010). The major radiation of streptaxids in Africa is particularly notable with approximately 1,000 described species (Bruggen, 1967; de Winter & Gittenberger, 1998; Rowson et al., 2010) and evidence from the East African fossil record that streptaxid genera, as with other extant East African stylommatophoran genera, were established by the Miocene, with the presence of species morphologically similar to extant taxa (Pickford, 1995, 2009). In Southeast Asia, species diversity within the Streptaxidae consists of approximately 130 nominal species in 13 genera (Bruggen, 1967, 1972; Richardson, 1988; Schileyko, 2000) but Asian streptaxids include deep level structure and have an Asian sister group, the family Diapheridae (Sutcharit, et al., 2010). Although empty shells may be relatively common, living examples can be difficult to find and this goes some way to explain why their internal anatomy is rarely described.

Prior to our current investigations 14 nominal streptaxid species were recorded from Thailand and attributed to four genera: *Discartemon* Pfeiffer, 1856, *Oophana* Ancey, 1884, *Haploptychius* Möllendorff, 1906, and *Perrottetia* Kobelt, 1905 (Panha, 1996; Hemmen & Hemmen, 2001; Siriboon et al., 2013). Our land snail surveys throughout Thailand have led to the discovery of many new species including several that we place in *Indoartemon* Forcart, 1946, and *Carinartemis*, new genus, that were previously unrecorded from Thailand. *Indoartemon* ranges from Sri Lanka to Myanmar, southern China and to Vietnam (Kobelt, 1906; Zilch, 1961; Richardson, 1988; Schileyko, 2000); while *Carinartemis*, new genus, is known only from the west of Thailand.

Indoartemon and *Carinartemis*, new genus, are distinguished from *Discartemon* by their oblique-heliciform shells with the last whorl displaced from the columellar axis. *Discartemon* shells may be flattened to heliciform, with whorls generally not displaced from the axis. *Indoartemon* and *Carinartemis*, new genus, differ from *Oophana*, *Haploptychius*, and *Perrottetia* by the presence of a parietal lamella and palatal lamella on the aperture. *Carinartemis*, new genus, has a distinctively wide and sharp peripheral keel of the penultimate whorl, allowing it to be readily distinguished from *Indoartemon*, *Oophana*, *Haploptychius*, and *Perrottetia* (Richardson, 1988; Schileyko, 2000).

In recording three species of *Indoartemon* and two new species of *Carinartemis*, new genus, from Thailand we describe three new species and provide the first descriptions of *Indoartemon* and *Carinartemis*, new genus, internal anatomy.

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MATERIAL AND METHODS

Specimens were collected from the central region of Thailand and provisional identifications made based on the publications of Gude (1903) and Kobelt (1905–1906), followed by critical determinations by comparison with relevant type specimens. Living snails were photographed before killing and stored at –20 C° prior to being defrosted and preserved in 70% ethanol for anatomical study. Shell height (H), shell width (W), shell angle (SA) were measured, and whorl count followed the methods of Burch & Pearce (1990) and Siriboon et al. (2013). Shells were imaged using a digital camera attached to a microscope and with Cell'D Imaging Software. The genitalia of preserved specimens of three new species were carefully dissected and examined under a stereo-microscope and composite anatomical drawings made based on specimens using camera lucida. Radulae were removed from the buccal mass then soaked in 10 % NaOH, cleaned in distilled water, examined and photographed under SEM (JEOL, JSM-5410 LV). Tissues were critical point dried from absolute ethanol and penial and vaginal wall structures were examined under SEM (PHILIPS, XL30).

Descriptions of apertural dentition follow Pilsbry (1916). In descriptions of genitalia 'proximal' is used in relation to the genital orifice and 'distal' refers to the region furthest away from the genital orifice. Other abbreviated genital characters follow Stoliczka (1871), Berry (1963), Verdcourt (2000), Herbert (2002), Sutcharit et al. (2010), and Siriboon et al. (2013): ag, albumen gland; at, atrium; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hd, hermaphroditic duct; ov, oviduct; p, penis; pa, penial appendix; ph, penial hook; pp, penial papilla; pr, penial retractor muscle; ps, penial sheath; psr, penial sheath retractor muscle; sv, seminal vesicle; ta, talon; v, vagina; vd, vas deferens.

Examined material was deposited in the following institutions: NHMUK, The Natural History Museum, London; CUMZ, Chulalongkorn University Museum of Zoology, Bangkok; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; NMW, National Museum of Wales, Cardiff, UK; ZRC, Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore.

SYSTEMATICS

Family Streptaxidae Gray, 1860

Genus *Indoartemon* Forcart, 1946

Odontartemon (Odontartemon): Kobelt, 1905: 91 (non Pfeiffer, 1856). Thiele, 1931: 730.
Oophana (Indoartemon) Forcart, 1946: 215. Benthem Jutting, 1954: 95.
Indoartemon: Zilch, 1960: 562. Richardson, 1988: 223–225. Schileyko, 2000: 776, 777.

Type species. *Streptaxis eburnea* Pfeiffer, 1861, by original designation.

Remark. Shells of *Oophana* and *Indoartemon* are similar but there are differences in the apertural dentition. *Indoartemon* possesses one parietal lamella and one palatal lamella; in addition basal and columellar lamellae are present in *I. layardianus* (Benson, 1853) and *I. cingalensis* (Benson, 1853). Apertural dentition of *Oophana* usually includes a single parietal lamella, palatal lamella, basal lamella, and columellar lamella. An upper palatal lamella or supracolumellar lamella are present in some species such as *Oophana strangulatus* (Möllendorff, 1894), *O. diplodon* (Möllendorff, 1900), and *O. pachyglottis* (Möllendorff, 1900).

The first genital morphological study of *Indoartemon* presented here indicates that the following characters may be diagnostic for the genus; a long penis with a thin penial sheath extending about half of the penis length; penial hooks present. The vas deferens does not pass through the penial sheath. The seminal vesicle is about one and a half times longer than the length from the talon to the branching point of the seminal vesicle. In *Oophana* the vas deferens enters the penial sheath distally, penial hooks and a seminal vesicle are present (Berry, 1963).

Indoartemon eburneus (Pfeiffer, 1861)

(Figs 1, 3A, B, Table 1)

Streptaxis eburnea Pfeiffer, 1861: 23. Type locality: Cochin China.
Streptaxis eburneus: Pfeiffer, 1868: 447. Gude, 1903: 226, pl. 4, figs 4–6.
Odonartemon (Odonartemon) eburneus: Kobelt, 1905: 91, 92, pl. 58, figs 21–23. Thiele, 1931: 730.
Oophana (Indoartemon) eburnea: Forcart, 1946: 215.
Indoartemon eburneus: Zilch, 1960: 562, fig. 1196.

Material examined. A single syntype in the H. Cuming collection is designated here as the lectotype NHMUK 20120255 (Fig. 1A). Additional record CUMZ 5014 (16 shells; Fig. 1C), Wat Tam Phalom, Loei, Thailand. Limestone hills 400–600 m above the mean sea level (17°33'17.1"N, 101°52'4.3"E).

Remarks. The oblique-heliciform shell possesses 7½ whorls and is a translucent glossy white with distinct sutures; fine transverse ridges diminish below the periphery. The embryonic shell is smooth and large with about 2½ whorls. The periphery is shouldered, the last whorl axially deflected and umbilicus open. Aperture semi-ovate, peristome discontinuous and expanded. Apertural dentition with one parietal and one palatal lamella (Fig. 3A).

Indoartemon laevis (Blanford, 1899) from Myanmar is distinctive with a smaller shell, lower spire and a basal lamella. *Indoartemon eburnea* is superficially similar to *I. cingalensis* from Sri Lanka, however, the last whorl is less deviated from the vertical axis and a columellar lamella is present.

Shells from Thailand (Fig. 3B) are slightly larger than the lectotype (Fig. 3A). However, apertural dentition and shell shape correspond and the size difference is interpreted as intra-specific variation.

***Indoartemon prestoni* (Gude, 1903)**
(Figs. 1, 3C, D, Table 1)

Streptaxis prestoni Gude, 1903: 322, 323, pl. 12, figs 17–19. Type locality: Lampun, Siam.
Haploptychius prestoni: Kobelt, 1906: 140, 141, pl. 62, figs 16–18. Zilch, 1961: 84. Richardson, 1988: 219.
Oophana (Indoartemon) prestoni: Benthem Jutting, 1954: 96.

Material examined. Of the two specimens mentioned by Gude (1903: 323) the single syntype in the lot NHMUK 1922.8.29.5 (Fig. 3C) is here designated as the lectotype. Additional record: CUMZ 5015 (12 shells; Fig. 3D), Wat Tam Ra-Khang, Si Samrong, Sukhothai, northern central lowlands, Thailand. Isolated limestone hills reaching about 200 m above mean sea level (17°9.6'6.0"N, 99°33'35.7"E).

Remarks. An oblique-heliciform shell with 7–7¾ whorls, white, glossy, translucent with distinct sutures. Fine transverse ridges diminish below the periphery. Smooth embryonic shell with about 2½ whorls. Periphery rounded, earlier whorls do not extend beyond the diameter of the axially deflected last whorl. Umbilicus open. Aperture subcircular, peristome thickened and expanded. Apertural dentition composed of one parietal lamella and palatal lamella (Fig. 3D).

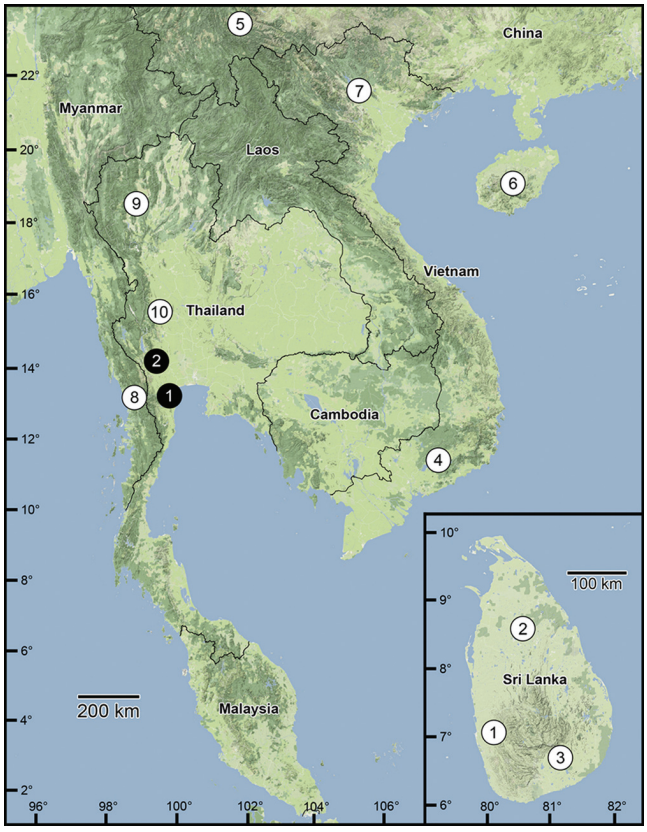

Fig. 1. Distribution map of *Indoartemon* spp. and *Carinartemis* spp. *Indoartemon* spp (white circle): (1) *Indoartemon cingalensis* (Benson, 1853); (2) *Indoartemon layardianus* (Benson, 1853); (3) *Indoartemon glacilis* (Collett, 1898); (4) *Indoartemon eburneus* (Pfeiffer, 1861); (5) *Indoartemon fuchsianus* (Gredler, 1881); (6) *Indoartemon bidens* (Möllendorff, 1883); (7) *Indoartemon tridens* (Möllendorff, 1898); (8) *Indoartemon laevis* (Blanford, 1899); (9) *Indoartemon prestoni* (Gude, 1903); and (10) *Indoartemon medius*, new species. *Carinartemis* spp. (black circle): (1) *Carinartemis vesperus*, new species; and (2) *Carinartemis striatus*, new species.

Indoartemon prestoni can be distinguished from *I. laevis* from Myanmar by its higher spire and distinct suture, regularly expanding whorls, deeper umbilicus and presence of a basal lamella. This species differs from *I. cingalensis* in its larger shell, lower spire, presence of a columellar lamella and in the last whorl being more deviated from the vertical axis. *Indoartemon prestoni* can be distinguished from *I. eburnea* by its lower spire with indistinct suture, the last whorl being more deviated from the vertical axis and a widely open umbilicus. *Indoartemon prestoni* has been placed in *Haploptychius* and

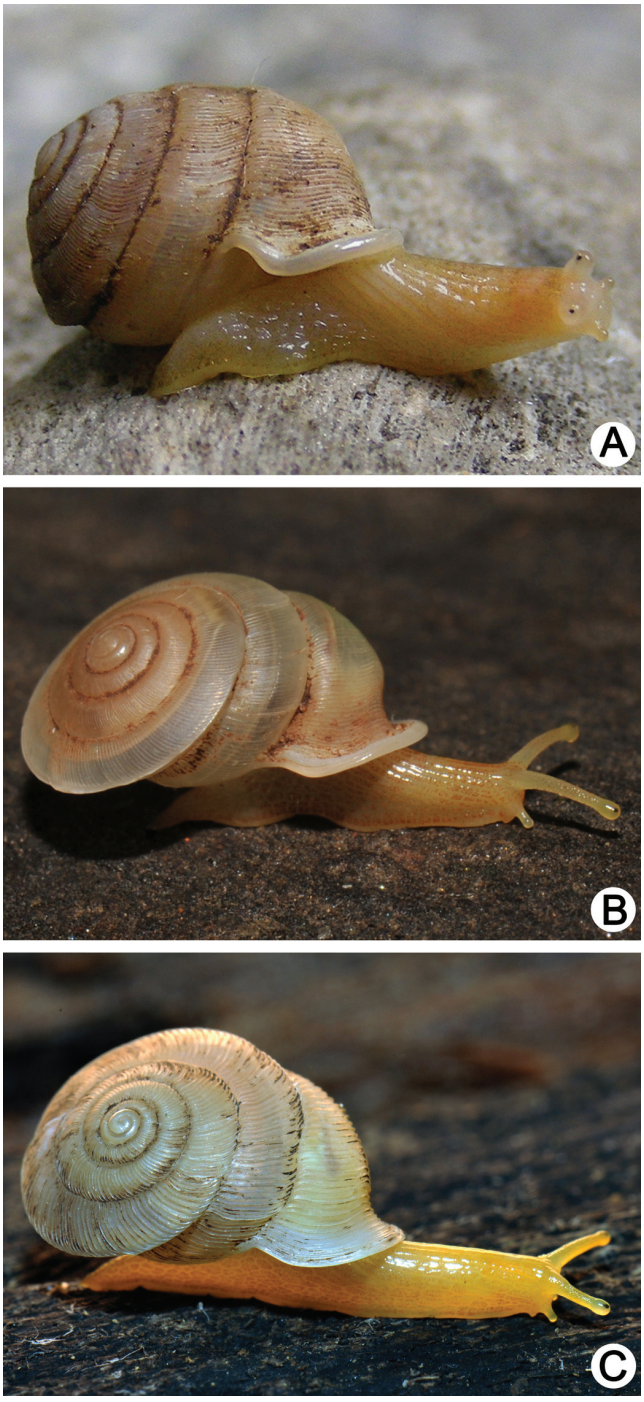

Fig. 2. Living snails of: A, *Indoartemon medius*, new species, paratype CUMZ 5017 (shell width about 8 mm); B, *Carinartemis vesperus*, new species, paratype CUMZ 6201 (shell width about 10 mm); C, *Carinartemis striatus*, new species, paratype CUMZ 6205 (shell width about 12 mm).

Oophana, but the presence of a single parietal lamella and a single palatal lamella confirm its position in *Indoartemon*.

Indoartemon medius Siriboon & Panha, new species
(Figs 1, 2A, 3E–G, 4A–C, 5A–I, Table 1)

Material examined. Holotype CUMZ 5016 (Fig. 3E). Measurement: height 8.8 mm, width 9.2 mm, 7 whorls. Paratypes: CUMZ 5017 (56 shells; Fig. 3F), CUMZ 6206 (28 specimens in ethanol), NHMUK 20130076 (2 shells), SMF (2 shells), and ZRC (2 shells).

Type locality. Wat Chuak Charoentham, Ban Rai, Uthai Thani, an isolated limestone hill about 200 m above mean sea level (15°16'26.3"N, 99°41'43.4"E).

Other material examined. Tam Lom-Tam Wang, Si Samrong, Sukhothai. Shells slightly smaller than specimens collected from Uthai Thani (CUMZ 5018, Fig. 3G).

Etymology. The specific epithet "*medius*" is derived from the Latin *"medius"* meaning "middle". It refers to the distribution range of this new species in central Thailand.

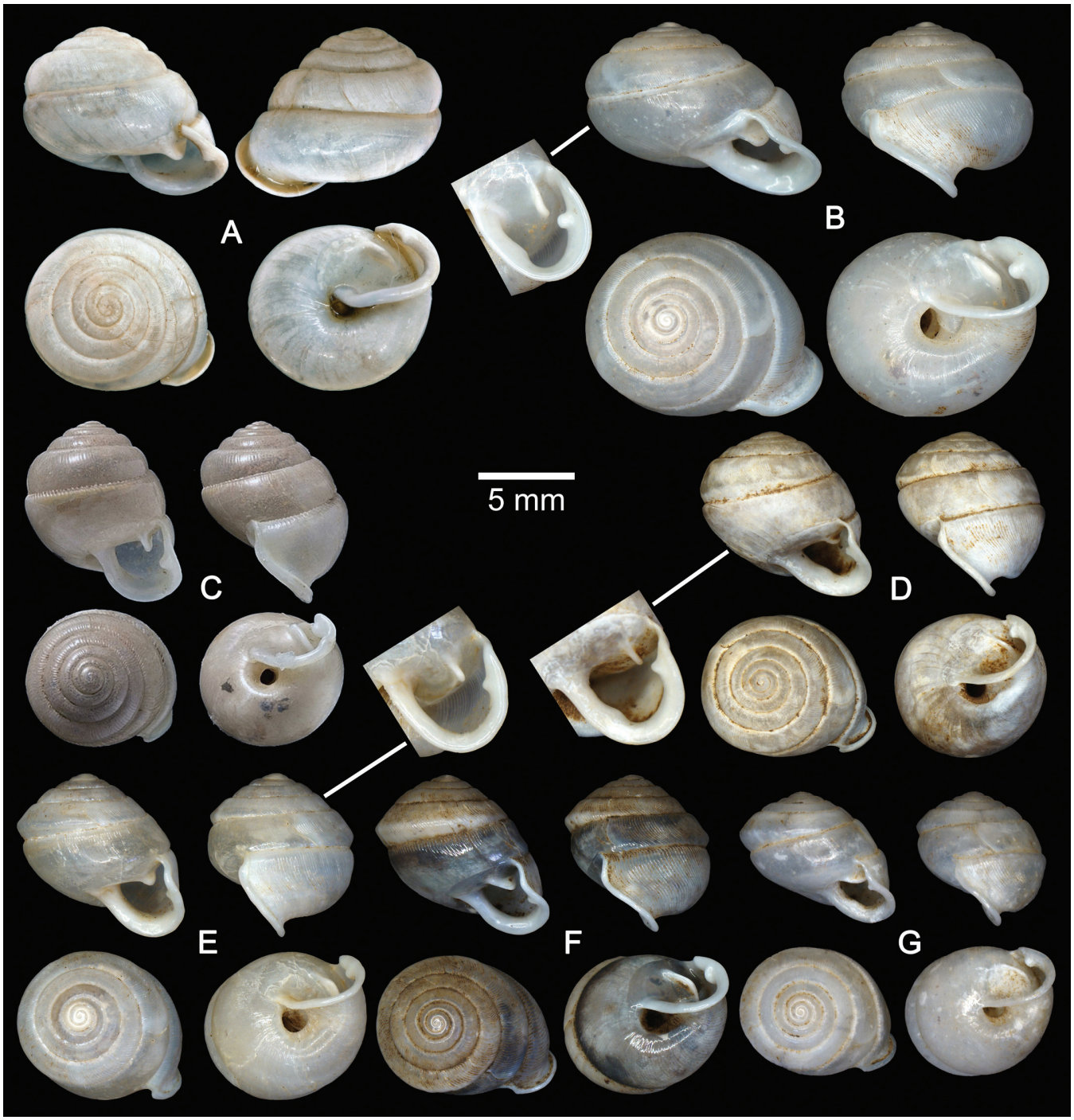

Fig. 3. Shells of *Indoartemon* spp: A, B, *Indoartemon eburneus*, (A) lectotype NHMUK 20120255, and (B) specimen CUMZ 5014, with apertural dentition, from Wat Tam Phalom, Loei; C, D, *Indoartemon prestoni*, (C) lectotype NHMUK 1922.8.29.5, and (D) specimen CUMZ 5015, with apertural dentition, from Wat Tam Ra-Khang, Si Samrong, Sukhothai. E–G, *Indoartemon medius*, new species, (E) holotype CUMZ 5016 with apertural dentition, (F) paratype CUMZ 5017, and (G) specimen CUMZ 5018 from Tam Lom-Tam Wang, Si Samrong, Sukhothai.

Table 1. Shell measurements of the three *Indoartemon* species and two *Carinatemis* species. Specimen collections and catalogue numbers indicated in parentheses.

Species, Locality and CUMZ no.	No. of Specimens	Ranges, Mean ± S.D. in mm of:				Number of Whorls
		Shell Height	Shell Width	H/W Ratio	Shell Angle	
Indoartemon eburneus (Pfeiffer, 1861)						
Wat Tam Phalom, Loei: (5014)	16	8.2–10.9 9.0±0.72	11.6–14.1 12.9±0.58	0.6–0.8 0.7±0.06	12.3–20.0 16.5±2.20	7¼–7¾
Indoartemon medius, new species						
Wat Chuak Charoentham, Ban Rai, Uthai Thani: (5016, 5017, 6206)	63	7.1–9.5 8.3±0.51	8.3–11.1 9.4±0.60	0.7–1.0 0.9±0.08	9.7–26.7 15.5±3.59	6¼–7
Tam Lom-Tam Wang, Si Samrong, Sukhothai: (5018)	19	6.6–7.4 7.0±0.25	7.2–8.6 7.8±0.39	0.8–1.0 0.9±0.06	12.4–35.5 16.9±4.86	6½–7
Indoartemon prestoni (Gude, 1903)						
Wat Tam Ra-Khang, Si Samrong, Sukhothai: (5015)	12	8.5–9.8 9.0±0.41	8.4–9.9 9.2±0.44	0.9–1.1 1.0±0.06	10.5–18.4 14.4±2.19	7–7¾
Carinartemis vesperus, new species						
Khao Kling, Khao Yoi, Phetchaburi: (5019, 5020, 6200, 6201)	69	6.3–8.3 7.1±0.44	8.8–10.7 10.7±0.37	0.6–0.9 0.7±0.06	42.1–66.0 57.0±4.44	6½–7
Khao Yoi, Phetchaburi: (6202)	8	6.6–8.0 7.0±0.36	8.9–9.9 9.4±0.36	0.7–0.8 0.8±0.06	43.4–60.1 52.2±5.65	6½–7
Carinartemis striatus, new species						
Tam Kra Sae, Sai Yok, Kanchanaburi: (6117, 6203, 6204, 6205)	16	8.0–9.9 8.7±0.53	11.4–12.2 11.9±0.26	0.7–0.8 0.7±0.05	39.9–51.3 47.3±3.42	7

Diagnosis. *Indoartemon medius*, new species, can be distinguished from *I. cingalensis* and *I. fuchsianus* (Gredler, 1881) in its higher spire, the last whorl being less deviated from the vertical axis, the left periphery of the penultimate whorl being keeled, and the absence of a columellar lamella. *Indoartemon laevis* differs from *I. medius*, new species, in its lower spire, the left periphery of the penultimate whorl being rounded and not extending beyond the diameter of the last whorl, and the presence of a basal lamella. *Indoartemon prestoni* possesses a distinct suture, the left periphery of the penultimate whorl extends beyond the diameter of the last whorl, and the umbilicus is wider. *Indoartemon medius*, new species, can be distinguished from the type species by its larger shell, the left periphery of the penultimate whorl being shouldered, last whorl being more deviated from the vertical axis, its wider umbilicus, and semi-ovate aperture.

Description. Shell oblique-heliciform, white, and translucent; whorls 7, spire conical with indistinct suture. Shell surface glossy, with fine transverse ridges that diminish below the periphery. Embryonic shell with about 2½ whorls and smooth surface; following whorls regularly expanded. Shell periphery keeled; last whorl axially deflected. Umbilicus narrow and deep. Aperture subcircular; peristome discontinuous, thickened and slightly expanded. Apertural dentition with one parietal lamella and one palatal lamella (Fig. 3E).

Radula. Teeth arranged in anteriorly V-shaped rows, each row containing 33–37 teeth with the formula (16-18)-1-(16-18); central tooth small, short, triangular with pointed cusp. Lateral and marginal teeth undifferentiated, unicuspid and lanceolate; lateral teeth gradually reduced in length and size with outer teeth much smaller and shorter than inner teeth (Fig. 5I).

Genital organs. Atrium (at) short. Proximal penis (p) long slender; becoming slightly broader before tapering distally. Penial sheath (ps) thin, extending about half of total penis length, penial sheath retractor muscle (psr) very thin, originating at atrium, inserting distally on penial sheath (Fig. 4A). Vas deferens (vd) slender, attached to distal end of penial sheath by a narrow band of connective tissue (Fig. 4B). Penial retractor muscle (pr) thin and very long, inserting distally on penis at the penis and vas deferens junction.

Internal wall of atrium possesses numerous atrial pores (Fig. 5A). Proximal penial wall with scattered and pale brown penial hooks about 3 hooks/200 μm^2; hooks withdrawn into penial papillae separated by low reticulated folds. Proximal penial hooks are minute (< 0.01 mm in length), tips obtuse and curved towards genital orifice (Fig. 5C, D). Distal penial wall with pale brown penial hooks about 5 hooks/200 μm^2; hooks located on penial papillae (pl). Penial papillae may extend across penial hook and adjacent areas with low reticulated folds (Fig. 5E, F). Distal minute penial hooks with obtuse tips (< 0.01 mm in length) expanded at base and curved towards genital orifice (Fig. 5G).

Vagina (v) short, stout, about quarter of total penis length. Gametolytic duct (gd) long, extending as far as albumin gland; gametolytic sac ovate (gs). Free oviduct (fo) stout and long. Oviduct (ov) enlarged and folded; prostate gland inconspicuous and bound to oviduct (Fig. 4A). Talon (ta) small, very short, and club shaped (Fig. 4C). Hermaphroditic duct (hd) bearing long seminal vesicle (sv) about one and half times longer than the length from talon to branching point of seminal vesicle. Vaginal wall with oblique parallel vaginal folds; vaginal hooks absent (Fig. 5H).

Animal. Live specimens exhibit yellowish to orange reticulated skin, and orange tentacular retractor muscles are visible through the semi-transparent body (Fig. 2A).

***Carinartemis* Siriboon & Panha, new genus**

Type species. *Carinartemis vesperus* Siriboon & Panha, new species.

Diagnosis. This new genus is noticeably distinct from *Discartemon* and *Perrottetia* by having a strong peripheral keel around nearly the entire penultimate whorl, in having the last whorl less inflated but strongly deviated from the vertical axis, and in having or lacking very thin parietal lamella. Whereas, *Discartemon* possesses a regularly coiled shell, the last whorl does not deviate from the columellar axis, and the apertural dentition varies, with at least a parietal lamella present. *Perrottetia* also has a smaller shell, has longitudinal furrows on outer wall of the last whorl, and always has two parietal and the other lamellae present.

In comparison, *Oophana* and *Indoartemon* have a more inflated last whorl, while the penultimate whorl is rounded to angular. *Oophana* has parietal, palatal, basal, and columellar lamellae, and *Indoartemon* has only parietal and palatal lamellae.

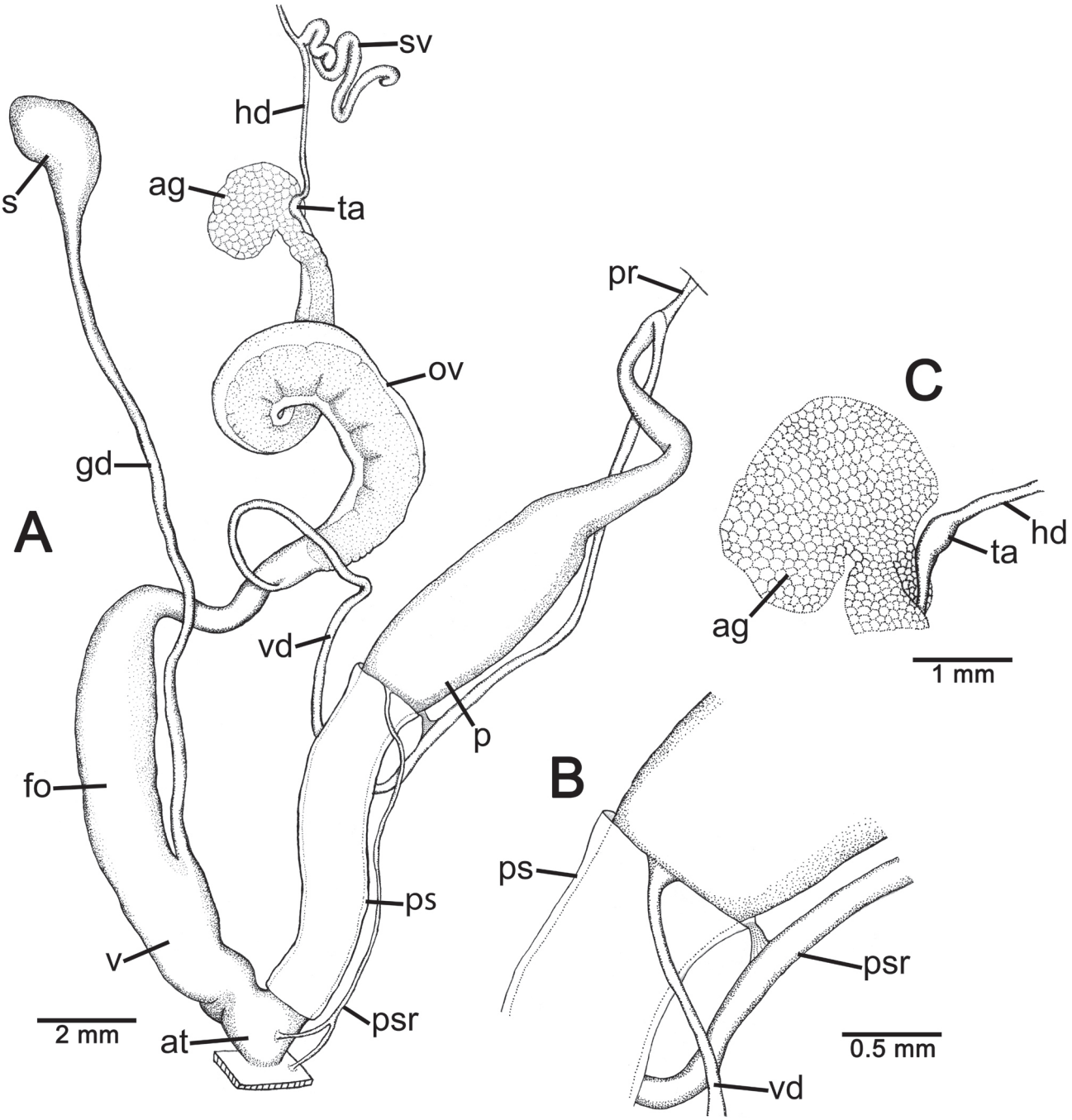

Fig. 4. Genitalia of *Indoartemon medius*, new species, paratype CUMZ 5017: A, reproductive system; B, attachment of vas deferens into distal end of the penial sheath; C, details of albumin gland and talon.

The new genus, *Carinartemis*, is superficially similar to *Haploptychius* and *Stemmatopsis* with the last whorl less inflated and much deviated from the vertical axis, and in having or lacking a lamella. However, *Haploptychius* differs from this new genus by having an angular to round peripheral keel around less than half of the penultimate whorl, and with a strong parietal lamella always present. The monotypic *Stemmatopsis* Mabille, 1887 is smaller, has a lower spire, a smooth shell surface, a rounded periphery of penultimate whorl, closed umbilicus, an aperture with an irregularly constricted shape, and a sinuous peristome (Fig. 6A; Mabille, 1887).

Description. Shell suboblique-heliciform, white, and translucent; whorls 7, spire low conical with distinct suture. Shell surface with transverse ridges. Embryonic shell with smooth surface; following whorls regularly expanding and penultimate whorl with very sharp and wide peripheral keel. Last whorl round and axially deflected. Umbilicus open and deep. Aperture subcircular, peristome expanded. Apertural dentition with or without parietal lamella and sometimes small other lamellae present.

Genitalia with short atrium; penis long; penial sheath thin to thick. Internal wall of introverted penis with brown penial hooks. Vagina short, free oviduct short to long. Seminal vesicle about as long as the length from the talon to the branching point of the seminal vesicle. Internal wall of vagina with oblique to arched parallel vaginal folds; vaginal hooks may be present.

Live specimens exhibit pale yellowish reticulated skin with brownish spots, and yellowish tentacular retractor muscles are visible through the semi-transparent body (Fig. 2B, C).

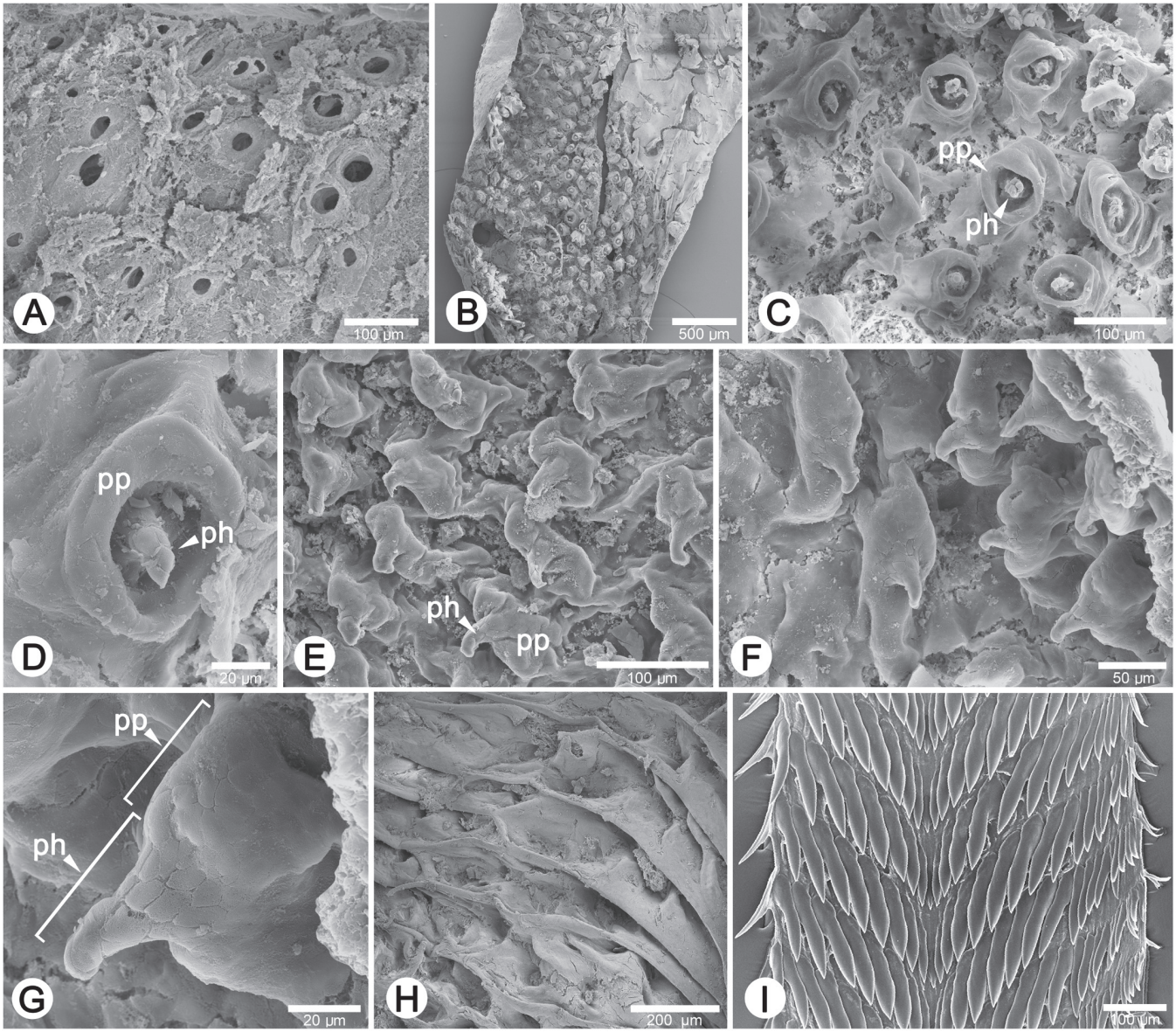

Fig. 5. Internal sculpture of genitalia of *Indoartemon medius*, new species, paratype CUMZ 5017: A, details of atrial pore on the atrium surface; B, low magnification shows arrangement of penial hooks; C, high magnification of penial hooks in proximal area; D, top view of penial hook, hooks shrunken in tubed penial papillae; E, low magnification of penial hook in distal area; F, lateral view of penial hook in distal area; G, high magnification of penial hooks in distal area; H, arrangement of vaginal folds; I, radula morphology.

Etymology. The generic name *Carinartemis* is derived from the Latin "*carina*" meaning "keel", and Greek "*artemis*" meaning "goddess of the chase". It refers to this carnivorous snail that has a prominent peripheral keel on penultimate whorl.

Remarks. The new genus currently comprises two new species. They are uncommon and seemed to be restricted to the limestone outcrops in western Thailand.

***Carinartemis vesperus* Siriboon & Panha, new species**
(Figs 1, 2B, 6B–E, 7A, B, 8A–F, Table 1)

Type material. Holotype CUMZ 5019 (Fig. 6B). Measurement: shell height 6.9 mm, shell width 9.6 mm, 7 whorls. Paratypes: CUMZ 5020 (3 shells), 6200 (60 shells; Fig. 6C, D), 6201 (2 specimens in ethanol; Figs 2B, 7A, B, 8A–F), NHMUK 20130077 (2 shells), SMF (2 shells), and ZRC (2 shells).

Type locality. Khao Kling, Khao Yoi District, Phetchaburi, Thailand. Rock crevices on isolated limestone hill reaching about 100 m above mean sea level (13°15'36.5"N, 99°48'14.8"E).

Other material examined. Khao Yoi, Khao Yoi District, Phetchaburi (CUMZ 6202). Khao Yoi, Phetchaburi (NMW.1955.158.25233, Fig. 6E).

Etymology. The specific epithet "*vesperus*" from a Latin term for "west" refers to the locality of the new species in the west of Thailand.

Diagnosis. *Carinartemis vesperus*, new species, can be distinguished from *H. mirificus* (Möllendorff, 1894) in having a higher spire, peripheral keel around nearly the entire penultimate whorl, a subcircular aperture, and in lacking apertural lamellae. While *H. mirificus* has a lower spire, a peripheral keel around less than half of the penultimate

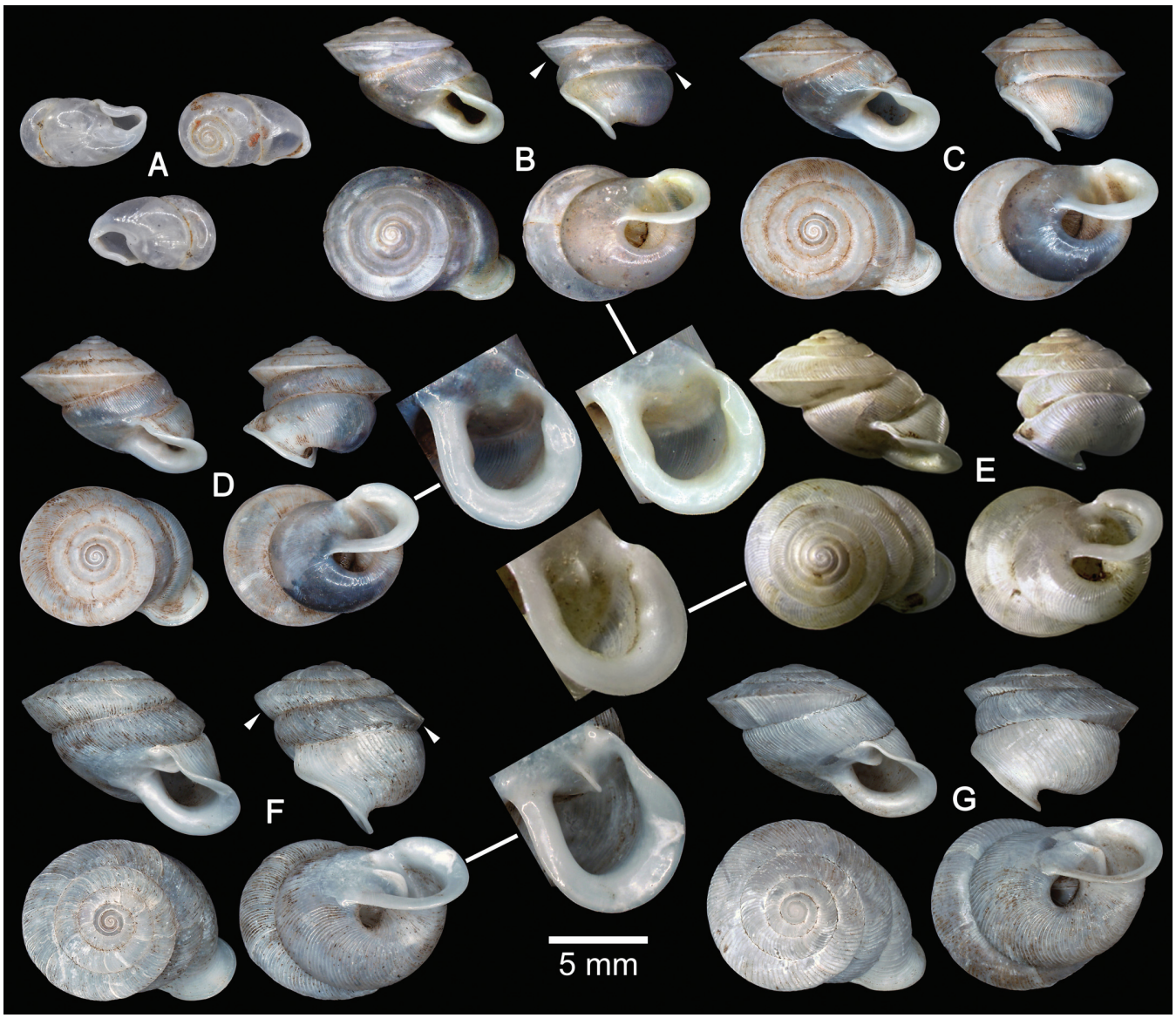

Fig. 6. A, Shell of *Stemmatopsis poirieri* lectotype MNHN 26980; B–E, Shells of *Carinartemis vesperus*, new species, (B) holotype CUMZ 5019 with apertural dentition, (C, D) paratype CUMZ 6200 from Khao Kling, Khao Yoi District, Phetchaburi, and (E) specimen NMW 1955.158.25233 from Khao Yoi, Petchaburi; F, G, *Carinartemis striatus*, new species, (F) holotype CUMZ 6203 with apertural dentition, and (G) paratype CUMZ 6117 from Tam Kra Sae, Sai Yok, Kanchanaburi.

whorl, a triangular aperture, and a strong and triangular parietal lamella.

Compared with *H. exacutus* (Gould, 1856) and *H. sankeyi* (Benson, 1859), this new species differs by having a strong peripheral keel around nearly the entire penultimate whorl, having the last whorl less inflated and much deviated from the vertical axis, and in lacking strong apertural lamellae. Whereas, these two species exhibit a strong peripheral keel over less than half of the penultimate whorl, and have the last whorl inflated and less deviated from the vertical axis. The apertural dentition of *H. exacutus* has two parietal lamellae and *H. sankeyi* has a strong parietal lamella.

Carinartemis vesperus, new species, differs from *C. striatus*, new species, by having a smaller shell with weaker transverse

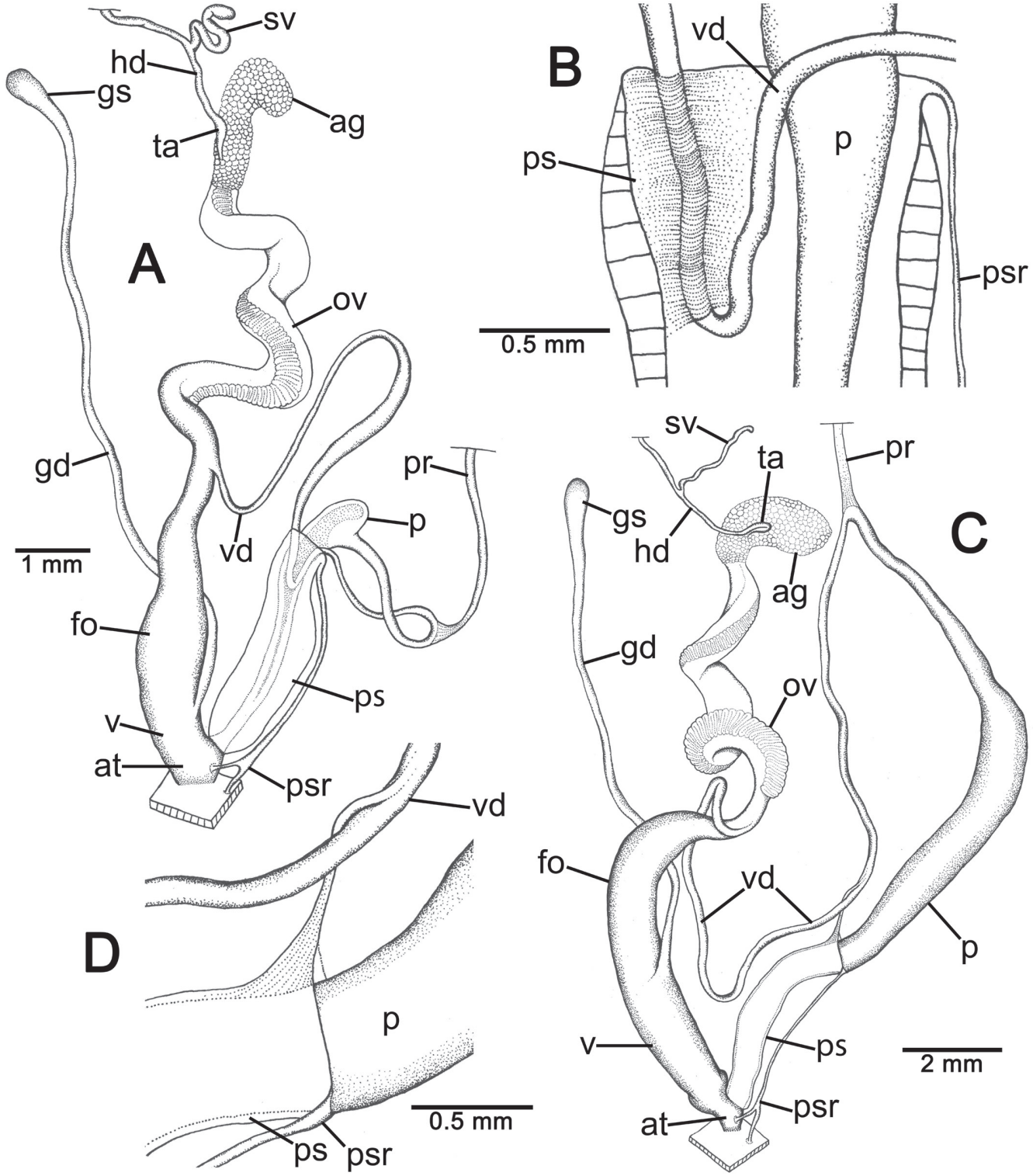

Fig. 7. Genitalia of *Carinartemis* spp: A, B, *Carinartemis vesperus*, new species, paratype CUMZ 6201, (A) reproductive system, and (B) insertion of vas deferens into penial sheath; C, D, *Carinartemis striatus*, new species, paratype CUMZ 6205, (C) reproductive system, and (D) attachment of vas deferens into distal end of the penial sheath.

ridges, the area below the periphery of the penultimate whorl smooth, a short longitudinal furrow in the umbilical area, and in lacking apertural lamellae. The genitalia have a short penis and vagina, and a thick penial sheath with the vas deferens passing it. Penial papillae are absent, and vaginal hooks are present. Whereas *C. striatus*, new species, has a larger shell, strong transverse ridges over the entire shell, no longitudinal furrow in the umbilical area, and has a prominent parietal

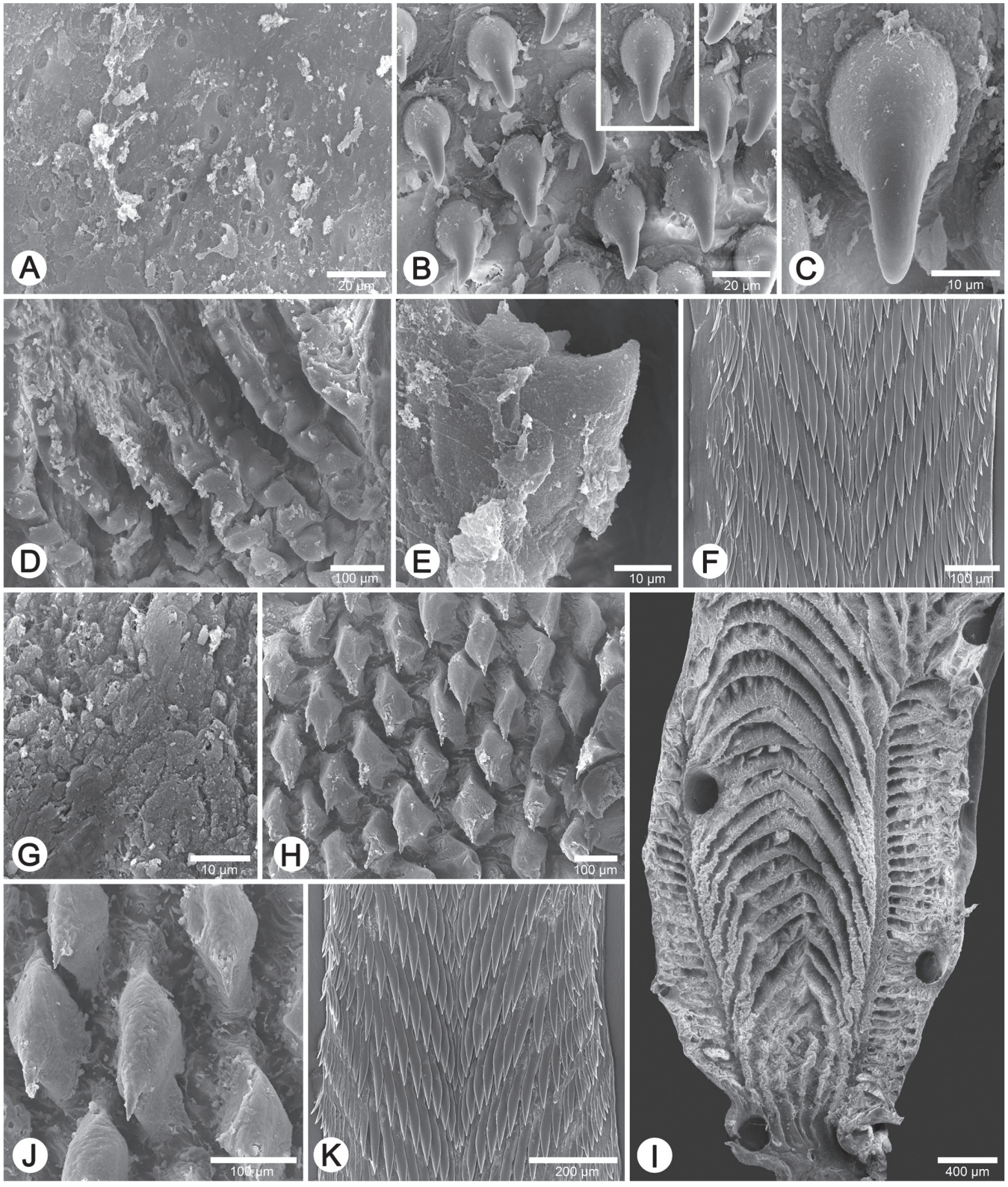

Fig. 8. Internal sculpture of genitalia of *Carinartemis* spp: A–F, *Carinartemis vesperus*, new species, paratype CUMZ 6201, (A) details of atrial pore on the atrium surface, (B) high magnification of penial hooks, (C) top view of penial hook, (D) arrangement of vaginal folds with hooks, (E) high magnification of vaginal hook, and (F) radula morphology. G–K, *Carinartemis striatus*, new species, paratype CUMZ 6205, (G) details of atrium surface, (H) low magnification shows arrangement of penial hooks, (I) low magnification shows arrangement of vaginal folds, (J) high magnification of penial hooks, and (K) radula morphology.

lamella. The genitalia have a long penis and vagina and a very thin penial sheath with the vas deferens attached to its distal end. Penial papillae are present, and vaginal hooks are absent.

Description. Shell suboblique-heliciform, white and translucent; whorls 7, spire conical with distinct suture. Shell surface glossy, with thin and fine transverse ridges; ridges disappear below periphery of penultimate whorl and around umbilicus. Embryonic shell with about 2½ whorls and smooth surface; following whorls regularly expanding. Shell periphery wide and sharply keeled around nearly entire penultimate whorl; last whorl axially deflected. Umbilicus widely open and deep with short longitudinal furrow. Aperture subcircular, peristome discontinuous, thickened, and expanded. Apertural dentition usually without lamellae, but sometimes with small parietal lamella, and rarely with very small other lamellae (Fig. 6B).

Radula. Teeth arranged in anteriorly V-shaped rows, each row containing 47–49 teeth with the formula (23-24)-1-(23-24); central tooth small, short, triangular with pointed cusp. Lateral and marginal teeth undifferentiated, unicuspid, and lanceolate; lateral teeth gradually reduced in length and size with outer teeth much smaller and shorter than inner teeth (Fig. 8F).

Genital organs. Atrium (at) short. Proximal penis (p) long, slender; becoming slightly broader with short pouch before tapering distally. Penial sheath (ps) thick, extending about fourth-fifths of total penis length; penial sheath retractor muscle (psr) very thin, originating at atrium and body wall (Fig. 7A). Vas deferens (vd) long, slender; slightly broadened before tapering distally; passes through about one-tenth of penial sheath length before entering into penis distally (Fig. 7B). Penial retractor muscle (pr) thin and very long, inserting distally on penis at the penis and vas deferens junction.

Internal wall of atrium smooth with numerous atrial pores (Fig. 8A). Penial papillae absent; pale brown penial hooks present, about 40 hooks/200 μm^2. Penial hooks short (< 0.03 mm in length), expanding at base, tips obtuse and curved towards genital orifice (Fig. 8B, C).

Vagina (v) very short and stout. Gametolytic duct (gd) long, extending as far as albumin gland; gametolytic sac ovate (gs). Free oviduct (fo) long, proximally large with equivalent diameter with vagina, and tapering to smaller tube distally. Oviduct (ov) enlarged and folded; prostate gland inconspicuous and bound to oviduct. Talon (ta) small, short and club shaped. Hermaphroditic duct (hd) bearing seminal vesicle (sv) about as long as the length from talon to branching point of seminal vesicle (Fig. 7A).

Vaginal wall with transparent vaginal hooks about 8 hooks/200 μm^2; hooks located on oblique parallel vaginal folds. Vaginal hooks short (< 0.04 mm in length), expanding at base, tips obtuse slightly curving away from genital orifice (Fig. 8D, E).

Distribution. This new species seems to be the restricted to limestone in western Thailand at the type locality and at Khao Yoi, Phetchaburi, the limestone karst about 10 km east of the type locality.

Remarks. Shell variation can be observed in five paratypes by having very small parietal lamella and the detectable upper palatal, palatal, basal and columellar lamellae (Fig. 6D). In addition, a single shell from Khao Yoi, Phetchaburi (Fig. 6E; NMW.1955.158.25233) has a strong parietal lamella and four other very small peripheral lamellae. However, we considered this conspecific based on the characters of thin and fine transverse ridges and broadly expanded apertural lip, and because it was collected within the range of this species. However, further anatomical and molecular data of the newly collected specimen with precise locality will elucidate whether this represents intraspecific variation or a separate taxon.

Carinartemis striatus Siriboon & Panha, new species

(Figs 1, 2C, 6F, G, 7C, D, 8G–K, Table 1)

Type material. Holotype CUMZ 6203 (Fig. 6F). Measurement: shell height 9.2 mm, shell width 11.4 mm, 7 whorls. Paratypes: CUMZ 6117 (5 shells; Fig. 6G), CUMZ 6204 (3 shells), CUMZ 6205 (1 specimen in ethanol; Figs 2B, 7A, B, 8G–I), NHMUK 20130611 (2 shells), SMF (2 shells), and ZRC (2 shells).

Type locality. Tam Kra Sae, Sai Yok, Kanchanaburi, Thailand. A limestone mountain reaching about 200 metres above mean sea level (14°6'23.5"N, 99°9'58.0"E).

Etymology. The specific epithet from the Latin *"stria"* meaning "furrow", in reference to the strong transverse ridges or radial striation on the shell surface.

Diagnosis. *Carinartemis striatus*, new species, can be distinguished from *H. mirificus* in its larger shell, higher spire, strong transverse ridges over the entire shell, subcircular aperture, broadly expanded peristome, and small parietal lamella. Whereas *H. mirificus* has a smaller shell, lower spire, nearly smooth shell surface, triangular aperture and a strong and triangular parietal lamella.

Compared with *H. exacutus* and *H. sankeyi*, this new species differs by having a strong peripheral keel around nearly the entire penultimate whorl, the last whorl less being inflated and much deviated from the vertical axis, and with strong transverse ridges over the entire shell. In comparison, these two species have a strong peripheral keel over less than half of penultimate whorl, and have the last whorl inflated and less deviated from vertical axis. The transverse ridges of *H. exacutus* disappear below the periphery of the penultimate whorl and it has two distinct parietal lamellae.

Description. Shell oblique-heliciform, white, dull, and translucent; whorls 7, spire low conical with distinct suture. Shell surface glossy, with strong transverse ridges and varices present. Embryonic shell with about 2½ whorls and smooth surface; following whorls regularly expanding.

Shell periphery wide and sharply keeled around nearly the entire penultimate whorl; last whorl axially deflected. Umbilicus open and shallow. Aperture semi-ovate, peristome discontinuous, thickened, expanded and reflected. Apertural dentition of one parietal lamella (Fig. 6F).

Radula. Teeth arranged in anteriorly V-shaped rows, each row containing 45–49 teeth with the formula (22-24)-1-(22-24); central tooth small, short, triangular with pointed cusp. Lateral and marginal teeth undifferentiated, unicuspid and lanceolate; lateral teeth gradually reduced in length and size with outer teeth much smaller and shorter than inner teeth (Fig. 8K).

Genital organs. Atrium (at) short. Penis (p) long, slender, becoming slightly broad in middle and then tapering distally. Penial sheath (ps) thin, extending about quarter of total penis length; penial sheath retractor muscle (psr) very thin, originating at atrium and body wall, inserting distally on penial sheath (Fig. 7C). Vas deferens (vd) slender, very long, attached to distal end of penial sheath with very thin connective tissue (Fig. 7D). Penial retractor muscle (pr) thin and very long, inserting distally on penis at the penis and vas deferens junction.

Internal wall of atrium generally corrugated with sparse atrial pores (Fig. 8G). Penial wall with pale brown penial hooks, about 1 hook/200 μm^2; hooks located on irregular trapezoidal papillae (pl). Penial hooks short (< 0.04 mm in length), slightly expanding at base, tips sharp and curved towards genital orifice (Fig. 8H, J).

Vagina (v) short and stout. Gametolytic duct (gd) long, extending as far as albumin gland; gametolytic sac (gs) ovate. Free oviduct (fo) long, proximally large with equivalent diameter with vagina, and tapering to a smaller tube distally. Oviduct (ov) enlarged and folded; prostate gland inconspicuous and bound to oviduct. Talon (ta) small, very short and club shaped. Hermaphroditic duct (hd) bearing seminal vesicle (sv) about as long as the length from talon to branching point of seminal vesicle (Fig. 7C).

Proximal vaginal wall with undulated parallel vaginal folds, arched distally; transverse parallel cavity present; vaginal hooks absent (Fig. 8I).

Distribution. This new species was found from the limestone karst near the very famous historic site.

Remarks. Apparently rare. Recent extensive searching revealed the living animal for the first time.

DISCUSSION

Indoartemon has been included in two molecular phylogenetic studies (Rowson et al., 2010; Sutcharit et al., 2010). Rowson et al. (2010) came to the conclusion that the Streptaxoidea were of Laurasian Mesozoic origin and *Indoartemon* came within a 'Streptaxines' clade with Early Cenozoic origin and a current distribution ranging from South America, Africa and Madagascar to Southeast Asia. Thus the 'Streptaxine' clade has established distinct lineages over an extremely wide geographical range. Currently, a total of 21 genera within the subfamily Streptaxinae Gray, 1860 sensu Schileyko (2000) are recognised, most only on the basis of shell characters but the genital systems of several examples have been studied (Gerlach & Bruggen, 1999; Schileyko, 2000). *Streptartemon* Kobelt, 1905, from South America and *Seychellaxis* Schileyko, 2000, from the Seychelles in addition to sharing similar oblique-heliciform shells with *I. medius*, new species, also exhibit shared anatomical features of their reproductive organs, namely a penial sheath extending about half of total penis length, a vas deferens entering the penis distally and the presence of a narrow band of connective tissue connecting the vas deferens to the distal margin of the penial sheath. *Streptartemon* and *Seychellaxis* fell into two distantly-related clades in the molecular phylogeny of Rowson et al. (2010). These shared characters cannot be demonstrated to have any phylogenetic value and may be plesiomorphic. These and other morphological characters will be better understood when they are mapped on a molecular phylogenetic tree.

The cladogenesis event leading to the *Indoartemon* lineage was dated roughly to the Eocene/Oligocene boundary by Rowson et al. (2010). Thus on current evidence the genus can be interpreted as having existed for about 35 Ma although the relationship of *Indoartemon* and possibly closely related genera such as *Oophana* has not been established based on molecular criteria and they could be part of the same lineage. The current distribution of *Indoartemon* ranges widely from Sri Lanka to areas of Southeast Asia (Fig. 1) but the records are widely discontinuous and generally based on very few records. The absence of any records from India is notable. Three hypotheses might account for this pattern, which are not mutually exclusive: 1) repeated long distance dispersal; 2) current distributions are relicts of a previously wide ranging distribution; 3) *Indoartemon* has been significantly under-recorded. Current information does not allow us to strongly favour one of these hypotheses over another but the distribution of the 'Streptaxine' clade does demonstrate a history of successful dispersal since the Middle Eocene. We also see no reason why *Indoartemon* should have been significantly under-recorded in comparison with other groups. Molecular phylogenetic evidence should help to clarify the historical biogeography of *Indoartemon* by showing any patterns of dispersal inferred by nested tree configurations and also reveal the genetic distance between species as an indication of the chronological history of *Indoartemon*.

The finding live specimens of the *Carinartemis*, new genus, in each type locality in the west is fortunate. Both *Carinartemis vesperus*, new species, and *Carinartemis striatus*, new species, are rarely collected except as adult shells. The shell characters alone can discriminate between the two new species, however, the genitalia provide further evidence that the two new species are distinct taxa.

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