

## The land snail genus *Macrochlamys* Gray, 1847 from Thailand, with descriptions of five new species (Pulmonata: Ariophantidae)

Arthit Pholyotha<sup>1,2</sup>, Chirasak Sutcharit<sup>2\*</sup> and Somsak Panha<sup>2\*</sup>

**Abstract.** The taxonomic status of the limacoid genus *Macrochlamys* Gray, 1847 in Thailand has long been plagued by much ambiguity due to the inability to distinguish members from each other, and a few other genera, by shell morphology alone. The taxonomy of the Thai species is evaluated resulting in recognition of seven species, including five new species. The new species, *Macrochlamys aurantia*, *M. coleus* and *M. tanymentula* from Kanchanaburi Province (West Thailand), and *M. caverna* and *M. lemma* from Lopburi Province (Central Thailand), are distinguished and described based on shell, animal colouration, radula and genitalia characters. The status of *Macrochlamys brunnea* Möllendorff, 1902b is at present unclear. Although described from Bangkok, no material identifiable as this species was found in recent extensive surveys and it is provisionally retained in the genus without anatomical evaluation. *Macrochlamys kelantanensis* Möllendorff, 1902a is re-described with additional morphological and anatomical information. The five new species appear to have a restricted distribution in Western and Central Thailand, whereas *M. kelantanensis* is more wide-ranging, from Thailand to Malaysia. Detailed descriptions and illustrations of the shell morphology, external morphology, genital anatomy and radulae are provided. The results show that despite the shells being morphologically similar, aspects of classical morphology based taxonomy for *Macrochlamys* species, especially the genitalia morphology, remain useful and reliable for species delimitation.

**Key words.** terrestrial snails, limacoid snail, taxonomy, systematics, Indochina, limestone

### INTRODUCTION

The land snail genus *Macrochlamys* Gray, 1847 is one of the most speciose in the family Ariophantidae Godwin-Austen, 1888. The genus comprises over a hundred described species distributed from South to Southeast Asia and the southern part of China (Blanford & Godwin-Austen, 1908; Schileyko, 2003). Recent extensive land snail surveys in Thailand have revealed a relatively large species diversity within the “*Macrochlamys-Sarika*” complex and highlights the issue of often ambiguous and misapplied *Macrochlamys* species names (Solem, 1966; Maneevong, 2000; Sutcharit & Panha, 2008). This study attempts to elucidate the Thai species of *Macrochlamys* sensu Godwin-Austen (1883) based on the shell, radula and genitalia characters.

“*Macrochlamys*” was first proposed by Benson (1832) without a description, and subsequently made available in Gray (1847). Godwin-Austen (1883: 76–122) provided the generic description that forms the basis for its wide acceptance and adoption in subsequent works (i.e., Blanford

& Godwin-Austen, 1908; Zilch, 1959; Schileyko, 2003; Raheem et al., 2014). In earlier works, Godwin-Austen (1883–1899) classified most ariophantid snails with a semi-transparent, polished and depressed to subglobose shell as *Macrochlamys* sensu Godwin-Austen (1883). Later, Godwin-Austen (1907) and Blanford & Godwin-Austen (1908) refined the classification of the Indian Ariophantidae and indicated that while many genera, such as *Taphrospira* Blanford, 1905, *Sarika* Godwin-Austen, 1907, *Parvatella* Blanford & Godwin-Austen, 1908, *Syama* Blanford & Godwin-Austen, 1908 and *Rasama* Laidlaw, 1932a, are conchologically similar, the reproductive anatomy and the mantle lobes reveal significant discriminatory taxonomic characters. Subsequent systematic revisions of various limacoid snails confirms the taxonomic importance of the reproductive organs for distinguishing taxa at both the generic and specific level. Examples are the revisions of the Australian Helicarionoidea by Hyman & Ponder (2010, 2016), the Southeast Asian and African Ariophantidae by Solem (1966) and Winter (2008) and the Southeast Asian Dyakiidae by Liew et al. (2009) and Sutcharit et al. (2012).

Species attributed to *Macrochlamys* sensu Godwin-Austen (1883) has a spirally coiled epiphallid caecum and a penis with a verge, flagellum, gametolytic organ and dart apparatus (Blanford & Godwin-Austen, 1908; Schileyko, 2003). Godwin-Austen (1907) and Solem (1966) suggest that most of the “*Macrochlamys*” species from Peninsula Malaysia, Indochina and Southern China without a coiled epiphallid caecum belong to the genus *Sarika*. In Thailand, although 11 species have been historically placed in the

<sup>1</sup>Biological Sciences Program, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand

<sup>2</sup>Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand; Email: somsak.pan@chula.ac.th; jirasak4@yahoo.com (\*corresponding authors)

genus “*Macrochlamys*” based on shell morphology (e.g., Panha, 1996; Hemmen & Hemmen, 2001) only one is retained in this study and the rest should be more properly assigned to other genera. Two of them, “*M. anceps* (Gould, 1844)” and “*M. pataniensis* Morgan, 1885”, have a shell with a keeled last whorl. The former has since been placed into the *Holkeion* (Blanford & Godwin-Austen, 1908: 240), while genitalia information shows that the latter should be transferred to *Pseudoplecta* Laidlaw, 1932b (Panha, unpublished data). “*Macrochlamys pedina* (Benson, 1865)”, “*M. diadema* Dall, 1897” and “*M. asamurai* Panha, 1997” have been anatomically examined and moved to *Sarika* (see Godwin-Austen, 1899; Blanford & Godwin-Austen, 1908; Sutcharit & Panha, 2008). Four other species, “*M. pumicata* (Morelet, 1875)”, “*M. dugasti* Morlet, 1891”, “*M. limbata* Möllendorff, 1894” and “*M. ochtogyra* Möllendorff, 1902b” also do not belong to *Macrochlamys* sensu Godwin-Austen, 1883 as they possess an un-coiled epiphallal caecum unique to *Sarika* (see Maneevong, 2000; Panha, unpublished data). “*Macrochlamys molecula* (Benson, 1859)” is clearly not a *Macrochlamys* with its dome-shaped shell, an uncoiled epiphallal caecum, and lack of dart apparatus and gametolytic duct (Stoliczka, 1871; Blanford & Godwin-Austen, 1908: 122). However, further study is required to determine its appropriate generic placement. The only remaining species, “*M. brunnea* Möllendorff, 1902b”, currently has no ascribed genitalia data, and is provisionally retained in *Macrochlamys* following the original description. Six other species of *Macrochlamys* sensu Godwin-Austen (1883) are found in Thailand. *Macrochlamys kelantanensis* Möllendorff, 1902a is herein re-described, and the other five are herein described as new species based on shell, external morphology, radula and genitalia characters.

## MATERIAL AND METHODS

The specimens were collected across Thailand and from some areas in Peninsular Malaysia. Live specimens were photographed, euthanised by two-Step methods (AVMA, 2013), and then stored at  $-20^{\circ}\text{C}$  prior to fixing and preserving in 70% (V/V) ethanol for anatomical study. Specimens were initially identified using Stoliczka (1871), Godwin-Austen (1883–1907) and Blanford & Godwin-Austen (1908) then subsequently compared to the relevant type specimens. Reproductive organs from 3–10 specimens of each species were dissected for examination. Shells and genitalia were imaged using a digital camera (DSLR D700 - Nikon) and a stereomicroscope with Cell’D Imaging Software. Radulae were extracted, soaked in 10% (W/V) sodium hydroxide, cleaned with distilled water and then examined under scanning electron microscopy (SEM; JEOL, JSM-6610 LV). The formulae and shape of radula are described. In the material examined sections, shells refer to empty shells while specimens refer to specimens preserved in ethanol. Descriptions of all new species herein are attributed to the first and third authors, Pholyotha & Panha, respectively.

In descriptions of the reproductive organs, ‘proximal’ refers to the region closest to the genital opening and ‘distal’ refers

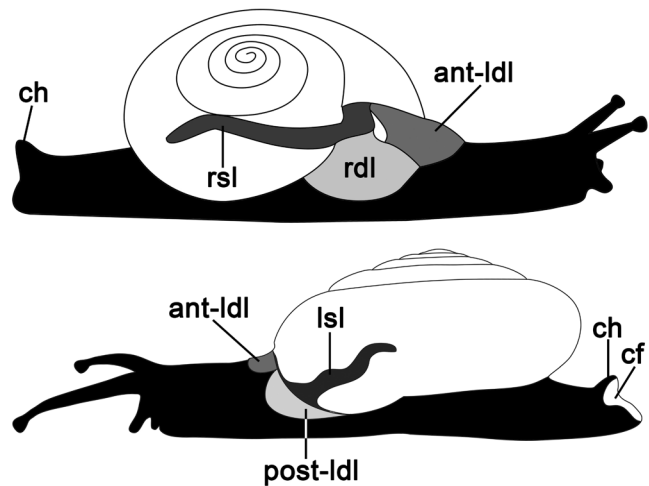


Fig. 1. Schematic drawing of the external features and mantle terminology of *Macrochlamys*. Abbreviations: ant-ldl, anterior left dorsal lobe; cf, caudal foss; ch, caudal horn; lsl, left shell lobe; post-ldl, posterior left dorsal lobe; rdl, right dorsal lobe; rsl, right shell lobe.

to the region furthest away. The genitalia terminology and abbreviations follow Blanford & Godwin-Austen (1908), Solem (1966) and Sutcharit & Panha (2008): ant-ldl, anterior left dorsal lobe; at, atrium; da, dart apparatus; cf, caudal foss; ch, caudal horn; drm, dart retractor muscle; e, epiphallus; ec, epiphallal caecum; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hf, head filament; lsl, left shell lobe; ov, oviduct; p, penis; pc, penial caecum; pg, prostate gland; post-ldl, posterior left dorsal lobe; pp, penial pilaster; prm, penial retractor muscle; pv, penial verge; rdl, right dorsal lobe; rsl, right shell lobe; ss, sperm sac; tf, tail filament; v, vagina, and vd, vas deferens.

**Institutional abbreviations.** 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; ZRC, Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore.

## SYSTEMATICS

### Family Ariophantidae Godwin-Austen, 1888

#### Subfamily Macrochlamydinae Godwin-Austen, 1888

#### Genus *Macrochlamys* Gray, 1847

*Macrochlamys* Gray, 1847: 169 – Benson, 1832: 13, 76 [unavailable]; Benson, 1836: 350, 351 [unavailable]; Stoliczka, 1871: 246; Godwin-Austen, 1883: 76–84; Blanford & Godwin-Austen, 1908: 77–79; Zilch, 1959: 323; Thiele, 1931: 628; Schileyko, 2003: 1322.

*Tanychlamys* Benson, 1834: 89 [unavailable] – Stoliczka, 1871: 247. *Orobia* Albers, 1860: 57.

**Type species.** *Helix vitrinoides* Deshayes, 1831, by monotypy.



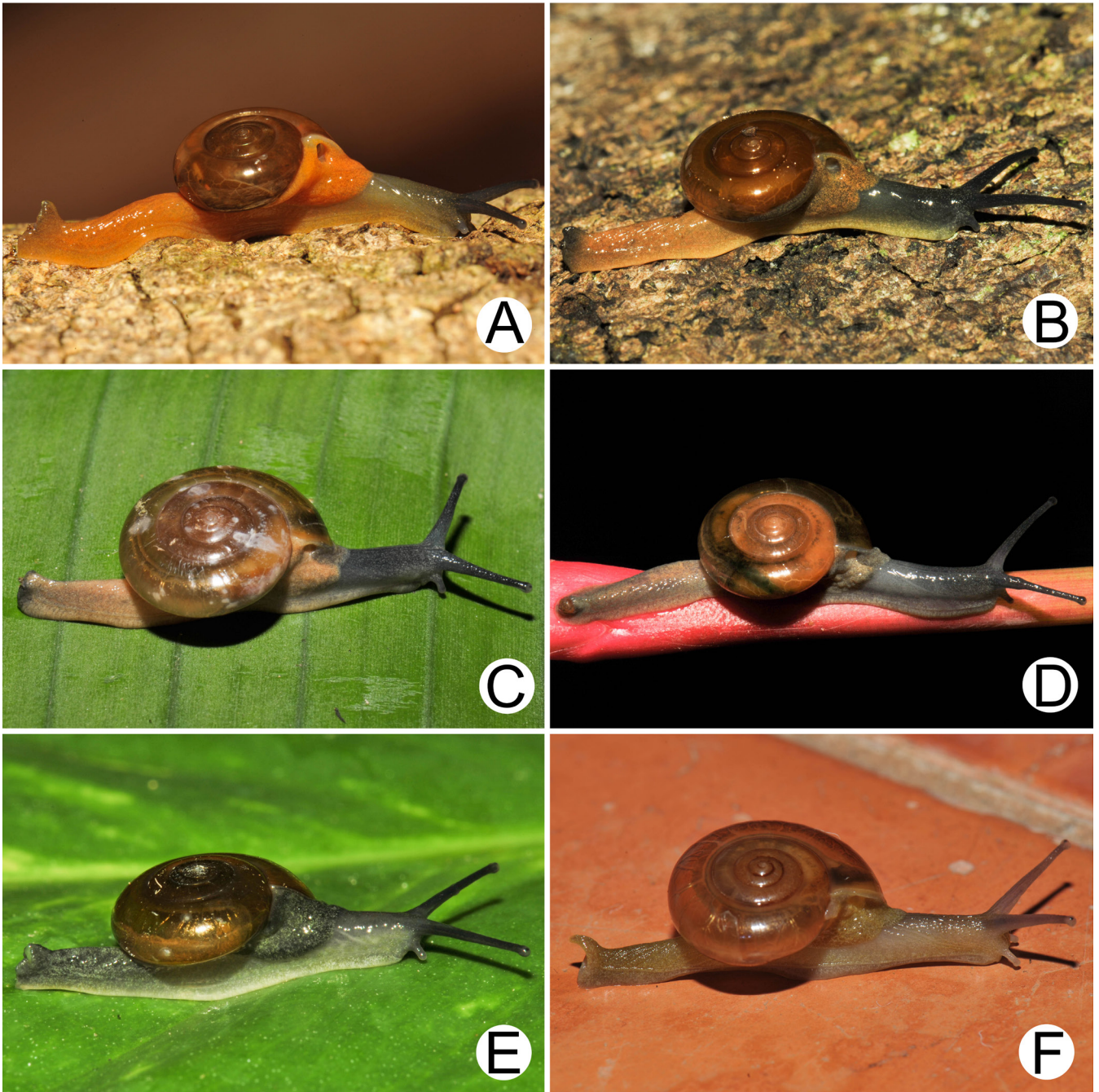


Fig. 2. Living snails of *Macrochlamys* spp. from Thailand. A, *Macrochlamys aurantia* new species, paratype (CUMZ 7103), Thong Pha Phum, Kanchanaburi, shell width about 15 mm; B, *M. coleus* new species, paratype (CUMZ 7106), Sai Yok, Kanchanaburi, shell width about 15 mm; C, *M. caverna* new species, paratype (CUMZ 7109), Tha Wung, Lopburi, shell width about 17 mm; D, *M. lemma* new species, paratype (CUMZ 7116), Ban Mi, Lopburi, shell width about 15 mm; E, *M. tanymentula* new species, paratype (CUMZ 7119), Thong Pha Phum, Kanchanaburi, shell width about 10 mm; F, *M. kelantanensis* (CUMZ 7125), Lam Kaen, Phang-Nga, shell width about 20 mm.

**Diagnostic description.** Shell small to large, dextral, depressed to semi-globose, thin, translucent, surface smooth and shiny, with 4–6 whorls. Last whorl rounded to slightly shouldered. Aperture lunate and normally with simple lip. Columellar margin slightly reflected near umbilicus. Umbilicus open or minutely open.

Genitalia with spirally coiled epiphallic caecum to which retractor muscle is attached. Flagellum, gametolytic organ,

dart apparatus with retractor muscle and penial verge well developed. Animal with well-developed mantle edge with two shell-lobes and three dorsal-lobes (Fig. 1). Body colour variable, from black or grey to colourful orange or yellow (Fig. 2). Sole tripartite, caudal foss and caudal horn present.

Radula with symmetric tricuspid central tooth, asymmetric tricuspid lateral teeth and bicuspid marginal teeth.



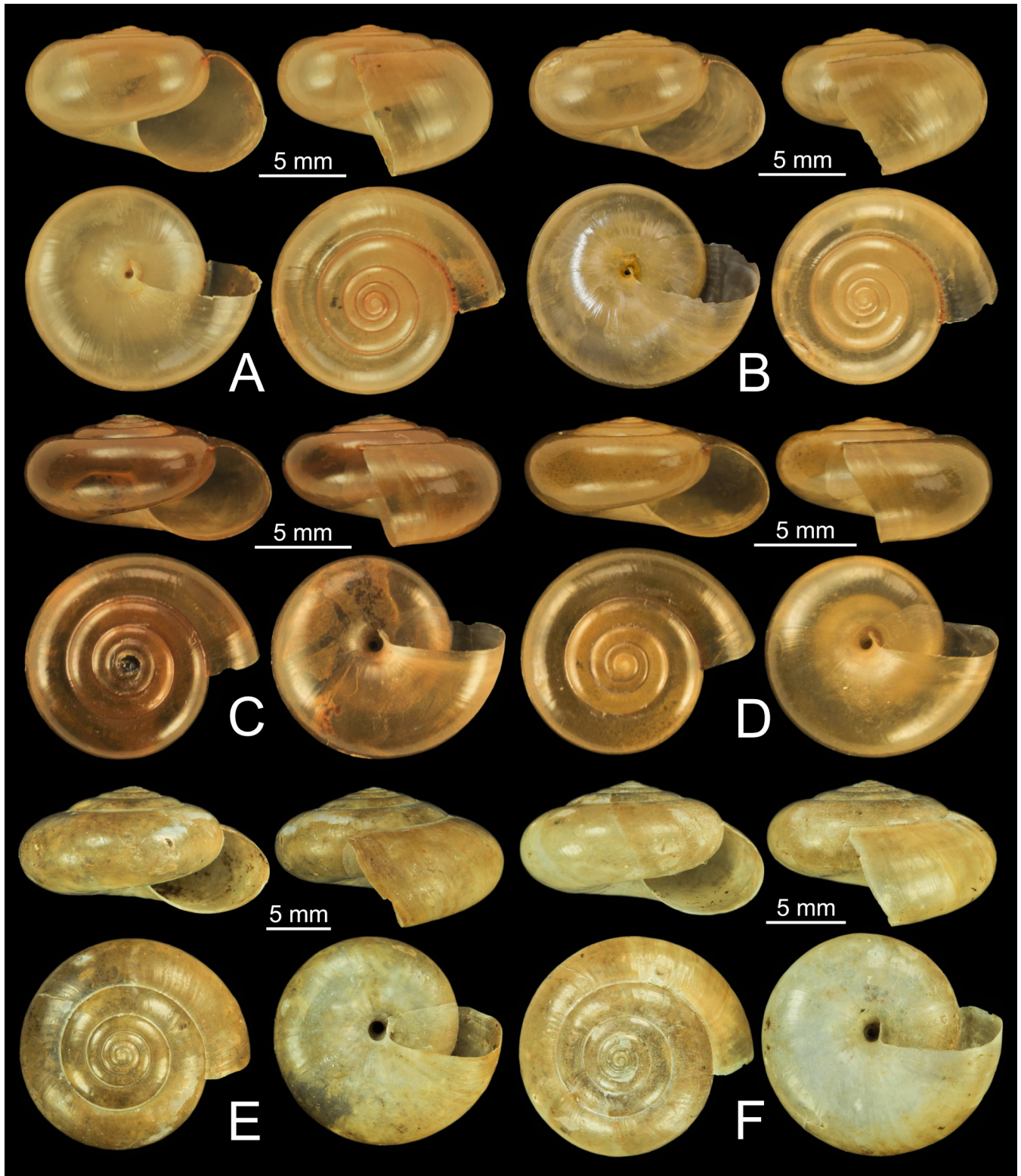


Fig. 3. Shells of *Macrochlamys aurantia* new species (A, B), *M. coleus* new species (C, D), and *M. caverna* new species (E, F). A, *Macrochlamys aurantia* holotype (CUMZ 7101); B, paratype (CUMZ 7102); C, *M. coleus* holotype (CUMZ 7104); D, paratype (CUMZ 7105); E, *M. caverna* holotype (CUMZ 7107); F, paratype (CUMZ 7108).



***Macrochlamys aurantia* Pholyotha & Panha, new species**

(Figs. 2A, 3A, B, 4A–E, 6A–C)

**Material examined.** Holotype (Fig. 3A; shell height 8.0 mm, shell width 14.0 mm, aperture height 6.0 mm, aperture width 7.2 mm, 5 $\frac{1}{8}$  whorls) (CUMZ 7101), limestone outcrop at Wat Uthum Phon Wanaram (Temple), Huai Kayeng Village, Thong Pha Phum District, Kanchanaburi Province, Thailand, 14°41'52.6"N, 98°31'32.3"E. Paratypes: three shells (Fig. 3B; shell height 8.0 mm, shell width 13.9 mm, aperture height 6.5 mm, aperture width 7.1 mm, 5 $\frac{1}{8}$  whorls) (CUMZ 7102), 12 specimens (CUMZ 7103), one shell (NHMUK), one shell (ZRC.MOL.13771), same data as holotype.

**Etymology.** The specific name “*aurantia*” is from Latin “*aurantium*” meaning “orange”, and refers to the prominent orange or reddish orange posterior part of its body.

**Description.** Shell medium-sized (Fig. 3A, B; shell height up to 8.2 mm; shell width up to 14.0 mm), dextral, comparatively depressed, thin but not fragile, semi-translucent, shiny and yellowish brown in colour. Shell surface smooth with fine growth lines. Embryonic shell small, about 2 $\frac{1}{2}$  whorls with smooth surface. Whorls 5–6, regularly increasing. Suture wide and deeply channelled. Spire depressed, apex little raised, spire angle about 152–156°. Last whorl large, periphery rounded. Aperture oval-lunate, open obliquely, lip simple. Columellar edge slightly thickened and a little reflected over the narrowly open umbilicus.

**Genital organs.** Atrium (at) short. Penis prolonged, slightly enlarged and cylindrical-shaped. Distally cylindrical and corresponding to penial verge. Penial caecum (pc) slightly prolonged. Epiphallus (e) slender tube, about two times length of penis. Epiphallic caecum (ec) coiled about one circle, located at middle of epiphallus and attached with thick penial retractor muscle (prm). Flagellum (fl) large, irregular coiled and length around half of epiphallus length. Vas deference (vd) slim tube connected between distal end of epiphallus and free oviduct (Fig. 4A).

Internal wall of penis with very small and oblique wrinkled penial pilasters (pp). Penial verge (pv) small, thick and located at distal end of penis (Fig. 4B).

Vagina (v) long, cylindrical-shape, about same length as penis. Dart apparatus (da) small, cylindrical-shape and situated at proximal end of vagina. Gametolytic sac (gs) prolonged and bulbous. Gametolytic duct (gd) long and cylindrical (two spermatophores in Fig. 4A). Free oviduct (fo) a long slender tube, proximal end encircled with thick brownish tissue. Oviduct (ov) large lobules, with prostate gland (pg) running alongside oviduct (Fig. 4A).

Spermatophore long, needle-shape and translucent (Fig. 4C–E). Head filament (hf) short, gradually thinning to terminal point (Fig. 4D). Sperm sac (ss) a cylindrical capsule, containing sperm mass. Tail filament (tf) very long and

cylindrical. Region close to sperm sac bearing three spines. First one dichotomous and split into two short spines, second one curved, located on same base as previous, third one simple, long and curved (Fig. 4D). Region furthest from sperm sac with small spine cluster near tip (Fig. 4E). Out of 10 specimens examined, seven contain one spermatophore and three contain two spermatophores in gametolytic organs.

**Radula.** Teeth arranged in a U-shape, with about 103 teeth in each row with formula (48-(12-10)-1-(10-11)-54). Central tooth symmetrical, tricuspid with large and lanceolate mesocone, ectocones small and pointed cusps. Lateral teeth asymmetrical tricuspid. Endocone small, located near tip, mesocone large, triangular with pointed cusp. Ectocone larger than edocone and located near tooth base. Marginal teeth start around tooth number 10–12, obliquely bicuspid, elongate and narrower than others. Endocone large, ectocone smaller with pointed cusp (Fig. 6A–C).

**External features.** Animal with reticulated skin. Head to eye stalks dark grey, body and tail deep yellow-orange. Caudal foss (cf) long and narrow. Caudal horn (ch) raised, large and greyish-orange. Mantle edge (shell lobes and dorsal lobes) well developed, dark to bright orange in colour. Shell lobes large and long. Right shell lobe (rsl) larger and longer than left shell lobe (lsl). Dorsal lobes large and broad. Right dorsal lobe (rdl) larger than both anterior left dorsal lobe (ant-ldl) and posterior left dorsal lobe (post-ldl). Snails secrete light orange slime when disturbed (Fig. 2A).

**Distribution and habitat.** *Macrochlamys aurantia* new species was usually found on the surface of limestone walls and in rock crevices. Some individuals were encountered creeping on the leaves of a bush or tree trunk close to the limestone outcrop during our surveys. This species is probably locally endemic, and is currently known only from the type locality, where the population density is rather abundant.

**Remarks.** *Macrochlamys aurantia* new species can be distinguished by the depressed spire, yellowish colour, large and rounded last whorl, and a wide and deep-channelled suture. The genitalia have long penis and vagina, one circle of coiled epiphallic caecum and a small dart apparatus located at the base of the vagina opposite the penis. Spermatophore has three spines at the proximal end and a cluster of small spines at the distal end of the tail filament.

This new species can be distinguished from *M. consepta* (Benson, 1860) and *M. chaos* Blanford, 1905 from Myanmar by its depressed shell with a wide deeply impressed suture, and broad last whorl and aperture. In contrast, *M. consepta* has an almost flat shell with shallow suture, and the last whorl and aperture are not much broader. *Macrochlamys chaos* has a conoidly depressed shell with shallow suture, and narrow last whorl and aperture. In addition, this new species can be distinguished from all other known species by its spermatophore with three spines at the proximal end, and the cluster of small spines at the distal end of the tail filament.

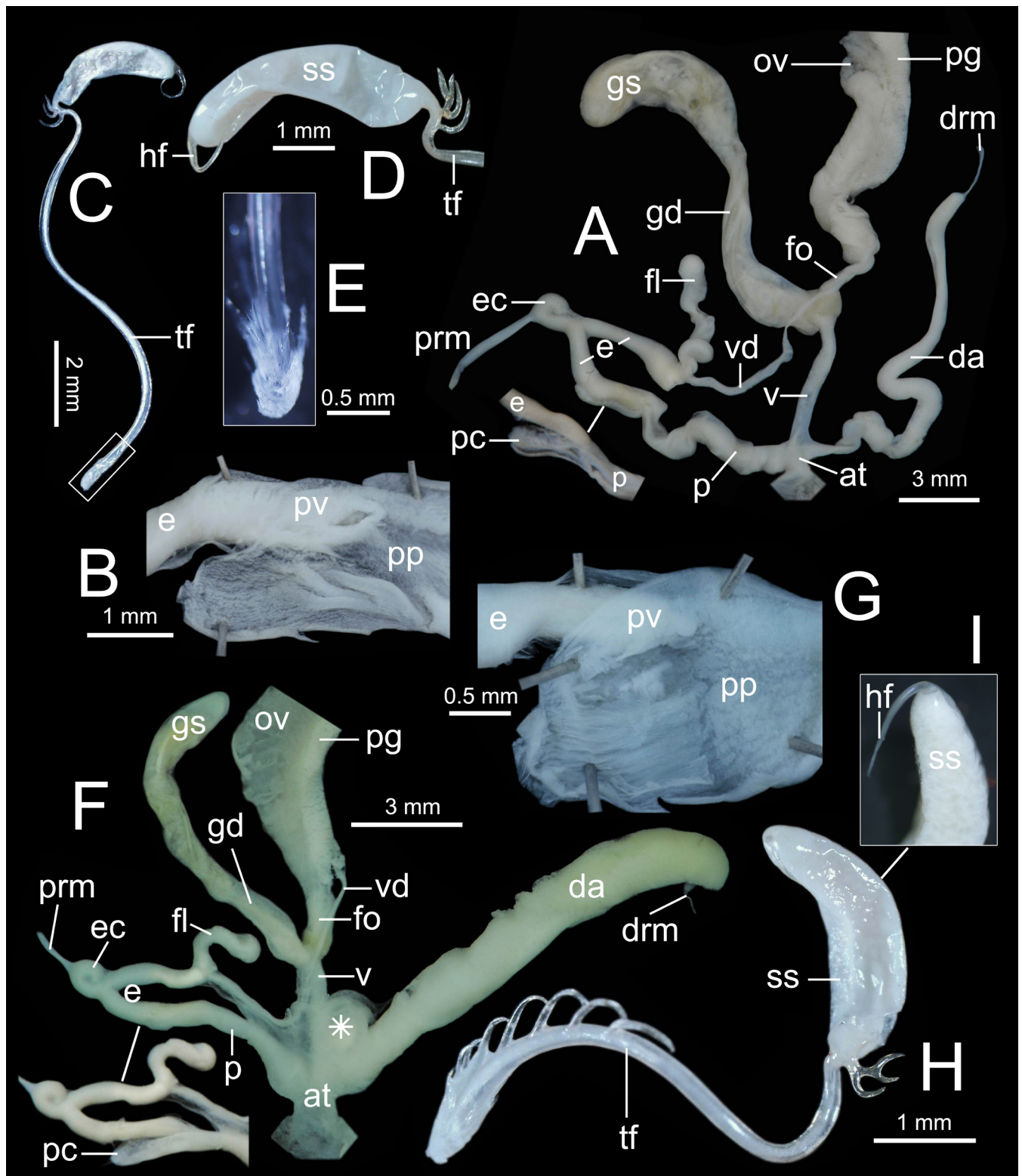


Fig. 4. Genitalia of *Macrochlamys aurantia* new species (A–E), and *M. coleus* new species (F–I). A–E, *Macrochlamys aurantia* paratype (CUMZ 7103): A, whole reproductive system; B, internal structure of penis with penial verge; C, spermatophore; D, detail of spines between sperm sac and tail filament; E, spines on the end of tail filament. F–I, *Macrochlamys coleus* paratype (CUMZ 7106): F, whole reproductive system; G, internal structure of penis with penial verge; H, spermatophore; I, head filament. Abbreviations: at, atrium; da, dart apparatus; drm, dart retractor muscle; e, epiphallus; ec, epiphallic caecum; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hf, head filament; ov, oviduct; p, penis; pc, penial caecum; pg, prostate gland; pp, penial pilaster; prm, penial retractor muscle; pv, penial verge; ss, sperm sac; tf, tail filament; v, vagina and vd, vas deferens. Asterisk indicates the tissue casting.



***Macrochlamys coleus* Pholyotha & Panha, new species**  
(Figs. 2B, 3C, D, 4F–I, 6D–F)

**Material examined.** Holotype (Fig. 3C; shell height 6.6 mm, shell width 13.0 mm, aperture height 5.0 mm, aperture width 6.2 mm,  $5\frac{1}{2}$  whorls) (CUMZ 7104), limestone outcrops at Wat Sunantha Wanaram (Temple), Sai Yok District, Kanchanaburi Province, Thailand,  $14^{\circ} 32'01.6''\text{N}$ ,  $98^{\circ} 50'13.8''\text{E}$ . Paratypes: one shell (Fig. 3D; shell height 6.0 mm, shell width 12.3 mm, aperture height 4.5 mm, aperture width 6.1 mm,  $5\frac{1}{4}$  whorls) (CUMZ 7105), 10 specimens (CUMZ 7106), same data as holotype.

**Etymology.** The specific epithet “*coleus*”, from the Latin word meaning “sheath”, refers to the well-developed tissue covering between the vagina and dart apparatus.

**Description.** Shell medium-sized (Fig. 3C, D; shell height up to 6.6 mm; shell width up to 13.0 mm), dextral, depressed, slightly thick, translucent brown in colour. Shell surface nearly smooth, with very fine growth lines. Embryonic shell surface smooth, with about  $2\frac{1}{2}$  whorls. Whorls 5–6, increasing regularly. Suture wide and shallow, channel-shaped. Spire depressed, apex slightly raised with spire angle of about  $148\text{--}152^{\circ}$ . Last whorl well rounded. Aperture crescent ovoid shaped, obliquely open, with simple lip. Columellar margin little developed and slightly reflected near umbilicus. Umbilicus narrowly open.

**Genital organs.** Atrium (at) short. Penis prolonged, cylindrical-shaped with rounded bulge corresponding to penial verge. Penial caecum (pc) slightly prolonged. Epiphallus (e) slender tube about two times longer than penis. Epiphallic caecum (ec) coiled about one circle, located at middle of epiphallus and attached with thick penial retractor muscle (prm). Flagellum (fl) short, cylindrical shaped and stretched around half of epiphallus length. Vas deference (vd) a thin tube connected between distal end of epiphallus and free oviduct (Fig. 4F).

Inner penial wall supported proximally with small and irregular wrinkled penial pilasters (pp), distally with thin longitudinal and wrinkled folds. Penial verge (pv) very small and short, situated at distal end of penis (Fig. 4G).

Vagina (v) slightly long, almost same length as penis and cylindrical. Dart apparatus (da) long, enlarged cylindrical shape, located at proximal end of vagina, with thick connective tissue encircled at proximal end (asterisk in Fig. 4F). Gametolytic sac (gs) elongate and bulbous. Gametolytic duct (gd) long and cylindrical (one spermatophore in Fig. 4F). Free oviduct (fo) short, about similar length to flagellum, proximal end encircled with brownish tissue. Oviduct (ov) large lobules with prostate gland (pg) running alongside (Fig. 4F).

Spermatophore long, needle-shaped and translucent (Fig. 4H). Head filament (hf) short, gradually tapering to a point (Fig. 4I). Sperm sac (ss) enlarged, cylindrical capsule-shaped with sperm mass. Tail filament (tf) long, curved with many

spines. Region close to sperm sac bear a single trichotomous spine divided into three pointed tips. Middle region with a row of five, long curved spines. Region furthest away from sperm sac contains small cluster of short spines (Fig. 4H).

**Radula.** Each row contains about 92 teeth with formula (45-(12-11)-1-(11-12)-46). Central tooth symmetric tricuspid. Lateral teeth asymmetric tricuspid. Marginal teeth obliquely bicuspid starting from tooth number 11–12 (Fig. 6D–F).

**External features.** Animal with reticulated skin. Head, eye stalks and body dark grey, and tail orange (Fig. 2B). Caudal foss (cf) long and narrow. Caudal horn (ch) large and dark grey in colour. Mantle edge (shell lobes and dorsal lobes) well developed, orange with black pigmented spots spread all over. Shell lobes and dorsal lobes similar in morphology to *M. aurantia* new species. Snails secrete light orange slime when disturbed.

**Distribution and habitat.** This new species is currently known only from the type locality, an area of limestone outcrops with a relatively low population density. The snails were mostly found on decaying leaf litter or sometimes climbing on limestone walls.

**Remarks.** *Macrochlamys coleus* new species is distinguished by a depressed shell, dark brown in colour, and rather shallowly channelled suture. The genitalia have one circle of coiled epiphallic caecum, and dart apparatus with a thick connective tissue encircling the proximal end. Its spermatophore has a single trichotomously branched spine at the proximal end, five long spines in the middle, and a cluster of small spines at the distal end of tail filaments. Its radula morphology is very similar to *M. aurantia*.

This new species is close to *M. aurantia* new species, but can be differentiated by its small last whorl and shallow channel-shaped suture. Anatomically, the genitalia have a short flagellum and well-developed connective tissue surrounding the proximal end of the dart apparatus; characters missing in *M. aurantia* new species. In addition, the spermatophore of this new species has a trichotomous spine on the tail filament close to the sperm sac and a row of long and curved spines on the middle part of the tail filament, while *M. aurantia* new species has one dichotomous spine and two simple spines on the tail filament close to the sperm sac. This new species differs from *M. hypoleuca* (Blanford, 1865) and *M. nebulosa* (Blanford, 1865) from Myanmar by its depressed shell with a broad last whorl and dark brown shell colour. In comparison, *M. hypoleuca* has a two-toned shell that is brown above the periphery and white below, while *M. nebulosa* has a conoidal, depressed, shell that is bluntly angulated at the periphery.

***Macrochlamys caverna* Pholyotha & Panha, new species**

(Figs. 2C, 3E, F, 5A, B, 6G–I)

**Material examined.** Holotype (Fig. 3E; shell height 8.6 mm, shell width 17.2 mm, aperture height 5.6 mm, aperture

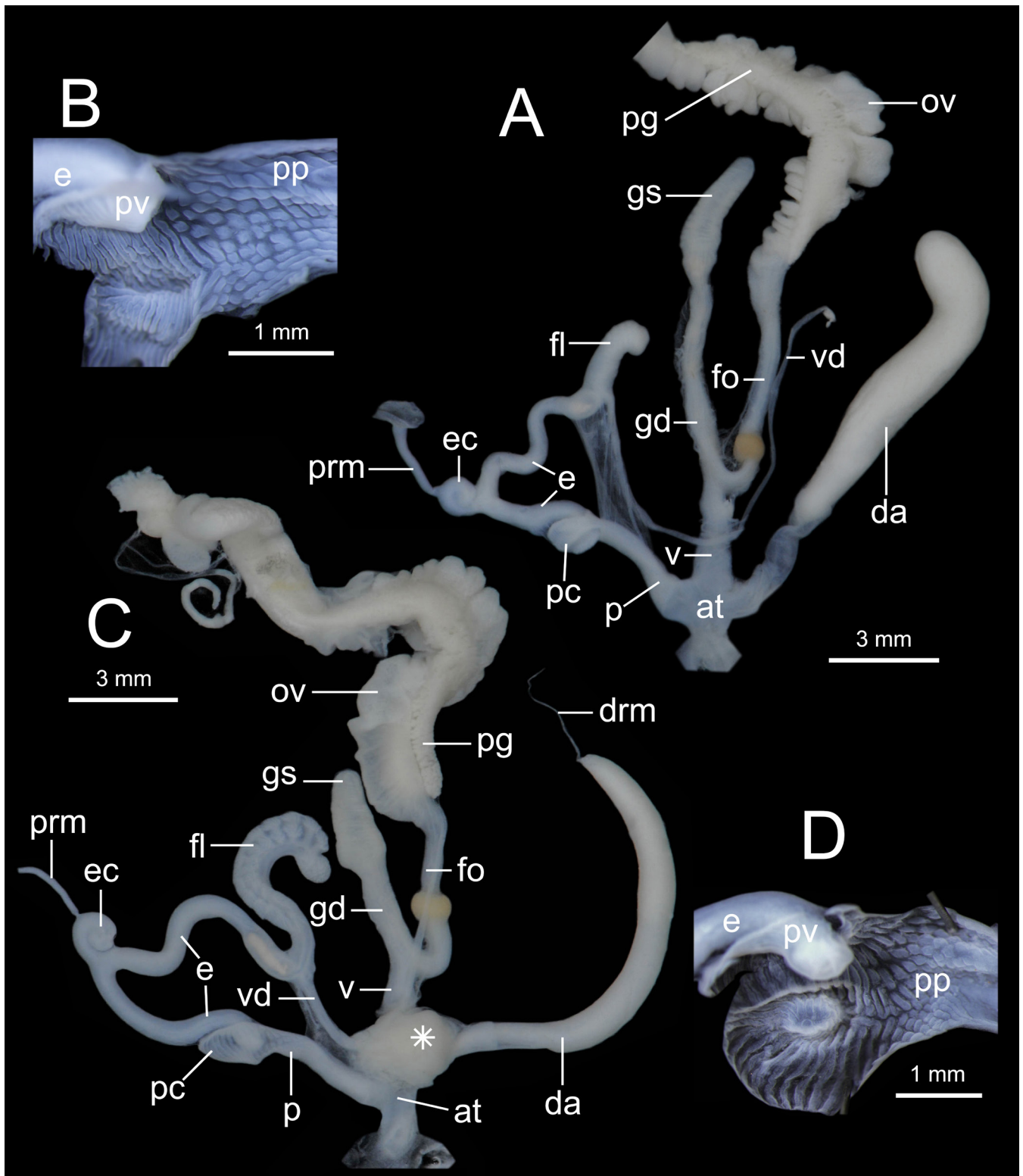


Fig. 5. Genitalia of *Macrochlamys caverna* new species (A, B), and *M. lemma* new species (C, D). A, B, *Macrochlamys caverna* paratype (CUMZ 7109): A, whole reproductive system; B, internal structure of penis with penial verge. C, D, *Macrochlamys lemma* paratype (CUMZ 7116): C, whole reproductive system; D, internal structure of penis with penial verge. Abbreviations: at, atrium; da, dart apparatus; drm, dart retractor muscle; e, epiphallus; ec, epiphallic caecum; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hf, head filament; ov, oviduct; p, penis; pc, penial caecum; pg, prostate gland; pp, penial pilaster; prm, penial retractor muscle; pv, penial verge; ss, sperm sac; tf, tail filament; v, vagina and vd, vas deferens. Asterisk indicates the tissue casting.



width 8.0 mm,  $6\frac{1}{4}$  whorls) (CUMZ 7107), limestone outcrops at Wat Khao Samo Khon (Temple), Tha Wung District, Lopburi Province, Thailand,  $14^{\circ} 54'05.9''\text{N}$ ,  $100^{\circ} 30'29.5''\text{E}$ . Paratypes: 55 shells (Fig. 3F; shell height 8.1 mm, shell width 15.0 mm, aperture height 5.4 mm, aperture width 7.2 mm,  $6\frac{1}{8}$  whorls) (CUMZ 7108), seven specimens (CUMZ 7109), five shells (NHMUK), five shells (ZRC.MOL.13772), same data as holotype. Non type material: 11 shells (CUMZ 7110), three specimens (CUMZ 7111), Wat Tham Chang Pueak (Temple), Tha Wung District, Lopburi Province, Thailand,  $14^{\circ} 54'08.7''\text{N}$ ,  $100^{\circ} 30'08.6''\text{E}$ ; 20 shells (CUMZ 7112), eight specimens (CUMZ 7113), Khao Mon Ing Dharma Practice Place, Ban Chi, Ban Mi District, Lopburi Province, Thailand,  $14^{\circ} 55'29.0''\text{N}$ ,  $100^{\circ} 31'00.3''\text{E}$ .

**Etymology.** The specific epithet “*caverna*” is derived from the Latin “*cavus*” meaning “hole or hollow”, in reference to the open and deep umbilicus.

**Description.** Shell medium-sized (Fig. 3E, F; shell height up to 8.6 mm; shell width up to 17.2 mm), dextral, depressed, somewhat thin, translucent, shiny, and pale reddish-brown. Shell surface smooth with obvious microscopic growth lines. Embryonic shell surface smooth, small with  $2\frac{1}{2}$  whorls. Whorls 5–6, regularly increasing. Suture wide and shallow. Spire convex, apex raised. Spire angle about  $134\text{--}142^{\circ}$ . Last whorl narrow with rounded periphery. Aperture ovate-lunate, obliquely open, lip simple. Columellar margin slightly thickened and reflected close to umbilicus. Umbilicus widely open and deep.

**Genital organs.** Atrium (at) short. Penis prolonged tube-shaped. Distal end with short and swollen penial caecum (pc) that corresponds to penial verge inside. Epiphallus (e) cylindrical, about two times penis length. Epiphallic caecum (ec) coiled about one circle and located proximally about one-third of epiphallic length. Penial retractor muscle (prm) short and thick. Flagellum (fl) enlarged and short, about one-third of epiphallic length. Vas deference (vd) a long, thin tube, connected between distal end of epiphallus and free oviduct (Fig. 5A).

Internal wall of penis proximally with oblique trapezoid penial pilasters (pp) and distally around penial caecum with long and narrowed pilasters surrounding penial verge (pv). Penial verge short, triangular-shaped and located at distal end of penis (Fig. 5B).

Vagina (v) about same length as penis and cylindrical. Dart apparatus (da) large and cylindrical, located at proximal end of vagina. Gametolytic sac (gs) prolonged and bulbous, gametolytic duct (gd) long and cylindrical. Free oviduct (fo) about same length as penis, proximally encircled with thick brownish tissue close to gametolytic duct and free oviduct junction at about one-fourth of its length. Oviduct (ov) large lobules; prostate gland (pg) running alongside oviduct (Fig. 5A).

**Radula.** Each row consists of 93 teeth with formula (47-(13-12)-1-(12-13)-45). Central tooth symmetrical tricuspid.

Mesocone large and lanceolate. Lateral teeth asymmetrical tricuspid with small endocone, large mesocone. Ectocone larger than endocone. Elongate and obliquely bicuspid marginal teeth start from tooth number 12–13 (Fig. 6G–I).

**External features.** Animal with dark grey head and tentacles that gradually becomes paler posteriorly into the yellowish body and tail. Caudal foss (cf) and caudal horn (ch) large and slightly dark grey in colour. Mantle edge well developed, shell lobes and dorsal lobes grey, except right dorsal lobe (rdl) which has yellowish colouration (Fig. 2C). Snails secrete yellowish slime when disturbed.

**Distribution and habitat.** Population density of this new species was generally high and abundant where found. They tend to live in small limestone hills in the Tha Wung and Ban Mi Districts, Lopburi Province.

**Remarks.** *Macrochlamys caverna* new species can be distinguished by its rather depressed shell with a wide and shallow suture and a widely open and deep umbilicus. Its genitalia have a short penial caecum, one circle of coiled epiphallic caecum, a rather long vagina and free oviduct, and very large dart apparatus that is located at the base of the vagina opposite the penis. Radula morphology of this species is very similar to *M. aurantia* new species.

*Macrochlamys caverna* new species can be distinguished from *M. aurantia* new species and *M. coleus* new species by its more elevated spire, shallow suture, widely open umbilicus and oblique trapezoid penial pilasters on the penial wall. In contrast, both *M. aurantia* new species and *M. coleus* new species have a depressed spire, channelled suture, narrow umbilicus, and small wrinkled and longitudinal folds on the penial wall. The rounded last whorl and wide open umbilicus of this new species differs from *M. benoitii* (Crosse & Fischer, 1863) from Indochina and *M. malaccana* (Pfeiffer, 1854) from Peninsular Malaysia. *Macrochlamys benoitii* has a shouldered last whorl and narrow umbilicus, while *M. malaccana* has a comparatively broader last whorl and minute umbilicus.

#### ***Macrochlamys lemma* Pholyotha & Panha, new species** (Figs. 2D, 5C, D, 7A, B, 10A–C)

**Material examined.** Holotype (Fig. 7A; shell height 7.2 mm, shell width 15.9 mm, aperture height 5.0 mm, aperture width 7.6 mm) (CUMZ 7114), limestone outcrops at Wat Khao Wongkot (Temple), Sanam Chaeng Village, Ban Mi District, Lopburi Province, Thailand,  $15^{\circ} 00'58.7''\text{N}$ ,  $100^{\circ} 32'38.5''\text{E}$ . Paratypes: two shells (Fig. 7B; shell height 6.3 mm, shell width 15.0 mm, aperture height 5.6 mm, aperture width 7.0 mm,  $5\frac{5}{8}$  whorls) (CUMZ 7115), 47 specimens (CUMZ 7116), two shells (NHMUK), one shell (ZRC.MOL.13773), same data as holotype.

**Etymology.** The specific name, derived from Greek “*lemma*” meaning “peel, husk or sheath”, is in reference to the well-developed tissue casing or sheath between the vagina and dart apparatus.

**Description.** Shell medium-sized (Fig. 7A, B; shell height up to 7.6 mm; shell width up to 17.0 mm), dextral, depressed to low-conical, thin, semi-translucent, shiny and pale yellowish in colour. Shell surface smooth with thin growth lines. Embryonic shell surface smooth, small, with about 2½ whorls. Whorls 5–6, increasing regularly, with shallowly impressed suture. Spire profile from low conical to nearly flat with just a little convexity. Spire angle about 147–159°. Last whorl narrow with well-rounded periphery. Aperture crescent-shaped, obliquely open with simple lip. Columellar margin slightly reflected near umbilicus. Umbilicus narrowly open and deep.

**Genital organs.** Atrium (at) large and slightly long. Penis long, cylindrical in shape and distally with short and swollen penial caecum (pc) that corresponds to penial verge inside. Epiphallus (e) rather long, about two and half times of penis length, cylindrical and almost same diameter as penis. Epiphallic caecum (ec) coiled about one circle and located proximally about one-third of epiphallus length. Penial retractor muscle (prm) slightly thick. Flagellum (fl) long, about half of epiphallus length, with early stage of spermatophore formation inside. Vas deference (vd) a long tube connected between free oviduct and distal end of epiphallus (Fig. 5C).

Inner wall of penis proximally with oblique trapezoid penial pilasters (pp) and distally at penial caecum with long and transverse-folded surrounding penial verge (pv). Penial verge small, thick and located at distal end of penis (Fig. 5D).

Vagina (v) rather long, about two-thirds of penis length, cylindrically shaped with thick connective tissue encircled at vagina and dart apparatus junction (asterisk in Fig. 5C). Dart apparatus (da) somewhat large, long cylindrical and located near proximal end of vagina above penis junction. Gametolytic sac (gs) bulbous. Gametolytic duct (gd) thick and rather short. Free oviduct (fo) long, approximately same length as penis, cylindrical in shape, and proximally encircled with thick brownish tissue about middle of its length. Oviduct (ov) are large lobules with prostate gland (pg) running alongside (Fig. 5C).

**Radula.** Each row consists of 99 teeth with formula (48-(14-13)-1-(14-15)-50). Central tooth triangular tricuspid. Lateral teeth asymmetric tricuspid with very small endocone. Elongate bicuspid marginal teeth starting from tooth number 13–15 (Fig. 10A–C).

**External features.** Animal with reticulated skin. Head, eye stalks and body dark grey, and the tail is pale orange. Caudal foss (cf) and caudal horn (ch) grey. Mantle edge (shell lobes and dorsal lobes) well developed with mix of black and dull yellow (Fig. 2D). Snails secrete light yellowish slime when disturbed.

**Distribution and habitat.** *Macrochlamys lemma* new species was found living in rock crevices and surfaces of limestone karst. It is currently known only from the type locality, where it is moderately abundant.

**Remarks.** *Macrochlamys lemma* new species can be diagnosed by its depressed to low-conical shell, well-rounded last whorl, wide impressed suture, and deep umbilicus. The genitalia have one circle of coiled epiphallus caecum, a short penial caecum, thick connective tissue encircling the proximal end of dart apparatus, a long epiphallus and flagellum, large and long dart apparatus located near the proximal end of the vagina above the penis and a relative short gametolytic duct and sac. The radula morphology is very similar to *M. aurantia* new species.

*Macrochlamys lemma* new species differs from *M. caverna* new species by its narrow umbilicus, slightly short gametolytic organ, long epiphallus and flagellum, and the dart apparatus is located above the penis connection. In comparison, *M. caverna* new species has a wide umbilicus, long gametolytic organ, short epiphallus and flagellum, and the dart apparatus is located opposite the penis.

The shell profile of this new species is rather variable and vary from shells with a nearly flat spire with an apex that is just a little convex to shells with a low-conical spire. The reproductive tracts of both shell forms have been examined and appear to be identical. Both have genitalia structure of long epiphallus and flagellum, short gametolytic duct and sac, thick connective tissue encircling the proximal end of the dart apparatus and a large dart apparatus locating above the penis, which are regarded as distinguishing characters of this species.

#### *Macrochlamys tanymentula* Pholyotha & Panha, new species

(Figs. 2E, 7C, D, 9A, B, 10D–F)

**Material examined.** Holotype (Fig. 7C; shell height 5.4 mm, shell width 10.9 mm, aperture height 4.2 mm, aperture width 5.3 mm, 5½ whorls) (CUMZ 7117), limestone outcrops at Khao Lok, Tha Kha-nun Village, Thong Pha Phum District, Kanchanaburi Province, Thailand, 14° 44'13.7"N, 98° 38'30.7"E. Paratypes: one shell (Fig. 7D; shell height 5.5 mm, shell width 11.1 mm, aperture height 4.0 mm, aperture width 5.2 mm, 5¾ whorls) (CUMZ 7118), nine specimens (CUMZ 7119), same data as holotype.

**Etymology.** The specific name “*tanymentula*” is made up of the Greek word “*tany*” meaning “long or slender” and the Latin “*mentula*” meaning “male organ including epiphallus” to refer to the very long and slender epiphallus of the male organ.

**Description.** Shell medium-sized (Fig. 7C, D; shell height up to 5.5 mm; shell width up to 11.1 mm), dextral, globosely depressed, rather thin, shiny, translucent and light brown in colour. Shell surface smooth with thin growth lines. Embryonic shell smooth, with about 2½ whorls. Whorls 5–6, regularly increasing, with weakly impressed suture. Spire low conical to a little convex. Apex slightly raised with spire angle of about 151–154°. Last whorl large with rounded periphery. Aperture slightly large, ovately lunate in shape, obliquely open with simple lip. Columellar margin



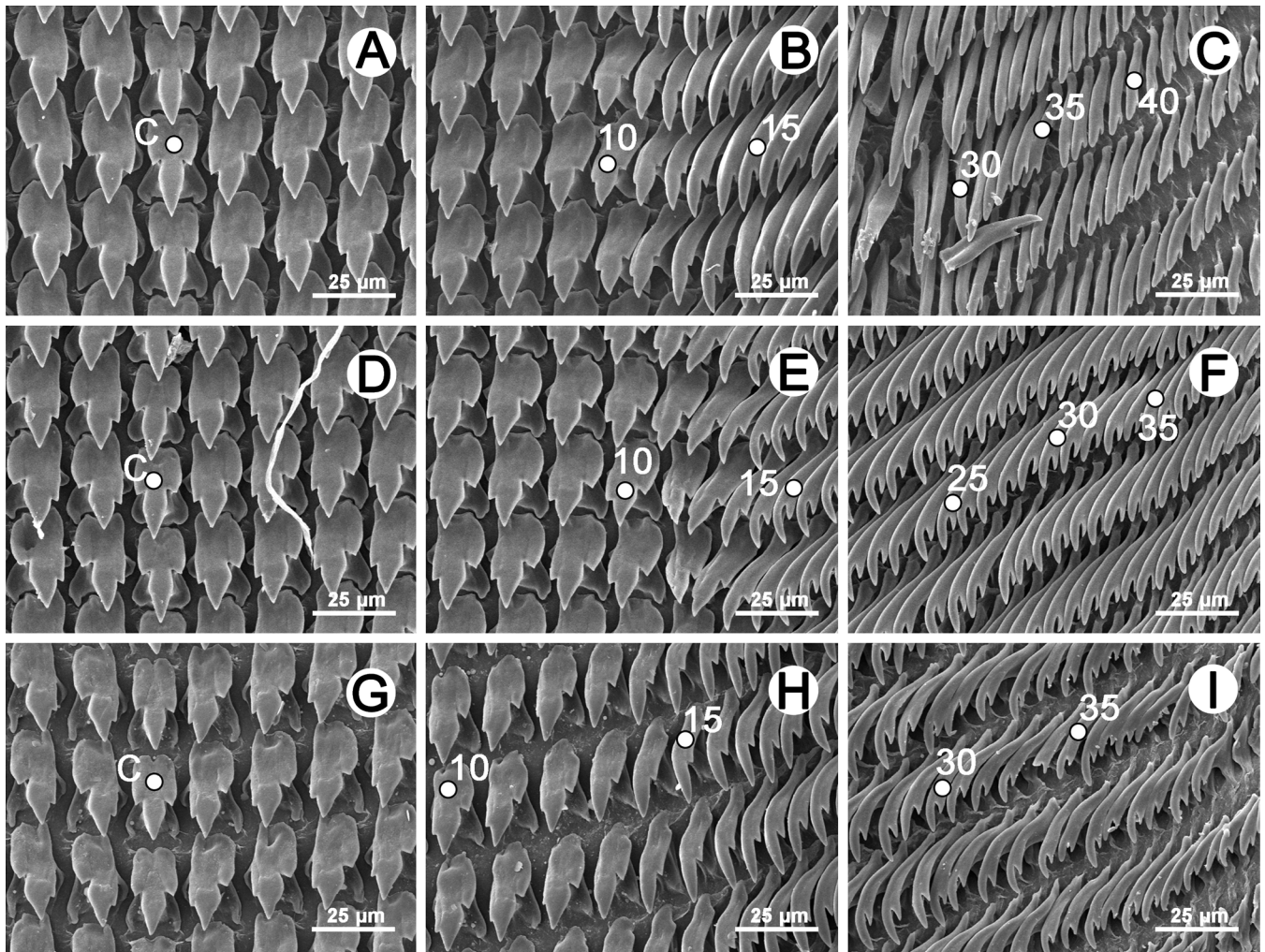


Fig. 6. SEM images of the radula of *Macrochlamys aurantia* new species (A–C) (paratype; CUMZ 7103), *M. coleus* new species (D–F) (paratype; CUMZ 7106), and *M. caverna* new species (G–I) (paratype; CUMZ 7109). Central tooth (indicated by ‘C’) with lateral teeth (A, D, G); lateral teeth with tricuspid marginal teeth transition (B, E, H); bicuspid marginal teeth (C, F, I).

gradually reflected near umbilicus. Umbilicus narrowly open and very small.

**Genital organs.** Atrium (at) very short. Penis (p) short, enlarged cylindrical in shape, and about two times greater than epiphallus diameter. Epiphallus (e) small, a slender tube about five times longer than penis. Epiphallic caecum (ec) coiled about one circle and located at middle of epiphallus. Penial retractor muscle (prm) thin. Flagellum (fl) very long, slender, and about half of epiphallic length. Vas deference (vd) a thin tube connected between free oviduct and distal end of epiphallus (Fig. 9A).

Internal wall of penis with small wrinkled longitudinal penial pilasters (pp). Penial verge (pv) slightly small, cylindrical-shaped and situated at distal end of penis (Fig. 9B).

Vagina (v) very short. Dart apparatus (da) large and cylindrical in shape, situated at proximal end of vagina. Gametolytic sac (gs) long and bulbous. Gametolytic duct (gd) long and cylindrical in shape. Free oviduct (fo) a small tube, approximately same length of penis, with thick brownish tissue near proximal end. Oviduct (ov) large lobules, with prostate gland (pg) running alongside (Fig. 9A).

**Radula.** Each row consists of about 99 teeth with formula (50-(14-12)-1-(12-13)-48). Central tooth symmetrical tricuspid with long and slender mesocone. Lateral teeth asymmetrical tricuspid with deeply indented endocone and ectocone. Bicuspid marginal teeth start from tooth number 12–14 (Fig. 10D–F).

**External features.** Animal with blackish grey reticulated skin, becoming pale yellow near foot sole and darker grey at eye stalks. Caudal foss (cf) large. Caudal horn (ch) raised with blackish grey colouration. Mantle edge well developed and blackish grey (Fig. 2E). Shell and dorsal lobes morphology similar to *M. aurantia* new species. Snails secrete yellowish-green slime when disturbed.

**Distribution and habitat.** *Macrochlamys tanymentula* new species has a narrow distribution and is currently known only from the type locality with a low population density. Snails were found among leaf litter on the ground or crawling on limestone walls.

**Remarks.** *Macrochlamys tanymentula* new species can be distinguished by its globosely depressed shell, with wide shallow suture and a very narrow umbilicus. The genitalia



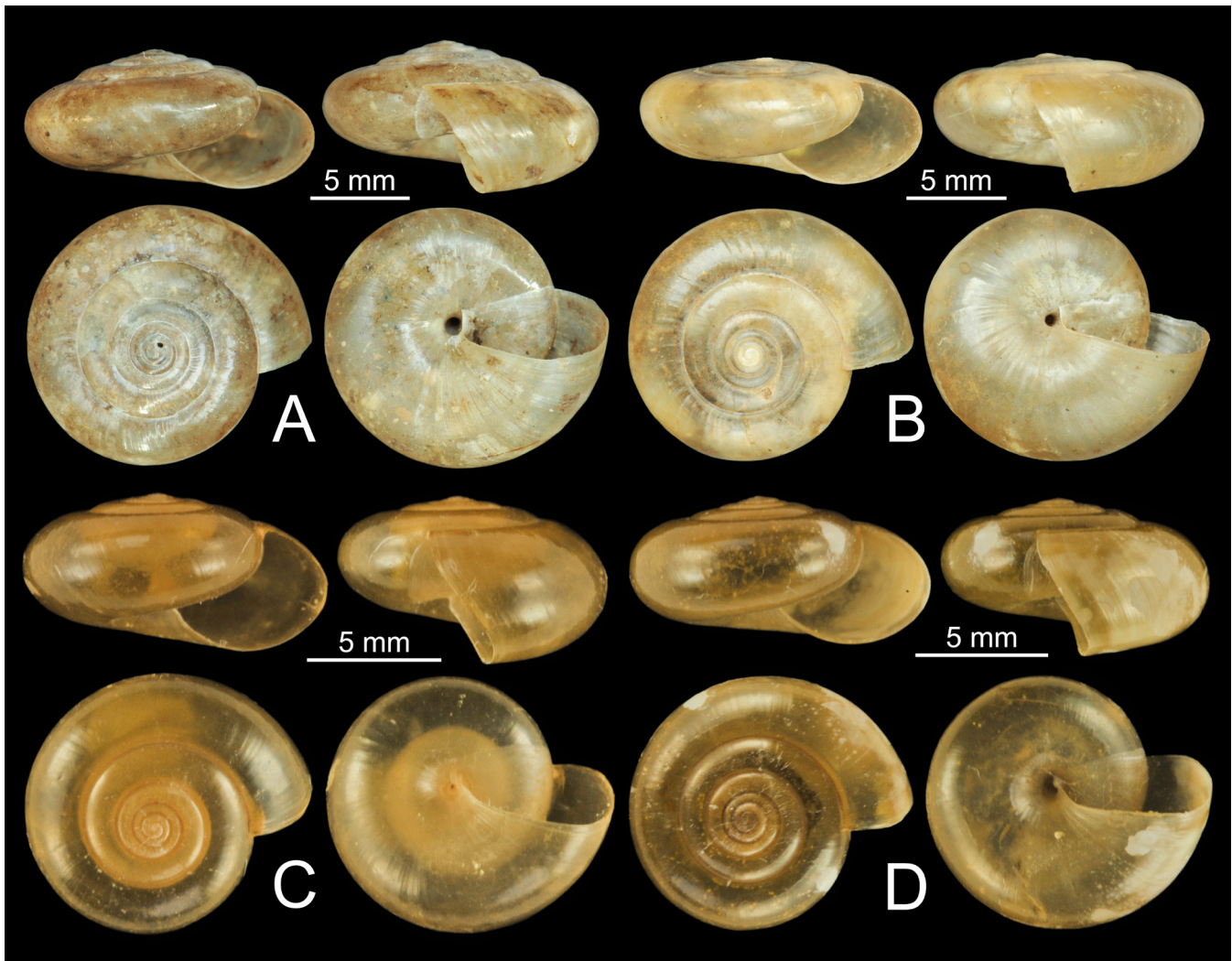


Fig. 7. Shells of *Macrochlamys lemma* new species (A, B), and *M. tanymentula* new species (C, D). A, *Macrochlamys lemma* holotype (CUMZ 7114); B, paratype (CUMZ 7115); C, *M. tanymentula* holotype (CUMZ 7117); D, paratype (CUMZ 7118).

have a very long and slender epiphallus and flagellum, coiled epiphallic caecum of about one circle, very short vagina, and a large dart apparatus located at the vagina base opposite the penis. Its radula morphology is very similar to *M. aurantia* new species.

This new species can be clearly distinguished from the other four new species proposed herein by its smaller shell with weakly impressed suture, narrow umbilicus, and very long epiphallus and flagellum, short vagina, and no penial caecum. The other four new species have relatively larger shells (Table 1), shorter epiphallus and flagellum, and with a short penial caecum. Furthermore, *M. aurantia* new species and *M. coleus* new species have a channel-shaped suture and orange to pale orange body colour, while *M. caverna* new species and *M. lemma* new species have oblique trapezoid penial pilasters inside the penis.

*Macrochlamys tanymentula* new species differs from *M. petasus* (Benson, 1859) and *M. aspides* (Benson, 1863) from Myanmar by its rounded last whorl and simple apertural lip. In comparison, *M. petasus* has a rounded to slightly subangulated last whorl, and the inside edge of the peristome is slightly expanded, while *M. aspides* has a

strongly thickened basal margin at the edge of the peristome (Blanford & Godwin-Austen, 1908). Compared with *M. notha* Blanford, 1905 from Myanmar and *M. brunnea* from Thailand, *M. tanymentula* new species has a smooth shell surface, relatively large and thin shell, with a slightly wider umbilicus. *Macrochlamys notha* has a dull shell with radial sculpture while *M. brunnea* has a relatively smaller shell and narrower umbilicus. *Macrochlamys stephoides* Stoliczka, 1873 from Malaysia has a higher spire compared to the depressed spire of *M. tanymentula* new species. In addition, Stoliczka (1873) mentioned that *M. stephoides* has similar genitalia to *M. indica* Benson sensu Godwin-Austen, 1883. In contrast, this new species has a very long epiphallus and flagellum (see Blanford & Godwin-Austen, 1908: 95).

***Macrochlamys brunnea* Möllendorff, 1902**  
(Fig. 8A)

*Macrochlamys brunnea* Möllendorff, 1902b: 155 (type locality: Bangkok, Muok Lek, Hinlap) – Hemmen & Hemmen, 2001: 44.

**Material examined.** Holotype (SMF 227090/1), Bangkok, Siam [Bangkok, Thailand]. Paratypes: one shell (SMF 227091/1), Bangkok, Thailand; four shells (SMF 227171/4),



Table 1. Comparison of shell and genital system of *Macrochlamys* species in Thailand.

Characters	<i>M. aurantia</i> new species	<i>M. coleus</i> new species	<i>M. caverna</i> new species	<i>M. lemma</i> new species	<i>M. tanymentula</i> new species	<i>M. brunnea</i>	<i>M. kelantanensis</i>
Shell width (mm) ranges, means $\pm$ SD and no. of specimens	11.7–14.0 12.8 $\pm$ 0.98 (n=6)	10.2–13.0 11.6 $\pm$ 0.99 (n=6)	13.2–17.2 14.3 $\pm$ 1.09 (n=11)	13.1–17.0 14.7 $\pm$ 1.54 (n=6)	9.6–11.1 10.6 $\pm$ 0.58 (n=5)	9.0*	16.7–24.0 20.0 $\pm$ 2.56 (n=9)
Shell height (mm) ranges, means $\pm$ SD and no. of specimens	6.5–8.2 7.5 $\pm$ 0.66 (n=6)	5.7–6.6 6.0 $\pm$ 0.35 (n=6)	7.3–8.6 7.6 $\pm$ 0.51 (n=11)	6.5–7.6 7.1 $\pm$ 0.40 (n=6)	4.9–5.5 5.2 $\pm$ 0.27 (n=5)	5.0*	9.0–13.0 11.4 $\pm$ 1.21 (n=9)
Shape of suture	Deep channel	Shallow channel	Impressed	Impressed	Impressed	Impressed	Impressed
Umbilicus	Narrowly open	Narrowly open	Widely open	Narrowly open	Narrowly open	Narrowly open	Narrowly open
Penial caecum	Present	Present	Present	Present	Absent	–	Absent
Inner wall of penis sculpture (proximal / distal)	Both with small wrinkles	Small wrinkled / small longitudinal and wrinkled folds	Trapezoid / lateral folds	Trapezoid / lateral folds	Both with weak wrinkles	–	Both with weak wrinkles
Epiphallus	Short	Short	Short	Rather long	Very long	–	Slightly long
Epiphallallic caecum	One circle	One circle	One circle	One circle	One circle	–	Two circles
Tissue casing	Absent	Present	Absent	Present	Absent	–	Absent
Vagina length	Long	Slightly long	Long	Slightly long	Short	–	Short
Position of thicken tissue on free oviduct	Base	Base	One-fourth from base	Near middle	Base	–	Base
Location of dart apparatus	Proximal end of vagina	Proximal end of vagina	Proximal end of vagina	Near proximal end of vagina	Proximal end of vagina	–	Proximal end of vagina

\*Shell measurement taken from the original description of Möllendorff (1902b).

Muok Lek, Siam [Muak Lek District, Saraburi Province, Thailand].

**Remarks.** *Macrochlamys brunnea* differs from its congeners in Thailand by its small size and globose shell (Table 1). Other distinguishing characters of this species are the depressed globose, shiny dark brown shell with a smooth surface and rounded periphery. The shell has a low conical spire, which is rather convex, with a slightly raised apex, and shallow suture. Its aperture is ovate-lunate in shape, opens obliquely and has a simple peristome. The columellar margin is gradually reflected near the narrowly open and very small umbilicus (Fig. 8A).

The generic placement of this species is tentative and requires verification since anatomical data is thus far unavailable. It is herein provisionally retained in the *Macrochlamys* as

originally proposed although this species can be assigned to either *Sarika* or *Macrochlamys* if based solely on shell morphology. Unfortunately, attempts to obtain topotypic specimens from Bangkok and accessible limestone outcrops in the Saraburi Province were unsuccessful and no specimens identifiable as *M. brunnea* could be found. This could be due to habitat loss and population decline as many limestone outcrops in this region are being quarried. Its current status is unclear.

***Macrochlamys kelantanensis* Möllendorff, 1902**  
(Figs. 2F, 8B–D, 9C, D, 10G–I)

*Macrochlamys hardwickei kelantanensis* Möllendorff, 1902a: 137 (type locality: Kelantan, Ostküste der Halbinsel Malacca [Kelantan, east coast of Peninsula Malaysia]) – Maassen, 2001: 110.

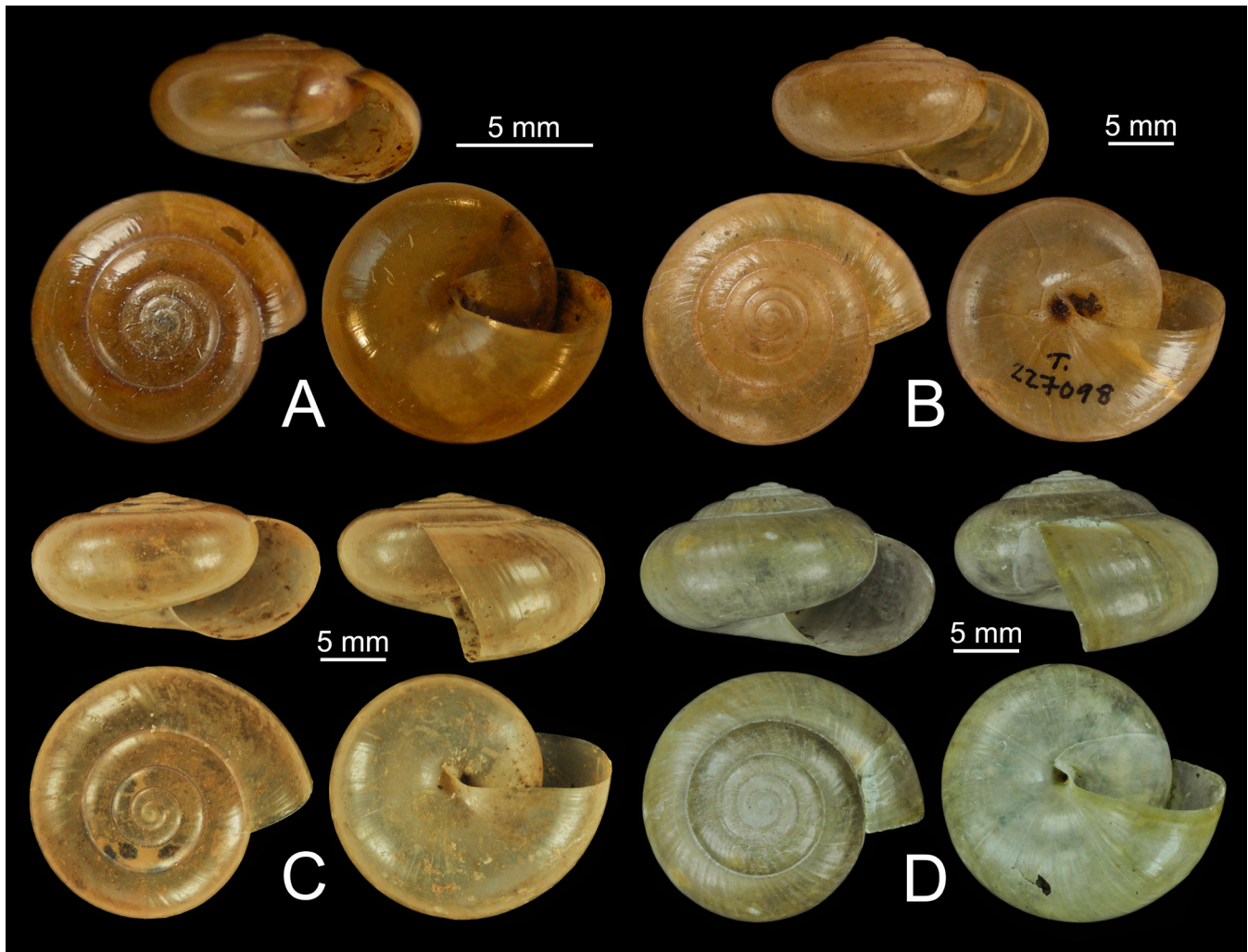


Fig. 8. Shells of *Macrochlamys brunnea* Möllendorff, 1902 (A), and *M. kelantanensis* Möllendorff, 1902 (B–D). A, *Macrochlamys brunnea* holotype (SMF 227090/1); B, *M. kelantanensis* holotype (SMF 227098); C, shell from Kedah, Malaysia (CUMZ 7130); D, shell from Chiang Rai, Thailand (CUMZ 7120).

**Material examined.** Holotype (SMF 227098), one paratype shell (SMF 227099), Kelantan, east coast of Peninsular Malaysia. Non type material: THAILAND. five shells (CUMZ 7120), 16 specimens (CUMZ 7121), Mae Chan District, Chiang Rai Province, 20° 08'38.7"N 99° 51'21.4"E; 32 specimens (CUMZ 7122), Nong Han, San Sai District, Chiang Mai Province, 18° 53'23.7"N 98° 59'54.7"E; two specimens (CUMZ 7123) Mae Sot District, Tak Province, 16° 43'26.9"N 98° 35'06.0"E; one shell (CUMZ 7124), 10 specimens (CUMZ 7125), Lam Kaen, Phang-Nga Province, 8° 35'48.5"N 98° 15'22.4"E; six specimens (CUMZ 7126), Koh Chang District, Trat Province, 12° 04'36.8"N 102° 22'02.6"E. MALAYSIA: 15 specimens (CUMZ 7127), Bukit Bunga, Kampung Jakar, Ayer Lanas, Kelantan, 5° 49'8.8"N 101° 54'40.4"E; one specimen (CUMZ 7128), Gunung Reng Batu Melintang, Jeli, Kelantan, 5° 42'54.1"N 101° 44'43.3"E; one shell (CUMZ 7132), 46 specimens (CUMZ 7129), Jalan Bunga, Merbok, Kedah, 5° 43'27.7"N 100° 23'22.3"E; one shell (Fig. 8C) (CUMZ 7130), 13 specimens (CUMZ 7131), Kampung Seberang Pekan, Baling, Kedah, 5° 41'13.4"N 100° 54'54.2"E.

**Description.** Shell medium to large (Fig. 8B–D; shell height up to 13.0 mm; shell width up to 24.0 mm), dextral, spire depressed to low-conical, thin, translucent, and pale brown in colour. Shell surface nearly smooth with very thin growth lines. Embryonic shell surface smooth, with about 2½ whorls. Whorls 5–6, regularly increasing. Suture impressed. Spire depressed conic to low conical. Apex raised with a spire angle of about 134–142°. Last whorl large with well-rounded periphery. Aperture crescent shape, open obliquely with simple lip. Columellar margin slightly reflected near umbilicus. Umbilicus narrowly open and deep.

**Genital organs.** Atrium (at) very short. Penis (p) short and cylindrical-shaped. Epiphallus (e) short, slightly smaller than penis diameter, about four times longer than penis. Epiphallic caecum (ec) somewhat enlarged, thick, almost same diameter as penis and coiled about two circles. Penial retractor muscle thin and long. Flagellum (fl) long, cylindrical-shaped, about same length as epiphallus. Vas deference (vd) a long tube between distal end of epiphallus and free oviduct (Fig. 9C).

Inner wall of penis supported with very small and irregular penial pilasters (pp). Penial verge (pv) small, cylindrical and located at distal end of penis (Fig. 9D).



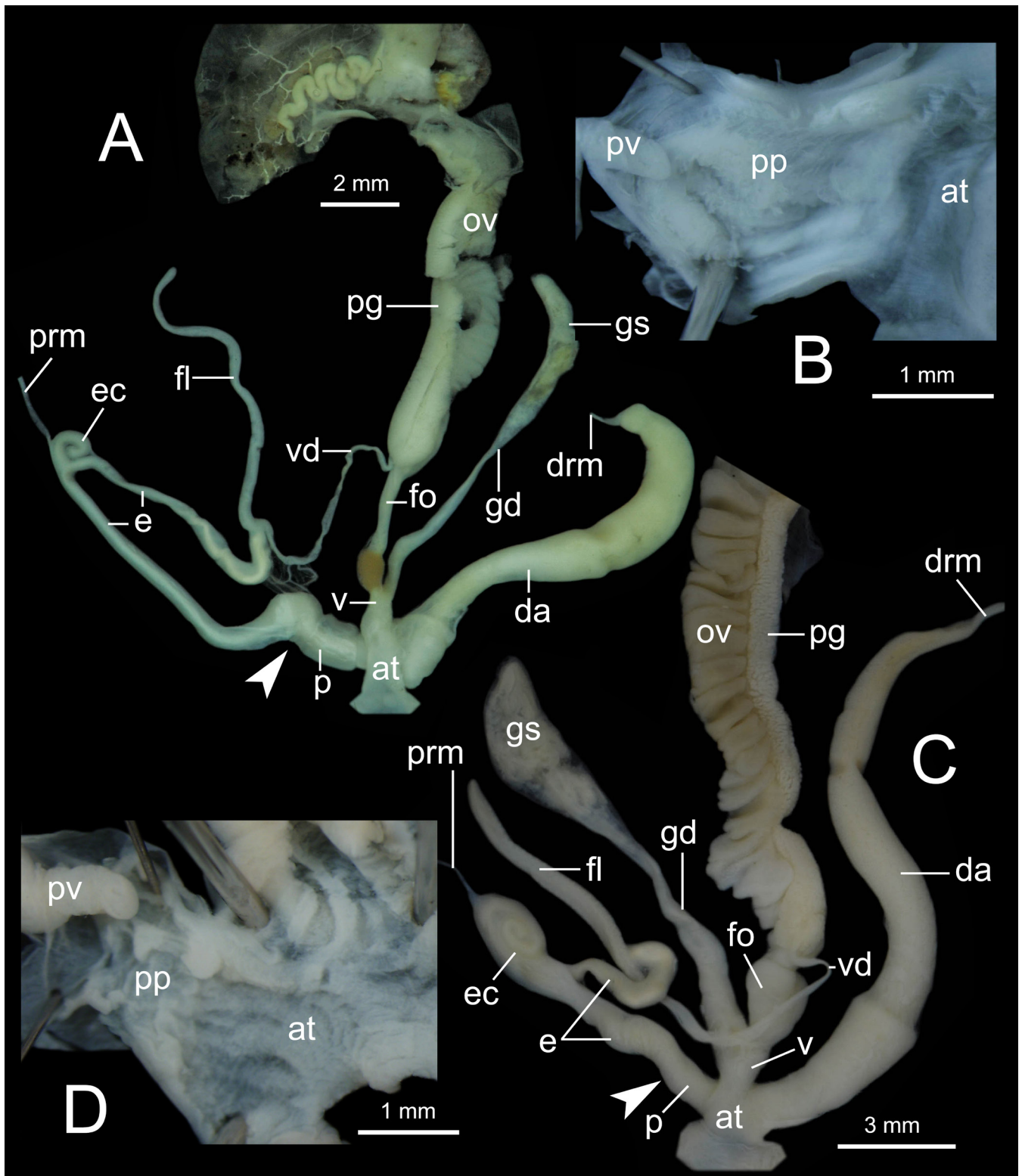


Fig. 9. Genitalia of *Macrochlamys tanymmentula* new species (A, B), and *M. kelantanensis* (C, D). A, B, *Macrochlamys tanymmentula* paratype (CUMZ 7119): A, whole reproductive system; B, internal structure of penis with penial verge. C, D, *Macrochlamys kelantanensis* (CUMZ 7125): C, whole reproductive system; D, internal structure of penis with penial verge. Abbreviations: at, atrium; da, dart apparatus; drm, dart retractor muscle; e, epiphallus; ec, epiphallic caecum; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hf, head filament; ov, oviduct; p, penis; pc, penial caecum; pg, prostate gland; pp, penial pilaster; prm, penial retractor muscle; pv, penial verge; ss, sperm sac; tf, tail filament; v, vagina and vd, vas deferens. Arrow indicates position of the penial verge.

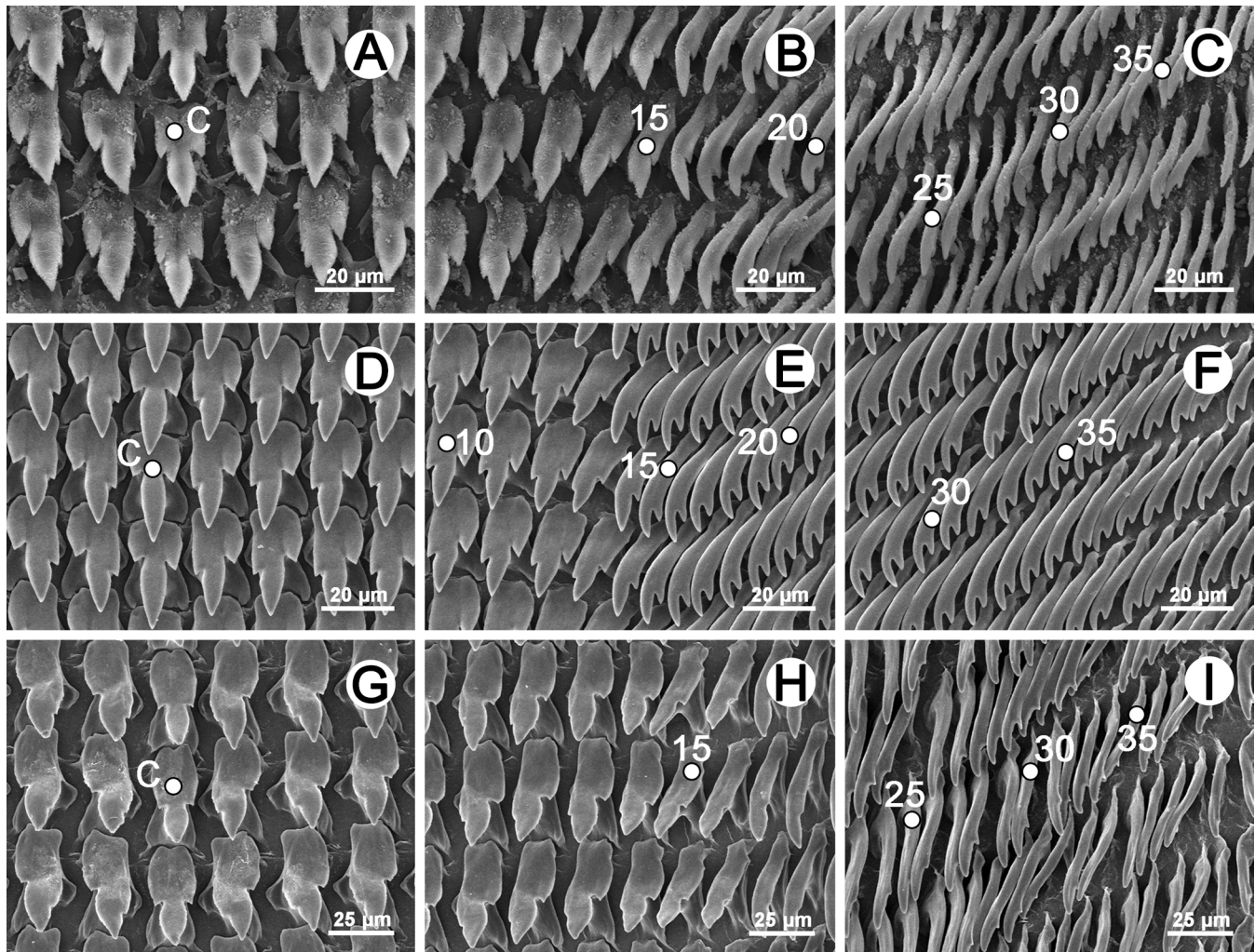


Fig. 10. SEM images of the radula of *Macrochlamys lemma* new species (A–C) (paratype; CUMZ 7116), *M. tanymentula* new species (D–F) (paratype; CUMZ 7119), and *M. kelantanensis* Möllendorff, 1902 (G–I) (CUMZ 7125). Central tooth (indicated by ‘C’) with lateral teeth (A, D, G); lateral teeth with tricuspid marginal teeth transition (B, E, H); bicuspid marginal teeth (C, F, I).

Vagina (v) short about same length as penis and cylindrical-shaped. Dart apparatus (da) very large, long and cylindrical, located at proximal end of vagina. Gametolytic sac (gs) bulbous; gametolytic duct (gd) long, cylindrical and slightly swollen near vagina. Free oviduct (fo) very short, triangular shape and entirely encircled with thick tissues. Oviduct (ov) large lobules; prostate gland (pg) runs alongside oviduct (Fig. 9C).

**Radula.** Radula morphology very similar to *M. aurantia* new species. Each row contains about 111 teeth with formula (55-(17-16)-1-(15-16)-55). Central tooth symmetrical tricuspid; mesocone large with dull cusp. Lateral teeth asymmetrical tricuspid with very small endocone. Marginal teeth with elongate bicuspid start around tooth number 15 to 17 (Fig. 10G–I).

**External features.** Animal with reticulated skin. Foot and body pale yellowish-grey, slightly darker on dorsal side. Head and tentacles darker grey. Caudal foss (cf) long and narrow, caudal horn (ch) raised, pale brownish colour. Mantle edge (shell lobes and dorsal lobes) well developed, dull brownish in colour (Fig. 2F). The snails secrete yellowish slime when disturbed.

**Remarks.** This species was originally nominated as a subspecies of *M. hardwickei* Godwin-Austen, 1883 from Lower Bengal, Sylhet and Western Assam (Möllendorff, 1902a). It is here raised to full species level. It differs from *M. hardwickei* sensu stricto by its larger shell, the cylindrically shaped penis, and enlarged and short cylindrical appearance of the free oviduct versus a smaller shell, enlarged and triangular-shaped penis, and extremely long free oviduct of *M. hardwickei* (see Godwin-Austen, 1883: 105–107, pl. 23, figs. 1–4; pl. 28, fig. 1). *Macrochlamys malaccana* from Peninsular Malaysia has a relatively smaller shell that bears a distinct dark brown spiral line at the suture (see Foon et al., 2017). Unfortunately, genitalia data of *M. malaccana* is not available for comparison.

*Macrochlamys kelantanensis* is usually ground dwelling and is often associated with anthropogenic habitats, such as plantations, fruit orchards, gardens or parks. This could explain their wide dispersal and it is believed to have been accidentally introduced through horticultural and agricultural trade activities.



Table 2. Taxon attributed to the *Macrochlamys* sensu Godwin-Austen, 1883 from Indochina and Myanmar classified by their maximum shell width and maximum whorl numbers. Data are taken from the original descriptions and additional references: Fischer & Dautzenberg (1904), Blanford & Godwin-Austen (1908) and Schileyko (2011). Taxa in bold are the Thai species treated in this study.

	Maximum number of whorls			
	whorl < 5	5 ≤ whorl < 6	6 ≤ whorl < 7	whorl ≥ 7
Small size (shell width ≤ 10 mm)	<i>M. kumahensis</i> <i>M. patens</i> <i>M. pauxillula</i> <i>M. perpaula</i>	<i>M. bartoni</i> <i>M. brunnea</i> <i>M. callojuncta</i> <i>M. causia</i> <i>M. curvilabris</i> <i>M. hatchongi</i> <i>M. noxia</i> <i>M. petasus</i> <i>M. pungi</i> <i>M. rejectella</i> <i>M. salwinensis</i> <i>M. spreata</i> <i>M. subpetasus</i>	<i>M. euspira</i> <i>M. jousoufi</i>	<i>M. ramburianus</i>
Medium size (10 < shell width < 20)	—	<b><i>M. aurantia</i> new species</b> <i>M. chaos</i> <b><i>M. coleus</i> new species</b> <i>M. declivis</i> <i>M. hypoleuca</i> <i>M. malaccana</i> <b><i>M. tanymentula</i> new species</b> <i>M. zero</i>	<i>M. aspides</i> <i>M. benoiti</i> <b><i>M. caverna</i> new species</b> <i>M. excepta</i> <b><i>M. lemma</i> new species</b> <i>M. nebulosa</i> <i>M. stenogyra</i> <i>M. stephoides</i>	<i>M. conseptia</i> <i>M. notha</i>
Large size (shell width ≥ 20 mm)	—	<i>M. douvillei</i> <i>M. glyptorhapha</i> <i>M. tenuigranosa</i>	<b><i>M. kelantanensis</i></b>	<i>M. despecta</i>

## DISCUSSION

In Thailand, the genus *Macrochlamys* sensu stricto currently comprises seven species, *M. kelantanensis* and *M. brunnea*, plus five new species proposed herein. The species in this genus bear a glossy, smooth and heliciform shell, which also occur in the *Parvatella*, *Rasama*, *Syama*, *Taphrospira*, and *Sarika* (Blanford & Godwin-Austen, 1908; Solem, 1966; Schileyko, 2003). This superficial resemblance may be attributed to convergence, presumably caused by a similar environmental enforcement (Barker, 2001; Hirano et al., 2014; Chiba & Cowie, 2016).

This work emphasises the genitalia as useful taxonomic characters for both generic and specific level delimitations. Unique genitalia characters of the genus *Macrochlamys* include the presence of a penial verge, a spirally coiled epiphalllic caecum, and the presence of a flagellum and dart apparatus (Blanford & Godwin-Austen, 1908; Schileyko, 2003). *Parvatella* has very similar genitalia, but has a shell with rapidly increasing last whorl, and is regarded to be a subgenus of *Macrochlamys* by Schileyko (2003). Compared to the four other aforementioned genera (see Introduction), *Rasama* has neither an epiphalllic caecum nor dart apparatus, *Syama* has a coiled epiphalllic caecum without a dart apparatus, *Taphrospira* has a straight epiphalllic caecum without a dart apparatus, and *Sarika* has a straight epiphalllic caecum with the dart apparatus present (Blanford & Godwin-

Austen, 1908; Schileyko, 2002, 2003). The diagnostic traits of the gain or loss of the epiphalllic caecum and dart apparatus, may reflect the phylogenetic relationships in many taxa (Hausdorf, 1998; Hyman et al., 2017). However, several studies have also pointed out that some genitalia characters show homoplasy, while some characters can be only used for higher level classification (Koene & Schulenburg, 2005; Hirano et al., 2014). Therefore, future studies combining comprehensive molecular phylogenetic analyses will be necessary to clarify the status of *Macrochlamys* with the other closely related genera.

In Indochina, including part of Myanmar, some 38 nominal species have been placed in the genus *Macrochlamys* based mainly on shell morphology (Morgan, 1885; Ancey, 1898; Fischer & Dautzenberg, 1904; Blanford & Godwin-Austen, 1908; Laidlaw, 1933; Panha, 1996; Hemmen & Hemmen, 2001; Maassen, 2001; Schileyko, 2011). The small and large shell-sized species (20 and five species, respectively) are obviously different from the species treated in this study (Tables 1, 2) and require no further elaboration. Remarks on the differences of the remaining 13 species bearing a medium-sized shell (Table 2) from the new species herein described are mentioned in the species treatment in this paper (see Remarks under the respective species). However, the reliability of the new species described herein are based largely on comparisons with the conchological characteristics of type specimens as most type material do not have

anatomical data for more reliable comparisons. All type specimens were examined except *M. benoiti*, *M. aspides*, and *M. strephoides*.

Thailand has extensive ranges of many isolated limestone hills, mountainous areas and various forests, and is recognised as a biodiversity hotspot harbouring a high diversity of land snails (Myers et al., 2000; Naggs et al., 2006). The five new species herein described were recorded exclusively on limestone karsts and appear to be restricted in distribution as well as being strictly allopatric. Because of the limited dispersal capabilities of land snails, the degree of isolation by the non-karstic areas will likely have a strong influence on their speciation (Barker, 2001). These limestone restricted snails can adapt to highly alkaline conditions, and the limestone provides numerous microhabitats allowing the snails to avoid predators and hide during aestivation periods. Limestone areas also support various specialised plant and fungal species that have adapted to grow in these conditions, which could serve as snail food resources.

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