

Unveiling the Diversity of the Semislug Genus *Durgella* Blanford, 1863 (Eupulmonata: Helicarionidae) from Thailand and Myanmar, with Description of Two New Species

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Received 14 February 2023 / Accepted 21 February 2024 / Published 11 June 2024

Communicated by Benny K.K. Chan

Durgella is a terrestrial semislug genus in the family Helicarionidae and currently comprises nine species recorded from Thailand and Myanmar. Two species, *D. concinna* and *D. raphiellus*, have been described based only on shell information, while the taxonomy of the remaining seven species is comprehensively treated herein using comparative morphology. Revised species descriptions are given for *D. levicula*, *D. erratica*, *D. siamensis*, and *D. libas*; *D. birmanica* (previously placed in the *Megaustenia*) is moved to this genus; and two species, *D. pentata* Pholyotha & Panha, sp. nov. and *D. nulla* Pholyotha & Panha, sp. nov., are described as new to science. Based on our findings, the combination of shell characters including shape, size, aperture, and umbilicus; the number of mantle extensions; and the genitalia, especially the penis, epiphallus, and dart apparatus, can be used to distinguish these nine species. Among these nine recognised species, only *D. nulla* Pholyotha & Panha, sp. nov. has no dart apparatus.

Key words: Comparative morphology, Durgellinae, Indochina, Land snail, Systematics, Taxonomic revision

BACKGROUND

The semislug genus *Durgella* Blanford, 1863, also known as ‘dancing semislugs’, is the type genus of the Durgellinae Godwin-Austen, 1888, a subfamily of the enormously diverse limacoid family Helicarionidae Bourguignat, 1877. According to MolluscaBase (2022), the genus currently comprises 21 nominal species. Members of this genus are tree-dwellers that occupy various tree-associated microhabitats such as tree trunks and leaves in tropical forests (Blanford and Godwin-Austen 1908). They are distributed from the subtropical forests of eastern India to the tropical or dry forests of Indochina, plus a few records from the Greater Sunda

Islands (Blanford and Godwin-Austen 1908; Solem 1966; Schileyko 2002; Vermeulen and Liew 2022).

Historically, the genus name *Durgella* was introduced without a description (Blanford 1863), and so its diagnostic characters are subject to validation. As is the case for several other groups of semislugs, the shell morphology is conservative compared to the other taxonomically informative structures, especially the reproductive organs, mantle edge development, and radula (Blanford and Godwin-Austen 1908; Solem 1966; Pholyotha et al. 2021a b). Godwin-Austen (1881) identified these structures by demarcating the genus based on the revision of its type species, *D. levicula* (Benson, 1859). Therefore, the genus is characterised by

Citation: Pholyotha A, Sutcharit C, Lwin N, Panha S. 2024. Unveiling the diversity of the semislug genus *Durgella* Blanford, 1863 (Eupulmonata: Helicarionidae) from Thailand and Myanmar, with description of two new species. Zool Stud 63:14. doi:10.6620/ZS.2024.63-14.

a very thin to membranous and vitriniform shell, a well-developed mantle, and a pectiniform radula (Godwin-Austen 1881; Blanford and Godwin-Austen 1908; Solem 1966). Since then, six species from Thailand and Myanmar and 15 species from other regions have been described or re-located to the genus. However, the genital anatomy of only five species (*D. levicula*, *D. assamica* Godwin-Austen, 1881, *D. mairangensis* Godwin-Austen, 1898, *D. rogersi* Godwin-Austen, 1907, and *D. libas* Solem, 1966) has been examined (Godwin-Austen 1881; Blanford and Godwin-Austen 1908; Solem 1966). The remaining taxa were provisionally assigned to this genus based solely on their shell traits, which are less informative. Since data on the genital anatomy and radular morphology of *Durgella* are scarce, the genus has been largely neglected for over a century.

Thailand and Myanmar are located in the Indo-Burma biodiversity hotspot (Myers et al. 2000), and are home to various endemic limacoid semislug taxa., i.e., *Durgella*, *Cryptosemelus* Collinge, 1902, *Parmarion* Fischer, 1855, *Megaustenia* Cockerell, 1912, and *Muangnua* Solem, 1966 (Blanford and Godwin-Austen 1908; Solem 1966; Hemmen and Hemmen 2001; Pholyotha et al. 2021a). These semislugs are often encountered in various habitats, especially limestone forests throughout Thailand; numerous ethanol-preserved specimens have been deposited in the Chulalongkorn University Museum of Zoology (CUMZ). Additionally, our 2015–2016 land snail survey in Myanmar, initiated by Fauna & Flora International (FFI), yielded many fresh specimens of durgellinids, which were also deposited in this museum. The newly collected material has prompted the taxonomic revision of all *Durgella* species recognised in Thailand and Myanmar. This study also provides new information on the mantle morphology, reproductive anatomy, and radulae of these species, together with their distribution. In addition, during our examination of the material, two new *Durgella* species from Thailand were encountered, and are herein described as new to science.

MATERIALS AND METHODS

Durgella specimens from Thailand and Myanmar were sampled from several localities including limestone and non-limestone habitats throughout the known distribution range of the genus (Fig. 1). The specimens from Myanmar were collected during 2015 to 2016 under an MoU between the Forest Department, the Ministry of Natural Resources and Environmental Conservation and Forestry, Myanmar, and FFI. The semislugs were obtained by direct visual searching and

hand collecting in favourable microsites, such as under leaves, trunks or branches. Prior to preservation, images of living specimens were taken using a Nikon camera (DSLR D850) with a Nikon 105 Macro lens (AF-S VR Micro-Nikkor 105 mm f/2.8G IF-ED). Living specimens were euthanised following the standard two-step protocol (American Veterinary Medical Association 2020), and then fixed in 95% (v/v) ethanol for further work. Identification of *Durgella* species was based on the original literature and several related publications (Godwin-Austen 1881 1883 1898 1907 1910; Blanford and Godwin-Austen 1908; Solem 1966), and comparisons with available type specimens and the reference collection. For shell morphology, adult specimens were measured for size, and whorls were counted using a stereoscopic light microscope. Dissections were performed on three to ten ethanol-preserved specimens of each species to study their external morphology and genital anatomy. Photographs of representative shells and genitalia were taken using the Nikon DSLR D850 with 105 mm macro lens, while the inner anatomy of the genitalia was imaged using a stereo microscope with the Cell'D Imaging Software. Radulae were prepared as previously described (Pholyotha et al. 2021a) and then observed and imaged using scanning electron microscopy (SEM; JEOL, JSM-6610 LV). All voucher specimens of *Durgella* spp. examined in this study have been deposited in the Chulalongkorn University Museum of Zoology (CUMZ), Bangkok, Thailand.

Morphological and anatomical abbreviations

In this study, the term ‘proximal’ refers to the region closest to the genital opening, while ‘distal’ refers to the region furthest away from the genital opening. Abbreviations used in images: ant-ldl (anterior left dorsal lobe), at (atrium), cf (caudal foss), ch (caudal horn), da (dart apparatus), el (portion of epiphallus nearer to penis), e2 (portion of epiphallus nearer to retractor muscle), ec (epiphallic caecum), fo (free oviduct), gd (gametolytic duct), gs (gametolytic sac), lsl (left shell lobe), p (penis), post-ldl (posterior left dorsal lobe), prm (penial retractor muscle), rdl (right dorsal lobe), rsl (right shell lobe), v (vagina), vd (vas deferens).

Institutional abbreviations: CUMZ, Chulalongkorn University, Museum of Zoology (Bangkok, Thailand); NHMUK, when citing lots deposited in The Natural History Museum (NHM, London, United Kingdom); SMF, Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Germany); ZMB, Museum für Naturkunde (Berlin, Germany).

RESULTS

TAXONOMY

Superfamily Helicarionoidea Bourguignat, 1877
 Family Helicarionidae Bourguignat, 1877
 Subfamily Durgellinae Godwin-Austen, 1888

Genus *Durgella* Blanford, 1863

Nanina (*Durgella*) Blanford, 1863: 76.

Macrochlamys (*Durgella*) – Stoliczka 1871: 248.

Durgella – Godwin-Austen 1881: 291. Godwin-Austen 1883: 142.
 Godwin-Austen 1898: 60. Godwin-Austen 1907: 205. Blanford
 and Godwin-Austen 1908: 213. Thiele 1931: 1007. Zilch 1959:
 327. Solem 1966: 49. Vaught 1989: 98. Schileyko 2002: 1297.

Type species: *Helix levicula* Benson, 1859,
 subsequent designation by Stoliczka (1871: 250).

Description: Shell subglobose to globose,
 imperforate to perforate, small to medium sized, thin to
 fairly solid, polished and pale to dark yellowish. Whorls
 3–4½ rapidly increasing, smooth or with microscopic
 sculpture on protoconch and teleoconch. Aperture large
 and oblique.

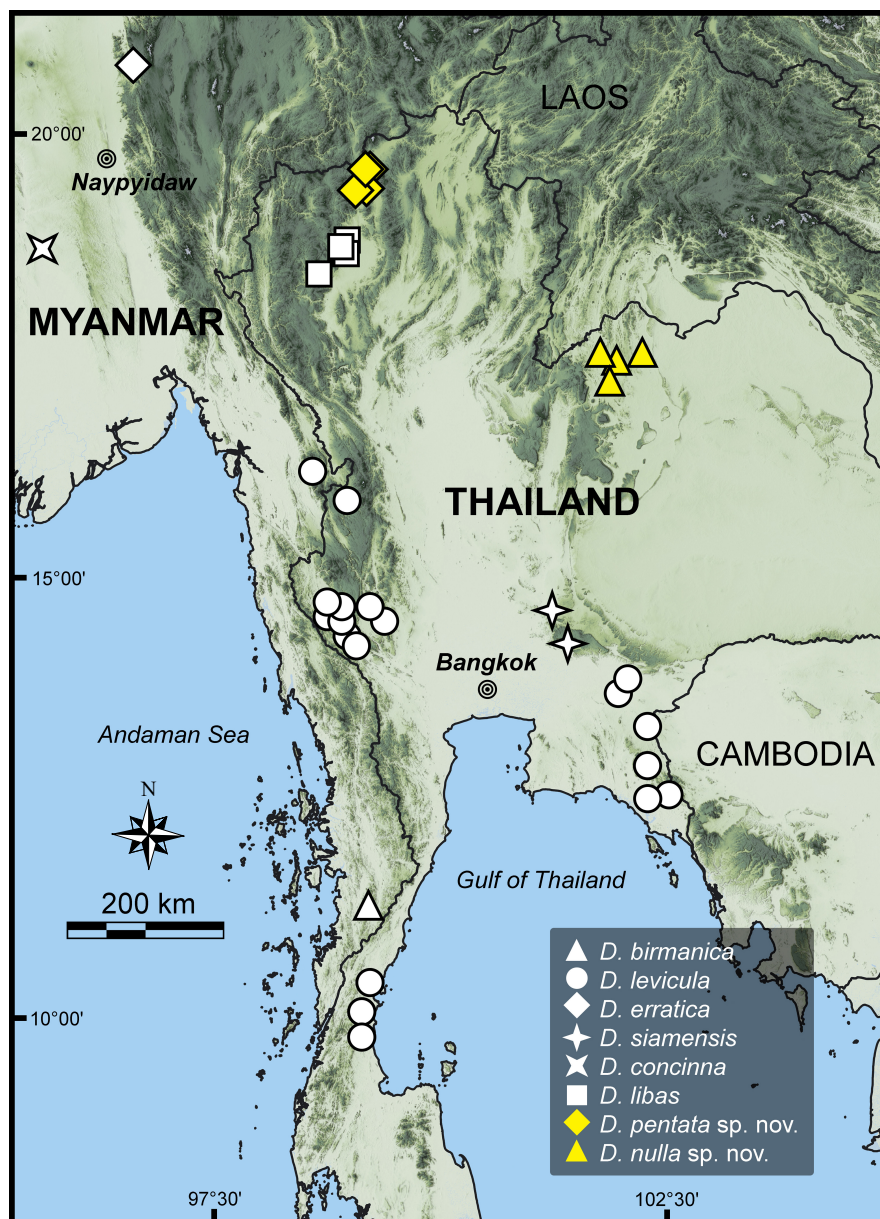


Fig. 1. Map of Thailand and Myanmar showing the geographic distribution of eight species of *Durgella* based on the specimens examined herein. Only *D. raphiellus* is not shown on the map, as its type locality of “Siam” [Thailand] is too imprecise.

Mantle extensions partially covering shell when fully extended; right shell lobe (rsl) broad and triangular; left shell lobe (lsl) triangular in shape, varying in width from narrow to broad, and reflected over the shell near the respiratory orifice (Figs. 2–4). Right dorsal lobe (rdl) broad, large, crescent shaped,

and reflecting to partially cover the shell. Left dorsal lobe (ldl) long, large, crescent shaped, and undivided (Fig. 2A, B) or divided (Fig. 2C, D) into anterior left dorsal lobe (ant-ldl) and posterior left dorsal lobe (post-ldl).

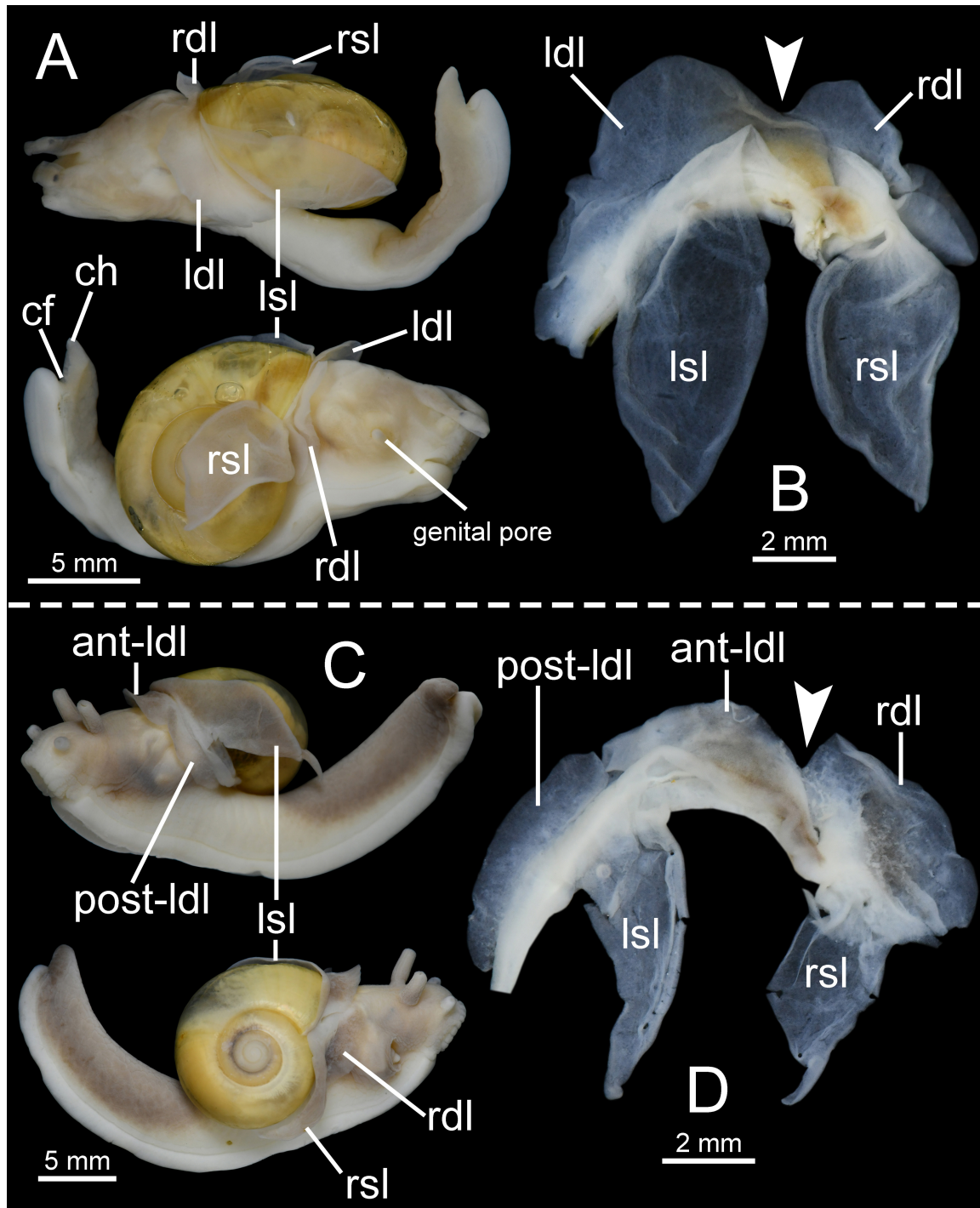


Fig. 2. Synoptic illustration of mantle extensions of the genus *Durgella*. A, B: four mantle extensions with left dorsal lobe undivided. C, D: five mantle extensions with left dorsal lobe divided into anterior and posterior left dorsal lobes. White arrow indicates pneumostome or breathing pore.

Genitalia with thin penial sheath, penial retractor muscle attached to epiphallallic caecum, very short vagina, and short to long gametolytic duct. Flagellum absent. Dart apparatus well-developed or absent.

Radular teeth arranged in a nearly straight line and gradually developing a curved edge. Central tooth generally reduced with small unicuspid, bicuspid or asymmetrical tricuspid. Lateral and marginal teeth undifferentiated, excessively numerous, elongated bicuspid with several tiny accessory ectoconal cusps on the outer edge (or pectiniform).

In life, anterior body varying in colour from pale yellowish-brown to blackish; posterior body generally yellowish-brown to reddish-brown, and with a black gradient that is darkest at the dorsal and lightest at the foot margin. Mantle extensions thin, transparent, and varying in colour from cream to yellowish, reddish-brown, or dark grey. Sole tripartite and lateral foot margin present. Caudal foss (cf) indented. Caudal horn (ch) long, large, and greatly overhung (Figs. 2A, C, 3, 4).

Habitat and behavior observations: After rainfall, these semislugs actively crawl on the leaves of plants, trunks or branches of bamboo, banana leaves, shrubs, or small trees. They also perform a tail flicking action when touched or disturbed; then, they often drop to the ground or are suspended in air by a long strand of sticky mucus from the posterior body to leaves or branches. This is probably an anti-predator behaviour that has also been observed in *D. mairangensis* Godwin-Austen, 1898 and *D. salius* (Benson, 1859), a species endemic to India (Godwin-Austen 1898; Blanford and Godwin-Austen 1908). In the resting stage or during aestivation, the semislugs normally attach themselves to the leaves or stems of plants by entirely withdrawing their body into the protective shell (Fig. 3C).

Many copulating pairs of *D. libas*, *D. pentata* sp. nov., and *D. nulla* sp. nov. were observed (Fig. 4D) in the humid and moist conditions of the rainy season, and they clearly exhibited reciprocal copulation. No direct observations of egg-laying were made in our survey, but many individuals produced clutches of 20–40 eggs within our mesh collecting bags; the eggs were translucent, whitish, soft, and oval to spherical shaped (Fig. 4A–C).

Remarks: The name *Durgella* was first proposed by W.T. Blanford (1863: 76) as a subgenus of *Nanina* Gray, 1834 without description or designation of a type species. Instead he only mentioned that it contained three nominal species, namely *Helix levicula* Benson, 1859, *Helix mucosa* Blanford & Blanford, 1861, and *Helix seposita* Benson, 1859. Later, F. Stoliczka (1871) re-described *Helix honesta* Gould, 1846 from Myanmar, and he also recognised *Durgella* as a subgenus of *Macrochlamys* Gray, 1847, and consecutively

designated *Helix levicula* as the type. However, the taxonomic treatment in Stoliczka (1871) was not accepted and has never been used. Later, Godwin-Austen (1881: 291) re-described *D. levicula* and discovered several unique characters from both *Nanina* and *Macrochlamys*; therefore, he raised *Durgella* as a distinct genus. This interpretation of the genus has been widely accepted (e.g., Blanford and Godwin-Austen 1908; Thiele 1931; Zilch 1959; Solem 1966; Schileyko 2002; Preece et al. 2022).

Concerning the type species designation, G. Nevill (1878: 24) erroneously designated *Helix honesta* Gould, 1846 as the type species. This designation is invalid because it does not involve an originally included nominal species (Blanford 1863; ICZN 1999: Art. 69).

***Durgella birmanica* (Pfeiffer, 1847)**

(Figs. 1, 3A, 5A–C, 6A, 9A, B, 11A, B)

Vitrina birmanica Pfeiffer, 1847: 65. Type locality: Mergui imperii Birmanorum [Myeik District, Tanintharyi Region, Myanmar]. Pfeiffer 1848: 498. Reeve 1862: *Vitrina* pl. 8, fig. 59. Hanley and Theobald 1876: 61, pl. 152, fig. 7.

Helicarion birmanicus [sic] – Tryon 1885: 177, pl. 41, fig. 42.

Cryptosoma ? birmanicum – Blanford and Godwin-Austen 1908: 212.

Megaustenia birmanicum – Solem 1966: 78.

Material examined: The type specimen could not be located. **MYANMAR:** Phra (Buddha) Cave, Tanintharyi Township, Tanintharyi Region (11°13'46.2"N, 99°10'34.3"E): CUMZ 14233 (4 preserved specimens).

Diagnosis: Shell globose, fragile, polished, and dark yellowish; animal with five mantle extensions; genitalia with very short vagina, short epiphallallic caecum, moderate gametolytic duct, and small dart apparatus.

Description: Shell (Figs. 5A–C, 9A, B). Shell globose, small to slightly medium sized (width up to 11.0 mm, height up to 5.4 mm), transparent, very thin, fragile, glassy, and dark yellowish or yellowish-corneous. Surface of protoconch smooth (Fig. 9A, B); surface of body whorl smooth. Spire slightly elevated; suture slightly impressed. Whorls 3¼–4, convex and rapidly increasing; last whorl enlarged and well-rounded. Aperture oblique, diagonal, roundly lunate, width greater than height; peristome simple. Columellar margin thin and little expanded near umbilicus. Umbilicus minute.

Genital organs (Fig. 6A). Atrium (at) enlarged and very short. Penis (p) long, cylindrical, and with thin penial sheath encircling about half of penis length. Epiphallus (e1 + e2) shorter than penis; e1 more slender and narrower than penis; e2 bulbous in shape and shorter than e1. Epiphallallic caecum (ec) short and small;

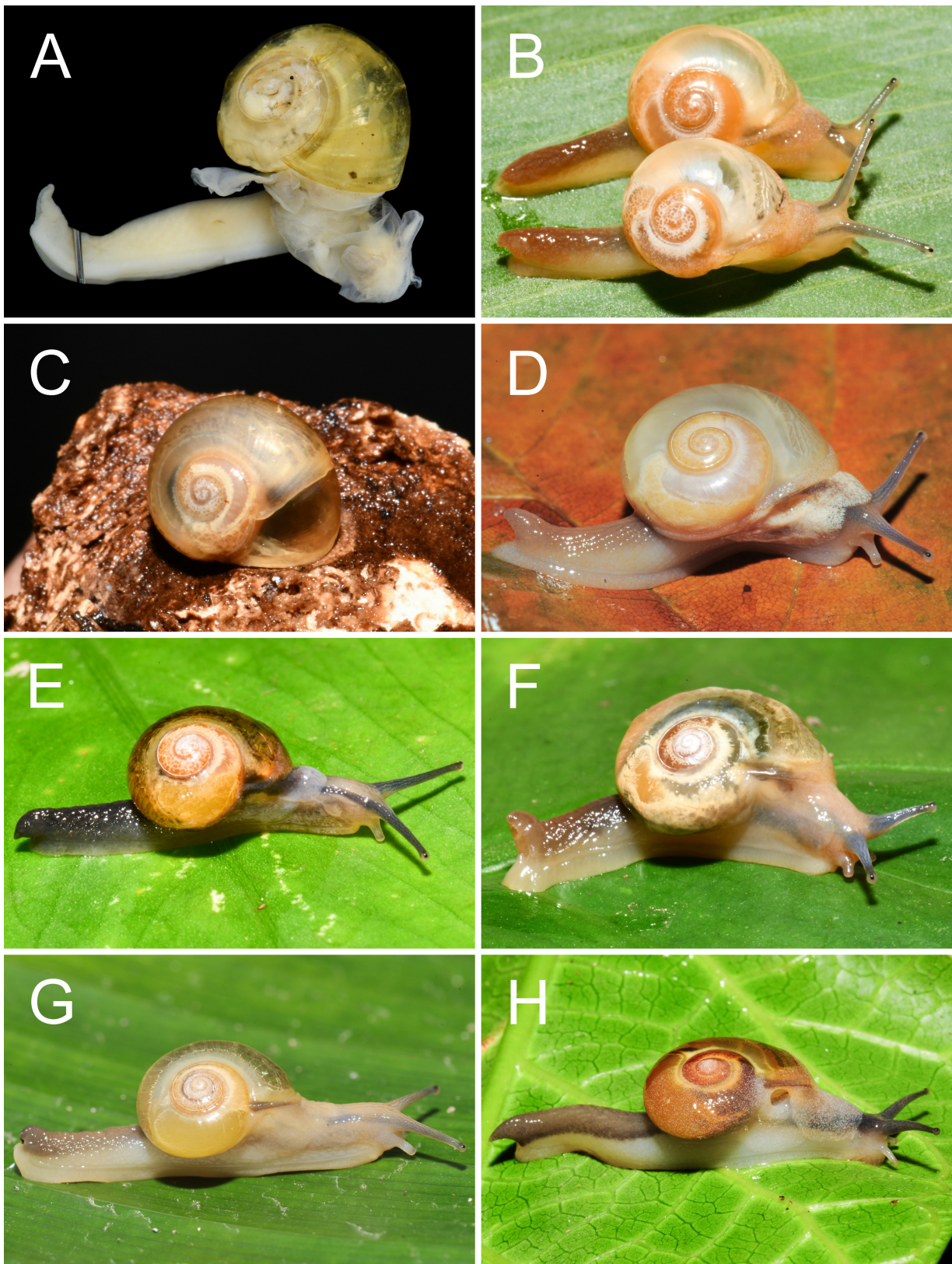


Fig. 3. Living snails of seven *Durgella* species. A: *D. birmanica* CUMZ 14233. B, C: *D. levicula*; B: CUMZ 14248; C: CUMZ 14250. D: *D. erratica* CUMZ 14234. E: *D. siamensis* CUMZ 14232. F: *D. libas* CUMZ 14237. G: *D. pentata* sp. nov. paratype CUMZ 14240. H: *D. nulla* sp. nov. paratype CUMZ 14228.

penial retractor muscle (prm) thin and attached at tip of epiphallid caecum. Vas deferens (vd) long and slender tube. Vagina (v) very short or inconspicuous. Dart apparatus (da) small, long cylindrical, and connected to atrium chamber. Gametolytic duct (gd) slightly shorter than penis, and enlarged at base with conical shape; gametolytic sac (gs) bulbous in shape. Free oviduct (fo) slightly shorter than penis; proximal part enlarged and bulbous; distal part slender and long cylindrical. Oviduct enlarged lobules; prostate gland running alongside oviduct.

Radula (Fig. 11A, B). Teeth numerous and pectiniform, arranged in wide-angled V-shaped rows, half row *ca.* 420 teeth. Central tooth reduced with two claw-shaped cusps. Lateromarginal teeth elongated bicuspid, outer edge serrated with three to six prominent cusps, diminishing gradually in size outwards. Outermost teeth slightly shorter than inner teeth.

External appearance (Fig. 3A). Animal with blackish body and light yellow near foot margin. Five mantle extensions well-developed and fleshy grey. Caudal horn raised, large, and blackish.

Distribution: This species is known from a single locality only at Phra (Buddha) Cave, Tanintharyi Region, Myanmar (Fig. 1).

Remarks: Concerning the authorship of this nominal name, Pfeiffer (1847) stated '*Vitrina birmanica* Phil.', and the specimen was from the R.A. Philippi collection. However, there is no clear evidence that Philippi provided him with the species name and description. Therefore, Pfeiffer (1847) is the sole author of this nominal name (ICZN 1999: Arts 50.1, 50.1.1).

Previous works placed this species in either the semislug genus *Helicarion* Férussac, 1821 or in *Megaustenia*, which is a replacement name of *Cryptosoma* Theobald, 1857 (Tryon 1885; Blanford and Godwin-Austen 1908; Solem 1966). However, *Helicarion* is mainly distributed in Australia (Schileyko 2002), while *Megaustenia* is native to mainland Southeast Asia (Schileyko 2002). Based on the shell characters, *D. birmanica* is distinct from all *Megaustenia* species because it has a small shell (9 mm) with 4 whorls, whereas *Megaustenia* spp. have much larger shells (18–25 mm) with fewer than 4 whorls

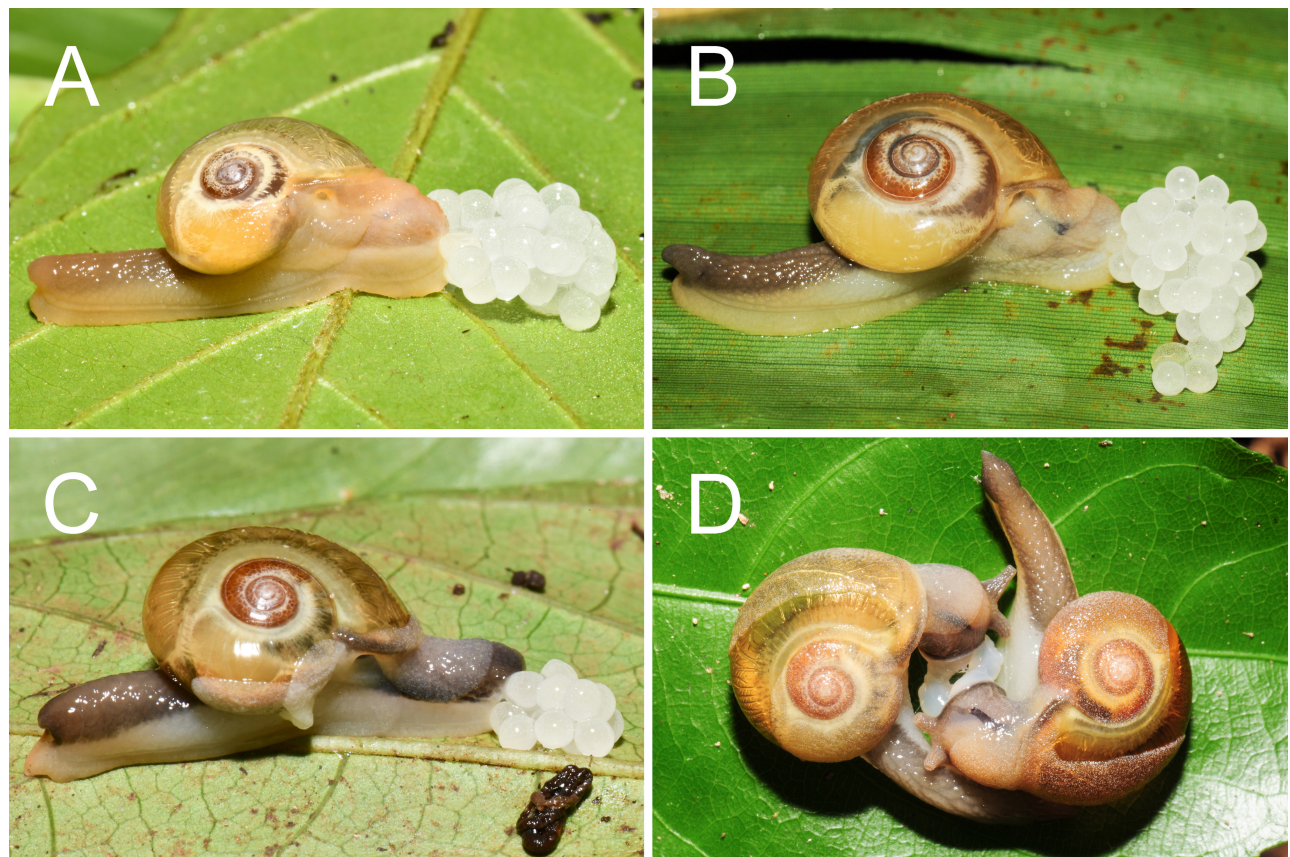


Fig. 4. Eggs and mating behavior of *Durgella* species recorded in the field. A: eggs of *D. libas* from Wachirathan Waterfall, Chiang Mai Province. B: eggs of *D. pentata* sp. nov. from Tham Chiang Dao, Chiang Mai Province. C: eggs of *D. nulla* sp. nov. from Phu Pha Lom, Loei Province. D: mating pairs of *D. nulla* sp. nov. from Phu Pha Lom, Loei Province.

(Table 1; Blanford and Godwin-Austen 1908; Solem 1966).

Several semislug specimens collected from the Tanintharyi Region (approximate type locality) in this study conform to the shell characteristics of *D. birmanica*. Our morphological study of shell sculpture, mantle morphology, genital anatomy, and radular morphology suggests that this species belongs to the genus *Durgella*.

***Durgella levicula* (Benson, 1859)**
(Figs. 1, 3B, C, 5D–F, 6B, C, 9C, D, 11C, D)

Helix levicula Benson, 1859: 391. Type locality: Phie Than, raro occurs [Payathonzu or Phaya Thone Zu, Kayin State, Myanmar]. Pfeiffer 1868: 48. Stoliczka 1871: 250. Hanley and Theobald 1876: 37, pl. 90, figs. 1, 4.
Nanina (Durgella) levicula: Blanford 1863: 81. Tryon 1886: 111, pl. 37, figs. 8, 9.
Nanina levicula – Nevill 1878: 26.
Durgella levicula – Godwin-Austen 1881: 291, pl. 20, figs. 1, 2 (shell), pl. 21, figs. 1, 3, 3a, 5 (anatomy). Godwin-Austen 1898: 61, pl. 76, fig. 1, 1a, 1b. Blanford and Godwin-Austen 1908: 213, fig. 75. Solem 1966: 49. Preece et al. 2022: 167, fig. 75a.

Material examined: *Holotype* NHMUK 1888.12.4.506 from Tenasserim (figured in Preece et al. 2022). **MYANMAR:** Mule-ik Range, Tenasserim

[Mulayit Taung (Hill), Kayin State, Myanmar]: NHMUK 1903.7.1.785 (18 shells). **THAILAND:** Khao Wang Khamen, Sai Yok District, Kanchanaburi Province (14°23'18.4"N, 98°55'30.5"E): CUMZ 14245 (10 preserved specimens). Sai Yok waterfall, Sai Yok District, Kanchanaburi Province (14°26'01.8"N, 98°50'53.0"E): CUMZ 14246 (3 preserved specimens). Wat Sunantha Wanaram, Sai Yok District, Kanchanaburi Province (14°32'05.1"N, 98°49'43.4"E): CUMZ 14247 (3 preserved specimens). Tham Than Lot, Si Sawat District, Kanchanaburi Province (14°39'44.8"N, 99°18'20.2"E): CUMZ 14248 (11 preserved specimens). Wat Tham Ong Chu School, Si Sawat District, Kanchanaburi Province (14°48'05.3"N, 99°05'03.6"E): CUMZ 14249 (1 preserved specimen). Sahakon Nikhom, Thong Pha Phum District, Kanchanaburi Province (14°44'35.7"N, 98°49'06.2"E): CUMZ 14250 (1 preserved specimen). Wat Tha Khanun, Thong Pha Phum District, Kanchanaburi Province (14°44'36.4"N, 98°38'15.7"E): CUMZ 14251 (7 preserved specimens). Wat Pa Tham Pha Daeng, Thong Pha Phum District, Kanchanaburi Province (14°38'44.7"N, 98°39'33.8"E): CUMZ 14252 (8 preserved specimens). Thee Lor Su, Umphang District, Tak Province (16°02'47.1"N, 98°51'09.2"E): CUMZ 14253 (22 preserved specimens). Wat Tham Khao Kriap, Lang Suan District, Chumphon

Table 1. Comparison of the morpho-anatomical characteristics of *Durgella* Blanford, 1863 and morphologically similar genera of helicarioideoan semislugs from mainland Southeast Asia. The genitalia characters depicted are in respect to type species, or otherwise stated. References: 1 = Blanford and Godwin-Austen (1908), 2 = Solem (1966), 3 = Schileyko (2002), 4 = Schileyko (2003), and 5 = Pholyotha et al. (2021a)

Genus (type species)	Shell			Genitalia			Radular teeth	Caudal horn	Ref.
	Shell size (width)	Umbilicus	Whorls	Dart apparatus	Epiphallic caecum	Flagellum			
<i>Durgella</i> Blanford, 1863 (<i>Helix levicula</i> Benson, 1859)*	small to medium	minute to narrow	3–4½	present ¹	present	absent	central unicuspid or asymmetrical bi- or tricuspid, lateromarginal bicuspid with several tiny cusps on outer side	present	1, 2, 3 this study
<i>Cryptaustenia</i> Cockerell, 1891 (<i>Vitrina planospira</i> Benson, 1859 (= <i>Vitrina succinea</i> Reeve, 1862))*	small to medium	minute	3–4½	present ²	absent	absent	central tricuspid, lateral bi- or tricuspid, marginal bicuspid	present	1, 2, 4
<i>Cryptosemelus</i> Collinge, 1902 (<i>Cryptosemelus gracilis</i> Collinge, 1902)*	small to medium	absent	3½–4	absent	absent	absent	central tricuspid, lateral tricuspid, marginal bicuspid	absent	5
<i>Megaustenia</i> Cockerell, 1912 (<i>Vitrina praestans</i> Gould, 1843)*	medium to large	absent	3–3½	present	present	present	central tricuspid, lateral tricuspid, marginal bicuspid	present	1, 2, 3

*Genitalia of the type species were examined. ¹*Durgella assamica* Godwin-Austen, 1881, *D. rogersi* Godwin-Austen, 1907 and *D. nulla* sp. nov. have no dart apparatus (Blanford and Godwin-Austen 1908; this study). ²*Cryptaustenia gadinodromica* Solem, 1966 have no dart apparatus (Solem 1966).

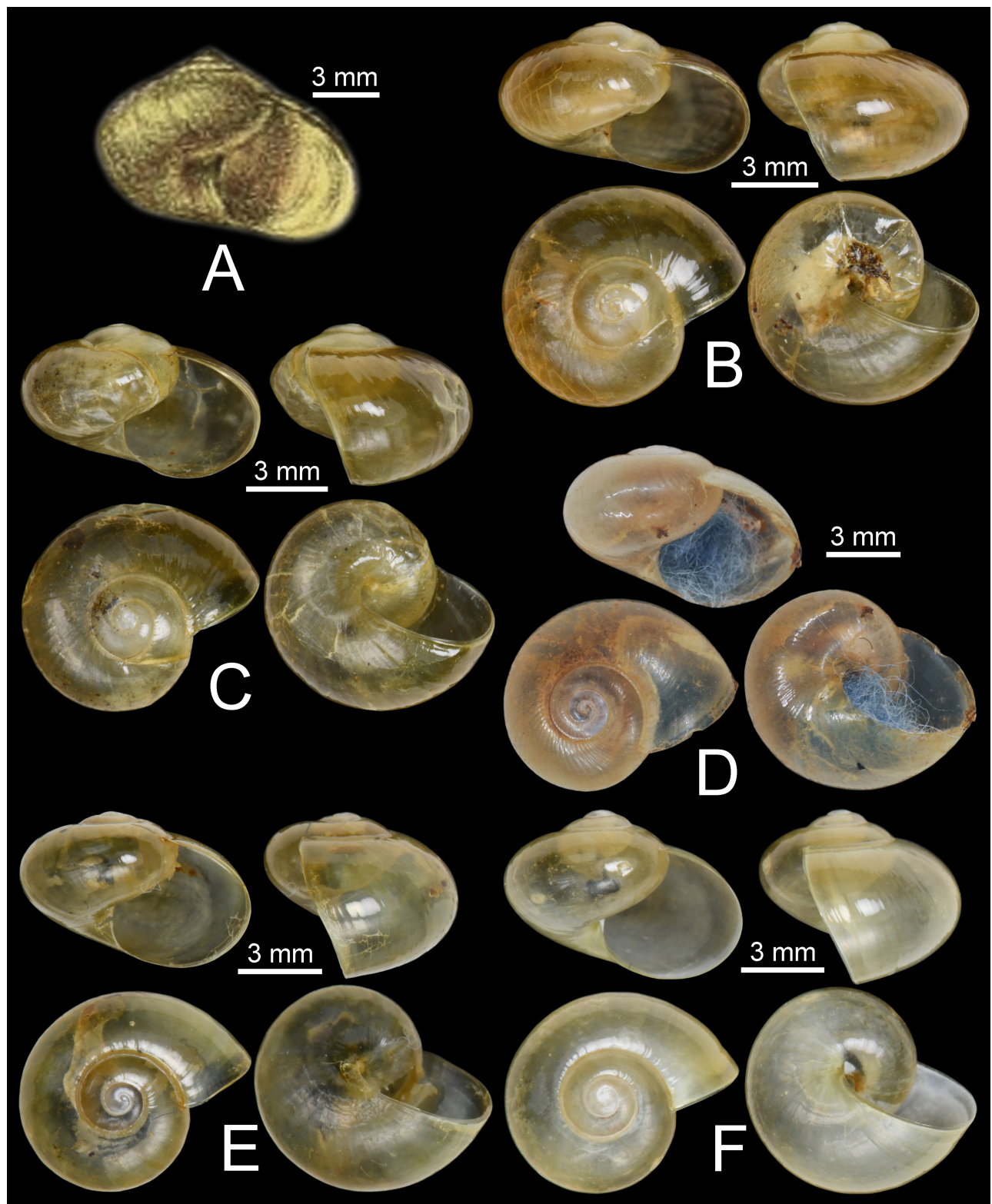


Fig. 5. Shells of *Durgella* species. A: *D. birmanica* modified from Hanley and Theobald (1876). B, C: *D. birmanica* CUMZ 14233. D–F: *D. levicula*; D: NHMUK 1903.7.1.785; E: CUMZ 14251; F: CUMZ 14245.

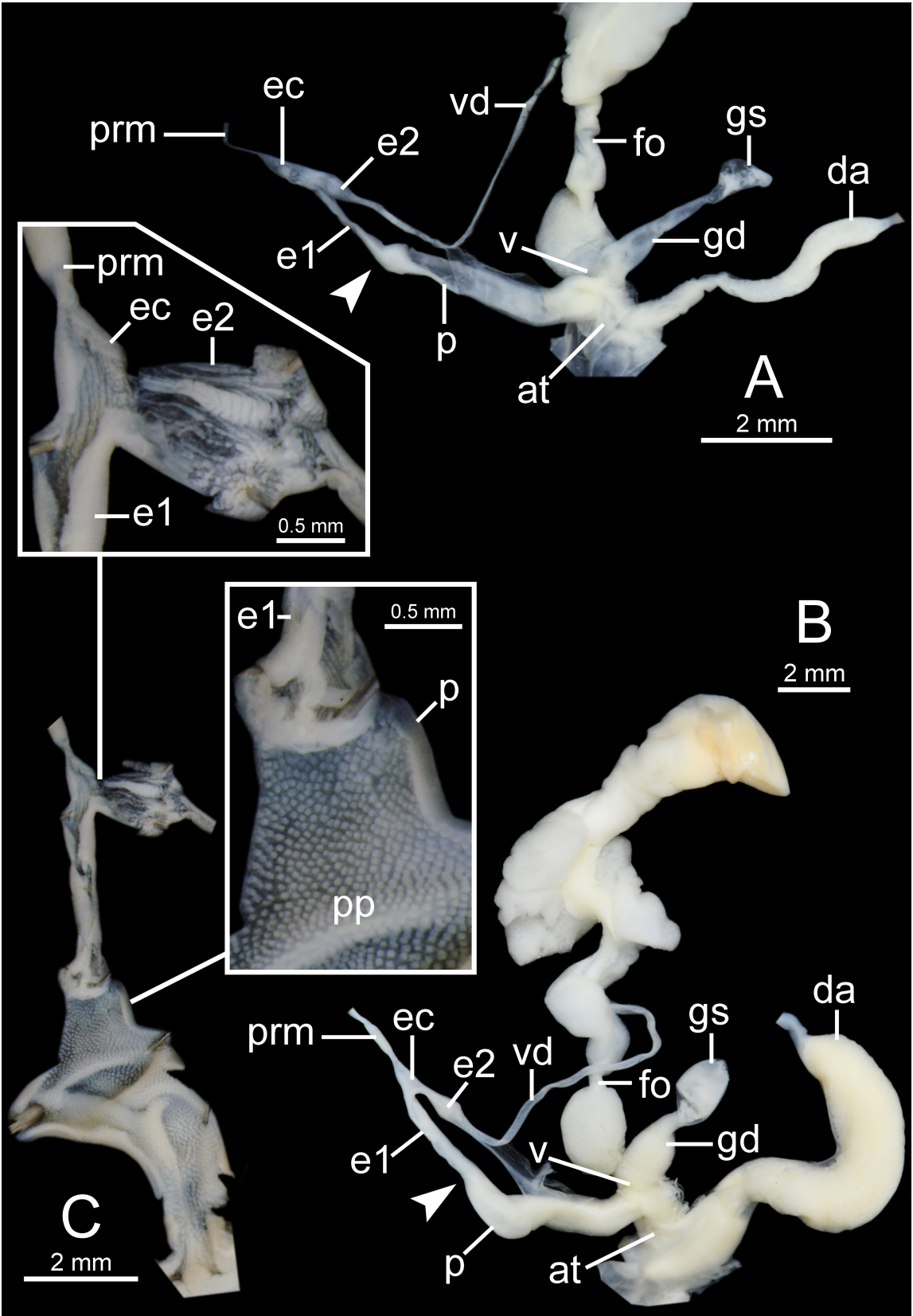


Fig. 6. Genitalia of *Durgella* species. A: *D. birmanica* CUMZ 14233. B, C: *D. levicula* CUMZ 14253; B: general view of the genital system; C: internal structure of the penis and epiphallus. White arrow indicates the end of the penis.

Province (9°49'02.9"N, 99°02'15.2"E): CUMZ 14254 (10 preserved specimens), 14255 (19 preserved specimens). Wat Phut Sadi Phupharam, Thung Tako District, Chumphon Province (10°05'36.1"N, 99°04'38.4"E): CUMZ 14256 (52 preserved specimens). Tham Krating Thong, Mueang Chumphon District, Chumphon Province (10°27'19.5"N, 99°06'23.7"E): CUMZ 14257 (13 preserved specimens). Bo Phloi, Bo Rai District, Trat Province (12°36'08.0"N, 102°33'18.3"E): CUMZ 14258 (9 preserved specimens). Wat Trok Nong Lang, Khlung District, Chanthaburi Province (12°32'16.5"N 102°16'35.8"E): CUMZ 14259 (2 preserved specimens). Ban Wang Ka Prae, Pong Nam Ron District, Chanthaburi Province (12°58'18.9"N, 102°16'12.5"E): CUMZ 14260 (15 preserved specimens). Wat Khao Singto, Mueang District, Sa Kaeo Province (13°59'24.3"N, 102°00'25.9"E): CUMZ 14261 (2 preserved specimens). Tham Phet Pho Thong, Khlung Hat District, Sa Kaeo Province (13°24'49.2"N, 102°19'37.7"E): CUMZ 14262 (8 preserved specimens), 14263 (12 preserved specimens). Wat Tham Khao Maka, Mueang District, Sa Kaeo Province (13°47'09.2"N, 101°56'53.7"E): CUMZ 14264 (11 preserved specimens), 14265 (5 preserved specimens).

Diagnosis: Shell globose, fragile, polished, pale to dark yellowish, and aperture roundly lunate; animal with four mantle extensions; genitalia with very short vagina, short epiphallic caecum, thick penial retractor muscle, rather short gametolytic duct, and very large dart apparatus.

Description: Shell (Figs. 5D–F, 9C, D). Shell globose, small to medium (width up to 11.0 mm, height up to 7.0 mm), transparent, thin, fragile, polished, and dark yellowish or pale yellowish with olive tinge. Protoconch surfaces sculptured with faint spiral furrows (Fig. 9C, D). Spire slightly elevated; suture slightly impressed. Whorls 3–4, convex and rapidly increasing; body whorl smooth, enlarged, and well-rounded. Aperture oblique, diagonal, roundly lunate, width as long as height; peristome thin, simple. Columellar margin thin and little expanded near umbilicus. Umbilicus minute.

Genital organs (Fig. 6B, C). Atrium (at) enlarged and very short. Penis (p) long, cylindrical, and thin penial sheath encircling about half of penis length. Inner sculpture of penis uniform throughout with small conical penial pilasters (pp). Epiphallus (e1 + e2) slightly shorter than penis; e1 more slender and narrower than penis; e2 short and bulbous shape. Inner sculpture: e1 with small and longitudinal dash-like pilasters; e2 with one very enlarged longitudinal pilaster. Epiphallic caecum (ec) short and small; penial retractor muscle (prm) thick and attached at tip of epiphallic caecum. Vas deferens (vd) long and thin tube.

Vagina (v) very short or inconspicuous. Dart apparatus (da) very large, long cylindrical, and connected to atrium chamber. Gametolytic duct (gd) shorter than half of penis length, and more enlarged at base; gametolytic sac (gs) enlarged and bulbous. Free oviduct (fo) shorter than penis; proximal part enlarged and bulbous; distal part small and cylindrical. Oviduct enlarged lobules; prostate gland running alongside oviduct.

Radula (Fig. 11C, D). Teeth pectiniform and numerous with half row *ca.* 400 teeth. Central tooth very reduced to tiny unicuspid. Lateromarginal teeth elongated bicuspid and outer edge serrated with tiny 3- to 8-point cusps. Outermost teeth slightly shorter than inner teeth.

External appearance (Fig. 3B, C). Posterior body with light to dark reddish-brown on dorsal and light yellow near foot margin; anterior body light yellow to reddish-brown. Four mantle extensions well-developed and light reddish-brown. Caudal horn raised, large, and blackish.

Distribution: The type locality and the newly collected sample suggest that this species is widespread in western, southern, and eastern Thailand, and the neighboring areas in Kayin State, Myanmar (Fig. 1).

Remarks: In terms of shell morphology alone, *D. levicula* is similar to *D. birmanica*, but it is easy to distinguish by the number of mantle extensions. *Durgella levicula* has four mantle extensions (undivided left dorsal lobe; Fig. 2B), whereas *D. birmanica* has five mantle extensions (left dorsal lobe divided into two lobes; Fig. 2D). In addition, the genitalia of *D. levicula* differ from *D. birmanica* by the larger dart apparatus.

***Durgella erratica* (Godwin-Austen, 1888)**

(Figs. 1, 3D, 7A–C, 9E, F, 10A, 11E, F)

Austenia ? erratica Godwin-Austen, 1888: 241. Type locality: Pingoung, Shan Hills [Pyinyaung, Mandalay Region, Myanmar].

Durgella erratica – Blanford and Godwin-Austen 1908: 216. Godwin-Austen 1910: 292, pl. 131, fig. 2, 2a.

Material examined: *Syntypes* NHMUK 1895.1.1.4–6 (3 shells) from Pingoung, Shan Hills [Pyinyaung, Mandalay Region, Myanmar]. **MYANMAR:** Pegu [Pyay District, Bago Region]: NHMUK 1906.1.1.60 (2 shells). Bassein [Patheingyi District, Ayeyarwady Region]: NHMUK 1906.1.1.102 (1 shell). Pyinyaung, Mandalay Region (20°51'08.7"N, 96°23'56.6"E): CUMZ 14234 (11 shells, 251 preserved specimens).

Diagnosis: Shell depressedly subglobose, fairly solid, sharply descending in front, and narrowly opened umbilicus; animal with four mantle extensions; genitalia with very short vagina, short epiphallic caecum, thick and large penial retractor muscle, moderate and cylindrical gametolytic duct, and very large dart

apparatus.

Description: Shell (Figs. 7A–C, 9E, F). Shell depressedly subglobose, small to medium sized (width up to 11.7 mm, height up to 6.7 mm), fairly solid, smooth, polished, pale golden amber or pale yellowish with olive tinge. Protoconch surfaces rather smooth or sculptured with dimly spiral furrows (Fig. 9E, F). Spire slightly elevated; suture slightly impressed. Whorls $3\frac{1}{4}$ – $3\frac{1}{2}$, convex, rapidly increasing; last whorl enlarged, rounded, and descending. Aperture oblique, roundly lunate, width greater than height; peristome thin. Columellar margin rather thick and slightly expanded near umbilicus. Umbilicus narrow.

Genital organs (Fig. 10A). Atrium (at) enlarged and very short. Penis (p) long, cylindrical, and with thin penial sheath encircling from atrium to nearly half of penis length. Epiphallus (e1 + e2) shorter than penis; e1 slender and narrower than penis; e2 slender and slightly longer than e1. Epiphallic caecum (ec) short and small;

penial retractor muscle (prm) thick, and attached at tip of epiphallic caecum. Vas deferens (vd) long and thin tube. Vagina (v) very short. Dart apparatus (da) very large, long cylindrical, and connected to atrium chamber. Gametolytic duct (gd) cylindrical and about half of penis length; gametolytic sac (gs) not enlarged. Free oviduct (fo) cylindrical, half of penis length, and enlarged slightly near vagina. Oviduct and prostate gland very small.

Radula (Fig. 11E, F). Teeth pectiniform and numerous with half row *ca.* 445 teeth. Central tooth very reduced to tiny bicuspid. Lateromarginal teeth narrowly elongate bicuspid, outer edge with inconspicuous (nearly absent) serrated cusp. Outermost teeth shorter than inner teeth.

External appearance (Fig. 3D). Posterior body with pale reddish-brown on dorsal and light yellow near foot margin; anterior body light yellow or creamy. Four mantle extensions well-developed with creamy to

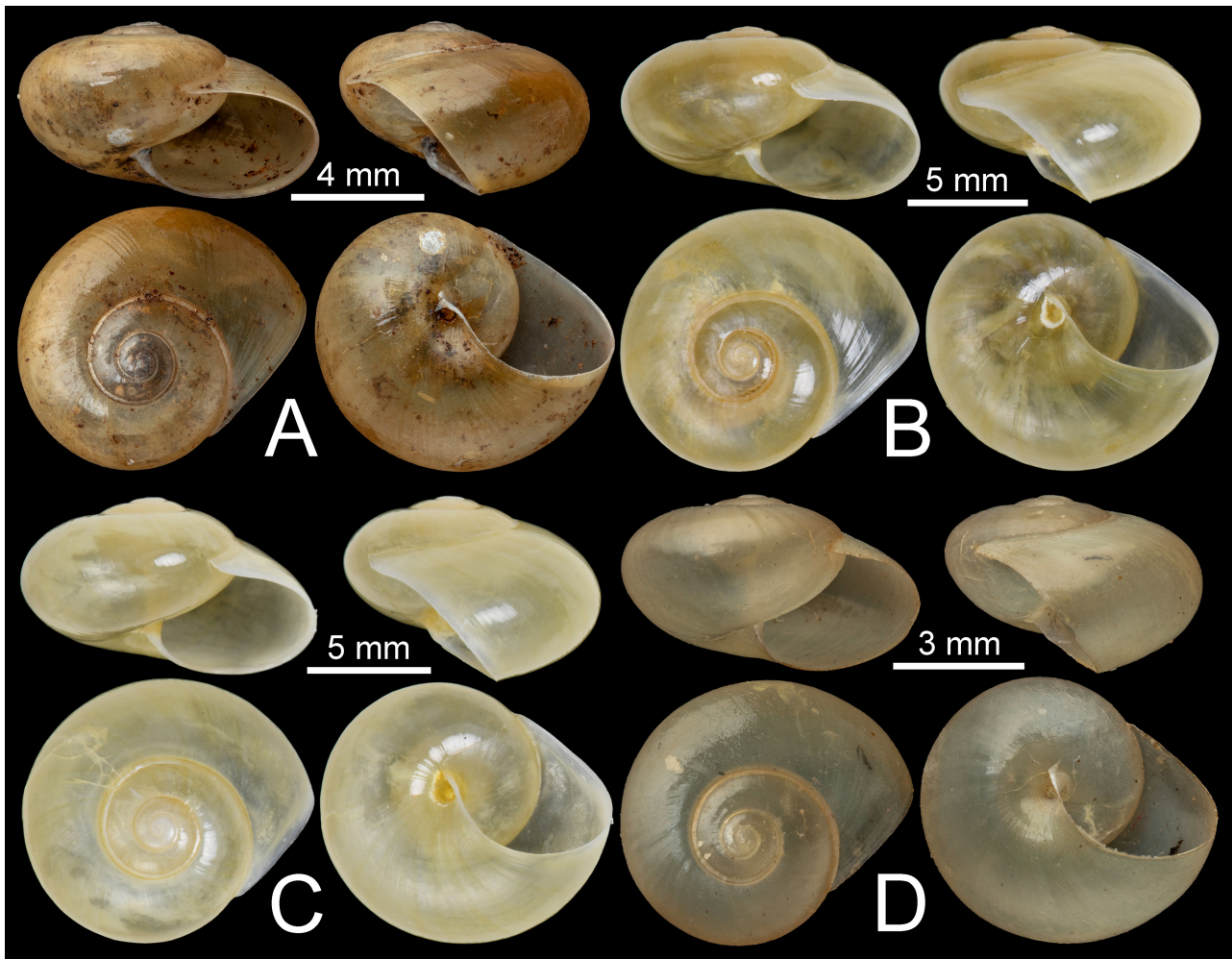


Fig. 7. Shells of *Durgella* species. A–C: *D. erratica*; A: syntypes NHMUK 1895.1.1.4–6; B, C: specimen CUMZ 14234. D: *D. concinna* syntype NHMUK 1865.9.3.15.

dark brown colour. Caudal horn raised, large, and pale reddish-brown.

Distribution: This species seems to be mostly restricted to limestone and mountainous areas in Pyinyaung, Mandalay Region, Myanmar (Fig. 1). This species was also found in Patheingyi District and Pyaw District, Myanmar (Godwin-Austen 1910).

Remarks: This species is easy to distinguish from most *Durgella* species known from Myanmar and Thailand by the last whorl being very descending and the relatively open umbilicus. The last whorl of other *Durgella* species has regular coiling and is not descending, and the umbilicus is generally very narrow. Among *Durgella* species with the body whorl descending in front (*D. siamensis*, *D. raphiellus*, and *D. concinna*), *D. erratica* differs from *D. siamensis* and *D. raphiellus* by having a more depressed shell and larger umbilicus. Anatomically, *D. erratica* has a relatively longer penis, thicker penial retractor muscle, and narrower gametolytic duct than *D. siamensis*. For further differences of this group, see the remarks under each species.

***Durgella concinna* Blanford & Godwin-Austen, 1908**
(Figs. 1, 7D)

Nanina levicula – Blanford 1865: 87. Nevill 1878: 26. (non Benson 1859).

Durgella concinna Blanford & Godwin-Austen, 1908: 215. Type locality: Thayet Myo [Thayet District, Magway Region], Prome [Pyaw District, Bago Region], and Akauktoung in Upper Pegu [Akauktoung, Pyaw District, Bago Region].

Material examined: Syntype NHMUK 1865.9.3.15 (1 shell; Fig. 7D) from Akauktoung, Pegu [Akauktoung, Pyaw District, Bago Region, Myanmar].

Diagnosis: Shell depressedly globose, small, fairly solid, polished, very descending in front, with narrowly opened umbilicus.

Description: Shell (Fig. 7D). Shell depressedly globose, small (width up to 7 mm, height up to 4 mm), fairly solid, smooth, polished, translucent, pale, almost whitish-horny. Spire low, convex, apex obtuse; suture shallow. Whorls 3½, rapidly increasing, slightly convex above; last whorl descending near aperture, rounded, and rather tumid beneath. Aperture oblique, roundly lunate; peristome thin. Columellar margin curved, vertical above, and slightly reflected. Umbilicus narrow.

Distribution: *Durgella concinna* is known from several localities in Magway (Fig. 1) and Bago regions in central Myanmar.

Remarks: *Durgella concinna* was nominated based on misidentified *D. levicula* specimens from central Myanmar (Blanford and Godwin-Austen 1908).

However, it differs from *D. levicula* in having the last whorl more descending near the aperture and a wider umbilicus. In contrast, *D. levicula* has a shell without a descending body whorl near the aperture and a tiny umbilicus.

The taxonomic status of *D. concinna* is still ambiguous because this species has a shell morphology that is very similar to *D. erratica*; it differs from the latter species by having a slightly smaller shell. Unfortunately, no specimens of *D. concinna* were found in our surveys, and so we could not compare their reproductive morphologies. Additional information is necessary to determine whether the difference in shell size represents size variation or distinct species. In this study, we retain *D. concinna* as a valid species per Blanford and Godwin-Austen (1908).

***Durgella raphiellus* (Martens, 1867)**
(Fig. 8A)

Helicaron raphiellus Martens, 1867: 69, pl. 12, fig. 9. Type locality: Siam [Thailand]. Tryon 1885: 177, pl. 40, figs. 36–38. Fischer and Dautzenberg 1904: 392. Saurin 1953: 113.

Durgella raphiellus – Inkhavilay et al. 2019: 83, fig. 39c.

Material examined: Syntypes ZMB/MOLL 5033 (2 shells; Fig. 8A) from Siam [Thailand].

Diagnosis: Shell subglobose, fragile, polished, pale golden-amber, and large body whorl very descending in front.

Description: Shell (Fig. 8A). Shell subglobose, small (width 7.5 mm, height 5 mm), thin, smooth, polished, pale golden-amber. Spire slightly elevated; suture slightly impressed. Whorls 3, convex and rapidly increasing; body whorl enlarged, well-rounded and descending. Aperture oblique, roundly lunate, width greater than height; peristome thin. Columellar margin simple and slightly expanded near umbilicus. Umbilicus minute.

Distribution: *Durgella raphiellus* is only known from the type locality in Thailand, and its exact locality is unknown.

Remarks: This species was described by Martens (1867) based on two specimens with ‘Siam’ as the type locality, which is very rough and covers a wide geographical area. However, the itinerary of E. von Martens indicates that he arrived in mainland Southeast Asia and made stops in ‘Bangkok’ and ‘Petshaburi’ for collecting specimens over a period of around three months (Martens 1876; Kabat and Boss 1997). This suggests that ‘Petshaburi’ [= Phetchaburi Province, Thailand] is the collection locality of this species, which is much more precise than ‘Siam’. Since this species was first discovered, there have been no additional specimens collected, records, or literature references.

Unfortunately, in our surveys we could not find any specimens that could be identified as this species for re-description.

Without further evidence of the soft-part anatomy depicted from the topotype; the taxonomic status and relationship of *D. raphiellus* is still provisional; therefore, we recognise it as valid species per Inkhavilay et al. (2019). However, *D. raphiellus* differs from *D. levicula* from peninsular Thailand by having a relatively smaller size and more descending last whorl. In addition, the apertural width is greater than the height in *D. raphiellus*, whereas these parameters are more equal in *D. levicula*.

***Durgella siamensis* Möllendorff, 1902**

(Figs. 1, 3E, 8B–D, 9G, H, 10B, C, 11G, H)

Durgella siamensis Möllendorff, 1902: 155. Type locality: Muoklek, Siam [Muak Lek District, Saraburi Province, Thailand]. Hemmen and Hemmen 2001: 43.

Bensonina (*Durgella*) *siamensis* – Fischer and Dautzenberg 1904: 395.

Material examined: *Syntype* SMF 227168/1 (1 shell) from Muoklek, Siam [Muak Lek District, Saraburi Province, Thailand]. **THAILAND:** Sarika Waterfall, Mueang District, Nakhon Nayok Province (14°18'31.3"N, 101°15'17.9"E): CUMZ 14232 (10 preserved specimens).

Diagnosis: Shell subglobose to globose, fragile, polished, dark yellow with a creamy tinge, and large body whorl very descending in front; animal with

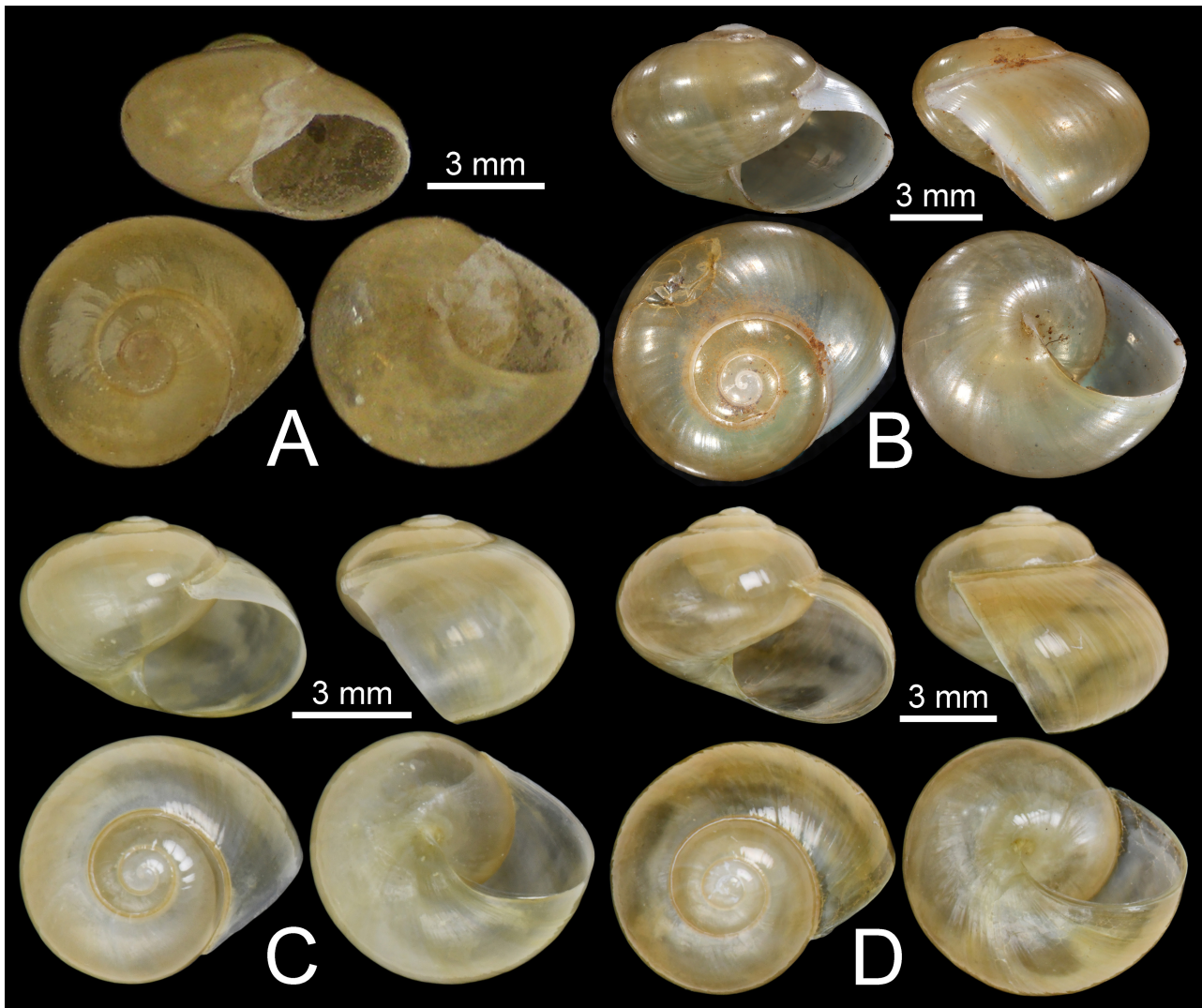


Fig. 8. Shells of *Durgella* species. A: *D. raphiellus* syntypes ZMB/MOLL 5033. B–D: *D. siamensis*; B: syntypes SMF 227168/1; C, D: CUMZ 14232.

blackish body and four mantle extensions; genitalia with very short vagina, rather long epiphallus, short epiphallic caecum, moderate gametolytic duct, and rather large dart apparatus.

Description: Shell (Figs. 8B–D, 9G, H). Shell subglobose to globose, small (width up to 9.3 mm, height up to 6.5 mm), transparent, smooth, thin, polished, and yellowish-corneous or dark yellow with creamy tinge. Protoconch smooth (Fig. 9G, H). Spire slightly elevated; suture slightly impressed. Whorls $3\frac{1}{2}$ –4, convex, rapidly increasing, last whorl enlarged, well-rounded, and descending. Aperture oblique, diagonal, roundly lunate, width greater than height; peristome thin. Columellar margin thin and little expanded near umbilicus. Umbilicus minute.

Genital organs (Fig. 10B, C). Atrium (at) enlarged and very short. Penis (p) long, cylindrical, and with thin penial sheath encircling from atrium to almost middle of penis. Inner sculpture of penis uniform throughout with small conical penial pilasters (pp). Epiphallus (e1 + e2) cylindrical and slightly longer than penis; inner sculpture of e1 and e2 with thin longitudinal folds, and one thickened longitudinal pilaster. Epiphallic caecum (ec) short and small; penial retractor muscle (prm) thick and attached at tip of epiphallic caecum. Vas deferens (vd) long and thin tube. Vagina (v) very short or inconspicuous. Dart apparatus (da) short, enlarged cylindrical, and connected to atrium chamber. Gametolytic duct (gd) slightly shorter than penis, proximally enlarged at base and then tapering distally; gametolytic sac (gs) enlarged and bulbous. Free oviduct (fo) slightly shorter than penis; proximal part enlarged and bulbous; distal end large and cylindrical. Oviduct enlarged lobules; prostate gland running alongside oviduct.

Radula (Fig. 11G, H). Teeth pectiniform, arrangement and shape similar to those of *D. levicula*, and with half row *ca.* 380 teeth. Central tooth very reduced to tiny unicuspid. Lateromarginal teeth elongated bicuspid, outer edge serrated with 3 to 6 cusps. Outermost teeth shorter than inner teeth.

External appearance (Fig. 3E). Animal with fleshy-grey on anterior body; posterior body blackish; foot margin pale grey. Four mantle extensions well-developed and dark grey, graduating to cream near foot margin. Caudal horn raised, large, and blackish.

Distribution: The type locality and the newly collected sample suggest that *D. siamensis* is probably restricted to the Saraburi and Nakhon Nayok provinces, central Thailand (Fig. 1).

Remarks: *Durgella siamensis* was originally described by O.F. von Möllendorff (1902) based on specimens collected by H. Fruhstorfer, a butterfly collector, from Muaklek [Muak Lek District, Saraburi

Province], central Thailand. In this study, we collected specimens from Nakhon Nayok Province, very close to the type locality, and found that *D. siamensis* tended to vary in shell shape between the subadult (Fig. 8C) and fully grown (Fig. 8D) specimens. The subadult shell of this species is similar to *D. raphiellus* (Fig. 8A), but the latter species differs by having a more depressed and slightly smaller shell. Because of the shell similarity between *D. siamensis* and *D. raphiellus*, an anatomical investigation and molecular study are necessary to clarify their taxonomic status.

Durgella siamensis differs from *D. levicula*, a common and widespread species in Thailand, by the descending last whorl. Anatomically, *D. siamensis* has thin longitudinal folds on the inner sculpture of the epiphallus (e2) (Fig. 10C), whereas *D. levicula* has small longitudinal dash-like pilasters varying in length (Fig. 6C) on the inner sculpture of the epiphallus (e2).

***Durgella libas* Solem, 1966**

(Figs. 1, 3F, 4A, 12A, B, 13A, B, 14, 17A, B)

Durgella libas Solem, 1966: 50, figs. 7–9, 13b. Type locality: Wang Dao, North Thailand [Chiang Dao District, Chiang Mai Province, Thailand]. Panha 1996: 35. Hemmen and Hemmen 2001: 43. Inkhavilay et al. 2019: 83, figs. 19f, 57c.

Material examined: THAILAND: Wachirathan Waterfall, Chom Thong District, Chiang Mai Province (18°32'30.7"N, 98°35'53.6"E): CUMZ 14236 (4 preserved specimens). Phra-Ruesi Cave, Mueang District, Chiang Mai Province (18°48'24.5"N, 98°54'38.3"E): CUMZ 14237 (4 preserved specimens). San Ku, Mueang District, Chiang Mai Province (18°48'56.8"N, 98°53'38.7"E): CUMZ 14238 (7 preserved specimens). Doi Suthep-Pui Nature Trail, Mueang District, Chiang Mai Province (18°49'23.4"N, 98°53'23.6"E): CUMZ 14235 (1 preserved specimen).

Diagnosis: Shell depressedly subglobose, membranous, polished, dark yellow with a creamy tinge; animal with four mantle extensions; genitalia with slightly long and enlarged penis, rather long epiphallus, small epiphallic caecum, short gametolytic duct, and very large dart apparatus.

Description: Shell (Figs. 12A, B, 13A, B). Shell depressedly subglobose, small to medium (width up to 13.0 mm, height up to 7.6 mm), transparent, very thin (membranous) and fragile, polished, and dark yellow with creamy tinge. Protoconch surface sculptured with faint spiral furrows with regular malleation (Fig. 13A, B). Spire slightly elevated; suture slightly impressed. Whorls 4–4½, convex and rapidly increasing; last whorl smooth, enlarged, and well-rounded. Aperture oblique, diagonal, roundly lunate, broader than high, and apertural lip simple. Columellar margin thin and little

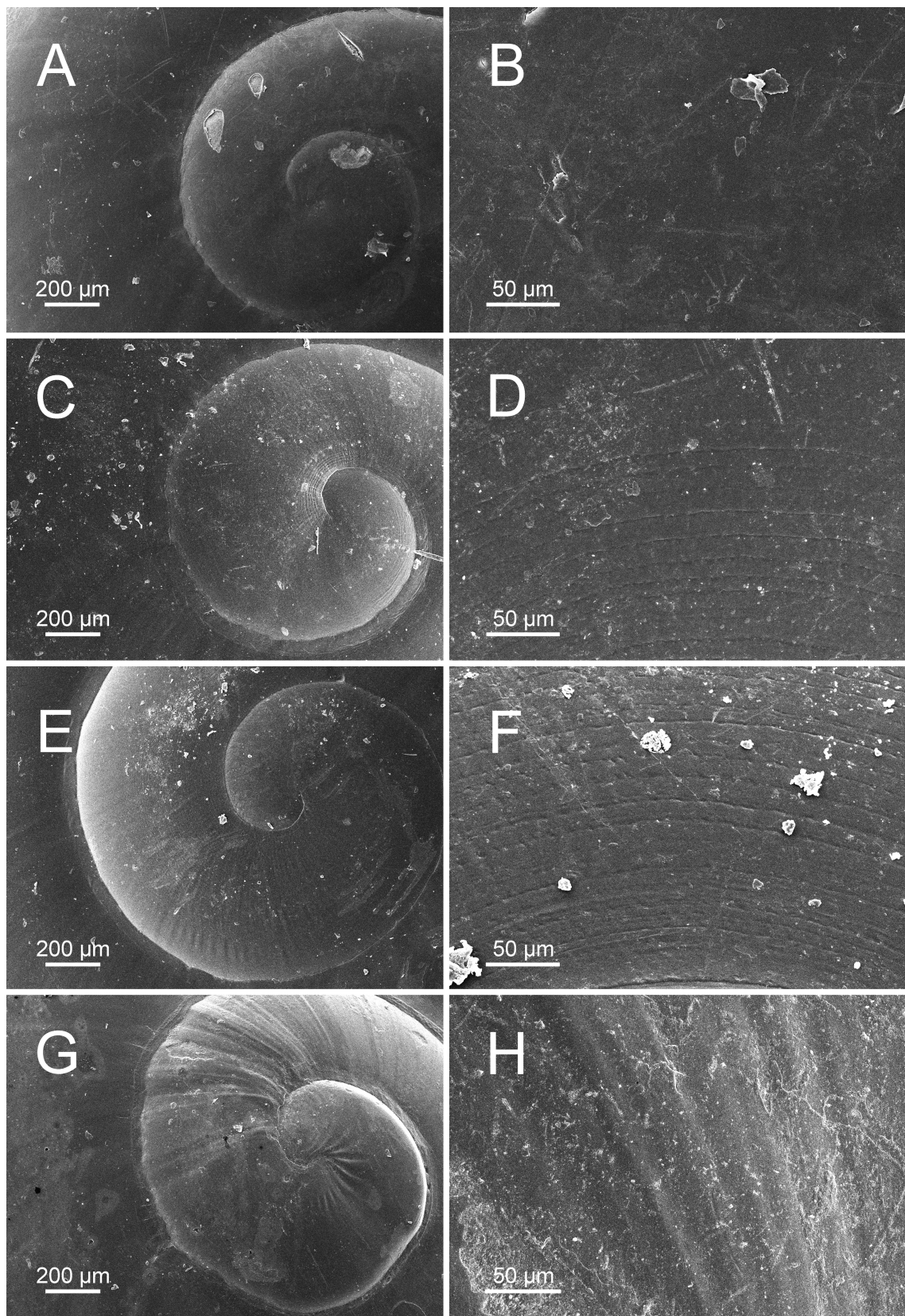


Fig. 9. Microsculpture of *Durgella* shells: protoconch and early teleoconch (first column), and close-up view of protoconch (second column). A, B: *D. birmanica* CUMZ 14233. C, D: *D. levicula* CUMZ 14251. E, F: *D. erratica* CUMZ 14234. G, H: *D. siamensis* CUMZ 14232.

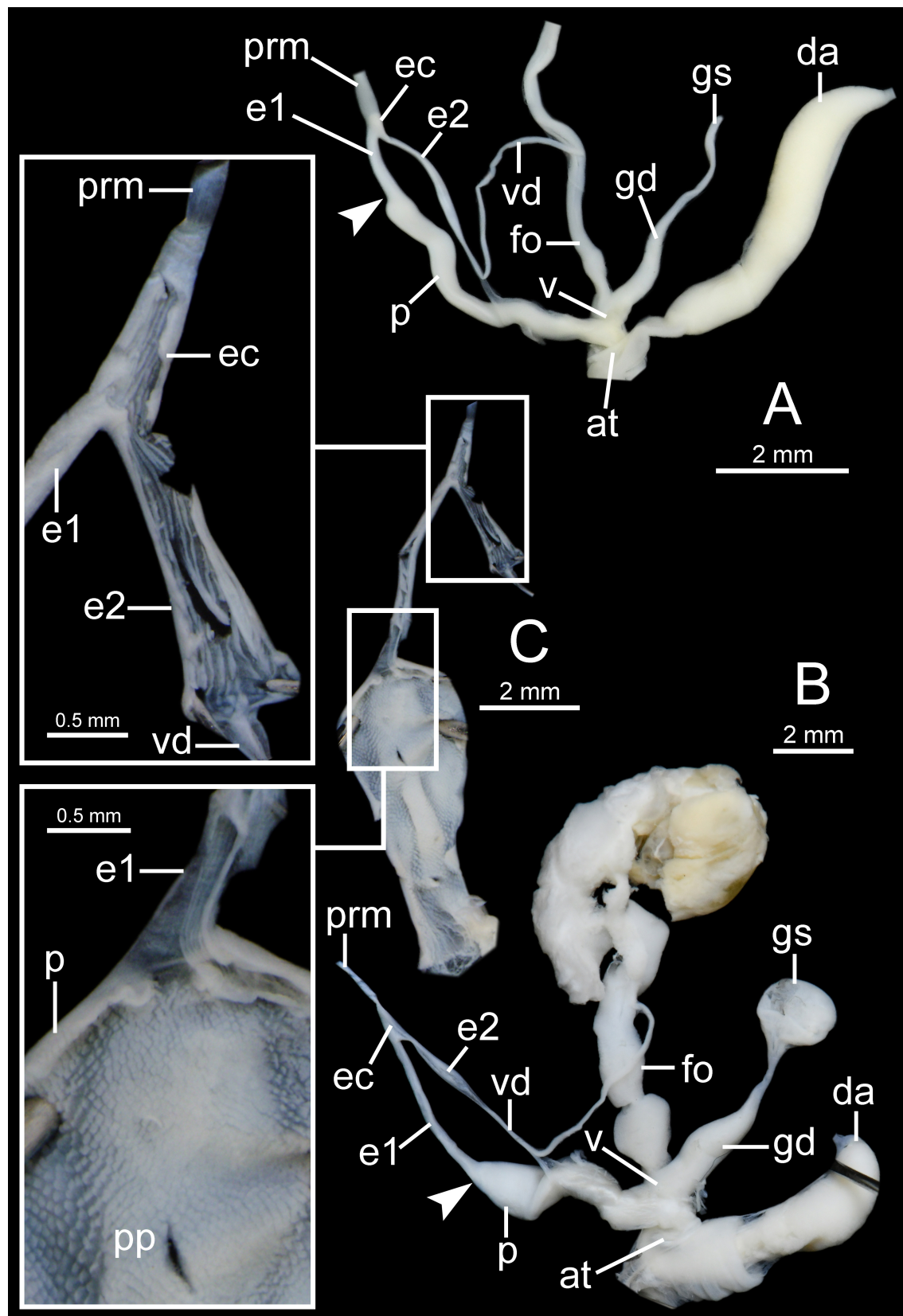


Fig. 10. Genitalia of *Durgella* species. A: *D. erratica* CUMZ 14234. B, C: *D. siamensis* CUMZ 14232; B: general view of the genital system; C: internal structure of the penis and epiphallus. White arrow indicates the end of the penis.

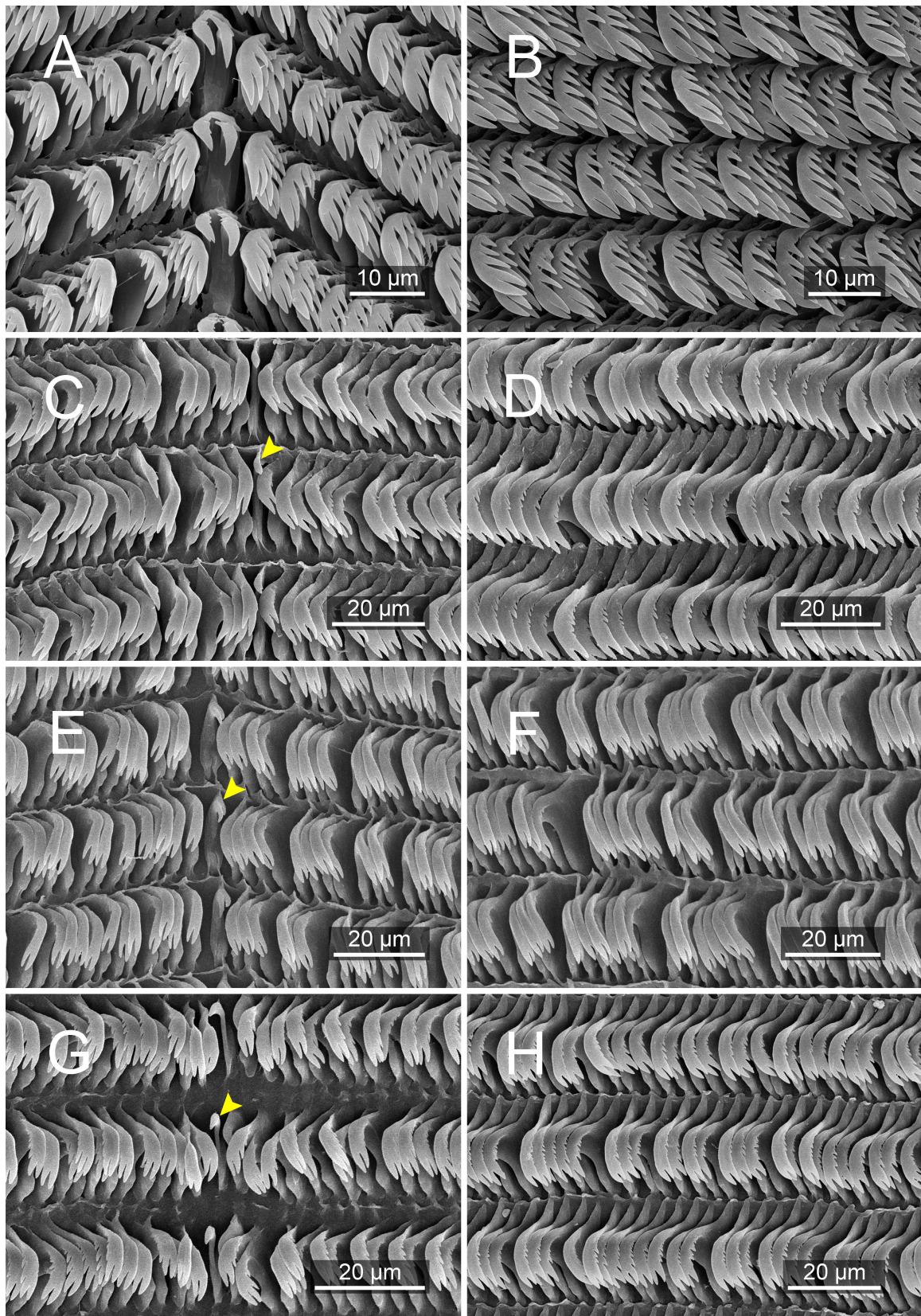


Fig. 11. Representative SEM images of the radula. A, B: *D. birmanica* CUMZ 14233. C, D: *D. levicula* CUMZ 14253. E, F: *D. erratica* CUMZ 14234. G, H: *D. siamensis* CUMZ 14232. Yellow arrow indicates the central tooth.

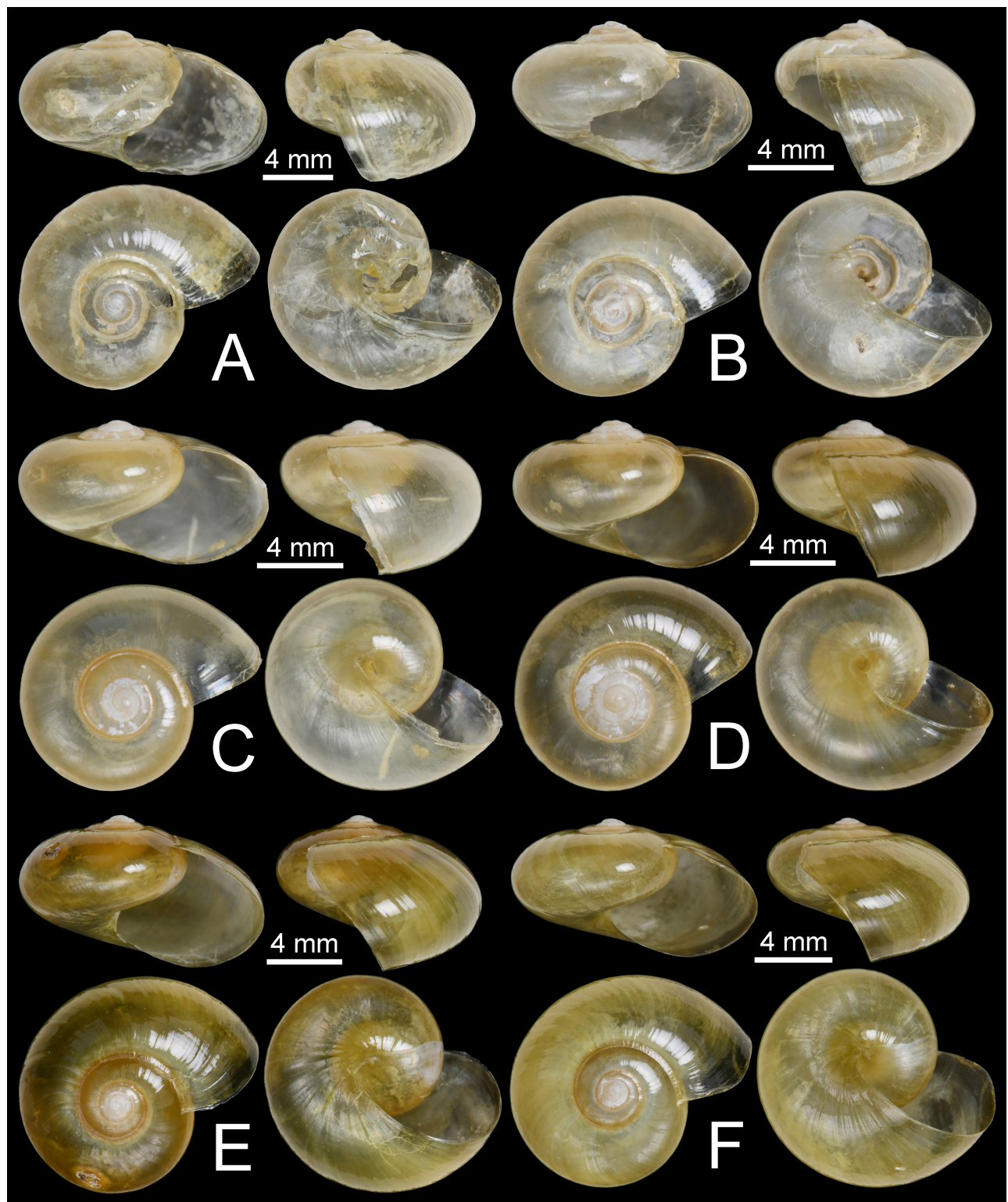


Fig. 12. Shells of *Durgella* species. A, B: *D. libas* CUMZ 14236. C, D: *D. pentata* sp. nov.; C: holotype CUMZ 14239; D: paratype CUMZ 14240. E, F: *D. nulla* sp. nov.; E: holotype CUMZ 14227; F: paratype CUMZ 14228.

expanded near umbilicus. Umbilicus minute.

Genital organs (Fig. 14). Atrium (at) enlarged and very short. Penis (p) slightly long, enlarged with irregular shape, and with thin penial sheath encircling from atrium to almost middle of penis. Inner sculpture of penis uniform throughout with small conical penial

pilasters (pp). Epiphallus (e1 + e2) same as penis length but its diameter much narrower; e1 rather long and slender; e2 shorter and bulbous. Inner sculpture: e1 with small longitudinal dash-like pilasters, and e2 with one large longitudinal pilaster. Epiphallic caecum (ec) short, small, and oblong; penial retractor muscle

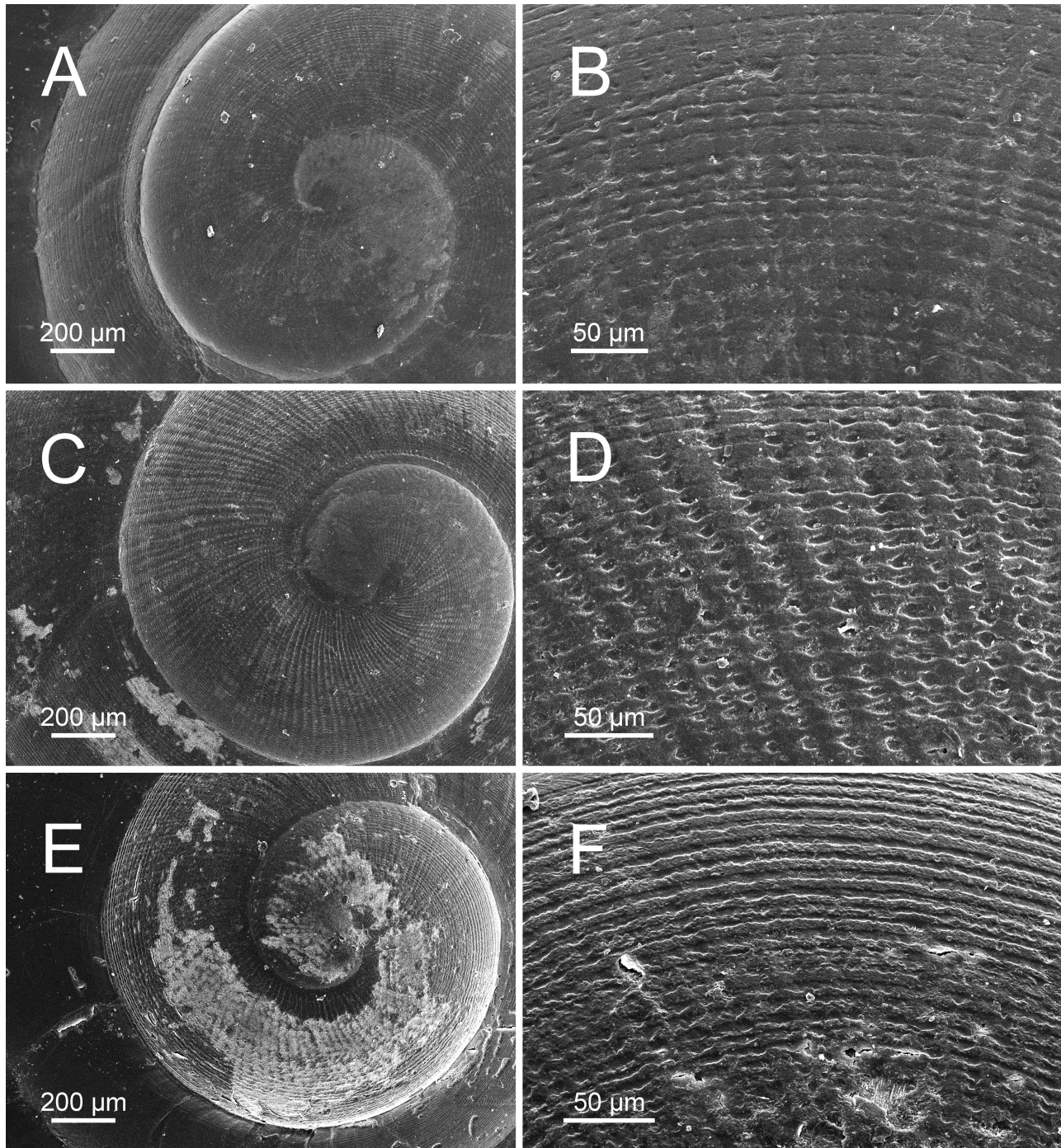


Fig. 13. Microsculpture of *Durgella* shells: protoconch and early teleoconch (first column), and close-up view of protoconch (second column). A, B: *D. libas* CUMZ 14236. C, D: *D. pentata* sp. nov. paratype CUMZ 14240. E, F: *D. nulla* sp. nov. paratype CUMZ 14228.

(prm) thick and attached at tip of epiphallic caecum. Vas deferens (vd) long and thin tube. Vagina (v) very short or nearly absent. Dart apparatus (da) rather short, enlarged cylindrical, and connected to atrium chamber. Gametolytic duct (gd) proximally enlarged and tapering

to smaller tube distally; gametolytic sac (gs) enlarged and bulbous. Free oviduct (fo) slightly shorter than penis; proximally enlarged and bulbous; distal part cylindrical. Oviduct enlarged lobules; prostate gland running alongside oviduct.

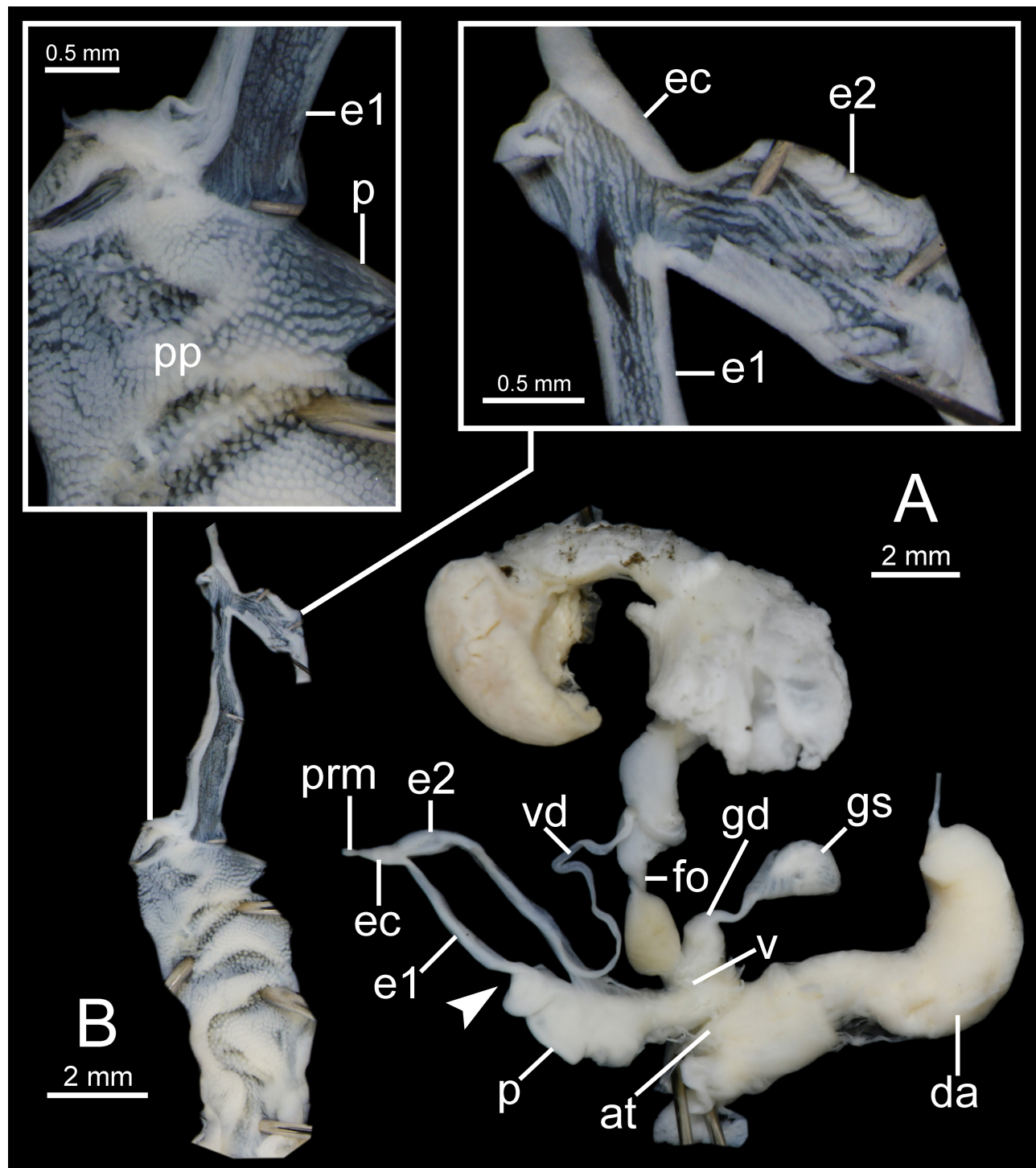


Fig. 14. Genitalia of *Durgella libas* CUMZ 14236. A: general view of the genital system and B: internal structure of the penis and epiphallus. White arrow indicates the end of the penis.

Radula (Fig. 17A, B). Teeth pectiniform, arrangement and shape similar to those of *D. levicula*, and with half row *ca.* 430 teeth. Central tooth very reduced to tiny unicuspid. Lateromarginal teeth elongated bicuspid and outer edge serrated with several tiny cusps. Outermost teeth shorter than inner teeth.

External appearance (Figs. 3F, 4A). Posterior body with pale reddish-brown to light yellow-brown on dorsal and light yellow near foot margin; anterior body light yellow or creamy. Four mantle extensions well-developed and creamy. Caudal horn raised, large, and reddish-brown.

Distribution: The species is known from Chiang Mai Province, northern Thailand (Fig. 1) and the newly collected samples suggest that this species prefers habitats in high mountainous areas.

Remarks: Solem (1966) listed the specimens from Ban Kao and Sai Yok [both from Kanchanaburi Province, western Thailand] as this species. However, we have collected many *Durgella* specimens from these two localities and found that the soft body colour, shells, and genital morphology are as those of *D. levicula* instead. Therefore, we conclude that *D. libas* is probably restricted to northern Thailand.

***Durgella pentata* Pholyotha & Panha, sp. nov.**

(Figs. 1, 3G, 4B, 12C, D, 13C, D, 15, 17C, D)

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Type material: *Holotype* CUMZ 14239 (Fig. 12C; width 11.5 mm, height 6.7 mm). *Paratypes* same locality as holotype: CUMZ 14240 (52 preserved specimens; Fig. 12D; width 11.0 mm, height 6.5 mm), 14241 (24 preserved specimens), NHMUK (2 shells).

Other material examined: **THAILAND:** Wat Tham Klaeb (Wat Tham Nguang Chang), Chiang Dao District, Chiang Mai Province (19°33'32.3"N, 99°03'46.2"E): CUMZ 14242 (7 preserved specimens). Pha Daeng Cave-Luang Cave, Chiang Dao District, Chiang Mai Province (19°34'40.7"N, 99°03'43.4"E): CUMZ 14243 (1 preserved specimen). Ban Pang Mayao, Chiang Dao District, Chiang Mai Province (19°26'10.5"N, 99°04'09.2"E): CUMZ 14244 (20 preserved specimens).

Type locality: Tham Chiang Dao, Chiang Dao District, Chiang Mai Province, Thailand (19°23'37.5"N, 98°55'39.6"E).

Diagnosis: Shell depressedly subglobose, thin, polished, dark yellow with a creamy tinge, and aperture roundly lunate, broader than high; animal with five mantle extensions; genitalia with very short vagina, small epiphallic caecum, short gametolytic duct, and very large dart apparatus.

Description: Shell (Figs. 12C, D, 13C, D). Shell depressedly subglobose, small to medium (width up to 11.7 mm, height up to 7.2 mm), transparent, polished, smooth, and yellowish-corneous or dark yellow with a creamy tinge. Protoconch surface sculptured with faint spiral furrows and regular strong malleation (Fig. 13C, D). Spire slightly elevated; suture impressed. Whorls 4–4½, convex, rapidly increasing; last whorl enlarged and well-rounded. Aperture oblique, diagonal, roundly lunate, width greater than height; peristome simple. Columellar edge thin and little expanded near umbilicus. Umbilicus minute.

Genital organs (Fig. 15). Atrium (at) enlarged and very short. Penis (p) long, cylindrical, and with thick penial sheath encircling about half of penis length. Inner sculpture of penis with longitudinal penial ridges from proximal to near middle and then transforming to small conical penial pilasters (pp). Epiphallus (e1 + e2) slightly shorter than penis; e1 cylindrical and narrower than penis; e2 short and bulbous shape. Inner sculpture: e1 with one thickened longitudinal fold running from proximal to near middle; e2 distally with dense papillae, and one thickened longitudinal pilaster. Epiphallic caecum (ec) short and small; penial retractor muscle (prm) thick and attached at tip of epiphallic caecum. Vas deferens (vd) long and slender tube. Vagina (v) very short or inconspicuous. Dart apparatus (da) very large, long cylindrical, and connected to atrium chamber. Gametolytic duct (gd) short, about half of penis length, proximally enlarged and then tapering to smaller and slender tube; gametolytic sac (gs) enlarged and bulbous. Free oviduct (fo) shorter than penis; proximally enlarged and bulbous; distal part shorter and cylindrical. Oviduct enlarged lobules; prostate gland running alongside oviduct.

Radula (Fig. 17C, D). Teeth pectiniform and numerous with half row *ca.* 380 teeth. Central tooth reduced to bicuspid. Lateromarginal teeth elongated bicuspid, unclear separation between endocone and ectocone and outer edge serrated with inconspicuous cusps. Outermost marginal teeth shorter, smaller, and more conspicuous serrated cusps than inner teeth.

External appearance (Figs. 3G, 4B). Dorsal of posterior body yellow to dark brown and then transforming to light yellow below foot margin; anterior body light yellowish. Five mantle extensions well-developed and creamy. Caudal horn raised, large, and yellowish-brown to dark brown.

Etymology: The specific name “*pentata*” is from the Greek word meaning five, referring to the presence of five mantle extensions.

Distribution: The new species is known from Tham Chiang Dao and the vicinity of Chiang Dao District, Chiang Mai Province, northern Thailand

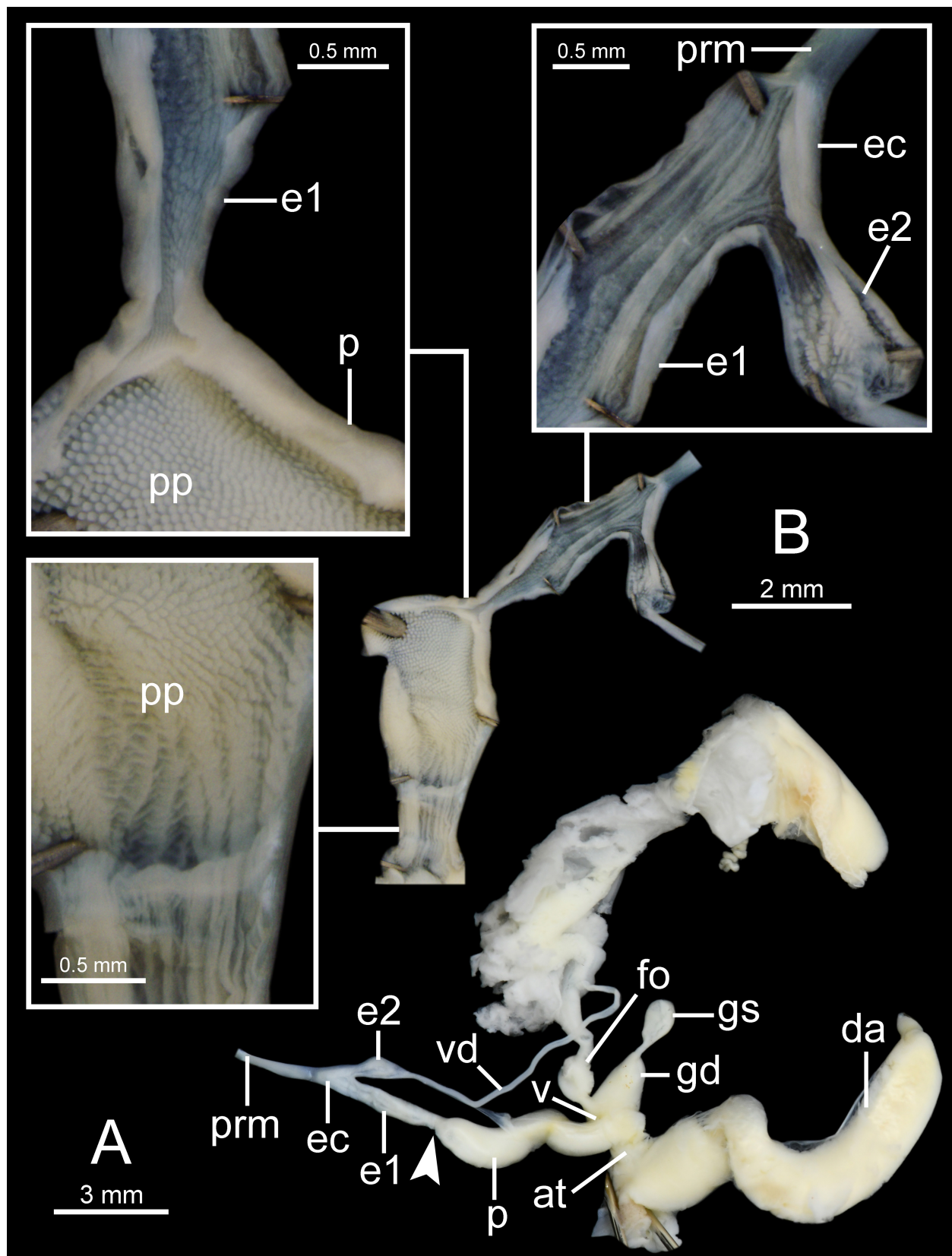


Fig. 15. Genitalia of *Durgella pentata* sp. nov. paratype CUMZ 14240. A: general view of the genital system and B: internal structure of the penis and epiphallus. White arrow indicates the end of the penis.

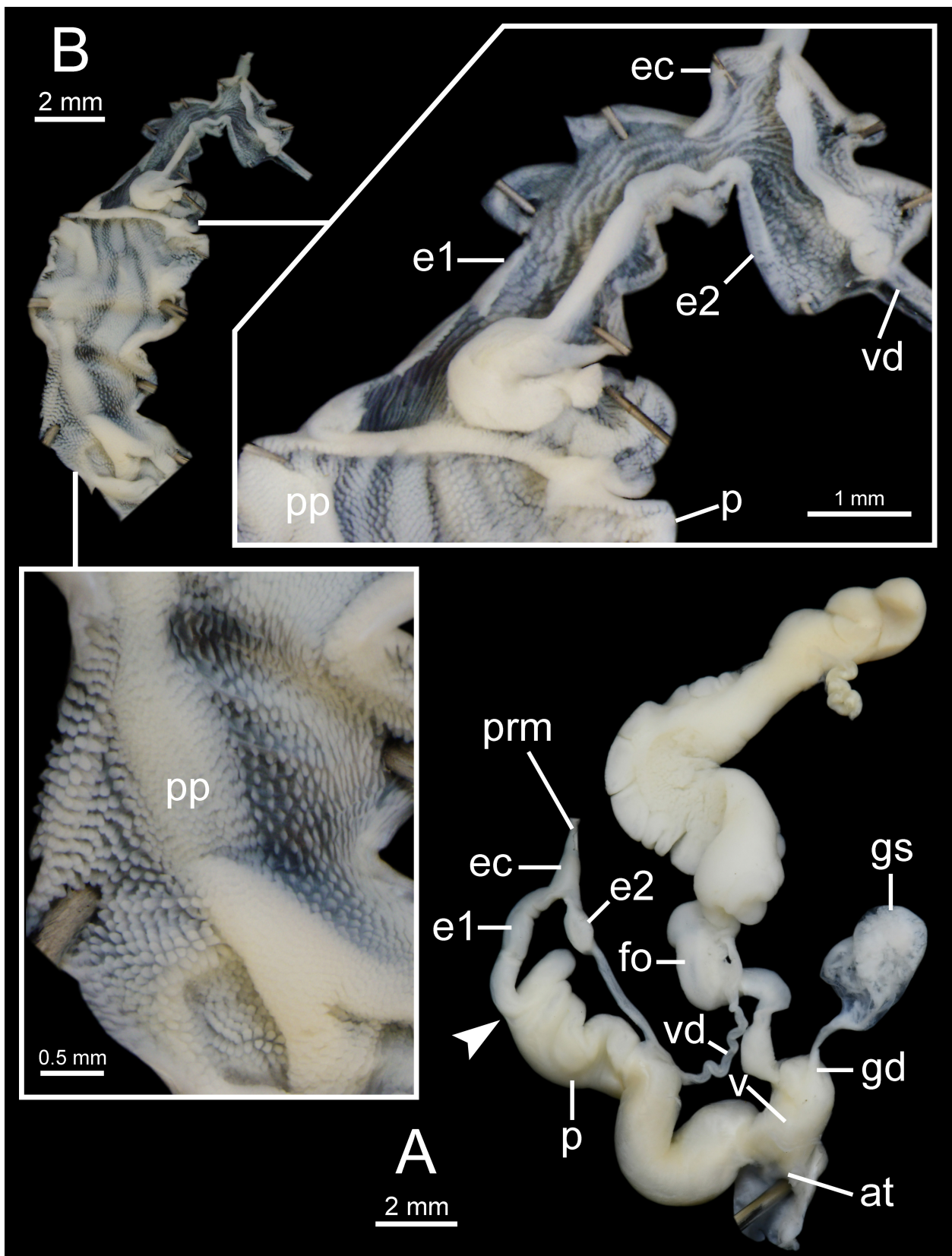


Fig. 16. Genitalia of *Durgella nulla* sp. nov. paratype CUMZ 14228. A: general view of the genital system and B: internal structure of the penis and epiphallus. White arrow indicates the end of the penis.

(Fig. 1).

Remarks: *Durgella pentata* sp. nov. differs from *D. levicula*, *D. erratica*, *D. siamensis*, and *D. libas* in the presence of five mantle extensions, while the other species have four mantle extensions. This new species

also differs from the others by having a protoconch sculptured with strong malleation, while *D. levicula*, *D. erratica*, and *D. siamensis* have rather smooth or faint spiral furrows without malleation, and *D. libas* has spiral furrows with faint malleation.

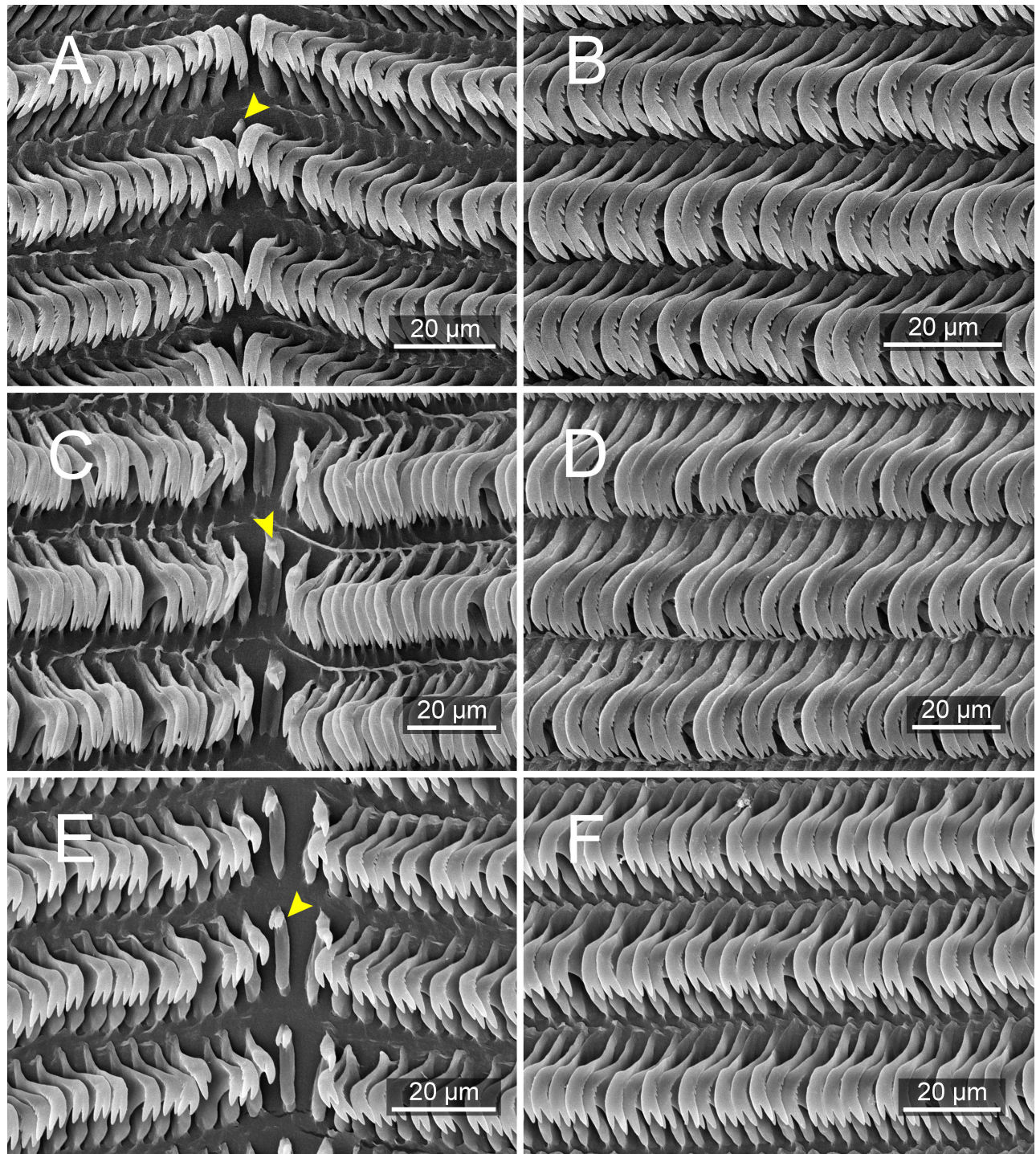


Fig. 17. Representative SEM images of the radula. A, B: *D. libas* CUMZ 14238. C, D: *D. pentata* sp. nov. paratype CUMZ 14240. E, F: *D. nulla* sp. nov. paratype CUMZ 14228. Yellow arrow indicates the central tooth.

Compared with *D. libas*, the species with the nearest geographic distribution, this new species possesses a smaller penis, shorter epiphallus, and inner penile structure with proximal longitudinal ridges transforming to distal small conical shapes. In contrast, *D. libas* has a larger penis, longer epiphallus, and inner penile sculpture with small conical shapes throughout the entire chamber.

In contrast to the other species with five mantle lobes (*D. birmanica* and *D. concinna*), this new species has a larger shell, lower spire, and more enlarged dart apparatus than *D. birmanica*. Compared with *D. concinna*, this new species has a larger and thinner shell with a minute umbilicus, and without a descending body whorl near the aperture.

***Durgella nulla* Pholyotha & Panha, sp. nov.**

(Figs. 1, 3H, 4C, D, 12E, F, 13E, F, 16, 17E, F)
 urn:lsid:zoobank.org:act:0C470A9B-2B16-489F-B8BA-017009FACC56

Type material: Holotype CUMZ 14227 (Fig. 11E; width 12.9 mm, height 7.6 mm). *Paratypes* same locality as holotype: CUMZ 14228 (19 preserved specimens; Fig. 11F; width 12.9 mm, height 7.1 mm), NHMUK (2 shells).

Other material examined: **THAILAND**: Wat Tham Pha Pu, Mueang District, Loei Province (17°34'43.4"N, 101°42'37.2"E): CUMZ 14229 (8 preserved specimens). Wat Tham Pha Sing, Wang Saphung District, Loei Province (17°17'28.0"N, 101°49'40.1"E): CUMZ 14230 (1 preserved specimen). Wat Tham Phupha Thamsathit, Suwannakhuha District, Nong Bua Lam Phu Province (17°37'38.4"N, 102°10'15.3"E): CUMZ 14231 (12 preserved specimens).

Type locality: Phu Pha Lom, Mueang District, Loei Province, Thailand (17°33'15.9"N, 101°52'04.9"E).

Diagnosis: Shell depressedly subglobose, membranous, polished, dark yellowish with olive tinge; animal with two different colours: upper body dark brown or blackish and from lower body to foot margin creamy; four mantle extensions; genitalia with very large penis, short gametolytic duct, and without dart apparatus.

Description: Shell (Figs. 12E, F, 13E, F). Shell depressedly subglobose, medium to large (width up to 13.5 mm, height up to 7.6 mm), transparent, smooth, very thin and fragile, polished, and dark yellowish with olive tinge. Protoconch surface sculptured with strong spiral furrows with or without malleation on furrows (Fig. 13E, F). Spire slightly elevated; suture little impressed. Whorls $4\frac{1}{4}$ – $4\frac{1}{2}$, convex, rapidly increasing; body whorl enlarged and rounded; aperture oblique,

roundly lunate, diagonal, width greater than height; peristome simple. Columellar margin thin and little expanded near umbilicus. Umbilicus minute.

Genital organs (Fig. 16). Atrium (at) enlarged and very short. Penis (p) long, enlarged cylindrical, and with thin penial sheath encircling about half of penis length. Inner sculpture of penis with uniformly small conical penial pilasters (pp) throughout. Epiphallus (e1 + e2) shorter than half of penis length; e1 more slender and narrower than penis; e2 shorter and bulbous in shape. Inner sculpture: e1 with small conical knobs arranged on longitudinal folds, and one very large and smooth longitudinal fold; e2 distally with dense papillae, and one large longitudinal fold. Epiphallic caecum (ec) short, slightly enlarged; penial retractor muscle (prm) thickened and attached at tip of epiphallic caecum. Vas deferens (vd) long and thin tube. Vagina (v) long and enlarged cylindrical. Dart apparatus (da) absent. Gametolytic duct (gd) short, proximally enlarged and then tapering to a small tube; gametolytic sac (gs) enlarged and bulbous shape. Free oviduct (fo) about half of penis length, proximally enlarged, and distally cylindrical. Oviduct enlarged lobules; prostate gland running alongside oviduct.

Radula (Fig. 17E, F). Teeth pectiniform and numerous with half row *ca.* 460 teeth. Central tooth very reduced to tiny bicuspid. Lateromarginal teeth elongated bicuspid and outer edge serrated with 3 to 6 tiny cusps, gradually diminishing in size outwards. Outermost marginal teeth shorter, smaller, and with more conspicuous serrated cusps than inner teeth.

External appearance (Figs. 3H, 4C, D). Posterior body with dark brown or blackish on dorsal and immediately transforming to yellow or cream near foot margin; anterior body light yellowish-brown to dark brown. Four mantle extensions well-developed and light cream in colour. Caudal horn raised, large, and blackish.

Etymology: The specific name “*nulla*” is from the Latin adjective meaning not any, none, nobody, or no, and refers to the absence of dart apparatus.

Distribution: The new species is known from Loei and Nong Bua Lam Phu provinces in northeastern Thailand (Fig. 1).

Remarks: Comparing the two new species described herein, *D. nulla* sp. nov. has four mantle extensions and no dart apparatus, whereas *D. pentata* sp. nov. has five mantle extensions and a large dart apparatus. *Durgella nulla* sp. nov. also differs from all other species from Thailand and Myanmar in the absence of a dart apparatus, whereas this organ appears in all other recognised species examined in this study.

Among species without a dart apparatus, *D. assamica* from Assam and *D. rogersi* from the Andaman Islands have a smaller subglobose shell with a long

gametolytic organ (Godwin-Austen 1881; Blanford and Godwin-Austen 1908), whereas *D. nulla* sp. nov. possesses a larger and depressedly subglobose shell with a short gametolytic organ and is locally endemic to Thailand.

DISCUSSION

In mainland Southeast Asia, there has long been confusion about the taxonomy of land snails that have a vitriniform or globosely helicoid shell with three to four whorls. These snails are called semislugs, and are members of the genera *Cryptaustenia*, *Cryptosemelus*, *Durgella*, and *Megaustenia* (Blanford and Godwin-Austen 1908; Solem 1966; Schileyko 2002 2003; Pholyotha et al. 2021a). Generally, these genera have similar shells, but the appearance of the live animal, genitalia, and radulae can be used to differentiate them (see Table 1). The presence of a caudal horn is a character shared among *Cryptaustenia*, *Durgella*, and *Megaustenia*, whereas it is absent in *Cryptosemelus*. By the absence of a flagellum, *Durgella* resembles *Cryptaustenia* and differs from *Megaustenia*. Most of the genitalia characters of *Cryptaustenia* and *Durgella* overlap, but radular morphology is a powerful character in distinguishing these two genera. *Durgella* has a radula with a much-reduced central tooth and numerous minute pectiniform lateromarginal teeth, whereas *Cryptaustenia* has a radula with large and triangular-shaped central tooth, bi- or tricuspid lateral teeth, and bicuspid marginal teeth (Blanford and Godwin-Austen 1908; Solem 1966; Schileyko 2002 2003; Pholyotha et al. 2021a).

The southern Indian semislug genus *Satiella* Blanford & Godwin-Austen, 1908 also has a shell, mantle extensions, and pectiniform radula like those of *Durgella*, but it differs from the latter genus in some anatomical traits. The genitalia of *Satiella* have no dart apparatus and the penis has a penial verge (Blanford and Godwin-Austen 1908), whereas the dart apparatus of most *Durgella* species is generally well-developed (except disappeared in three species: *D. assamica*, *D. rogersi*, and *D. nulla* sp. nov.), and the penis does not have a penial verge (Blanford and Godwin-Austen 1908; Solem 1966). Because of the lack of molecular information, the relationships between *Durgella* and related genera cannot be explained in this study. In the future, comprehensive information on the anatomical structure and molecular phylogenetics might help to elucidate their evolutionary relationships.

Unlike the external shell morphology, which is very reduced and conserved, the soft part anatomies, including the mantle extensions, genitalia, and radula,

are taxonomically informative and can be used to differentiate *Durgella* species. Our results show that this genus can be divided into three groups. First, the species with four mantle extensions (Fig. 2B) and a well-developed dart apparatus include *D. erratica*, *D. levicula*, *D. siamensis*, and *D. libas*. Second, the species with five mantle extensions (Fig. 2D) and the presence of a dart apparatus include *D. birmanica* and *D. pentata* sp. nov. Lastly, the single species with four mantle extensions and no dart apparatus is *D. nulla* sp. nov. Unfortunately, this subdivision cannot currently be applied to other *Durgella* species because the mantle extensions were only briefly mentioned in previous works, although the dart apparatus was more obviously observed. Of all *Durgella* species for which genitalia have been examined, *D. assamica* and *D. rogersi* lack a dart apparatus, whereas *D. mairangensis* has a well-developed dart apparatus (Godwin-Austen 1881 1883 1898 1907 1910; Blanford and Godwin-Austen 1908; Solem 1966). As a next step towards enhancing our understanding of the evolution of the dart apparatus as well as the presence of both four and five mantle extensions occurring within the same genus, the genus *Durgella* is an interesting and suitable candidate for investigation. Future research on the genus should include more material and will also require incorporation of molecular phylogenetic analyses.

Based on the previous records and the recent field survey data, all *Durgella* species show high levels of local endemism, except for *D. levicula*. Regarding the distribution of *D. levicula*, although several localities in Thailand were surveyed, only some localities in the western, southern and eastern parts of the country were found to harbour this species. The geographical populations of *D. levicula* are possibly shaped by sea level fluctuation in the last glacial periods recorded in tree-dwelling *Amphidromus* snails (Prasankok et al. 2007), or by association with human activities reported in ground-dwelling *Sarika* snails (Pholyotha et al. 2022) and freshwater *Pomacea* snails (Dumidae et al. 2021). However, no molecular phylogenetic analysis of *D. levicula* is available, and so further research on this issue would help elucidate the phylogeographical history of this species.

CONCLUSIONS

Our findings have demonstrated that at least nine valid species of the genus *Durgella* occur in Thailand and Myanmar, of which two species from Thailand, *D. pentata* sp. nov. and *D. nulla* sp. nov., are newly described herein. All species previously recorded from Myanmar and Thailand have been listed and re-described

in this study, namely *D. birmanica*, *D. erratica*, *D. levicula*, *D. libas*, *D. raphiellus*, *D. siamensis*, and *D. concinna*. Unfortunately, our intensive survey did not yield new material for *D. concinna* from Myanmar or *D. raphiellus* from Thailand, and the current taxonomy of these two species remains doubtful.

Acknowledgments: This work and the new species names were registered with ZooBank under urn:lsid:zoobank.org:pub:47CC0281-1C88-4C0B-84BD-26B7F082D535. We are grateful to all members of the Animal Systematics Research Unit, Chulalongkorn University for their kind help during field trips and technical support, and the Fauna & Flora International (FFI) and Ministry of Natural Resources and Environmental Conservation Forest Department, Myanmar for the preparation of permission documents and data collection in Myanmar. We are also indebted to J. Ablett, F. Naggs, and H. Taylor (NHM, London); R. Janssen, K.-O. Nagel, and S. Hof (SMF, Frankfurt); and T. von Rintelen and C. Zorn (ZMB, Berlin) for allowing the authors to examine the collections and photographs. This study was approved by the Chulalongkorn University Animal Care and Use Committee (CU-ACUC; approval number 1723018). This study was mainly funded through grants received from The Thailand Research Fund (TRF-DPG628001) and the Center of Excellence on Biodiversity (BDC-PG2-160012), and was also supported by the Ratchadapisek Somphot Fund for Postdoctoral Fellowship, Chulalongkorn University to S.P. and A.P. In addition, special thanks go to anonymous reviewers for providing valuable comments and suggestions on the manuscript.

Authors' contributions: AP and CS collected specimens, created illustrations and species descriptions, and wrote the manuscript. NL and SP obtained funds for this work. All authors participated in revising the manuscript and approved the final version.

Competing interests: All authors declare that they have no conflict of interest.

Availability of data and materials: All specimens are deposited in museum collections stated in the paper.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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