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The operculate micro land snail genus *Dicharax* Kobelt & Möllendorff, 1900 (Caenogastropoda, Alycaeidae) in Thailand, with description of new species

Parin Jirapatrasilp[1], Barna Páll-Gergely[2], Chirasak Sutcharit[1], Piyoros Tongkerd[1]

1 *Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand*

2 *Plant Protection Institute, Centre for Agricultural Research, Herman Ottó út 15, H-1022 Budapest, Hungary*

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Corresponding author: Piyoros Tongkerd (piyorose@hotmail.com)

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Abstract

This study reviews the *Dicharax* species in Thailand. Altogether ten *Dicharax* species are reported, four of which are new to science and described herein. They are *Dicharax borealis* Jirapatrasilp & Páll-Gergely **sp. nov.**, *Dicharax burchi* Jirapatrasilp & Páll-Gergely **sp. nov.**, *Dicharax panhai* Jirapatrasilp & Páll-Gergely **sp. nov.** and *Dicharax pongrati* Jirapatrasilp & Tongkerd **sp. nov.** *Alycaeus davisi* Godwin-Austen, 1914 is regarded as a junior subjective synonym of *Alycaeus cucullatus* Theobald, 1870 (= *D. cucullatus*) based on a similar depressed-conical shell shape, a long sutural tube and a sharp swelling behind the peristome. Furthermore, the type locality of *Alycaeus pratatensis* Panha & Burch, 1997 (= *D. pratatensis*) had to be amended. Most important characters to distinguish *Dicharax* species are the general shell shape and relative lengths of teleoconch regions, whereas the spiral striation of R1, the shape of swelling of R3, the outer peristome crenulation and protrusion, and the exterior opercular sculpture show large intraspecific variability.

Key Words

Cyclophoroidea, Gastropoda, Mollusca, taxonomy

Introduction

Alycaeidae Blanford, 1864 is a family of cyclophoroidean operculate land snails. The alycaeid shell is characterized by a sutural tube that corresponds with numerous perpendicular microtunnels as described by Páll-Gergely et al. (2016). This taxon has been treated as a subfamily of Cyclophoridae by several authors including Bouchet et al. (2017), whereas it has been treated as a family of its own by other sources (e.g. Egorov 2013). Based on the unique gas exchange system of the shell and the presence of synapomorphic genital anatomical characters, Páll-Gergely et al. (2020b) proposed to treat this taxon at the family level, which is followed here. This family ranges from western India to Japan, including Indonesia in the south. This group is known to be particularly diverse in three regions, (1) the southeastern Himalaya, (2) Peninsular Malaysia and Sumatra, and (3) northern Vietnam, northern Laos and southern China (Páll-Gergely et al. 2017, 2020b, Aravind and Páll-Gergely 2018, Páll-Gergely 2019, Sajan et al. 2020). In Southeast Asia, alycaeid taxa from Laos, Vietnam, and Peninsular Malaysia have received attention in the past few years (Foon and Liew 2017, Páll-Gergely et al. 2017), whereas the taxa from Thailand have remained poorly studied. Eleven alycaeid species were described from Thailand before 2010, mostly classified as members of *Alycaeus* Baird, 1850 (BEDO 2017; Table 1). However, reports of some species in the checklist of Thai land snails (Solem 1966, Hemmen and Hemmen 2001) are questionable as these were listed without illustrations to confirm their correct identification (i.e. *Dicharax diplochilus* (Möllendorff, 1887), *Dicharax fimbriatus* (Bavay & Dautzenberg, 1912) and *Dioryx bacca* (Pfeiffer, 1863)).

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Table 1. List of species in the family Alycaeidae reported from Thailand. Some species recorded in Solem (1966) and Hemmen and Hemmen (2001) are exempted due to dubious identification.

Species [Original genus]	Type locality	Distribution records	References
Alycaeus conformis Fulton, 1902	Perak State, Malaysia	**Malaysia:** Kelantan, Pahang, Selangor and Johor **Thailand:** Bangpae waterfall, Phuket	Fulton (1902), Páll-Gergely et al. (2016, 2020b), Foon and Liew (2017)
Alycaeus gibbosulus Stoliczka, 1872	Penang Island, Malaysia	Peninsular Malaysia **Thailand:** Khao Chong, Trang	Stoliczka (1872), Habe (1965), Foon and Liew (2017), Páll-Gergely et al. (2020b)
Alycaeus somwangi Dumrongrojwattana & Maassen, 2008	Lub Lae Cave, Chonburi Province, Eastern Thailand	Only the type locality	Dumrongrojwattana and Maassen (2008), Páll-Gergely et al. (2020b)
Chamalycaeus canaliculatus (Möllendorff, 1894) [*Alycaeus*]	Samui Islands, Gulf of Siam	Only the type locality	Möllendorff (1894), Páll-Gergely et al. (2017, 2020b)
Dicharax caudapiscis Páll-Gergely & Hunyadi, 2018	Wat Tham Pla, approx. 9 km south-southwest from Mae Sai, Chiang Rai Province, Northern Thailand	Only the type locality	Páll-Gergely and Hunyadi (2018), Páll-Gergely et al. (2020b)
Dicharax cucullatus (Theobald, 1870) (syn. nov. *Alycaeus davisi* Godwin-Austen, 1914) [*Alycaeus*]	Shan States	**Myanmar:** Shan State **Thailand:** Doi Chiang Dao, Doi Ang Khang and Doi Inthanon, Chiang Mai	Theobald (1870), Godwin-Austen (1914), Páll-Gergely et al. (2020b), this study
Dicharax notus (Godwin-Austen, 1914) [*Alycaeus*]	Fort Stedman, Burma	**Myanmar:** Shan State **Thailand:** Tham Luang Sa Koen, Nan	Godwin-Austen (1914), Páll-Gergely et al. (2020b), this study
Dicharax omissus (Godwin-Austen, 1914) [*Alycaeus*]	Siam and Shan boundary	**Myanmar:** Shan State **Thailand:** Tham Mae Lana, Mae Hong Son	Godwin-Austen (1914). Páll-Gergely et al. (2020b), this study
Dicharax pratatensis (Panha & Burch, 1997) [*Alycaeus*]	Doi Chiang Dao, Chiang Mai Province, Northern Thailand [non Pratat cave, Erawan National Park, Kanchanaburi Province]	Only the type locality	Panha and Burch (1997), this study
Dicharax stuparum Páll-Gergely & Hunyadi, 2018	50 m before Wat Phra That Doi Tung, around the car park, Doi Tung, Chiang Rai Province, Northern Thailand	Only the type locality	Páll-Gergely and Hunyadi (2018), Páll-Gergely et al. (2020b)
Dicharax borealis Jirapatrasilp & Páll-Gergely sp. nov.	Tham Ban Luang, Doi Ang Khang, Chiang Mai Province, Northern Thailand	Only the type locality	This study
Dicharax burchi Jirapatrasilp & Páll-Gergely sp. nov.	Tham Phaya Nakharat, Khon Kaen Province, Northeastern Thailand	**Myanmar:** Hsihseng centre, Shan State **Thailand:** Doi Chiang Dao, Chiang Mai and Ban Soppong, Mae Hong Son	This study
Dicharax panhai Jirapatrasilp & Páll-Gergely sp. nov.	Pratat cave, Erawan National Park, Kanchanaburi Province, Western Thailand	Only the type locality	Páll-Gergely et al. (2020b), this study
Dicharax pongrati Jirapatrasilp & Tongkerd sp. nov.	Doi Chiang Dao, Chiang Mai Province, Northern Thailand	Only the type locality	This study
Dioryx distortus (Haines, 1855) [*Cyclostoma*]	Siam	Thailand	Haines (1855), Kobelt (1902), Páll-Gergely et al. (2020b)
Stomacosmethis christae (Maassen, 2006) [*Alycaeus*]	at km 117.6 of road # 4 (Krabi – Phang Nga), Krabi Province, Southern Thailand	Only the type locality	Maassen (2006), Páll-Gergely et al. (2020b)
Stomacosmethis matchacheepiorum (Dumrongrojwattana & Maassen, 2008) [*Alycaeus*]	Khao Pratun Cave, Rayong Province, Eastern Thailand	Only the type locality	Dumrongrojwattana and Maassen (2008), Páll-Gergely et al. (2020b)
Stomacosmethis perakensis (Crosse, 1879) [*Alycaeus*]	Buket Pondong, Perak	**Malaysia:** Kedah and Perak **Thailand:** Banang Pupo, Yala	Crosse (1879), Foon and Liew (2017), Páll-Gergely et al. (2020b)
Stomacosmethis roebeleni (Möllendorff, 1894) [*Alycaeus*]	Samui Islands, Gulf of Siam	**Malaysia:** Perlis **Thailand:** Patthalung	Möllendorff (1894), Foon and Liew (2017), Páll-Gergely et al. (2020b)
Stomacosmethis somnueki (Panha & Patamakanthin, 2001) (syn. *A. huberi* Thach, 2018) [*Alycaeus*]	Ao Luk limestone areas, Krabi Province, Southern Thailand	Only the type locality	Panha and Patamakanthin (2001), Thach (2018), Páll-Gergely et al. (2020a, b)

Dicharax Kobelt & Möllendorff, 1900 (replacement name for *Charax* Benson, 1859, non *Charax* Scopoli, 1777 [Pisces]) is one of the seven genera of the Alycaeidae (Páll-Gergely et al. 2020b). It was originally described as a subgenus of *Alycaeus*, and was diagnosed as follows: "constriction broad, contiguous to the aperture, and divided more or less remotely from it, across the whorl, by a ridge which is hollow internally" (Benson 1859). That diagnosis was adopted by later authors (Kobelt 1902, Gude 1921, Egorov 2013). Páll-Gergely et al. (2017) elevated *Dicharax*

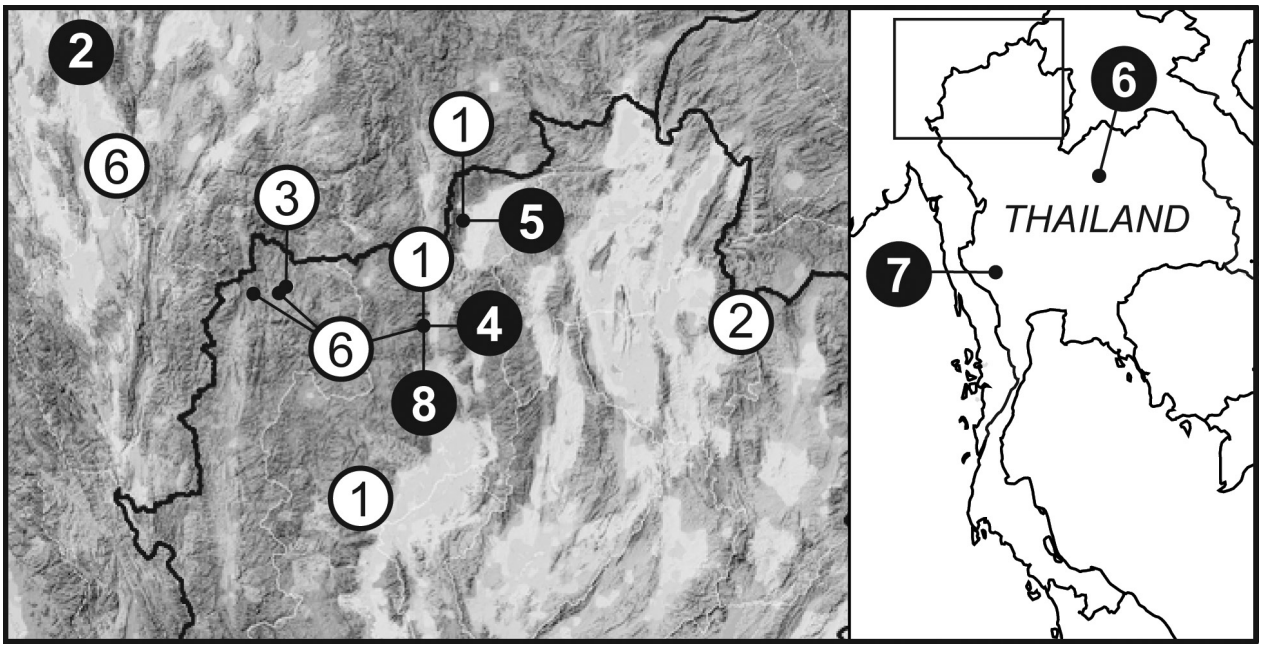

Figure 1. Geographical position of the type localities (white number in black circle) and other examined localities (black number in white circle) of *Dicharax* spp. in this study. No. **1**: *D. cucullatus*, **2**: *D. notus*, **3**: *D. omissus*, **4**: *D. pratatensis*, **5**: *D. borealis* sp. nov., **6**: *D. burchi* sp. nov., **7**: *D. panhai* sp. nov., **8**: *D. pongrati* sp. nov. The type localities of *D. cucullatus* and *D. omissus* (Shan States and Siam and Shan boundary, respectively) are general and not plotted in the figure.

to a full genus and questioned the conspicuous hollow ridge (termed swelling by Godwin-Austen 1914 and Páll-Gergely et al. 2017) as feature diagnostic of the genus, and defined *Dicharax* as having a low protoconch and lacking spiral striation on the entire shell. *Dicharax caudapiscis* Páll-Gergely & Hunyadi, 2018 and *D. stuparum* Páll-Gergely & Hunyadi, 2018 were described from Northern Thailand subsequently (Páll-Gergely and Hunyadi 2018). Following the genus definition of Páll-Gergely et al. (2017), as many as 164 nominal species were assigned to *Dicharax*, including three *Alycaeus* species that were formerly recorded from Thailand or "Siam", namely *A. davisi* Godwin-Austen, 1914, *A. omissus* Godwin-Austen, 1914, and *A. pratatensis* Panha & Burch, 1997 (Páll-Gergely et al. 2020b).

In the present paper, based on the examination of the CUMZ collections, the type locality of *D. pratatensis* has to be amended. The specimens from Pratat Cave, Kanchanaburi, western Thailand (the former type locality of *A. pratatensis*), are now described as a new species. Three additional species are also new to science and described from northern and northeastern Thailand. We also provide diagnoses to three nominal species based on the types and newly examined populations.

Material and methods

This study is based on material collected from throughout Thailand since 1996 which is now deposited in the collection of the Chulalongkorn University (CUMZ) (Fig. 1). Additional specimens from HA and UF were examined by BP-G. Live specimens were mostly collected from crevices in limestone outcrops, while empty shells were collected from the ground. Shells were measured using digital (scanning electron microscope) SEM images. The counting of the shell whorls (to the closest 1/8 whorl) follows Kerney and Cameron (1979). The nomenclature of external alycaeid shell features follows Páll-Gergely et al. (2017). The teleoconch is divided into three regions, namely; R1 (the beginning of the teleoconch to the beginning of the differently ribbed region along the suture), R2 (the differently ribbed area to the constriction) and R3 (the constriction to the peristome) (see Páll-Gergely et al. 2017: fig. 1a, b). The swelling on R3 is classified into either blunt (R3 gradually swollen; Páll-Gergely et al. (2017: fig. 2q)) or sharp (R3 abruptly swollen and the swelling is narrower and more elevated; Páll-Gergely et al. (2017: fig. 2r)). The peristome is double, and its two parts are termed "inner peristome" or "inner lip" and "outer peristome" or "outer lip" based on Liew et al. (2014: fig. 10) and Páll-Gergely et al. (2017).

Institutional abbreviations

CUMZ, Chulalongkorn University Museum of Zoology, Bangkok; FMNH, Field Museum of Natural History, Chicago; HA, Collection of András Hunyadi, Budapest; HNHM, Hungarian Natural History Museum, Budapest; NHM, The Natural History Museum, London; NHMUK, when citing specimen lots deposited in the NHM; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; UF, Florida Museum of Natural History, University of Florida, Gainesville; UMMZ, University of Michigan Museum of Zoology, Ann Arbor.

Other abbreviations

SH, shell height; SW, shell width.

Meaning of some Thai locality words

"Doi", Mount; "Tham", Cave; "Wat", Temple.

Results

Taxonomy and systematics

Family Alycaeidae Blanford, 1864

Dicharax Kobelt & Möllendorff, 1900

Alycaeus (*Charax*) Benson, 1859: 177; Pfeiffer 1865: 43, 44; Kobelt and Möllendorff 1897: 149, 150 (invalid; preoccupied by *Charax* Scopoli, 1777 [Pisces]).

Alycaeus (*Dicharax*) Kobelt & Möllendorff, 1900: 186 (replacement name for *Charax* Benson, 1859, non *Charax* Scopoli, 1777 [Pisces]); Kobelt 1902: 364; Gude 1921: 236.

Chamalycaeus (*Dicharax*) – Thiele 1929: 108; Wenz 1938: 478, fig. 1225; Egorov 2013: 37, fig. 66.

Chamalycaeus (*Sigmacharax*) Kuroda, 1943: 8; Egorov 2013: 37, 38.

Chamalycaeus (*Cipangocharax*) Kuroda, 1943: 11; Egorov 2013: 36.

Chamalycaeus (*Awalycaeus*) Kuroda, 1951: 73, 74; Egorov 2013: 35, 36.

Dicharax – Páll-Gergely and Asami 2017: 14; Páll-Gergely et al. 2017: 10, fig. 5; Páll-Gergely et al. 2020b: 48–53.

Type species. *Alycaeus hebes* Benson, 1857, by subsequent designation (Gude 1921: 236).

Dicharax cucullatus (Theobald, 1870)

Figs 2, 3, 4A, B, 5A, 6H

Alycaeus cucullatus Theobald, 1870: 396, 397, pl. 18, fig. 2. Type locality: Shan States [Myanmar]. Hanley and Theobald 1874: 39, pl. 96, figs 1, 4; Reeve 1878: pl. 2, sp. 12; Godwin-Austen 1914: 407, pl. 155, fig. 5; Tarruella and Domènech 2011: 72.

Alycaeus (*Charax*) *cucullatus* – Kobelt and Möllendorff 1897: 150.

Alycaeus davisi Godwin-Austen, 1914: 408, pl. 148, fig. 9, 9a. Type locality: Siam and Shan State boundary. New synonym.

Alycaeus (*Dicharax*) *cucullatus* – Kobelt 1902: 367, 368; Gude 1921: 244, 245.

Alycaeus (*Chamalycaeus*) *davisi* – Gude 1921: 226.

Dicharax cucullatus – Páll-Gergely et al. 2020b: 57, 58.

Dicharax davisi – Páll-Gergely et al. 2020b: 58.

Type material examined. ***Syntypes*** of *Alycaeus cucullatus* NHMUK 1888.12.4.951–952 from Shan States (2 shells; Fig. 2A). ***Syntypes*** of *Alycaeus davisi* NHMUK 1903.7.1.1630 from Shan States (4 shells; Fig. 2B).

Other material examined. CUMZ 7421 from Doi Chiang Dao, Chiang Mai Province, Thailand, 19°14'26.7"N, 98°52'49.8"E, 24–28 May 1997, coll. S. Panha, J.B. Burch, P. Dumrongrojwattana (1 shell; Figs 3A, 6H). CUMZ 5071 from Tham Ban Luang, Doi Ang Khang, Chiang Mai Province, Thailand, 19°52'13.7"N, 99°02'44.1"E, 17 Mar. 2000, coll. S. Panha, P. Tongkerd (34 shells; Figs 2C, D, 3B). CUMZ 7422 from Siribhum Waterfall, Doi Inthanon, Chiang Mai Province, Thailand, 18°32'48.5"N, 98°30'44.0"E, 13–15 Oct. 2009, coll. C. Sutcharit (71 shells; Figs 3C, 4A, B). CUMZ 7423 from Wachirathan Waterfall, Doi Inthanon, Chiang Mai Province, Thailand, 18°32'31.0"N, 98°35'53.8"E, 21 Jan. 2015, coll. P. Jirapatrasilp, R. Srisonchai, W. Siriwut, T. Seesamut, C. Sutcharit (10 shells; Fig. 3D). CUMZ 7424 from Doi Inthanon, 2,000 m a.s.l, Chiang Mai Province, Thailand, 18°35'08.5"N, 98°29'03.4"E, 21 Jan. 2015, coll. P. Jirapatrasilp, R. Srisonchai, W. Siriwut, T. Seesamut, C. Sutcharit (3 shells; Fig. 3E). CUMZ 7432 from Doi Inthanon, ~1,700–2,000 m a.s.l, Chiang Mai Province, Thailand, 18°35'08.5"N, 98°29'03.4"E, 5–6 Oct. 2020, coll. P. Jirapatrasilp, A. Pholyotha, W. Siriwut, N. Likhitrakarn, C. Sutcharit (6 specimens in ethanol; Fig. 5A).

Diagnosis. Shell medium-sized (SH up to 3.5 mm, SW up to 5.5 mm), depressed-conical. Spire ca. 1/5 of shell height. R1 with regular, strong ribs; R2 longer than R3; R2 with 49–57 ribs. R3 with sharp swelling near aperture. Aperture round. Inner peristome with four to five indentations, always with parieto-columellar indentation, sometimes weak at basal. Outer peristome fringed, slightly reflected but not conspicuous. Umbilicus round. Operculum multispiral with elevated lamella.

Distribution. Shan State, Myanmar (Gude 1921), and Chiang Mai Province, Thailand.

Remarks. This species was originally described from Shan State and diagnosed by its fringed peristome with five indentations (Theobald 1870). Later, Godwin-Austen (1914) described *Alycaeus davisi* with a less fringed peristome with four indentations from Siam and Shan State boundary. Upon examining the type specimens, both species agree in having a depressed-conical shell shape, a long R2 and a sharp swelling of R3 near the aperture (Fig. 2A, B). The types of *A. cucullatus* differ from those of *A. davisi* in having a more fringed peristome and more indentations. However, based on recently collected specimens, we conclude that this variation is to be interpreted as intraspecific as we found that this crenulation may vary even within the same population from nearly smooth (Fig. 4A) via slight (Fig. 4B) to strong (Fig. 2C, D). Because both species were described from the same geographical region, *Alycaeus davisi* is herein regarded as a junior subjective synonym of *Alycaeus cucullatus*. Refer to Discussion regarding the color of living specimen and variation in spiral striation.

Dicharax cucullatus differs from other species with similar shell shape and fringed peristome, i.e. *D. anthostoma* (Möllendorff, 1885) (Páll-Gergely et al. 2017: fig. 19a, b) from China, *D. ataranensis* (Godwin-Austen, 1914)

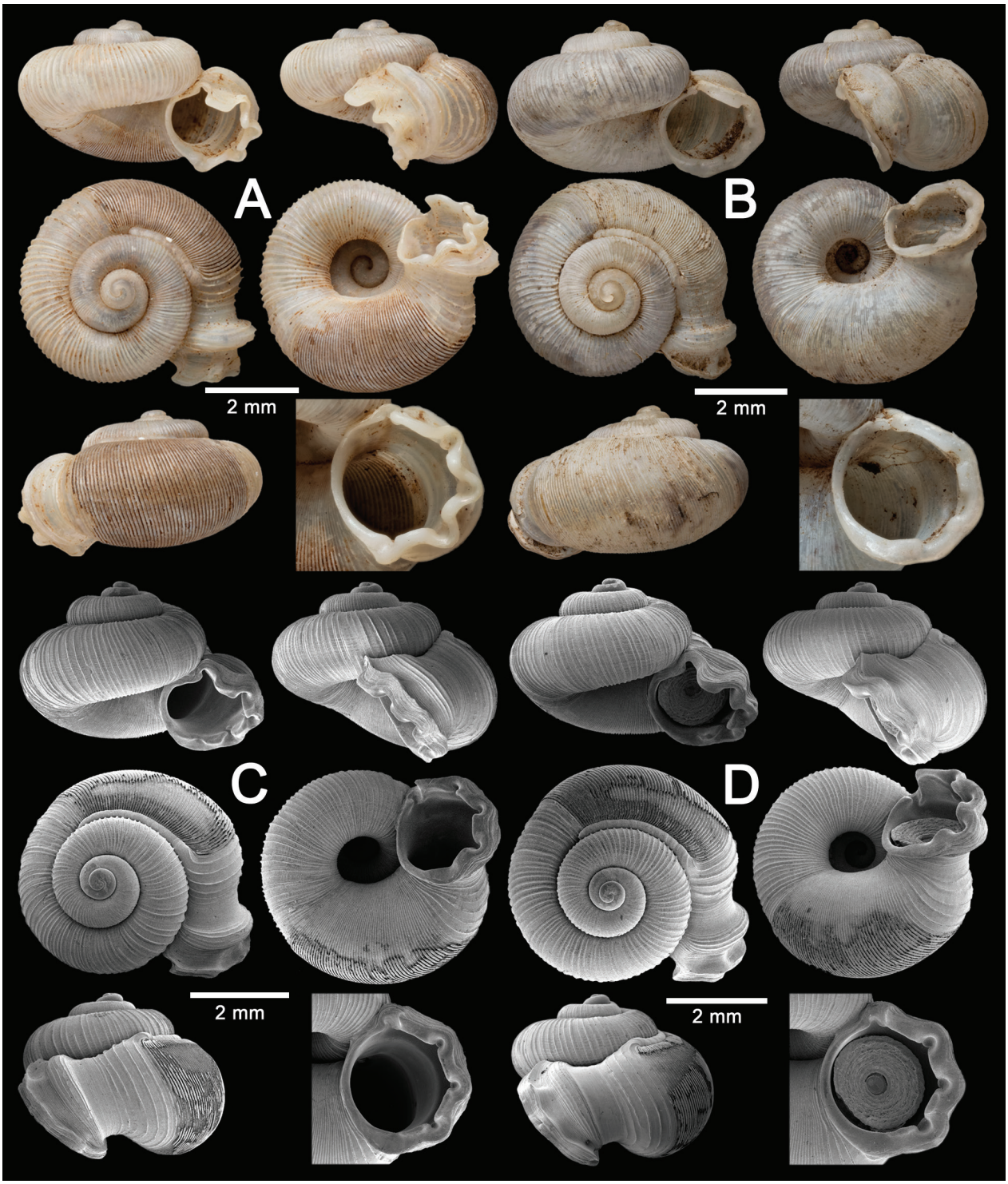

Figure 2. *Dicharax cucullatus* **A.** Syntype of *Alycaeus cucullatus*, NHMUK 1888.12.4.951; **B.** Syntype of *Alycaeus davisi*, NHMUK 1903.7.1.1630; **C, D.** Specimens CUMZ 5071 from Tham Ban Luang, Doi Ang Khang, Chiang Mai Province. Close-up images of the aperture not to scale. Photo: NHM (**A, B.**).

(Páll-Gergely et al. 2020b: figs 11, 12) from Myanmar and *D. fimbriatus* (Páll-Gergely et al. 2017: figs 35–37) from China and Vietnam in possessing a sharp swelling nearer to the aperture. In addition, *D. cucullatus* differs from *D. anthostoma* in having shorter distance between the inner and outer peristomes and from *D. ataranensis* in possessing a shorter R3. Although *D. tangmaiensis* (Chen & Zhang, 2001) (Páll-Gergely et al. 2020b: fig. 14) from Tongmai Town, Bomi County, Tibet Autonomous Region, China is very similar to *D. cucullatus*, the distance between both species' type localities is approximately 1,100 km. Thus, the status of *D. tangmaiensis* needs further scrutiny.

Some specimens from Doi Inthanon possess a more depressed shell with a lower spire, a very low swelling of R3

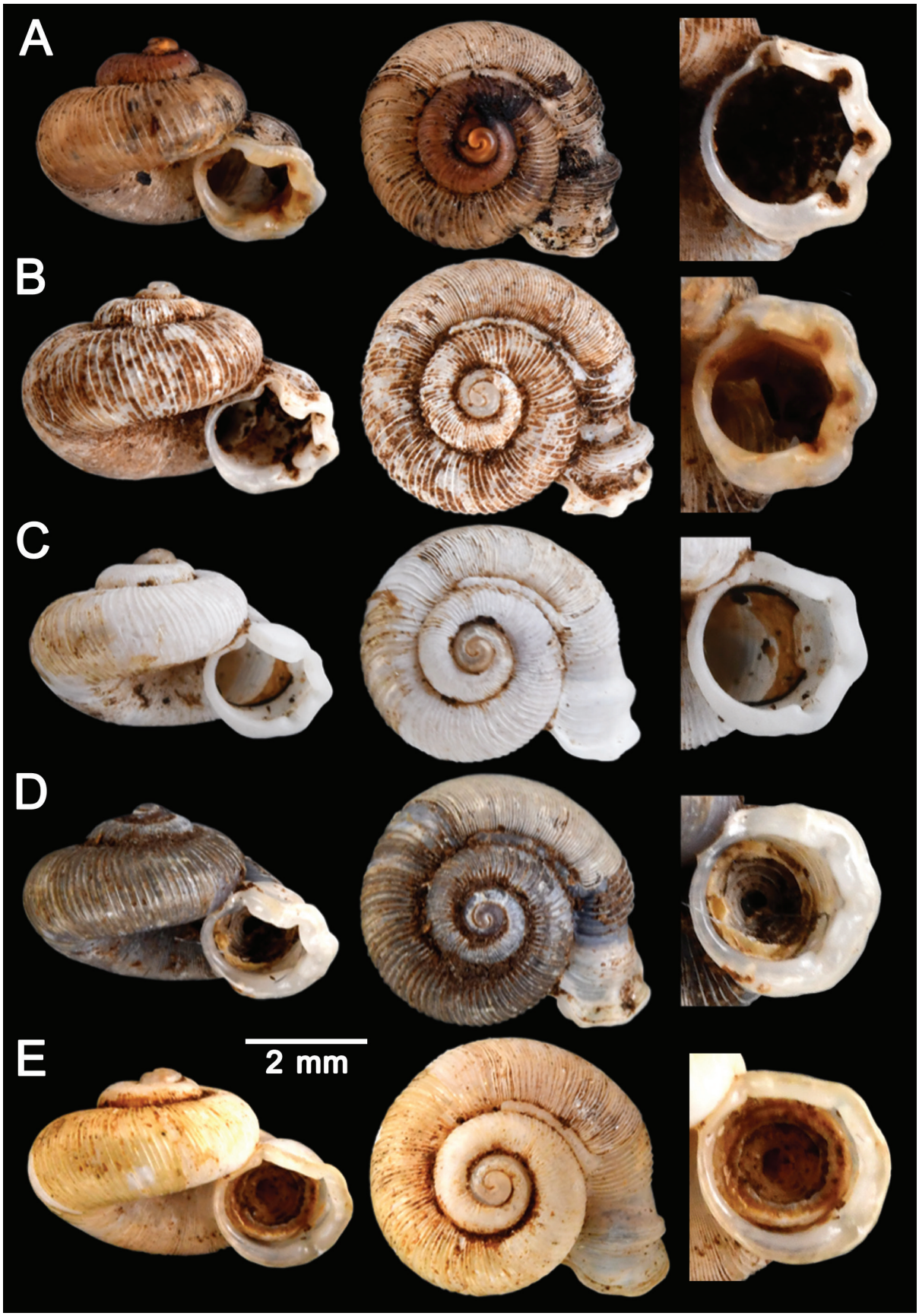

Figure 3. *Dicharax cucullatus* from Chiang Mai Province **A.** Specimen CUMZ 7421 from Doi Chiang Dao; **B.** Specimen CUMZ 5071 from Tham Ban Luang, Doi Ang Khang; **C.** Specimen CUMZ 7422 from Siribhum Waterfall, Doi Inthanon; **D.** Specimen CUMZ 7423 from Wachirathan Waterfall, Doi Inthanon; **E.** Specimen CUMZ 7424 from Doi Inthanon, 2000 m a.s.l. Close-up images of the aperture not to scale.

and a nearly smooth inner peristome (Fig. 4A) very similar to *D. borealis* sp. nov. However, *D. cucullatus* could be distinguished from *D. borealis* sp. nov. by a round aperture and always having a parieto-columellar indentation.

Dicharax notus (Godwin-Austen, 1914)

Figs 4C, D, 5B, 6E, 7A, B

Alycaeus notus Godwin-Austen, 1914: 411, pl. 155, fig. 12. Type locality: Fort Stedman, Burma [Maing Thauk or Mine Thauk located in the east side of Inle Lake south of Nyaungshwe, Nyaungshwe Township, Taunggyi District, Shan State, Myanmar].

Alycaeus (*Dicharax*) *notus* – Gude 1921: 262.

Dicharax notus – Páll-Gergely et al. 2020b: 69.

Type material examined. ***Syntypes*** NHMUK 1903.7.1.3065 from Fort Stedman (15 shells; Fig. 4C).

Other material examined. CUMZ 7425 from Tham Luang Sa Koen, Nan Province, Thailand, 19°22'00.1"N, 100°32'28.4"E, 19 Jan. 2017, coll. C. Sutcharit, A. Pholyotha (174 shells and 13 specimens in ethanol; Figs 4D, 5B, 6E, 7A, B).

Diagnosis. Shell small (SH up to 2.2 mm, SW up to 3.6 mm), depressed-conical. Spire ca. 1/5 of shell height. R1 with regular ribs; R2 as long as or shorter than R3; R2 with 48–50 ribs. R3 with low blunt central swelling, more elevated in newly examined population. Aperture round. Inner peristome without indentation, with parieto-columellar angle in newly examined population. Outer peristome expanded, reflected. Umbilicus round. Operculum multispiral either with or without elevated lamella.

Distribution. Shan State, Myanmar (Gude 1921), and Nan Province, Thailand.

Remarks. Similar to *D. cristatus* (Möllendorff, 1886) from China and Vietnam as well as *D. depressus* (Bavay & Dautzenberg, 1912) and the rounded peristome morph of *D. fimbriatus* (the latter two known from Pac Kha, northern Vietnam) in shell size and shape, length of R2 and R3, and position of the swelling in R3 (Páll-Gergely et al. 2017). The specimens from Nan Province, Thailand (Fig. 4D) differ from the type specimens in having a longer R3, a more shouldered R3 swelling, a stronger descending aperture, and a parieto-columellar angle. Despite those differences, we preliminarily identified the specimens from Nan Province as *D. notus*. Refer to Discussion regarding the color of living specimen and variation in operculum morphology.

Dicharax omissus (Godwin-Austen, 1914)

Figs 6A, 8A, B

Alycaeus omissus Godwin-Austen, 1914: 411, pl. 155, fig. 13. Type locality: Siam and Shan State boundary.

Alycaeus (*Chamalycaeus*) *omissus* – Gude 1921: 231.

Dicharax (?) *omissus* – Páll-Gergely et al. 2020b: 100.

Type material examined. ***Syntypes*** NHMUK 1903.7.1.1228 from Siam & Shan boundary (2 shells; Fig. 8A).

Other material examined. CUMZ 7426 from Tham Mae La Na, Mae Hong Son Province, Thailand, 19°34'28.9"N, 98°12'57.4"E, 19 Jan. 2017, coll. C. Sutcharit (1 shell; Figs 6A, 8B).

Diagnosis. Shell very small (SH up to 1.7 mm, SW up to 2.7 mm), depressed-conical. Spire ca. 1/4 of shell height. R1 with regular, strong ribs; R2 shorter than R3; R2 with 35–36 ribs. R3 with blunt central swelling. Aperture round. Inner peristome without indentation, with beak-like basal protrusion in newly examined population. Outer peristome expanded, not reflected. Umbilicus round.

Distribution. Border region between Thailand and Myanmar (Gude 1921), and Mae Hong Son Province, Thailand.

Remarks. The specimen from Mae Hong Son Province (Fig. 8B) exhibits stronger R1 ribs and possesses a beak-like protrusion at the base of the aperture, which is absent in the syntype (Fig. 8A). Apart from these differences, this specimen is nearly identical to the syntype in terms of shell size and shape, and R2 and R3 length. In addition, the locality of this specimen lies only approximately 12 km from the boundary between Thailand and Shan State, Myanmar. We thus identify this specimen as *D. omissus*. The most similar species to *D. omissus* is *D. notus*, which is larger and has reflected outer peristome.

Dicharax pratatensis (Panha & Burch, 1997)

Figs 6B, 8C, D

Alycaeus pratatensis Panha & Burch, 1997: 119–122, fig. 2a–c. Type locality: “Tham Pratat, Erawan National Park, Kanchanaburi Province, Thailand”, hereby emended to: “Doi Chiang Dao, Chiang Mai Province, Northern Thailand”.

Type material examined. ***Holotype*** CUMZ Cy 001 (Fig. 8C), ***paratypes*** CUMZ Cy 002 (2 shells; Fig. 8D), FMNH (1 shell), NHMUK 20200324 (2 shells) and UMMZ (1 shell) from Doi Chiang Dao, Chiang Mai Province, Thailand, 19°14'26.7"N, 98°52'49.8"E, 24–28 May 1997, coll. S. Panha, J.B. Burch, P. Dumrongrojwattana.

Other material examined. CUMZ 7427 from Doi Chiang Dao, Chiang Mai Province, Thailand, 19°14'26.7"N, 98°52'49.8"E, 24–28 May 1997, coll. S. Panha, J.B. Burch, P. Dumrongrojwattana (16 shells; Fig. 6B).

Diagnosis. Shell small (SH up to 2 mm, SW up to 3.2 mm), depressed-conical. Spire ca. 1/6 of shell height. R1 with regular, very strong ribs; R2 shorter than R3; R2 with 44–51 ribs. R3 with prominent, blunt swelling near aperture, anterior slope of swelling steeper than posterior slope. Aperture round. Inner peristome thickened, protruding, with slight parieto-columellar angle. Outer peristome expanded, not reflected. Umbilicus round. Operculum multispiral.

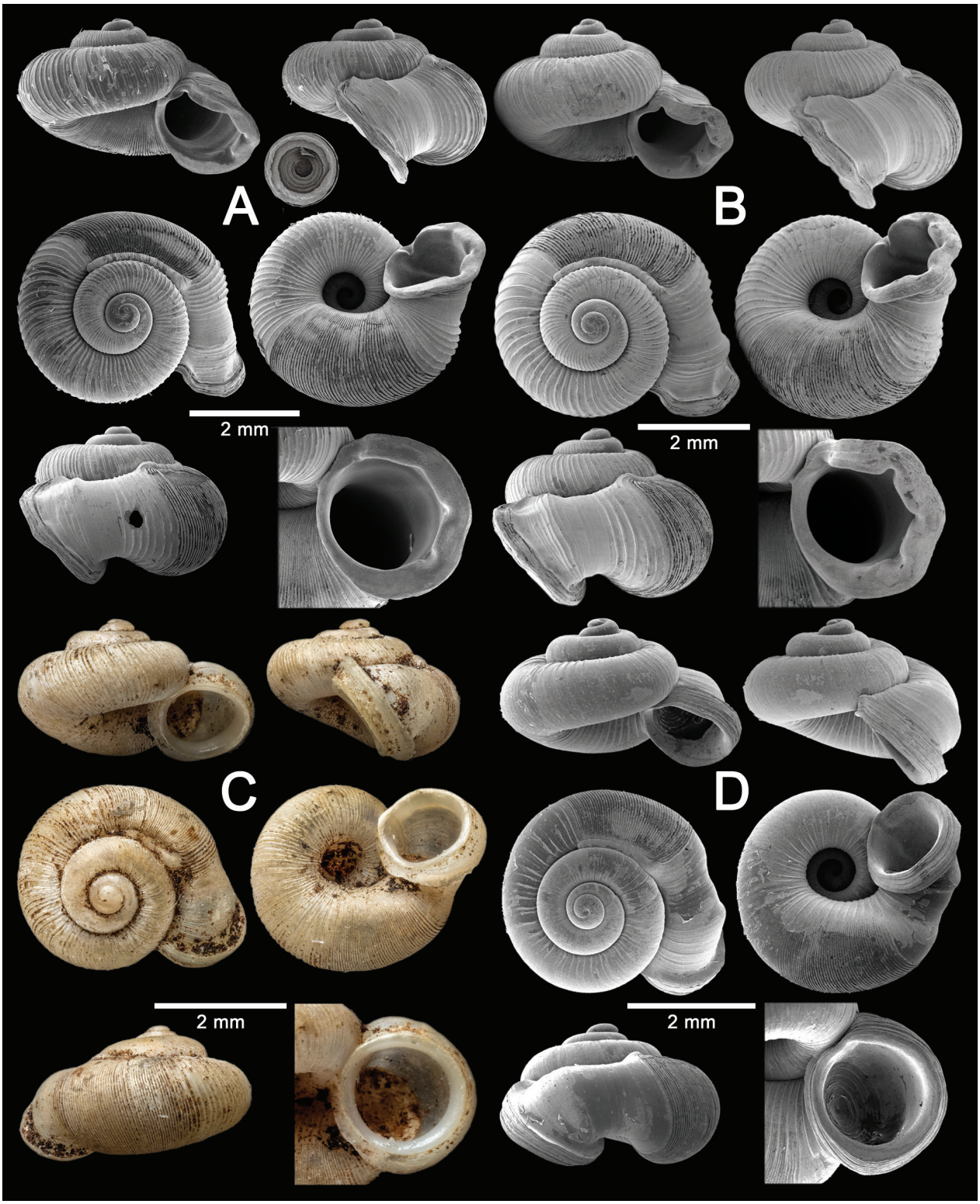

Figure 4. A, B. *Dicharax cucullatus*, specimens CUMZ 7422 from Siribhum Waterfall, Doi Inthanon, Chiang Mai Province; **A.** With operculum; **C, D.** *Dicharax notus* **C.** Syntype NHMUK 1903.7.1.3065; **D.** Specimen CUMZ 7425 from Tham Luang Sa Koen, Nan Province. Close-up images of the aperture not to scale. Photo: NHM (**C.**).

Distribution. Known only from Doi Chiang Dao, Chiang Mai Province, Thailand.

Remarks. Re-examination of the type materials (holotype Cy 001: Fig. 8C and paratypes Cy 002: Fig. 8D) deposited in CUMZ and figured in the original description (Panha and Burch 1997: fig. 2) revealed that the locality code associated with the types points to "Doi Chiang Dao". However, the locality of the paratypes of *Alycaeus pratatensis* deposited in SMF (inv. number: 331452) appears as "Tham Pratat, Erawan National Park, Kanchanaburi Province". After we compared all the type materials to the same specimen lots of both localities housed in the general CUMZ collections

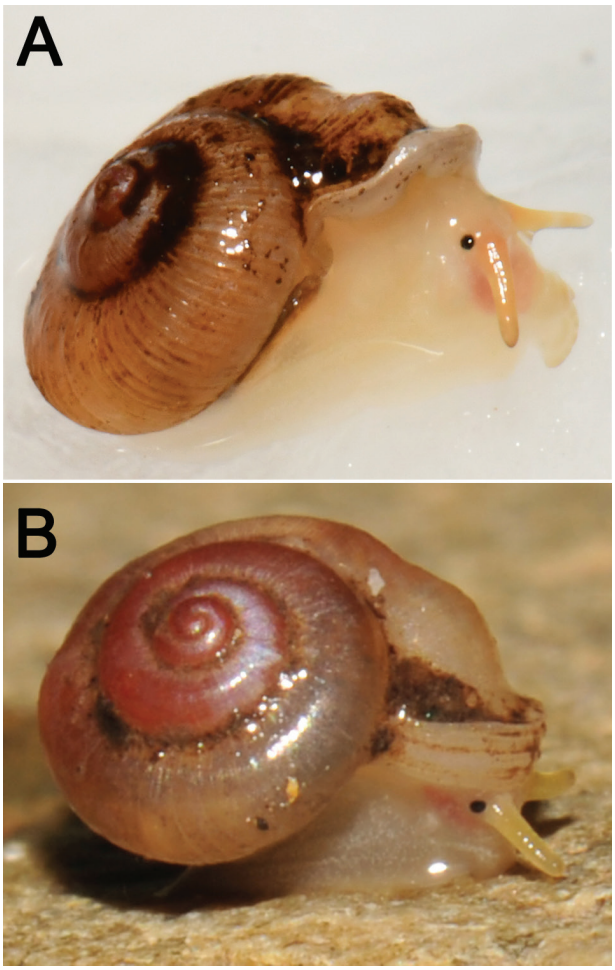

Figure 5. Living *Dicharax* specimens. **A.** *Dicharax cucullatus*, specimen CUMZ 7432 from Doi Inthanon, Chiang Mai Province; **B.** *Dicharax notus*, specimen CUMZ 7425 from Tham Luang Sa Koen, Nan Province. Both photographed in the laboratory. Not to scale. Photo: A. Pholyotha.

and communicated with S. Panha, it became evident that the type material might have been mis-allocated. We conclude that the published type locality of *A. pratatensis* (Tham Pratat, Erawan National Park, Kanchanaburi Province, Thailand) is incorrect, and another species (*Dicharax panhai* sp. nov.) lives there. Thus, the type locality of *A. pratatensis* is hereby amended to Doi Chiang Dao, Chiang Mai Province, Thailand. Páll-Gergely et al. (2020b: 71) transferred *A. pratatensis* to *Dicharax* based on the examination of paratype specimens deposited in the Senckenberg Museum (SMF 331452). However, the present study revealed that those shells and all other CUMZ specimens from Tham Pratat, Erawan National Park, Kanchanaburi Province, Thailand belong to *D. panhai* sp. nov. (see below).

***Dicharax borealis* Jirapatrasilp & Páll-Gergely, sp. nov.**

http://zoobank.org/80FC8FC0-D804-4BE6-B5F5-5CD400772BBF

Figs 6G, 9

Type material. ***Holotype*** CUMZ 5072/1 (Fig. 9), ***paratypes*** CUMZ 5072/2 (2 shells; Fig. 6G), NHMUK 20200325 (1 shell) and SMF (1 shell) from Tham Ban Luang, Doi Ang Khang, Chiang Mai Province, Thailand, 19°52'13.7"N, 99°02'44.1"E, 17 Mar. 2000, coll. S. Panha, P. Tongkerd.

Diagnosis. Shell medium-sized (SH up to 2.7 mm, SW up to 4.4 mm), depressed-conical. Spire ca. 1/6 of shell height. R1 with regular ribs; R2 twice longer than R3; R2 with ca. 72 ribs. R3 with very low, elongated swelling. Aperture oval. Inner peristome thickened, with three very shallow indentations, always without parieto-columellar indentation. Outer peristome expanded, not reflected. Umbilicus round.

Description. Shell medium-sized (SH up to 2.7 mm, SW up to 4.4 mm), depressed-conical, solid, translucent, pale yellowish. Shell outline oval in apical view, spire ca. 1/6 of shell height. Whorls ca. 4¼. Protoconch low, ca. two whorls, glossy and smooth. R1 ca. 1¾ whorls, with fine, regular ribs; with ca. 21 ribs in ¼ whorl adjoining R2, ribs sharper near suture and inside umbilicus than in middle of body whorl. Boundary between R1 and R2 distinct as R2 contains more close-set and thicker ribs than R1; R2 with ca. 72 ribs that are curved towards aperture; R2 ca. 1/3 whorl and twice longer than R3. Boundary between R2 and R3 distinct due to shallow constriction; R3 with fine growth lines; with very low and elongated swelling. Aperture oval; slightly oblique to shell axis. Peristome double with regular outer peristome. Inner peristome thick, expanded, with three very shallow indentations, always without parieto-columellar indentation. Outer peristome thinner, expanded, not reflected, multi-layered (visible mostly in lateral view). Umbilicus round, open, approximately one third of shell width. Operculum unknown.

Etymology. The specific epithet "*borealis*" refers to the occurrence of the new species from the northern mountain of Thailand.

Distribution. Known only from the type locality in Chiang Mai Province, Thailand.

Remarks. Differs from the sympatric *D. cucullatus* in having a wider shell, a rather oval outline, a shorter R3 with very low and elongated swelling, a less fringed and oval aperture and an inner peristome with three very shallow indentations, always without any parieto-columellar indentation.

***Dicharax burchi* Jirapatrasilp & Páll-Gergely, sp. nov.**

http://zoobank.org/8797FE78-84C5-4887-AF61-923C1E341734

Figs 6F, 10, 11A

Type material. ***Holotype*** CUMZ 7428/1 (Fig. 10A), ***paratypes*** CUMZ 7428/2 (1 shell and 6 specimens in ethanol; Fig. 6F), HNHM (1 shell), NHMUK 20200326 (2 shells) and SMF (2 shells) from Tham Phaya Nakharat, Khon Kaen Province, Thailand, 16°48'32.8"N, 101°57'23.9"E, 21 July 2020, coll. P. Tongkerd, A. Pholyotha.

Other material examined. UF 347279 from limestone pass 10.0 km NW Ban Soppong, Mae Hong Son Province, Thailand, 19°33.183'N, 98°11.533'E, 800 m a.s.l.,

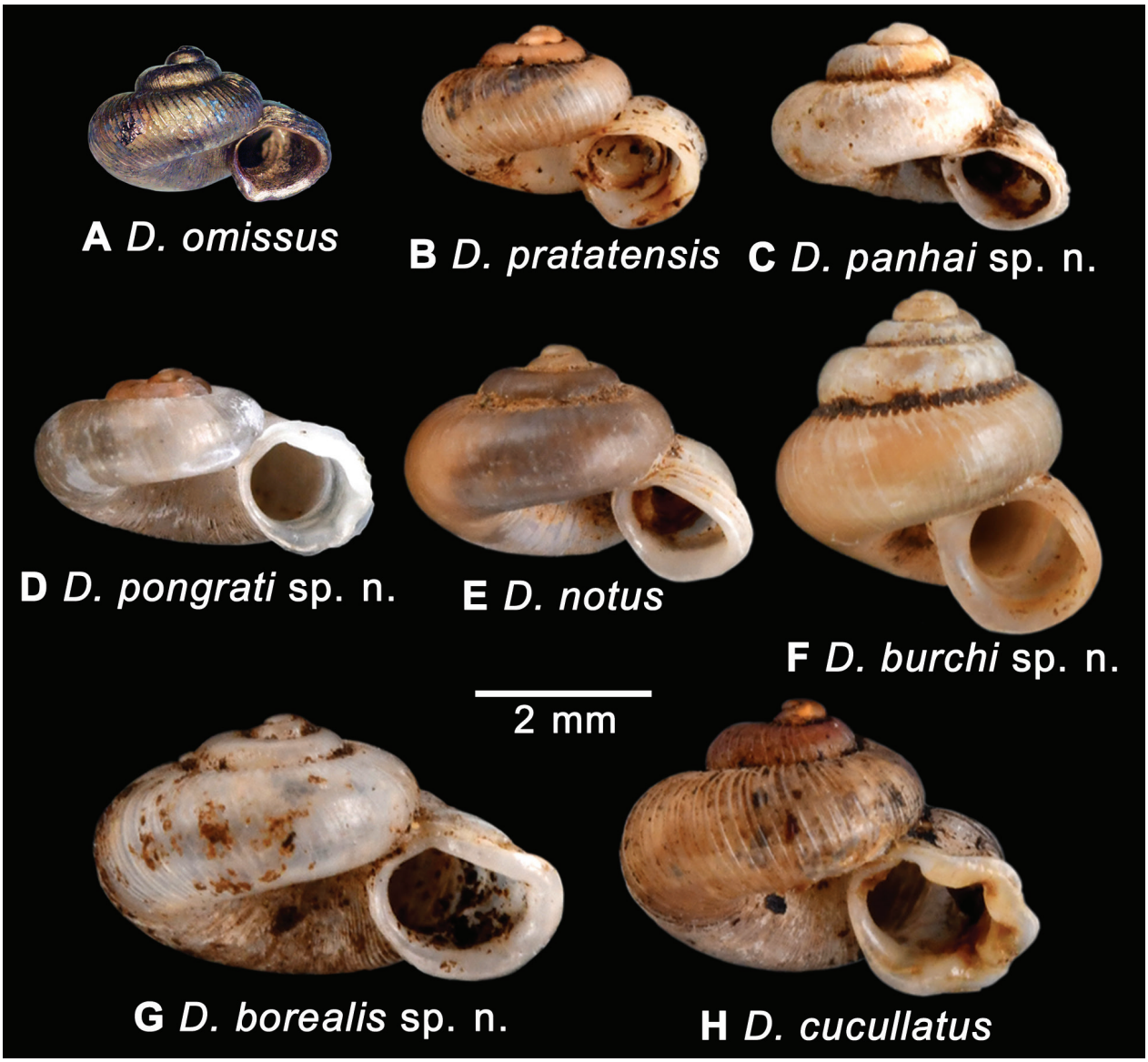

Figure 6. Synoptic view of the eight *Dicharax* taxa in Thailand. **A.** *Dicharax omissus*, specimen CUMZ 7426 (gold plated); **B.** *Dicharax pratatensis*, specimen CUMZ 7427; **C.** *Dicharax panhai* sp. nov., paratype CUMZ 7429/2; **D.** *Dicharax pongrati* sp. nov., paratype CUMZ 7430/2; **E.** *Dicharax notus*, specimen CUMZ 7425; **F.** *Dicharax burchi* sp. nov., paratype CUMZ 7428/2; **G.** *Dicharax borealis* sp. nov., paratype CUMZ 5072/2; **H.** *Dicharax cucullatus*, specimen CUMZ 7421.

23 Jun. 1987, coll. F.G. Thompson (1 shell; Fig. 10D). UF 345622 from 10.2 km WNW of Soppong, Road 1095, Mae Hong Son Province, Thailand, 19°33'N, 98°03'E, 820 m a.s.l., 20 Mar. 1988, coll. K. Auffenberg (3 shells). HA (locality code: 2018/41) from Hsihseng centre E ca. 6 km, right side of rd. + 500 m on unpaved rd., limestone hill, Shan State, Myanmar, 20°8.002'N, 97°18.024'E, 1000 m a.s.l., 7 Oct. 2018, coll. A. Hunyadi, K. Okubo, J.U. Otani (1 shell; Fig. 11A). CUMZ 7431 from Doi Chiang Dao, Chiang Mai Province, Thailand, 19°14'26.7"N, 98°52'49.8"E, 24–28 May 1997, coll. S. Panha, J.B. Burch, P. Dumrongrojwattana (4 shells; Fig. 10B, C).

Diagnosis. Shell small (SH up to 3.6 mm, SW up to 3.5 mm), conical. Spire ca. ½ of shell height. R1 with regular, strong ribs; R2 as long as R3; R2 with 36–43 ribs. R3 with either sharp and narrow or blunt and more elongated swelling in the middle of R3 or near aperture. Aperture round. Inner peristome blunt, slightly protruding. Outer peristome expanded (most conspicuously at the upper palatal position and near the umbilicus), reflected. Umbilicus partly or entirely covered by expanded outer peristome. Operculum multispiral.

Description. Shell small (SH up to 3.6 mm, SW up to 3.5 mm), conical, solid, semitransparent, yellowish to pale orange. Shell outline round in apical view, spire ca. ½ of shell height. Whorls approaching 5, last whorl large. Protoconch low, ca. two whorls, glossy and smooth. R1 ca. 2 whorls, with regular, strong ribs; with ca. 21 ribs in ¼ whorl adjoining R2, ribs sharper near suture and flatter near umbilicus, most prominent when approaching R2. Boundary between R1 and R2 distinct as R2 contains more close-set ribs than R1; R2 with 36–43 ribs that are

Figure 7. Close-up images of the aperture showing the operculum *in situ*. **A, B.** *Dicharax notus*, specimens CUMZ 7425; **A.** Without lamella; **B.** With elevated lamella; **C.** *Dicharax pongrati* sp. nov., paratype CUMZ 7430/2, without lamella, probably lost due to corrosion.

curved towards aperture; R2 ca. ¼ whorl, as long as R3. Boundary between R2 and R3 distinct due to shallow constriction; R3 smooth with indistinct growth lines; with either sharp and narrow or blunt and more elongated swelling in the middle of R3 or near aperture. Aperture round; slightly oblique to shell axis. Peristome double with prominent outer peristome. Inner peristome blunt, slightly protruding. Outer peristome strongly thickened, expanded, reflected, most conspicuously at the upper palatal position and near the umbilicus, multilayered (visible in lateral view). Umbilicus is partly or entirely closed by the reflected outer peristome. Operculum thin; multispiral ridges not significantly elevated.

Etymology. In honor of Prof. John B. Burch, a prominent American malacologist, who, together with Prof. S. Panha, extensively studied the taxonomy and systematics of micro land snails of Thailand.

Distribution. The new species is known from the type locality, Tham Phaya Nakharat, Khon Kaen Province, Northeastern Thailand. The other localities are Doi Chiang Dao, Chiang Mai Province and Ban Soppong, Mae Hong Son Province, Northern Thailand, and also from Shan State, Myanmar.

Remarks. Differs from *D. vestitus* (Blanford, 1862) from Moditoung [Modi Taung, Arakan Hills] (Fig. 11B), and its subspecies *D. v. akyabensis* (Godwin-Austen, 1914) from Baumi, Akyab [Sittwe] (Fig. 11C), both from Rhakhine State, Myanmar, by having a smaller shell with a higher spire, a longer last whorl and a less distinct and a narrower constriction between R2 and R3. Differs from *D. conicus* (Godwin-Austen, 1871) from Samiamri, E of the Kopili R., Assam State, India (Fig. 11D) in having a longer last whorl, more close-set ribs on R2, and the inner and outer peristomes are narrower and less reflected. Differs from *D. imitator* Páll-Gergely & Hunyadi in Páll-Gergely et al., 2017 from Guangxi, China in having a less smooth R1, a much thicker peristome, a longer R2, a shallower constriction between R2 and R3, the last whorl less oblique compared to the columellar axis and a less triangular aperture (Páll-Gergely et al. 2017).

This species exhibits the variation of R1 sculpture from nearly smooth (Fig. 10A) to distinctly ribbed (Fig. 10C, D) and R3 swelling from sharp (Fig. 10B, C) to blunter and longer by having the anterior slope of swelling steeper than posterior slope (Fig. 10D). In addition, the umbilicus is open, or covered by the reflected outer peristome. The latter trait even shows variation within the same population (maybe also depends on the age of the examined specimens).

Dicharax panhai Jirapatrasilp & Páll-Gergely, sp. nov.

http://zoobank.org/C6236997-4DFE-43BD-971B-29C5E071A89E

Figs 6C, 12A–C

Dicharax pratatensis – Páll-Gergely et al. 2020b: 71, 72.

Type material. ***Holotype*** CUMZ 7429/1 (Fig. 12A), ***paratypes*** CUMZ 7429/2 (16 shells; Figs 6C, 12B), HNHM (2 shells), NHMUK 20200327 (2 shells), paratypes of "*Alycaeus pratatensis* Cy 003" FMNH (2 shells), SMF 331452 (2 shells; Fig. 12C) and UMMZ (2 shells) from Tham Pratat, Erawan National Park, Kanchanaburi Province, Thailand, 14°23'50.8"N, 99°04'56.3"E, 230 a.s.l., 26 Oct. 1996, coll. S. Panha.

Diagnosis. Shell small (SH up to 2.4 mm, SW up to 3.1 mm), depressed-conical with triangular dorsal side and widened, sigmoid last whorl. Spire ca. 1/3 of shell height. R1 with regular, thread-like ribs; R2 twice shorter than R3; R2 with ca. 18 ribs. R3 with blunt central swelling. Aperture round. Inner peristome thick, protruding. Outer peristome expanded, not reflected. Umbilicus elliptical.

Description. Shell small (SH up to 2.4 mm, SW up to 3.1 mm), depressed-conical with triangular dorsal side and widened, sigmoid last whorl; solid, worn out white; the exact color of non-weathered (fresh) shells unknown. Shell outline oval in apical view, spire ca. 1/3 of shell height. Whorls ca. 4 and 1/8. Protoconch low, ca. two whorls, glossy and smooth. R1 ca. 1¾ whorls with fine, regular, thread-like ribs; with ca. 14 ribs in ¼ whorl adjoining R2, ribs sharper near suture and flatter near umbilicus. Boundary between R1 and R2 distinct as R2 contains more close-set ribs than R1; R2 with ca. 18 ribs that are curved towards aperture; R2 ca. 1/8 whorl, twice shorter than R3. Boundary between R2 and R3 distinct due to shallow constriction; R3 initially coils horizontally forming a flat base, but

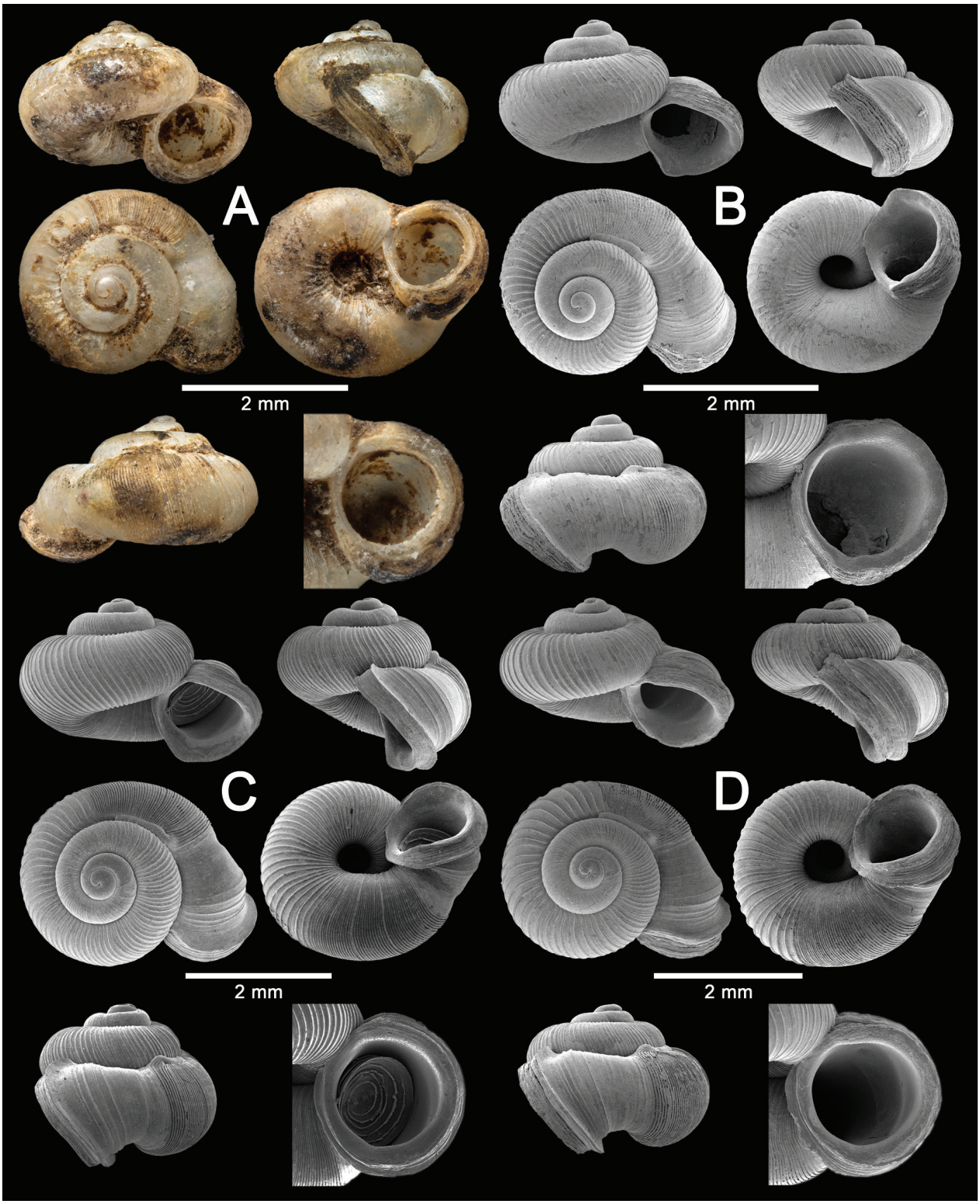

Figure 8. A, B. *Dicharax omissus* **A.** Syntype NHMUK 1903.7.1.1228; **B.** Specimen CUMZ 7426 from Tham Mae La Na, Mae Hong Son Province **C, D.** *Dicharax pratatensis* **C.** Holotype CUMZ Cy 001; **D.** Paratype CUMZ Cy 002 from Doi Chiang Dao, Chiang Mai Province. Close-up images of the aperture not to scale.

aperture strongly descent being strongly oblique to shell axis; R3 mostly smooth with indistinct growth lines that become stronger near aperture; with blunt central swelling. Aperture round; slightly oblique to shell axis. Peristome double with regular outer peristome. Inner peristome thick, protruding. Outer peristome slightly expanded, not reflected, multi-layered (visible mostly in lateral view). Umbilicus elliptical, open, slightly more than one third of shell width. Operculum unknown.

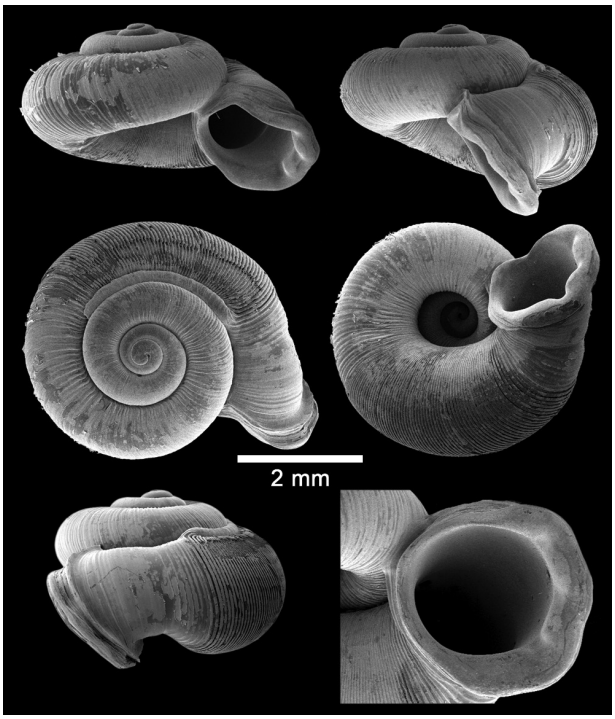

Figure 9. *Dicharax borealis* sp. nov., holotype CUMZ 5072/1.

Etymology. In honor of Prof. Somsak Panha, a prominent Thai malacologist and our beloved professor who initiated the taxonomic and systematic study of land snails and other terrestrial invertebrates in Thailand and surrounding areas of mainland Southeast Asia.

Distribution. The new species is known only from the type locality in Kanchanaburi Province, Thailand.

Remarks. Similar to *D. pratatensis* from Doi Chiang Dao, Chiang Mai Province, Thailand in having a depressed-conical shell shape and R3 with blunt swelling, but differs in having a conical apical part on a wide shell base, less distinct ribs of R1 and shorter R2 with less ribs. The short R2 and breathing tube is also exhibited in *D. abdoui* Páll-Gergely in Páll-Gergely et al., 2017 from Khammouane Province, Laos and *D. stuparum* from Chiang Rai Province, Northern Thailand, but *D. panhai* sp. nov. is larger, comprises more whorls, has a more elevated spire and a larger last whorl (Páll-Gergely et al. 2017, Páll-Gergely and Hunyadi 2018).

***Dicharax pongrati* Jirapatrasilp & Tongkerd, sp. nov.**

http://zoobank.org/92117A2E-1578-41D6-845C-8223B815B272

Figs 6D, 7C, 12D

Type material. ***Holotype*** CUMZ 7430/1 (Fig. 12D), ***paratypes*** CUMZ 7430/2 (56 shells; Figs 6D, 7C), HNHM (2 shells), NHMUK 20200328 (2 shells) and SMF (2 shells) from Doi Chiang Dao, Chiang Mai Province, Thailand, 19°14'26.7"N, 98°52'49.8"E, 24–28 May 1997, coll. S. Panha, J.B. Burch, P. Dumrongrojwattana.

Diagnosis. Shell medium-sized (SH up to 2.3 mm, SW up to 4.4 mm), lenticular, depressed-conical. Spire ca. ¼ of shell height. R1 with regular, thread-like ribs; R2 three times longer than R3; R2 with ca. 76 ribs. R3 strongly reduced, without swelling. Aperture round. Inner peristome with two shallow indentations. Outer peristome expanded, slightly reflected. Umbilicus elliptical. Operculum multispiral, with or without elevated lamella.

Description. Shell medium-sized (SH up to 2.3 mm, SW up to 4.4 mm), lenticular, depressed-conical, solid, translucent, yellowish to pale orange. Shell outline oval in apical view, spire ca. ¼ of shell height. Whorls ca. 4 and 1/8. Protoconch low, ca. two whorls, glossy and smooth. R1 ca. 1¾ whorls with fine, regular, thread-like ribs; with ca. 17 ribs in ¼ whorl adjoining R2, ribs more elevated and sharper near suture and flatter near umbilicus and at the edge of body whorl. Boundary between R1 and R2 distinct as R2 contains denser and thicker ribs than R1; R2 with ca. 76 ribs that are curved towards aperture; R2 ca. 1/3 whorl, three times longer than R3. Boundary between R2 and R3 distinct due to shallow constriction; R3 strongly reduced, without swelling, practically the constriction continues directly to outer peristome. Aperture round; slightly oblique to shell axis. Peristome double with regular outer peristome. Inner peristome slim, slightly protruding, with two shallow indentations. Outer peristome thickened, expanded, slightly reflected, multilayered (visible in lateral view). Umbilicus elliptical, open, approximately one third of shell width. Operculum either thin with low lamella or thick with elevated lamella.

Etymology. In honor of Pongrat Dumrongrojwattana, a Thai malacologist who has studied micro land snails of Thailand and was one of the collectors of this new species.

Distribution. The new species is known only from the type locality in Chiang Mai Province, Thailand.

Remarks. Differs from the sympatric and similar depressed-conical *D. pratatensis* in having a wider and more depressed shell, a much longer R2, a shorter R3 without a swelling and two shallow indentations at the inner peristome.

Discussion

Dicharax species inhabiting China, Laos and Vietnam have been revised recently by Páll-Gergely et al. (2017). Several other species have been included in *Dicharax* in a recent family-wise revision without examining species-level taxonomy (Páll-Gergely et al. 2020b). Here we report a total of ten *Dicharax* species from Thailand, six out of ten species being recorded from their type localities only, and the remaining species with additional occurrences within the vicinity of the type locality which ranges wider within Thailand or both Thailand and Myanmar. Nearly all *Dicharax* species are known from the northern mountainous region except for *D. panhai* sp. nov., the type locality of which is in the Tenasserim Range.

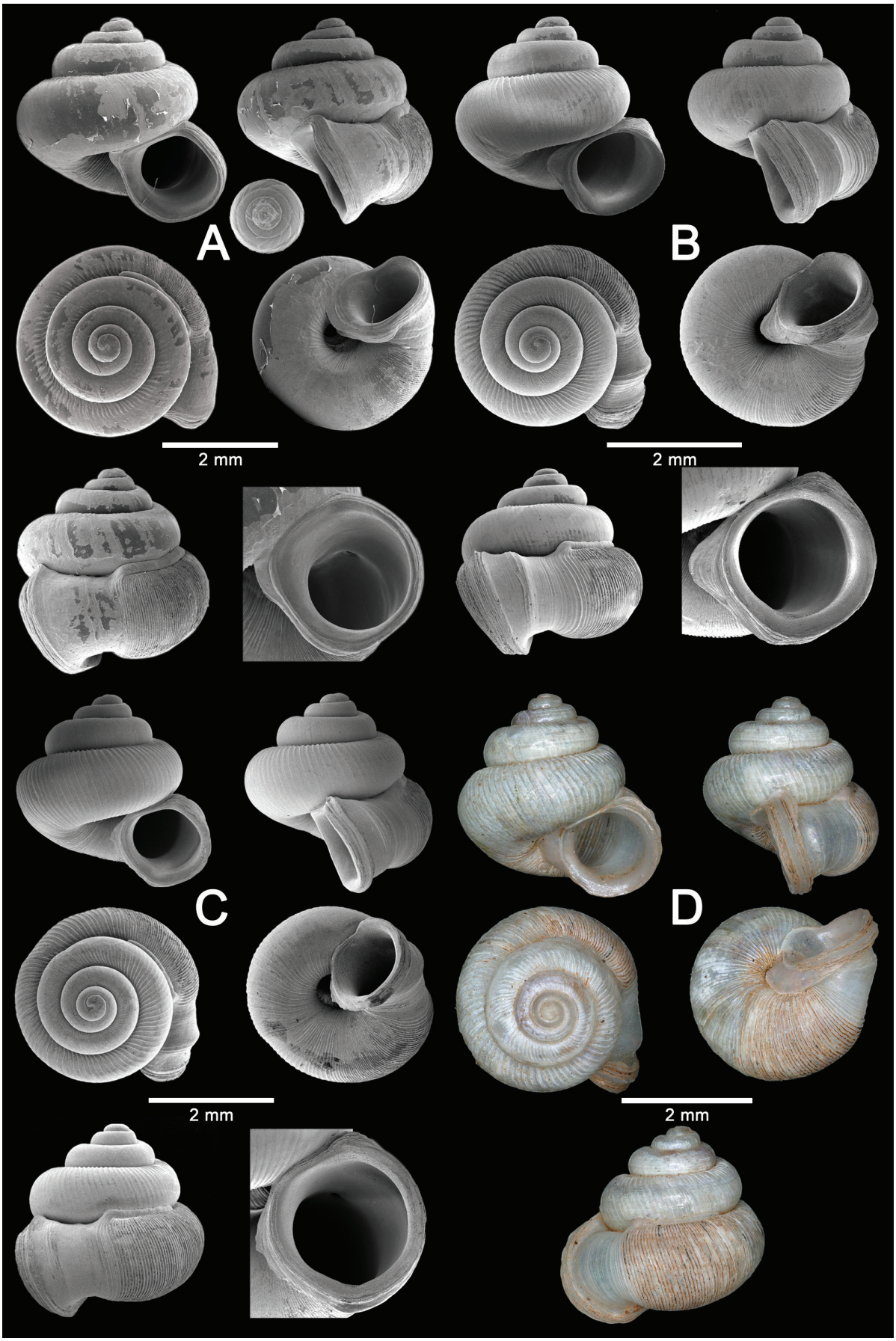

Figure 10. *Dicharax burchi* sp. nov. **A.** Holotype CUMZ 7428/1 with operculum; **B, C.** Specimen CUMZ 7431 from Doi Chiang Dao, Chiang Mai Province; **D.** Specimen UF 345622 from 10.2 km WNW of Soppong, Road 1095, Mae Hong Son Province. Close-up images of the aperture not to scale.

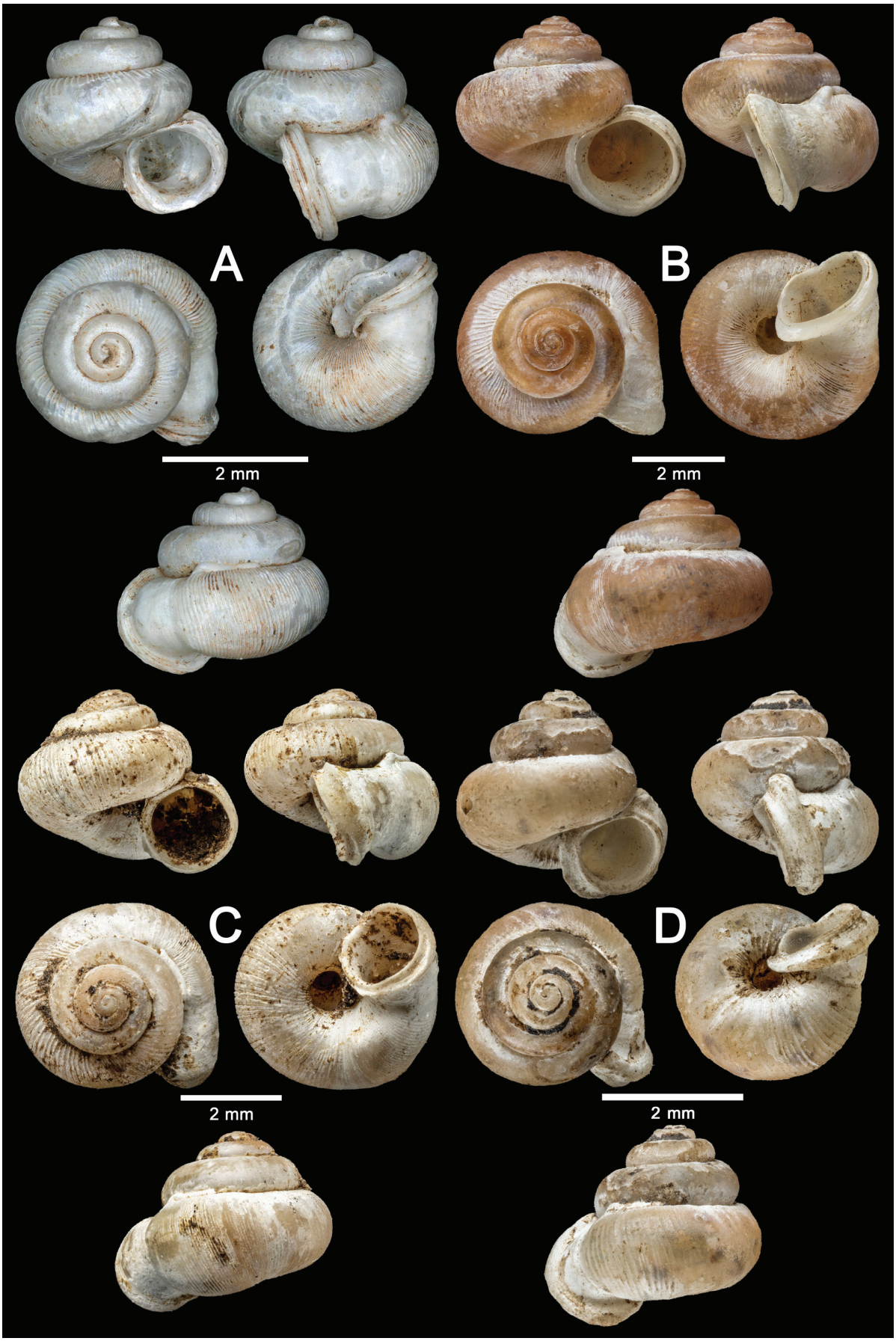

Figure 11. A. *Dicharax burchi* sp. nov., specimen HA (locality code: 2018/41) from Hsihseng centre E ca. 6 km, limestone hill, Shan State, Myanmar; **B.** *Dicharax vestitus*, holotype NHMUK 1906.4.4.53; **C.** *Dicharax vestitus akyabensis*, syntype NHMUK 1888.12.4.251–252; **D.** *Dicharax conicus*, syntype NHMUK 1903.7.1.2674. Photo: NHM (**B–D**).

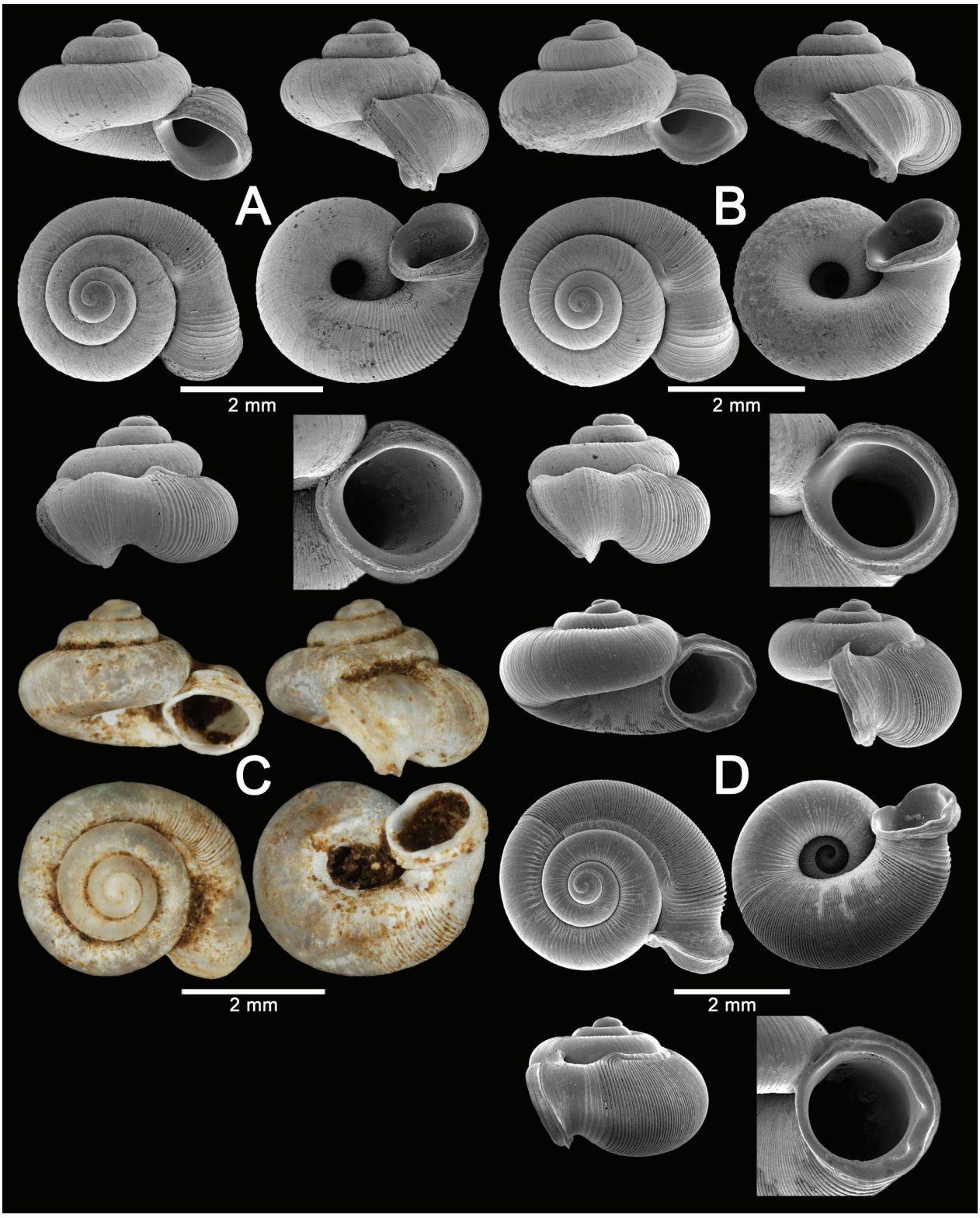

Figure 12. A–C. *Dicharax panhai* sp. nov. **A.** Holotype CUMZ 7429/1; **B.** Paratype CUMZ 7429/2; **C.** paratype SMF 331452 (paratype of "*Alycaeus pratatensis* Cy 003" from Tham Pratat, Erawan National Park, Kanchanaburi Province, Thailand). **D.** *Dicharax pongrati* sp. nov., holotype CUMZ 7430/1 Close-up images of the aperture not to scale. Photo: B. Páll-Gergely, courtesy Ronald Janssen (**C.**).

In addition, the populations here assigned to *D. burchi* sp. nov. inhabit a wide area from Myanmar to northeastern Thailand (Fig. 1) and shows considerable variation in terms of shell characters. Nevertheless, we currently refrain from describing local populations as subspecies. The disjunct distribution of *Dicharax* species has been

Table 2. Comparison of diagnostic conchological characters among *Dicharax* species in this study.

Species	Shell shape	Spire to shell height ratio	R2 length compared to R3	No. of R2 ribs	Swelling of R3	Aperture shape	Outer peristome	Inner peristome	Umbilicus
D. cucullatus	depressed-conical	~1/5	≥ R3	49–57	sharp; near aperture	round	fringed, slightly reflected but not conspicuous	with four to five indentations, always with parieto-columellar; sometimes weak at basal	round
D. notus	depressed-conical	~1/5	≤ R3	48–50	low blunt; central; more elevated in newly examined population	round	expanded, reflected	without indentation; with parieto-columellar angle in newly examined population	round
D. omissus	depressed-conical	~1/4	< R3	35–36	blunt; central	round	expanded, not reflected	without indentation; with beak-like basal protrusion in newly examined population	round
D. pratatensis	depressed-conical	~1/6	< R3	44–51	prominent, blunt; near aperture; anterior slope steeper than posterior slope	round	expanded, not reflected	without indentation; with slight parieto-columellar angle	round
D. borealis sp. nov.	depressed-conical	~1/6	> R3	~72	very low and elongated	oval	expanded, not reflected	with three very shallow indentations, always without parieto-columellar	round
D. burchi sp. nov.	conical	~1/2	~ R3	36–43	sharp and narrow or blunt and more elongated; central or near aperture	round	expanded, reflected, most conspicuously at the upper palatal position and near the umbilicus	without indentation	partly or entirely covered by expanded outer peristome
D. panhai sp. nov.	depressed-conical with triangular dorsal side	~1/3	twice shorter than R3	~18	blunt; central	round	expanded, not reflected	without indentation	elliptical
D. pongrati sp. nov.	lenticular, depressed-conical	~1/4	three times longer than R3	~76	not swelling	round	expanded, slightly reflected	with two shallow indentations	elliptical

reported in *D. diminutus* (Heude, 1885) from China, whereas some species, e.g. *D. fimbriatus* and *D. cristatus*, show a wide distribution range from China to Vietnam and Laos (Páll-Gergely et al. 2017). Additional, especially molecular phylogenetic analyses could reveal that the morphologically distinct populations currently treated as a single species might represent distinct species.

The alycaeid shell is complicated mostly due to the three clearly distinguishable regions of the teleoconch (R1, R2, R3) having their own characteristics of sculpture (the most important is the rib density), length and morphology. Previous revisions (Páll-Gergely et al. 2017, 2020b, Páll-Gergely and Auffenberg 2019) showed that most populations are recognizable, i.e. possess unique combinations of characters that distinguish them from other conspecific populations. Due to the high variability among populations, the most useful approach is being a lumper, in order not to over split the alycaeid genera and not to describe many unrealistic species (Páll-Gergely et al. 2020b: 27). Thus, instead of describing every recognizable population as distinct species (or even subspecies), we only distinguish species with unique character states, and attempt to apply existing nominal species to newly examined populations as much as possible. The latter is the situation for *D. notus* and *D. omissus*, which have so far been known from single populations. The populations we examined and identified as *D. notus* and *D. omissus*, differ from their respective type specimens in some characters, which we interpret as being insufficient for distinguishing them at species level. Moreover, both species are variable and widespread, as revealed by the examination of additional populations from Thailand and Myanmar (Páll-Gergely et al. in prep.).

The recent alycaeid revisions (Páll-Gergely et al. 2017, Páll-Gergely and Auffenberg 2019) also showed that most important characters to distinguish species are the relative lengths of regions (especially R2 and R3) and the general shell shape, whereas other characters, such as the shape of swelling on R3, and the crenulation and protrusion of outer peristome, show large intraspecific variability (although they can be useful in some cases to distinguish species). The new species described here are recognized based on the following characters (Table 2): (1) *Dicharax burchi* sp. nov. is recognized by its conical

shell shape with an elevated spire, even if the examined populations show variation in terms of rib strength and density, the shape of R3 swelling and the expansion of the outer peristome; (2) *Dicharax panhai* sp. nov. has a unique shell shape of a wide base and triangular dorsal side, and a short R2; (3) *Dicharax pongrati* sp. nov. has a lenticular, depressed-conical shell shape, an extremely long R2 and a very short R3; (4) *Dicharax borealis* sp. nov. has a depressed-conical shell shape, a very low and elongated R3 swelling and an inner peristome with three very shallow indentations. Although *D. borealis* sp. nov. could be interpreted as a *D. cucullatus* with a low R3 swelling, it is sympatric with a *D. cucullatus* population at the type locality of *D. borealis* sp. nov., which excludes conspecificity.

One population of *D. cucullatus* from Doi Ang Khang, Chiang Mai Province, Thailand exhibits the spiral striation on R1 (Fig. 2C, D). The spiral striation was rarely found in *Dicharax* and was reported in very few species (e.g. *D. candrakirana* Nurinsiyah & Hausdorf, 2017, one population of *D. depressus*). In those cases, the spiral striation is probably the part of lower shell layers and assumed not to be homologous with those of *Chamalycaeus* and *Metalycaeus* species (Páll-Gergely et al. 2017, 2020b). However, in this case the normal spiral striation which is elevated from the shell surface found in one *D. cucullatus* population could be regarded as homologous to the condition found in the other genera.

The variation on the exterior sculpture of the operculum has been rarely recorded. Foon and Liew (2017) noted the discrepancy of the operculum of two species, *Stomacosmethis roebeleni* (Möllendorff, 1894) and *Pincerna thieroti* (Morgan, 1885), between the original description and recently examined specimens. The original descriptions of both species described the opercula as entirely non-calcified (Morgan 1885, Möllendorff 1894), while the recently examined specimens exhibit the opercula with calcified exterior layers (Foon and Liew 2017). Moreover, Páll-Gergely et al. (2017) reported the variation from an operculum without elevated lamella to the presence of elevated lamella in *D. cristatus*, *D. depressus* and *D. fimbriatus*, and from smooth to multispiral (i.e. with low lamella) opercula in *D. fraterculus* (Bavay & Dautzenberg, 1900). However, these differences were compared between specimens from different localities. The only report about variation (presence or absence of the elevated lamella) within the same population was reported in *Metalycaeus nipponensis* (Reinhardt, 1877) (Páll-Gergely et al. 2020b). Here we first report the variation of the outer opercular surface in the same population in *Dicharax*, which is illustrated in *D. notus* in possessing an operculum either without (Fig. 7A) or with an elevated lamella (Fig. 7B). We thus suggest that this trait might be less advantageous in diagnosing different *Dicharax* species, and probably in other alycaeid genera.

The body coloration of living specimen has been scarcely reported compared to the shell color. Living specimens of both *D. cucullatus* (Fig. 5A) and *D. notus* (Fig. 5B) have a reddish orange shell with a pink apex and a light-yellow to pale orange body coloration. In addition, most *Dicharax* shells in this study have a reddish orange shell (Fig. 6). Comparing to other alycaeid species, *Stomacosmethis somnueki* (Panha & Patamakanthin, 2001) has a white, bright yellow or orange shell and a pale yellow body color (Panha and Patamakanthin 2001), whereas several species of *Alycaeus*, *Pincerna* and *Stomacosmethis* species from Peninsular Malaysia have a yellow shell with an orange apex and a pale yellow to gray body color (Foon and Liew 2017). The shell coloration could be used to classify some alycaeid genera to some extent. *Stomacosmethis* is usually bright yellow or orange, and *Alycaeus* is more colorful with reddish or yellowish tint compared to *Chamalycaeus* which has a similar shell but colorless (Páll-Gergely et al. 2020b). However, the light-yellow to pale orange body coloration is common, often associated with lighter colored shell and might not be different among genera.

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