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New and little-known species of *Clostophis* Benson, 1860 from Southeast Asia (Gastropoda: Eupulmonata: Hypselostomatidae)

Barna **Páll-Gergely**[1*] & András **Hunyadi**[2]

Abstract. The present paper describes six new species as follows: *Clostophis bactrianus*, new species (Peninsular Malaysia), *Clostophis thinbowguensis*, new species (Myanmar), *Clostophis obliquus*, new species (China: Guangxi), *Clostophis yoga*, new species (Vietnam), *Clostophis candidus*, new species (Vietnam) and *Clostophis charybdis*, new species (Vietnam). Additional information on shell morphology and distribution is presented for *Clostophis laidlawi* (Collinge, 1902), *Clostophis neglectus* (van Benthem Jutting, 1961) and *Clostophis sankeyi* Benson, 1860. Furthermore, *Hypselostoma lacrima* Páll-Gergely & Hunyadi, 2015 and *H. socialis* Páll-Gergely & Hunyadi, 2015 are transferred to *Clostophis*.

Key words. taxonomy, systematics, shell, conchology, apertural barriers, endemism

INTRODUCTION

Southeast Asia is a biodiversity hotspot for mammals and vascular plants (Myers et al., 2000) and certainly for invertebrates if a focused assessment were made. Land snails are mostly found in calcium-rich habitats, such as limestone rocks (Solem, 1974), because they need calcium-carbonate to build their shells. A large fraction of land snails are micro-molluscs that bear shells less than ca. 5 mm (Panha & Burch, 2005; Páll-Gergely et al., 2022), which can be most effectively collected via sediment sampling methods around limestone outcrops (Tweedie, 1961). The present paper follows several others concerning new species descriptions of the Hypselostomatidae (Páll-Gergely et al., 2015, 2019, 2020, 2022; Dumrongrojwattana et al., 2021) from China and Southeast Asian countries.

In the present paper we focus on the genus *Clostophis* Benson, 1860, which was originally described as a diplommatinid (Caenogastropoda) and has only been transferred to the stylommatophoran Hypselostomatidae recently (see Páll-Gergely et al., 2020). The currently known ten species of *Clostophis* are distributed from western Myanmar and Peninsular Malaysia to northern Vietnam and China's Guangxi Province. Although the terrestrial malacofauna of southern Thailand, Cambodia, and southern Vietnam is relatively well-known (Panha & Burch, 2005; Vermeulen et al., 2019a, b), *Clostophis* has not yet been reported there.

Clostophis species are characterised by tiny (1–2 mm) colourless or whitish (but never brown) shells and possess none or several apertural barriers. The genus *Angustopila*, which contains the smallest land snails (Páll-Gergely et al., 2022), are typically smaller (< 1 mm) and have less dense spiral striation on their shells.

Tonkinospira Jochum, Slapnik & Páll-Gergely, 2014 is a genus harbouring similar species to *Clostophis*, and while we may consider treating them as synonyms, currently there are some general, often not mutually exclusive differences which suggest they should be kept separated for the time being. Namely, *Tonkinospira* has a narrower umbilicus, more "compact" shell without a detached aperture, and no apertural denticles, while *Clostophis* species generally have wider umbilici, and may have detached apertures and possess apertural barriers.

Within *Clostophis*, some species (*C. lacrima*, *C. obliquus*, new species, *C. socialis*) are distinct from the others by possessing long apertural barriers. Although they may warrant a genus of their own, we refrain from erecting genus-group taxa in this taxonomically complex family with many unsolved problems.

Herein, six new species of *Clostophis* are described from Peninsular Malaysia, Myanmar, Vietnam, and China's Guangxi Province.

MATERIAL AND METHODS

Shells were manually brushed clean of mud using wet, fine, tapered brushes. The shells were examined without coating under a low vacuum SEM (Hitachi tm4000 Plus SEM at the Research and Instrument Core Facility of the Faculty

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[1]Plant Protection Institute, Centre for Agricultural Research, Herman Ottó street 15, H-1022, Budapest, Hungary; Email: pallgergely2@gmail.com (*corresponding author)

[2]Adria sétány 10G 2/5., H-1148, Budapest, Hungary

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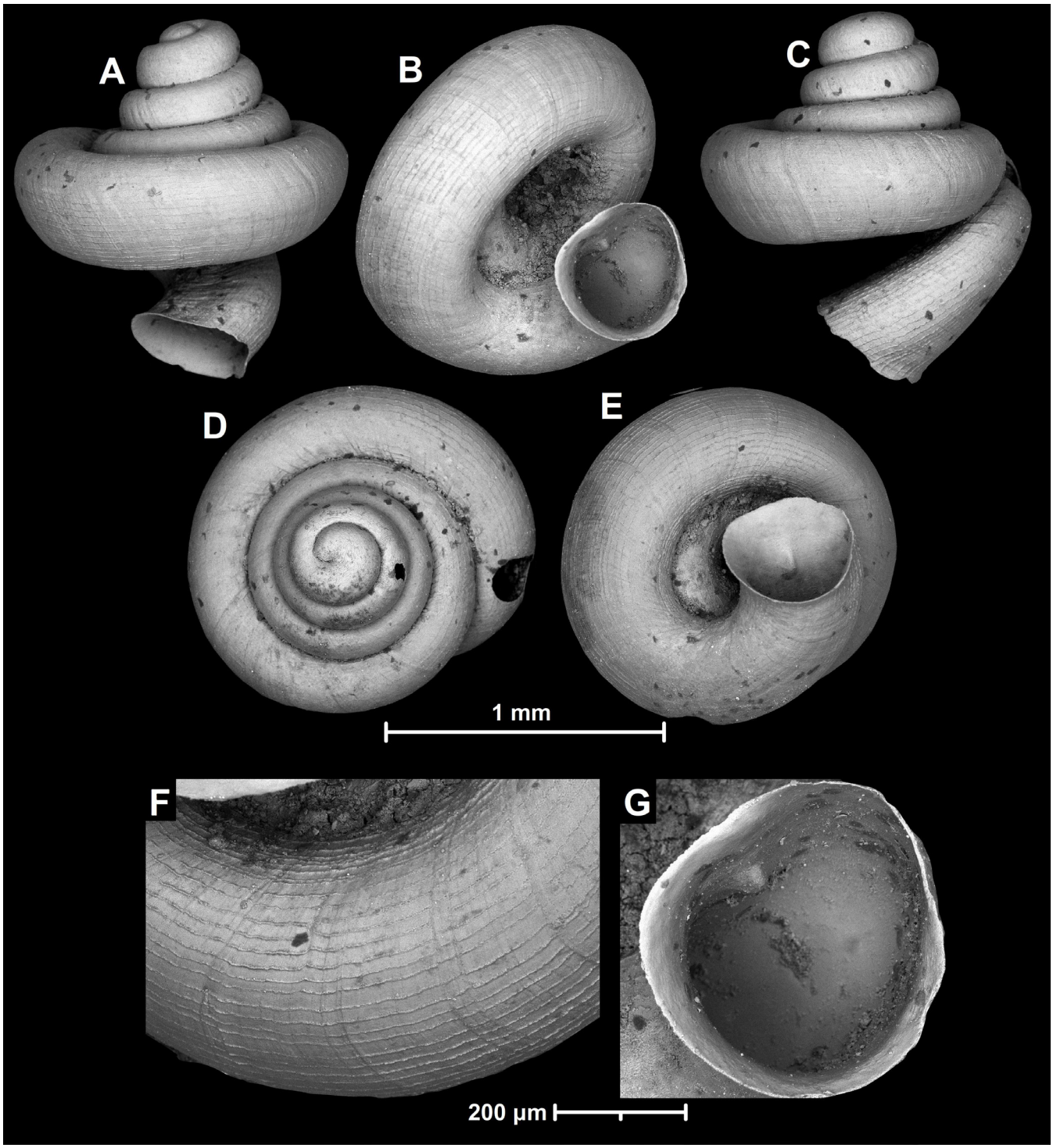

Fig. 1. *Clostophis sankeyi* Benson, 1860, from locality 2018/50.

of Science, Eötvös Loránd University, Budapest, Hungary). A Keyence vhx 5000 microscope was used to measure the shells. Shell whorl number was counted to the nearest quarter whorl according to Kerney & Cameron (1979).

Abbreviations.
HA: Collection András Hunyadi, Budapest, Hungary
HNHM: Hungarian Natural History Museum, Budapest, Hungary
MNHN: Muséum National d'Histoire Naturelle, Paris, France
NHM: The Natural History Museum, London, United Kingdom
NHMUK: when citing specimens deposited in the NHM
SH: shell height
SW: shell width (diameter)

SYSTEMATICS

Family Hypselostomatidae Zilch, 1959

Remarks. This taxon is treated as family by Schileyko (1998) and as a subfamily by Bouchet et al. (2017). So far, no molecular phylogeny is available that would help

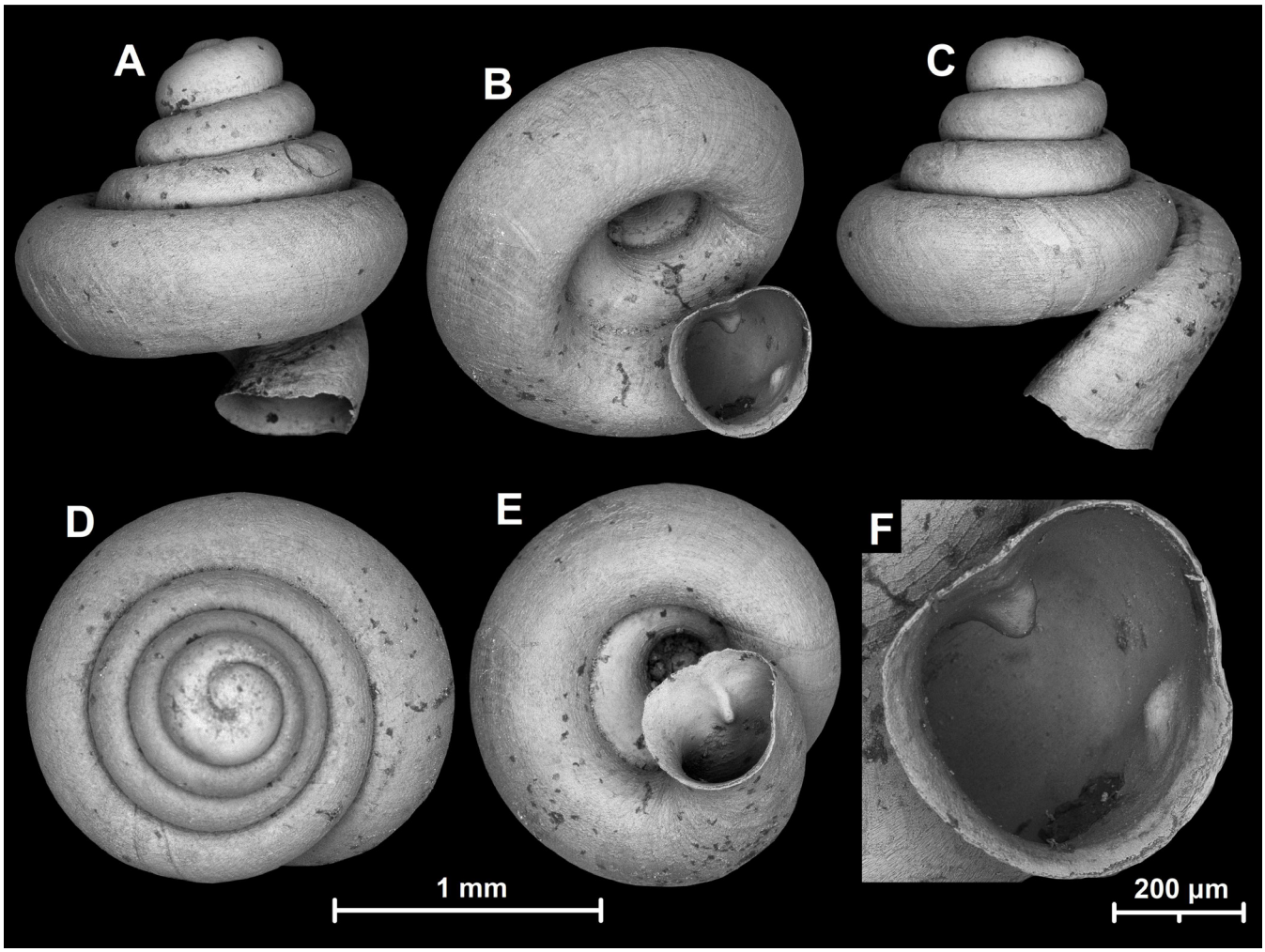

Fig. 2. *Clostophis sankeyi* Benson, 1860, from locality 2018/49a.

in understanding the systematics of hypselostomatids and related orthurethran groups. Therefore, the decision of which systematics to follow is arbitrary. To be consistent with our previous papers (Páll-Gergely et al., 2015, 2019, 2020, 2022), we treat Hypselostomatidae as an independent family.

Clostophis Benson, 1860

Clostophis Benson, 1860: 95.
Montapiculus Panha & Burch, 1999: 148.

Type species. *Clostophis sankeyi* Benson, 1860, by monotypy.

Remarks. This genus was redescribed and transferred from the Diplommatinidae to the Hypselostomatidae by Páll-Gergely et al. (2020).

Species from Peninsular Malaysia and Myanmar

Clostophis sankeyi Benson, 1860
(Figs. 1, 2)

Clostophis sankeyi Benson, 1860: 95.
Clostophis sankeyi — Páll-Gergely et al., 2020: 352, fig. 3A.

Material examined. 1 shell (coll. HA, Fig. 2), Myanmar, Mon Province, Mawlamyine centre ENE ca. 26 km, Dhammasa Cave, 8 m a.s.l., 16°30.403′N, 97°48.646′E (locality code 2018/49a), coll. A. Hunyadi, K. Okubo & J.U. Otani, 11 October 2018; 1 shell (coll. HA, Fig. 1), Myanmar, Mon Province, Mawlamyine NE ca. 14 km, Kalagon, Kha Yone Cave, 0 m a.s.l., 16°31.986′N, 97°42.910′E (locality code: 2018/50), coll. A. Hunyadi, K. Okubo & J.U. Otani, 11 October 2018.

Measurements (in mm). SH = 1.53, SW = 1.41 (2018/49a); SH = 1.34, SW = 1.22 (2018/50).

Remarks. In our previous paper (Páll-Gergely et al., 2020) we reported this species from two localities, but they were not figured. Here we figure both shells and add the following observation. The holotype and specimen from locality 2018/50 lack a parietal tooth (Fig. 1B, E, G), whereas the shell from locality 2018/49a has a blunt, low, but clearly visible parietal tooth (Fig. 2B, E). The presence or absence of the parietal tooth is best interpreted as part of intraspecific variability, because all other traits of the three examined available shells are similar.

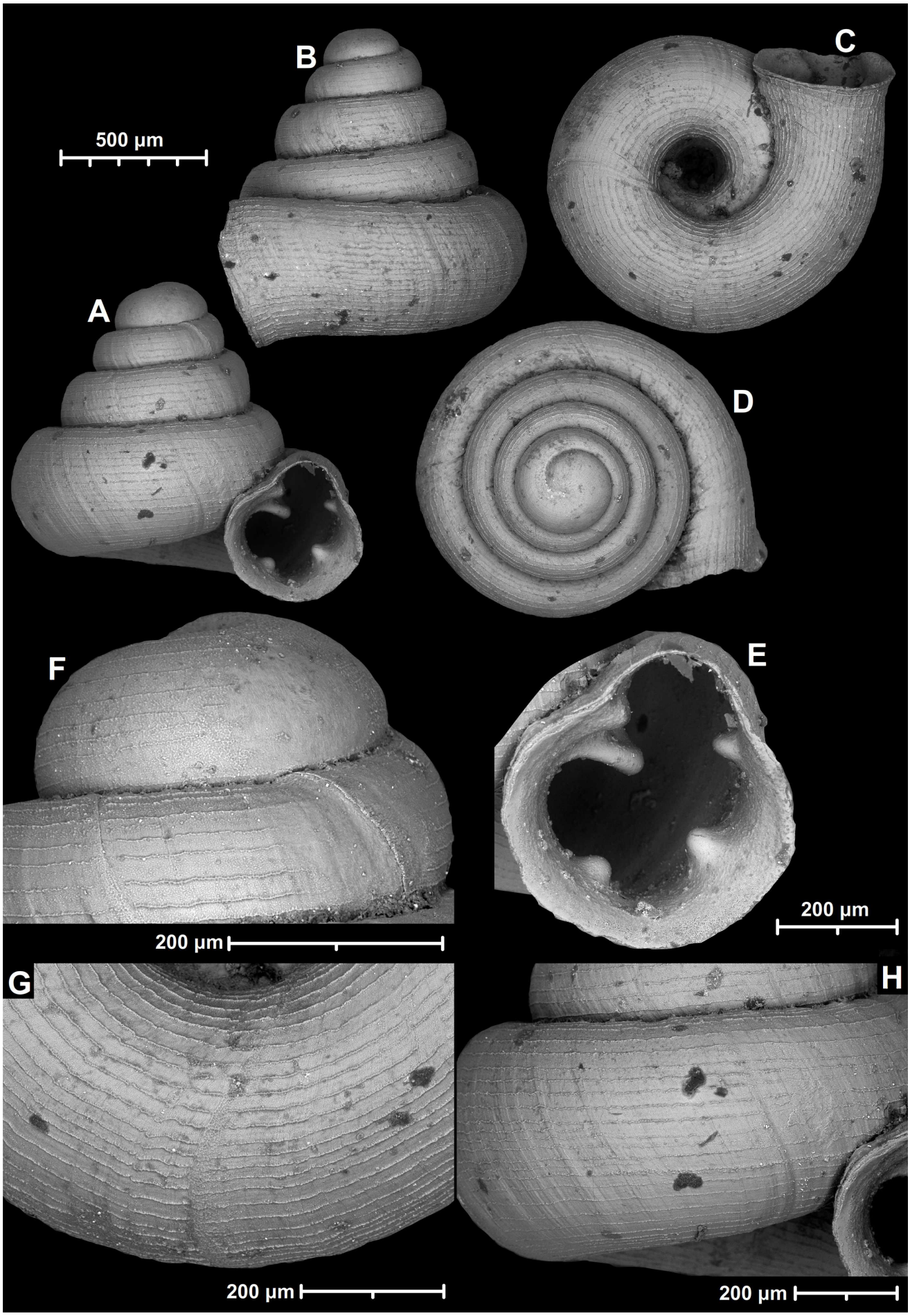

Fig. 3. *Clostophis laidlawi* (Collinge, 1902), locality 2013/30, specimen 2.

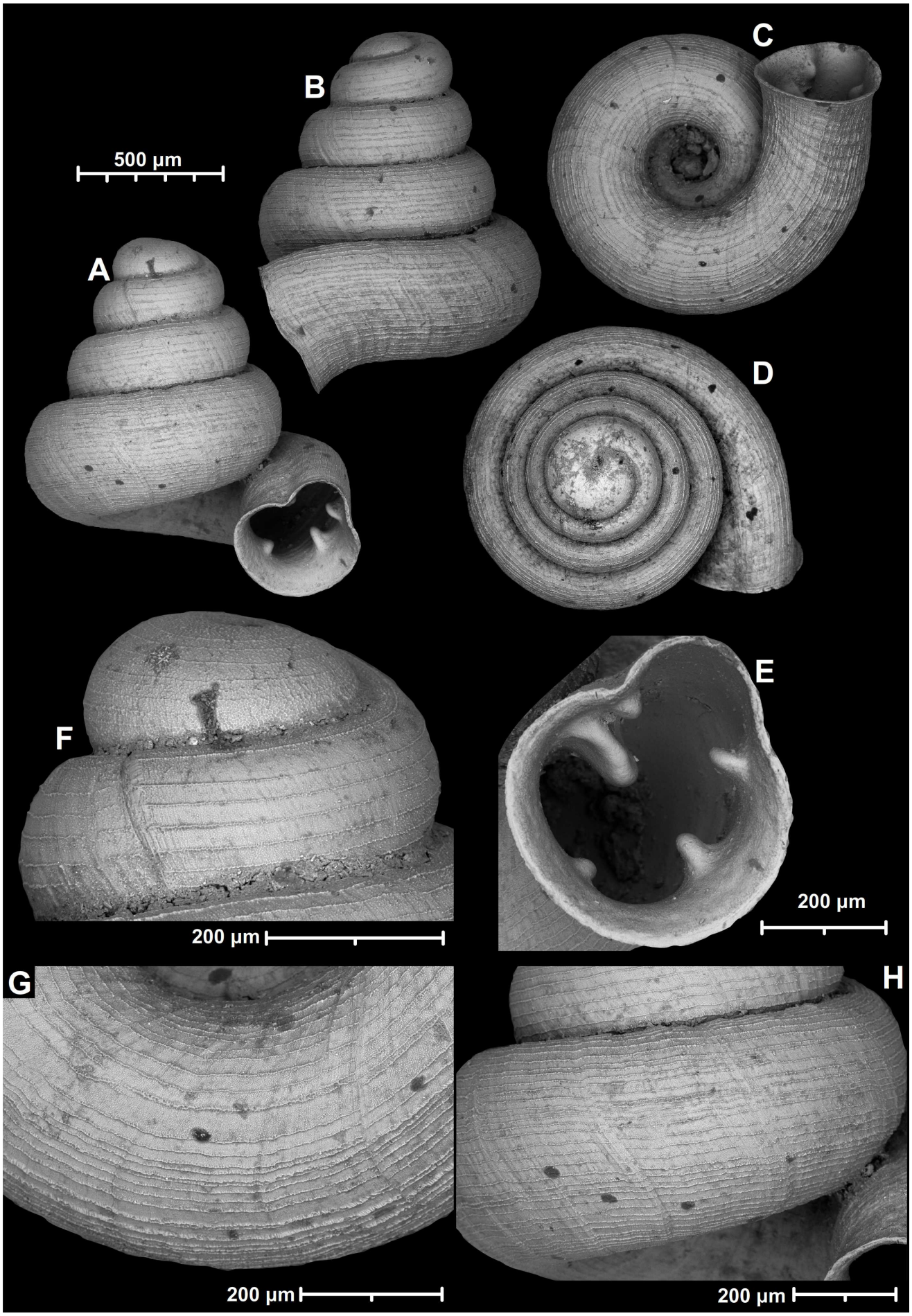

Fig. 4. *Clostophis laidlawi* (Collinge, 1902), locality 2013/30, specimen 1.

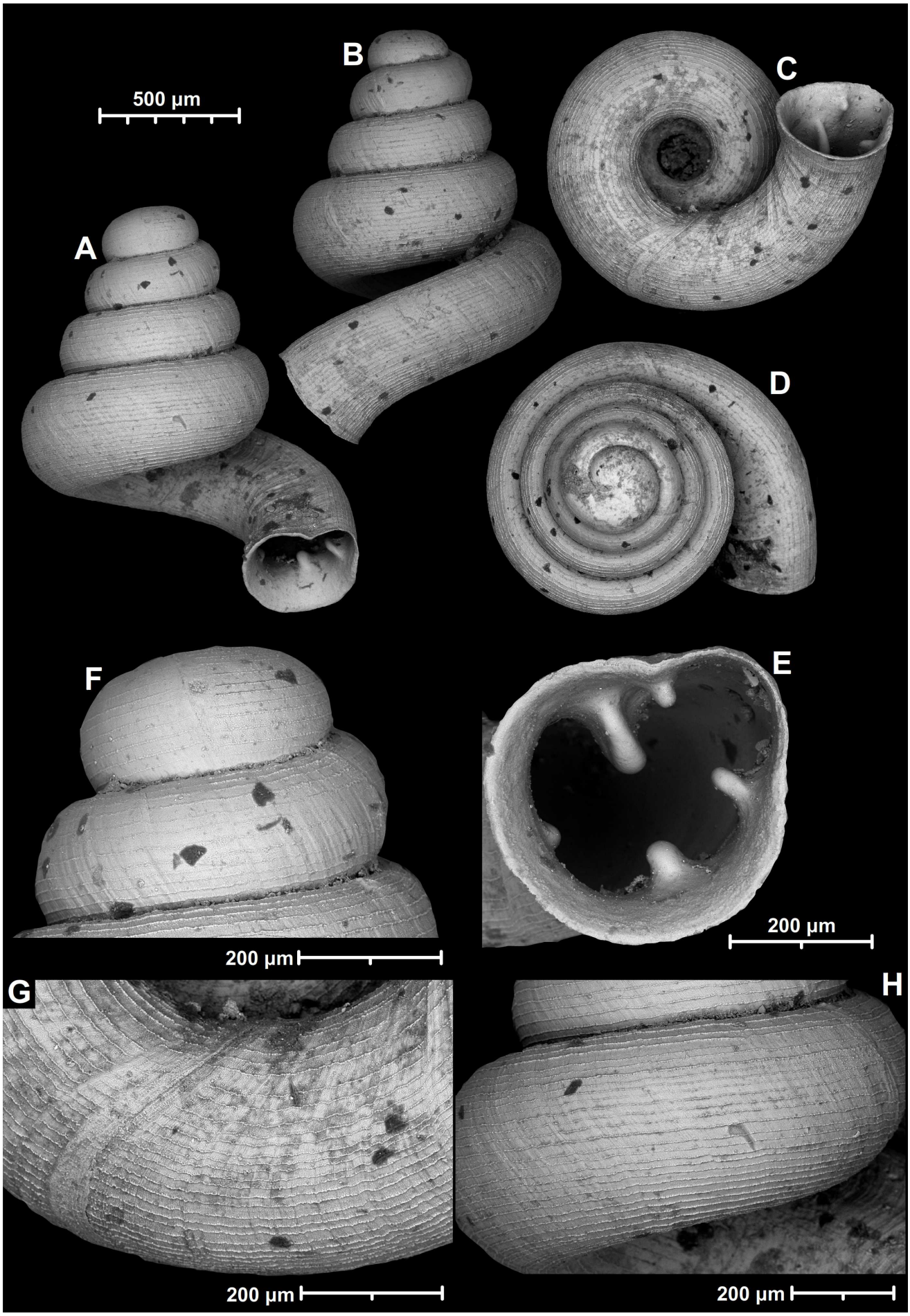

Fig. 5. *Clostophis laidlawi* (Collinge, 1902), locality 2013/30, specimen 3.

Clostophis laidlawi (Collinge, 1902)
(Figs. 3–5)

Hypselostoma laidlawi Collinge, 1902: 83, pl. 5, figs. 29, 30.
Gyliotrachela laidlawi — Laidlaw, 1933: 214.
Hypselostoma laidlawi — van Benthem Jutting, 1950: 19 (partim).
Paraboysidia laidlawi — van Benthem Jutting, 1961: 36, pl. 8, fig. 2b.
Paraboysidia laidlawi — Maassen, 2001: 74.

Material examined. 92 shells (coll. HA, Figs. 3–5), Malaysia, Pahang, 20 km SE of Jerantut, Gua Kota Gelanggi, below Gua Balai, 120 m a.s.l., 3°54.000′N, 102°28.412′E (locality code: 2013/30), coll. A. Hunyadi, 21 January 2013.

Remarks. This species was originally described to possess four apertural barriers ("a dorsal and ventral one situated on the upper and lower border of the peristome, and two smaller internal teeth, one on the right and one on the left of the peristomial teeth"). Van Benthem Jutting (1950) figured a shell from the British Museum, Natural History (currently NHM) that was collected at the type locality and possessed only two teeth (fig. 9 therein). She also mentioned that the 'holotype' of *C. laidlawi* was in Cambridge and was "so badly broken and delicate that an examination could not be allowed". However, Collinge (1902) did not mention the number of specimens he examined and did not select a holotype, therefore van Benthem Jutting's (1950) information about a shell being a holotype is incorrect. We also examined and imaged a shell from the NHM, which was collected at the type locality and originated from the author (Collinge) (Fig. 6). This shell is most probably the same one van Benthem Jutting (1950) also examined, and since it is from the type locality and from the author of the species, we treat it as a syntype of *H. laidlawi*. In a later paper, based on newly collected material at Ulu Tembeling, van Benthem Jutting (1961) described the species with two apertural barriers as *Paraboysidia neglecta*. It is evident that there are two distinct species (i.e., *H. laidlawi* with five teeth and *P. neglecta* with two) because they were collected syntopically at Ulu Tembeling and no intermediate forms are known.

We collected *Clostophis laidlawi* at one locality. Among the 92 adult shells, 26 had a 'normal' aperture (Fig. 3), whereas the apertures of the remaining 66 shells were slightly or strongly detached from the penultimate whorl (Figs. 4, 5). This shows that the detached last whorl is a part of the spectrum of variability within a population and suggests that this condition can rapidly develop in Hypselostomatidae.

Although Collinge (1902) mentioned only four apertural barriers, van Benthem Jutting (1961) found five, which matches with our observations. It is probable that Collinge simply overlooked the tiny angular tooth next to the parietal lamella.

Clostophis neglectus (van Benthem Jutting, 1961)
(Figs. 6, 7)

Hypselostoma laidlawi — van Benthem Jutting, 1950: 19, fig. 9 (partim).
Paraboysidia neglecta van Benthem Jutting, 1961: 36, pl. 8, fig. 2a. ["Biserat Caves, State of Jalor", and "Gua Che Yatin, Ulu Tembeling, Pahang"]
"*Hypselostoma laidlawi*" (referring to the figure in van Benthem Jutting (1950) as probably *Systenostoma* species) — Panha & Burch, 2002: 125.
Clostophis neglectus — Páll-Gergely et al., 2020: 352.

Material examined. 1 shell, probably syntype of *Hypselostoma laidlawi* (NHMUK 20191105, Fig. 6), Biserat Caves, Jalor, Patani, Malay, coll. Collinge; 7 shells + 3 juvenile/broken shells (coll. HA), Kelantan, 24.8 km from Gua Musang toward Kuala Krai, right side of Road #8, 160 m a.s.l., 4°55.193′N, 102°06.850′E, 100 m a.s.l. (locality code: 2013/26), coll. A. Hunyadi, 18 January 2013; 103 shells + 24 juvenile/broken shells (coll. HA, Fig. 7), Pahang, 15 km W of Bandar Pusat Jengka, Hutan Lipur Gunung Senyum, 90 m a.s.l., 3°41.862′N, 102°25.980′E (locality code: 2013/33), coll. A. Hunyadi, 23 January 2013.

Measurements (in mm). SH = 1.09–1.32, SW = 1.16–1.38, (n = 8).

Remarks. Regarding the confusion with *C. laidlawi*, see remarks under that species.

Clostophis bactrianus, new species
(Fig. 8)

Type material. Holotype (SH: 1.1 mm, SW: 1.6 mm) (HNHM 105324), Pahang, Gua Bama, 9 km from Kuala Lipis toward Padang Tungku, 120 m a.s.l., 4°11.652′N, 101°57.936′E (locality code: 2013/28), coll. A. Hunyadi, 19 January 2013. Paratypes: 24 shells (coll. HA), same data as for holotype.

Diagnosis. Uniquely characterised within the genus by the two low, blunt teeth on the columellar and basal side of the aperture.

Description. Shell conical, wider than high, apex blunt. Whorls rounded or slightly shouldered. Last whorl not detached from penultimate whorl, although aperture may be slightly protruding (parietal callus elevated from penultimate whorl). Protoconch consisting of 1.5 whorls, spirally striated except for the first ca. 0.25 whorl. Entire shell with 4.25 whorls. Umbilicus relatively narrow, less than one third of shell width. Entire teleoconch with strong, elevated, rather equidistant spiral striae (ca. 20–22 on body whorl in apertural view), and some weak, irregular radial growth lines. Aperture almost heart-shaped due to large sinulus. Parietal tooth pronounced, relatively short, reaches peristome. Palatal tooth also strong, elevated, but blunt. Sinulus clearly separated from rest of aperture due to strong parietal and palatal teeth.

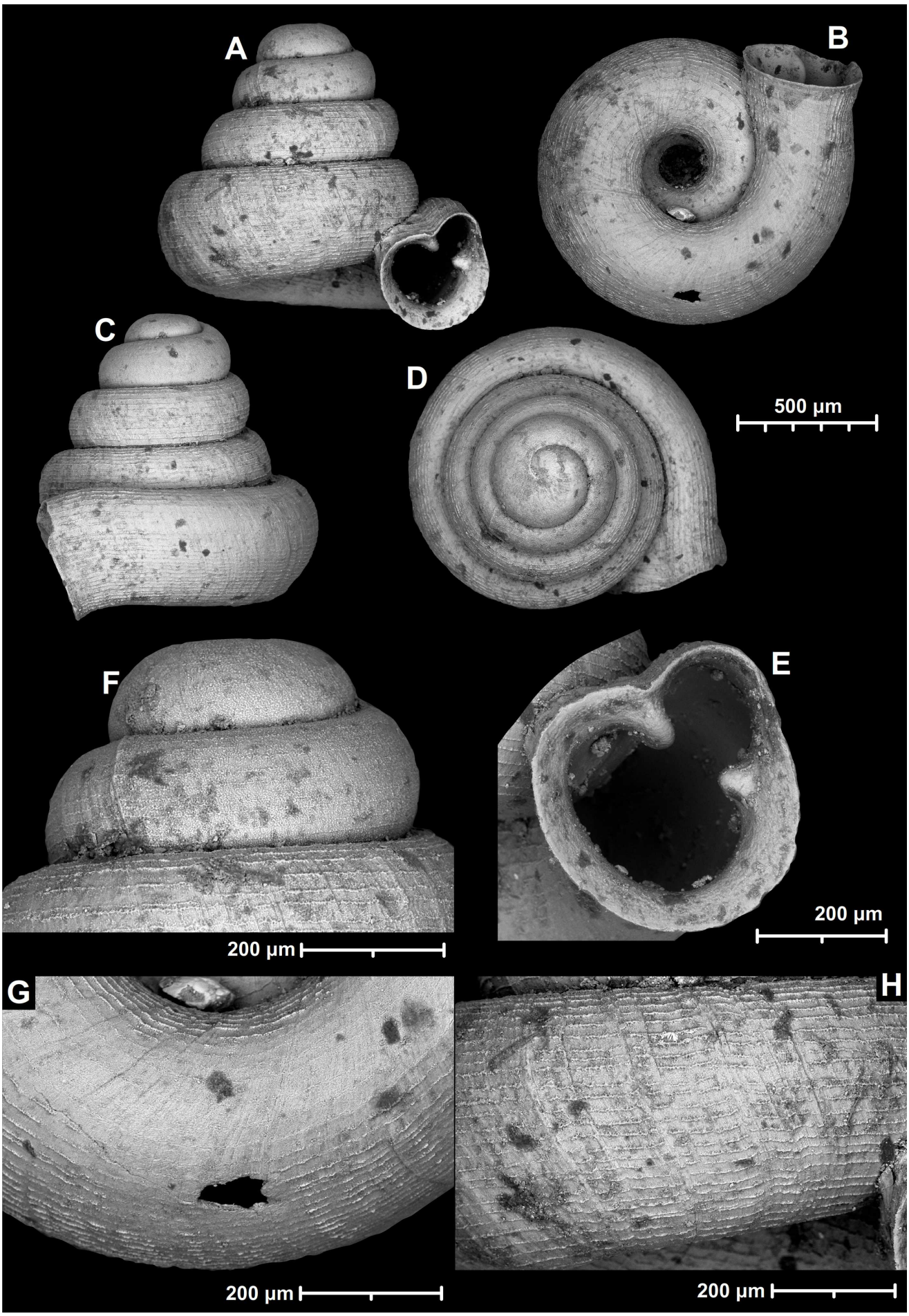

Fig. 6. *Clostophis neglectus* (van Benthem Jutting, 1961) (syntype of *C. laidlawi*: NHMUK 20191105).

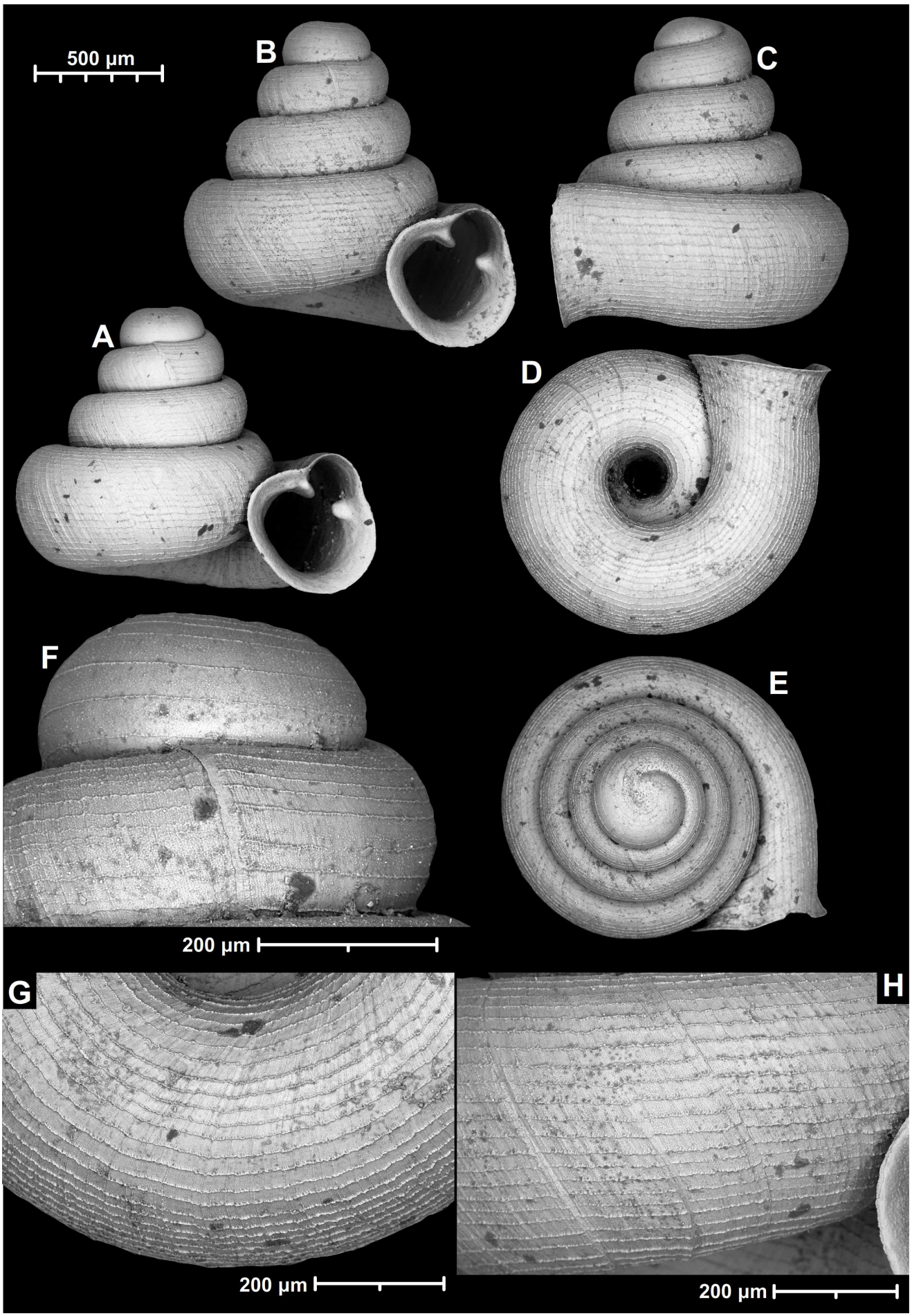

Fig. 7. *Clostophis neglectus* (van Benthem Jutting, 1961) from locality 2013/33. A, specimen 2; B–H, specimen 1.

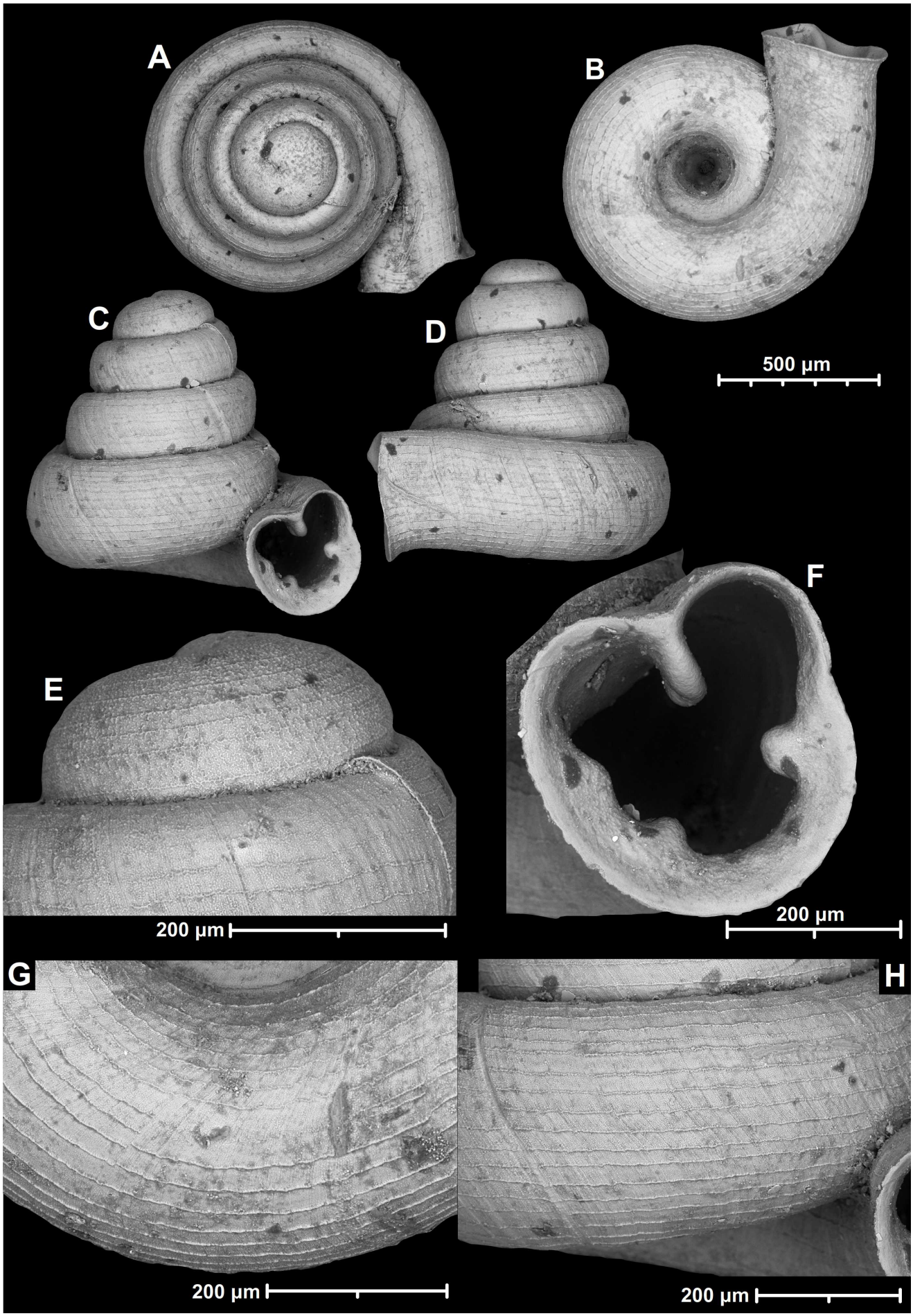

Fig. 8. *Clostophis bactrianus*, new species (holotype, HNHM 105324).

Two low, blunt denticles situated next to each other on the peristome on the basal and columellar sides of the aperture; the lower one is situated slightly left (i.e., direction of the columella) from the basal most point, whereas the upper one sits on the columellar side.

Measurements (in mm). SH = 0.94–1.05, SW = 1.03–1.06 (n = 4).

Differential diagnosis. *Clostophis bactrianus*, new species, differs from *C. neglectus* by the smaller shell size, the more elevated parietal tooth, the more basally-situated palatal tooth (and as a result, a larger sinulus), and the two low denticles on the columellar and basal sides of the aperture. *Clostophis laidlawi* has five apertural barriers.

Etymology. The specific epithet derives from the scientific name of the Bactrian camel (*Camelus bactrianus* Linnaeus, 1758). The two blunt columellar teeth of this new species resemble the two humps on the camel's back.

***Clostophis thinbowguensis*, new species**
(Fig. 9)

Type material. Holotype (SH: 1.27 mm, SW: 1.25 mm) (MNHN-IM-2000-38057), Myanmar, Tanintharyi Region, Thin Bow Gu Cave, Phayahran Camp; 11°11.38′N, 99°10.30′E; coll. F. Bréhier, 20 February 2015.

Diagnosis. Among species of *Clostophis* with the last part of the penultimate whorl attached to the penultimate whorl, *C. thinbowguensis*, new species, differs by the incurved last part of the last whorl, in combination with the presence of a single tooth (a parietalis) in the aperture.

Description. Shell conical, width and height equal or almost equal. Whorls rounded. Last whorl not detached from penultimate whorl, although aperture slightly protruding (parietal callus elevated from penultimate whorl). Protoconch consisting of slightly less than 1.5 whorls, its sculpture is not discernible due to corrosion of shell surface. Entire shell with 4.75 whorls. Umbilicus normally wide, ca. one third of shell width. Entire teleoconch corroded, except for the characteristic presence of dense spiral striation on the apertural and ventral side of the body whorl (counting them is not possible). Some weak, irregular radial growth lines are present. Aperture subcircular, sinulus wide and weakly isolated due to low, deeply situated parietal tooth. No additional apertural barriers present. Peristome slightly expanded, not reflected.

Measurements (in mm). SH = 1.27, SW = 1.25 (holotype).

Differential diagnosis. *Clostophis thinbowguensis*, new species, is similar to some *Angustopila* species, but differs from them by the generally larger size and the denser spiral striation. The most similar species is probably *Angustopila concava* due to the similar strongly oblique aperture, but that species is smaller, has a concave conical shell, and a more anteriorly situated lower parietal tooth.

Etymology. This new species is named after its type locality (Thin Bow Gu Cave).

Species with short apertural barriers

***Clostophis yoga*, new species**
(Figs. 10, 11)

Type material. Holotype (SH: 1.08 mm, SW: 0.97 mm) (HNHM 105325), Vietnam, Thanh Hóa Province, 23.7 km south of centre of Ngọc Lặc, Phúc Thịnh, Làng Miềng, rock wall above the village, 65 m a.s.l., 19°55.869′N, 105°22.196′E (locality code: 2020/38), coll. A. Hunyadi, 13 February 2020. Paratypes: 7 shells, same data as for holotype, coll. HA.

Additional material. 4 juvenile/broken shells, coll. HA, same data as for holotype.

Diagnosis. *Clostophis* species with a detached last quarter whorl are as follows: *C. candidus*, new species, *C. multiformis* Páll-Gergely & A. Reischütz, 2020, *C. proboscideus* (Panha & Burch, 1999) and *C. sankeyi*. Among them, *C. sankeyi* is similar to *C. yoga*, new species, in shell shape, but is much larger, has a wider umbilicus and at least a parietal tooth. The same is true for *C. proboscideus*, which has an even wider umbilicus than this new species. *Clostophis multiformis* has a domed dorsal side (shell shape is not concave conical as in this new species), possesses a parietal tooth, and its aperture does not turn towards the umbilicus. *Clostophis candidus*, new species, is similar to *Clostophis yoga* in lacking apertural barriers, but it is smaller, has a conical shell, and its aperture does not turn towards the shell axis.

Description. Shell concave conical, shell usually wider than high (as in figured paratype, Fig. 11). Whorls slightly, bluntly shouldered. Last ca. quarter whorl detached from penultimate whorl; aperture turns towards spire axis covering edge of umbilicus in ventral view. Therefore, width of body whorl is only slightly wider than that of the penultimate whorl. Protoconch consisting of ca. 1.25 whorls with pronounced spiral striations. Entire shell with 3.75–4 whorls. Umbilicus conspicuously oval, relatively narrow, occupies slightly less than one third of shell width (measured along a horizontal line in Figs. 10E and 11E). Teleoconch with weak, irregular radial lines and stronger, equidistant spiral striae (18–22 on body whorl in frontal view). Aperture subcircular, toothless, peristome slightly reflected, mostly at its columellar side.

Measurements (in mm). SH = 0.88–1.08, SW = 0.97–1.06 (n = 4).

Etymology. The specific epithet *yoga* (to be used as a noun in apposition) refers to the aperture that turns toward shell axis, resulting in a distorted shell shape and resembling a yoga position.

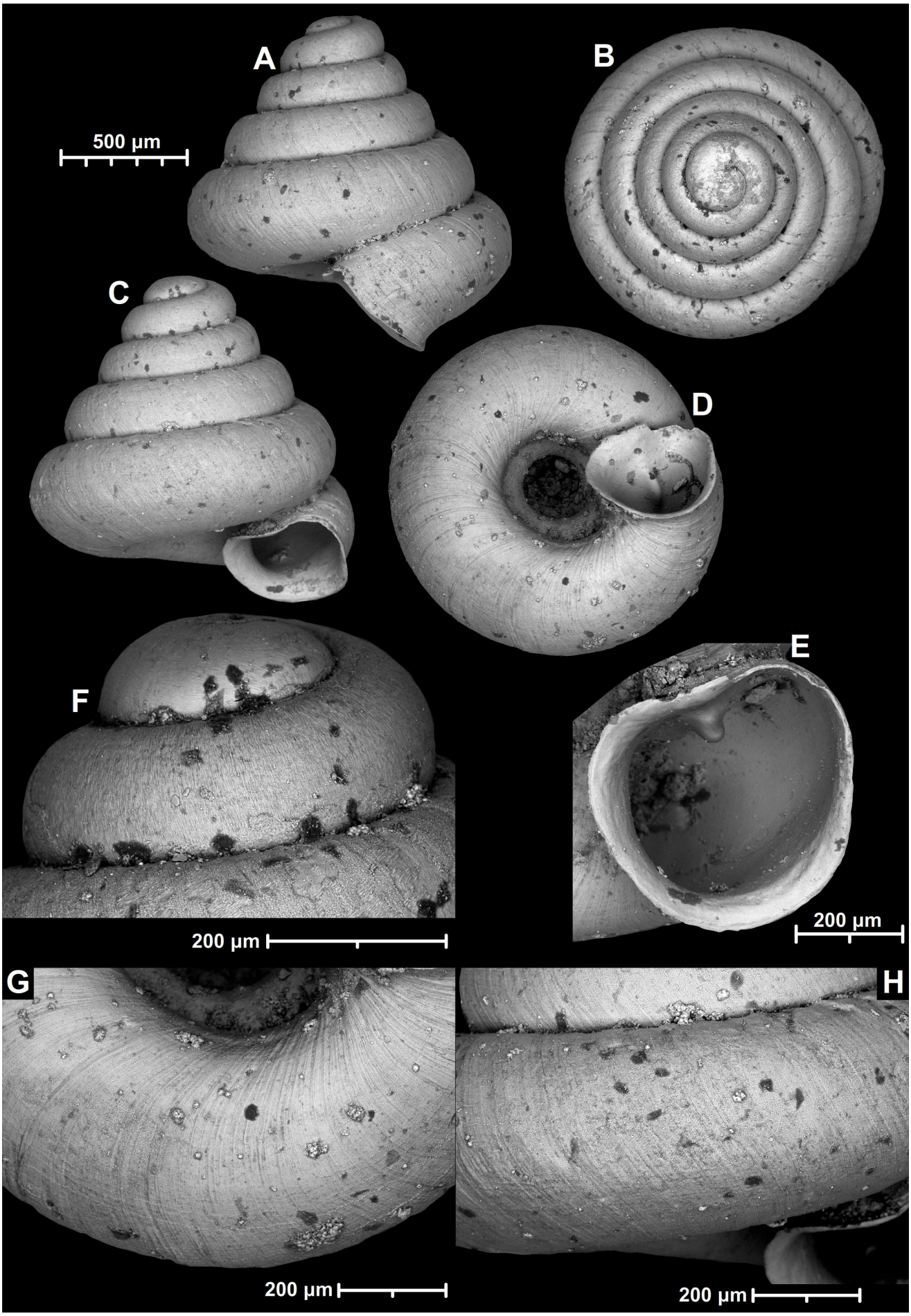

Fig. 9. *Clostophis thinbowguensis*, new species (holotype, MNHN-IM-2000-38057).

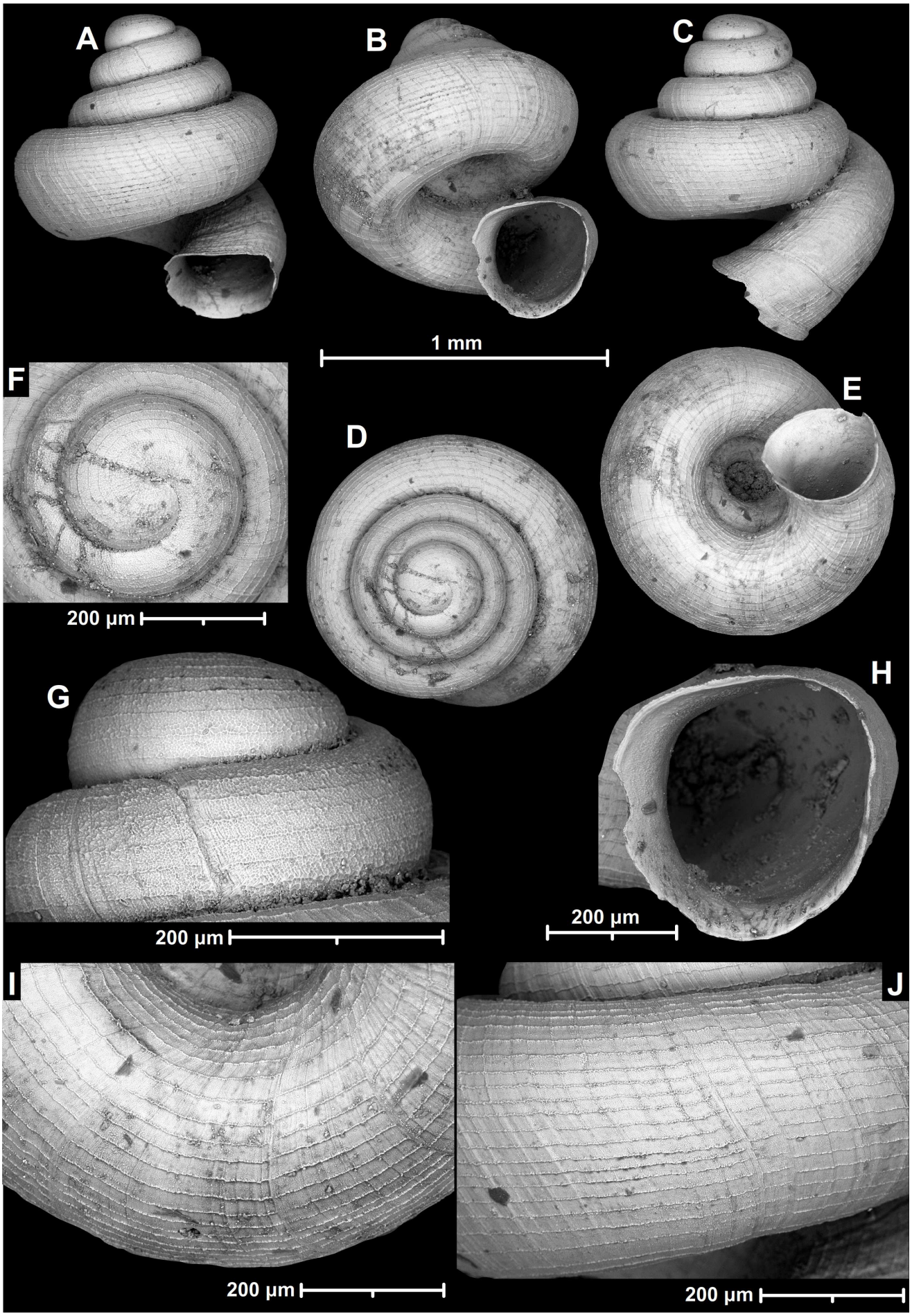

Fig. 10. *Clostophis yoga*, new species (holotype, HNHM 105325).

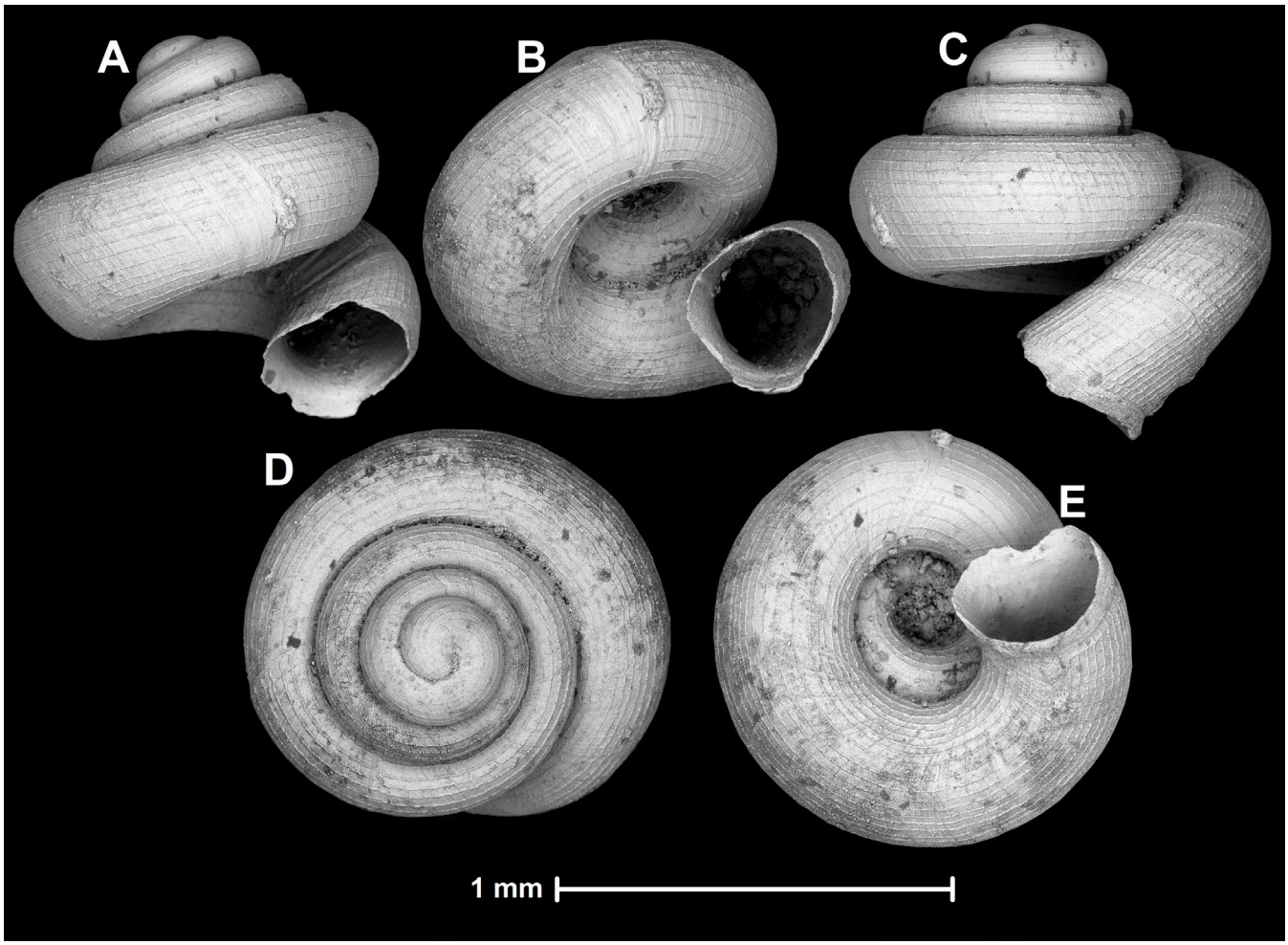

Fig. 11. *Clostophis yoga*, new species (paratype, coll. HA).

***Clostophis candidus*, new species**
(Fig. 12)

Type material. Holotype (SH: 1.03 mm, SW: 0.92 mm) (HNHM 105326), Vietnam, Lạng Sơn Province, Bắc Sơn District, Long Dong, 3.8 km north from junction of roads no. QL1B (main road) and 241, 390 m a.s.l., 21°56.728′N, 106°19.447′E (locality code: 2020/51), coll. A. Hunyadi, 18 February 2020. Paratypes: 10 shells, same data as for holotype.

Additional material. 2 juvenile/broken shells (coll. HA), same data as for holotype.

Diagnosis. *Clostophis* species with a detached aperture are as follows: *C. multiformis* Páll-Gergely & A. Reischütz, 2020, *C. proboscideus*, *C. sankeyi*, and *C. yoga*, new species. *Clostophis sankeyi* and *C. proboscideus* are larger, have a strongly concave conical shell shape, and possess at least one parietal tooth. The concave conical shell shape also differentiates *C. yoga*, new species, from *C. candidus*, new species. *Clostophis multiformis* has a dome-like, blunter apex (shell shape is not conical) and possesses a parietal tooth.

Description. Shell conical, higher than wide. Whorls rounded. Last part of body whorl (less than quarter whorl) detached from penultimate whorl. Protoconch consisting of ca. 1.25 whorls, finely spirally striated. Entire shell with ca. 4.25 whorls. Umbilicus rounded, slightly wider than one third of shell width. Teleoconch with weak, irregular radial lines and stronger, equidistant spiral striae (20–22 on body whorl in frontal view). Aperture subcircular, toothless, peristome slightly reflected, mostly at its columellar side.

Measurements (in mm). SH = 0.98–1.15, SW = 0.89–1.01 (n =4).

Etymology. The specific epithet *candidus* (bright, clear, transparent in Latin) refers to the clear, transparent shell.

***Clostophis charybdis*, new species**
(Figs. 13, 14)

Type material. Holotype (SH: 1.18 mm, SW: 1.12 mm) (HNHM 105327), Vietnam, Lạng Sơn Province, Bình Gia, eastern edge of the village, Di Chí Kéo Lèng (Thẩm Khuyên Cave), rock wall; 21°56.30′N, 106°23.82′E, 375 m a.s.l. (locality code: 2020/48), coll. A. Hunyadi, 17 February 2020. Paratype: 1 shell, coll. HA, same data as for holotype; 30 paratypes, coll. HA, Vietnam, Lạng Sơn Province, Bắc Sơn District, Long Dong, 3.8 km north from junction of roads no. QL1B (main road) and 241, 390 m a.s.l., 21°56.728′N, 106°19.447′E (locality code: 2020/51), coll. A. Hunyadi, 18 February 2020.

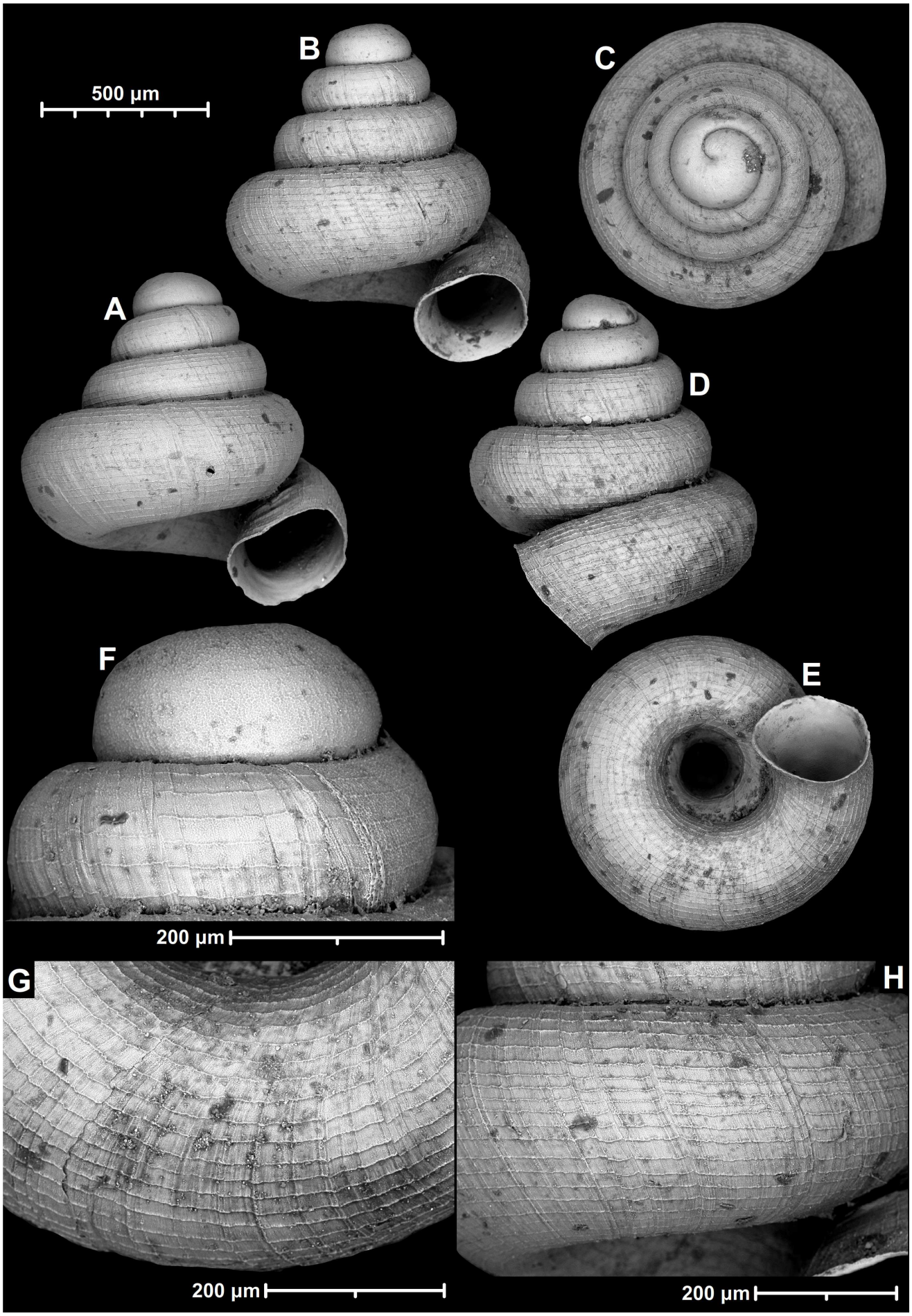

Fig. 12. *Clostophis candidus*, new species. A, paratype (coll. HA); B–H, holotype, HNHM 105326.

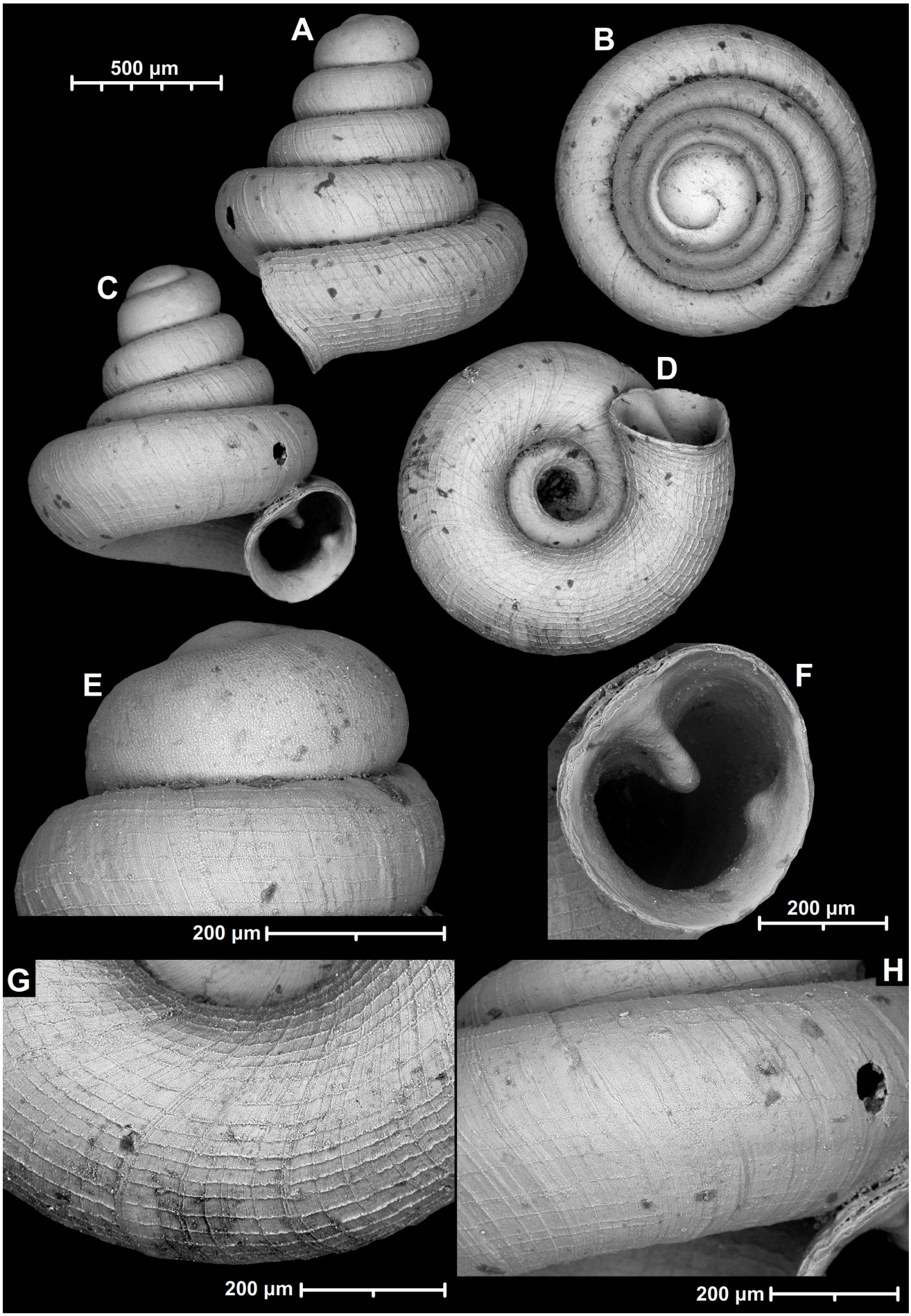

Fig. 13. *Clostophis charybdis*, new species (holotype, HNHM 105327).

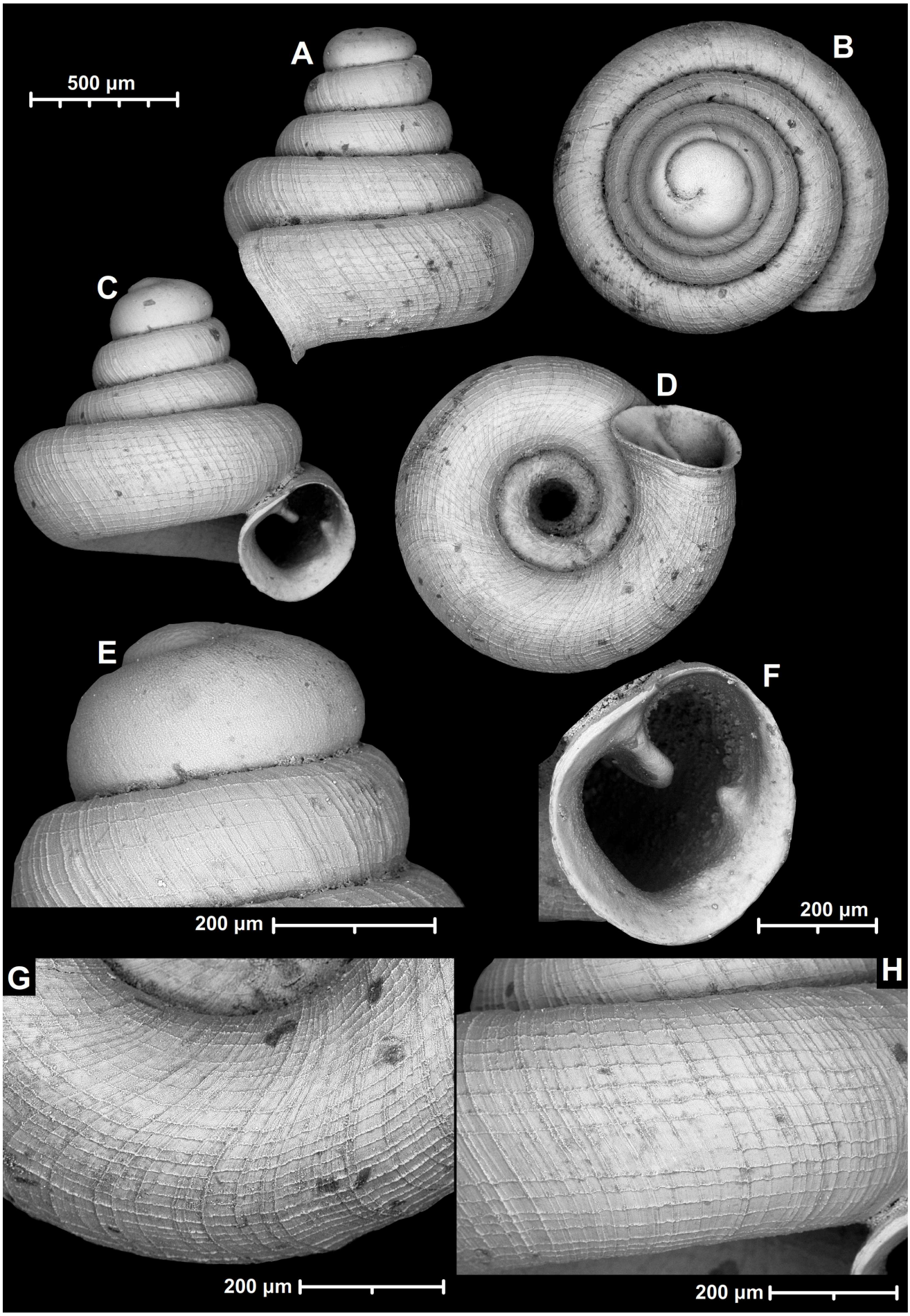

Fig. 14. *Clostophis charybdis*, new species (paratype, coll. HA).

Diagnosis. A concave conical *Clostophis* species with a wide umbilicus, a well-developed, elevated parietal, and a shorter, pointed palatal tooth situated slightly upper (more apically) than where the parietal tooth points.

Description. Shell concave conical, widest at its base, slightly higher than wide to slightly wider than high, body whorl conspicuously wider than penultimate whorl. Whorls very slightly, bluntly shouldered. Protoconch consisting of 1.25–1.5 whorls, finely pitted/granular, and spirally striated preceding the first teleoconch whorl. Entire shell consisting of 4.5–4.75 whorls, with relatively strong, irregular radial growth lines and equally strong, dense, equidistant spiral striae. Body whorl with few, ca. 16–18 spiral striae from apertural view. Umbilicus regularly growing, wide, shell width is ca. 2.5 times wider than umbilicus. Aperture oblique to shell axis, oval to rectangular with blunt sinulus area. Sinulus large, only slightly smaller than other side of aperture, and well separated due to elevated parietal tooth and palatal tooth. Parietal callus rather blunt, not smeared onto penultimate whorl. Peristome expanded, not reflected. Parietal tooth elevated straight, nearly reaching parietal callus. Parietal wall with a low but pointed tooth that is positioned slightly upper (more apically) compared to where the parietal tooth points.

Measurements (in mm). SH = 1.02–1.21, SW = 1.03–1.19 (n = 6).

Differential diagnosis. Among the *Clostophis* species possessing two parietal teeth, *Clostophis incurvus* Páll-Gergely & Vermeulen, 2020 has a conical shell with a narrower umbilicus, and *Clostophis platytrochus* Páll-Gergely & Hunyadi, 2020 also has a more conical shell and a more pronounced oblique aperture with a more basally-situated palatal tooth.

Etymology. Named after Charybdis, the large whirlpool (or sea monster) of the Greek mythology, referring to the whirlpool-like umbilicus.

Species with long apertural barriers

Remarks. The three species listed here (*C. lacrima*, *C. obliquus*, new species, and *C. socialis*) differ from all other *Clostophis* species in the long apertural barriers (in the case of *C. obliquus*, only the angulo-parietal lamella is long). These species are similar to other *Clostophis* species in shell size, shape, colour, and sculpture.

Clostophis lacrima (Páll-Gergely & Hunyadi, 2015)
(Figs. 15, 16)

Hypselostoma lacrima Páll-Gergely & Hunyadi, 2015 (in Páll-Gergely et al., 2015): 45, figs. 6, 8F–K.

Material examined. 2 shells (coll. HA), Vietnam, Lạng Sơn Province, Hữu Lũng District, Hữu Liên, 1,400 m west from Đông Lâm along road no. 241, 21°41.91′N, 106°21.77′E, 210 m a.s.l. (locality code: 2020/53), coll. A. Hunyadi, 19 February 2020.

Measurements (in mm). SW = 1.28–1.29, H: 1.35–1.36 (n = 6).

Remarks. This species, due to its colourless shell and dense spiral striation is transferred to the genus *Clostophis*.

This species was described from the Chinese Guangxi Province, ca. 105 km northeast from the new Vietnamese locality. The Vietnamese shells are slightly smaller (measurements of the Chinese shells are SW = 1.34–1.35, SH = 1.33–1.35) and their palatal fold is straight, whereas the Chinese specimens' palatal fold is slightly angled. These differences, however, do not justify their distinction as a separate species.

Clostophis obliquus, new species
(Fig. 17)

Type material. Holotype (SH: 1.19 mm, SW: 1.18 mm) (HNHM 105324), China, Guangxi, Liuzhou Shi, 12 km southeast from Douleyan Scenic Area, 110 m a.s.l., 24°13.666′N, 109°24.643′E (locality code: 2009/68), coll. A. Hunyadi, 6 October 2009. Paratypes: 3 shells, same as for holotype, coll. HA.

Diagnosis. A conical *Clostophis* species with four apertural barriers: outer part of angulo-parietal lamella tilts towards palatal wall, inner part longer, turns to opposite direction; two palatal folds short, thin (blade-like), oblique (descending inside aperture), situated in some distance from peristome; columellar tooth also short, blunt (knob-like).

Description. Shell conical, widest at its base, as high as wide. Whorls very slightly, bluntly shouldered. Protoconch consisting of 1.5 whorls, finely pitted/granular, and weakly spirally striated preceding the first teleoconch whorl. Entire shell consisting of 5 whorls, with relatively strong, irregular radial growth lines and equally strong, dense, irregularly spaced spiral striae. Body whorl with few, ca. 20–24 spiral striae from apertural view. Umbilicus regularly growing, normally wide, ca. one third of shell width. Aperture slightly oblique to shell axis, oval teardrop-shaped with a blunt sinulus. Sinulus small, well separated due to elevated angulo-parietal lamella and upper palatal tooth. Parietal callus rather blunt, not smeared to penultimate whorl. Peristome expanded, not reflected. Angulo-parietal lamella long, elevated, its outer part shorter, strongly oblique, tilts towards palatal wall, inner part longer, gradually (as it goes deeper) tilts towards columella. Palatal wall with two short blade-like, oblique lamellae; upper one nearly reaches peristome, its inner end is situated lower than the outer one; inner one situated slightly deeper, also oblique (outer end situated higher up, while inner end is lower). Columellar tooth also short, blunt (knob-like), situated in some distance from peristome.

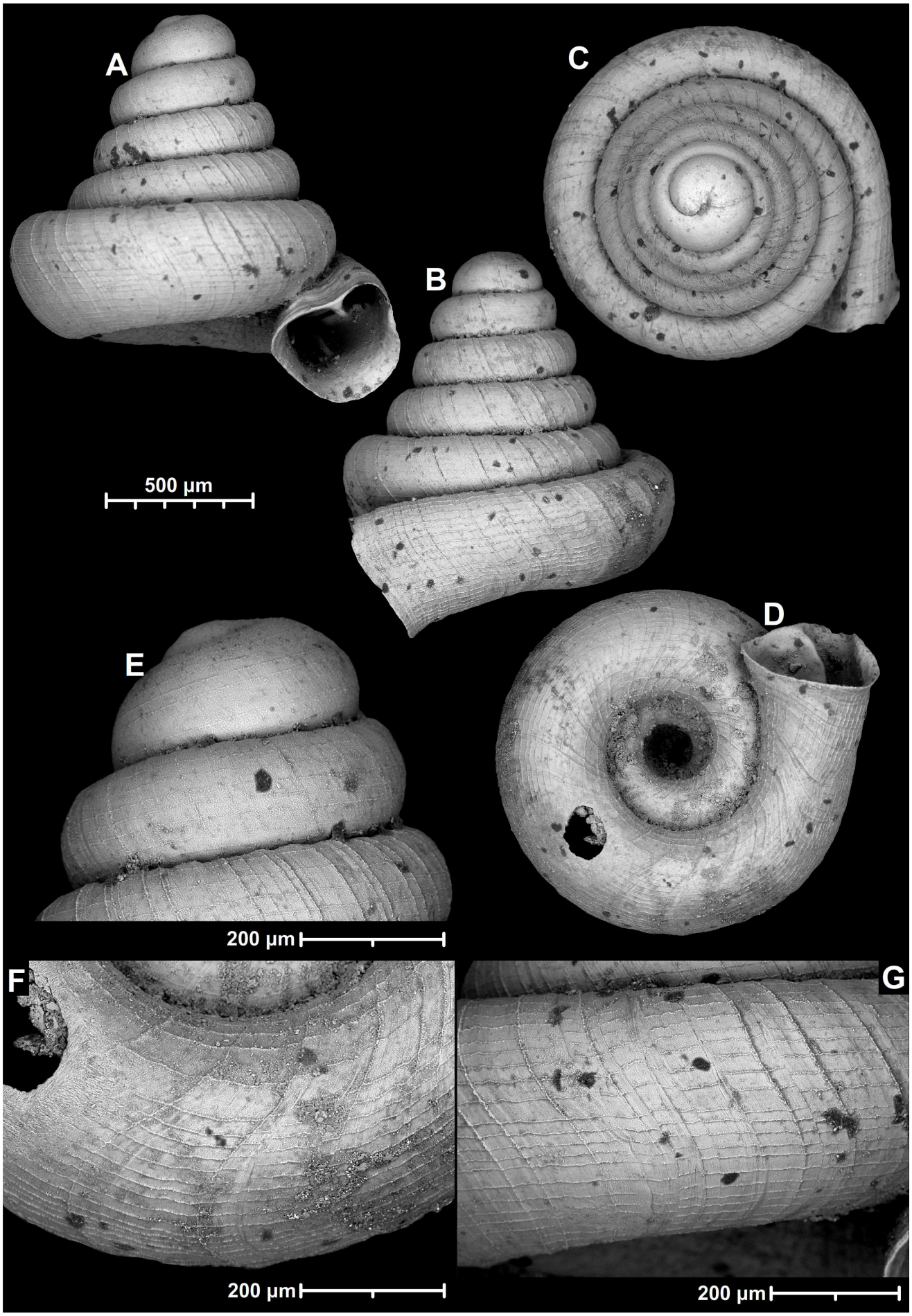

Fig. 15. *Clostophis lacrima* (Páll-Gergely & Hunyadi, 2015), from locality 2020/53.

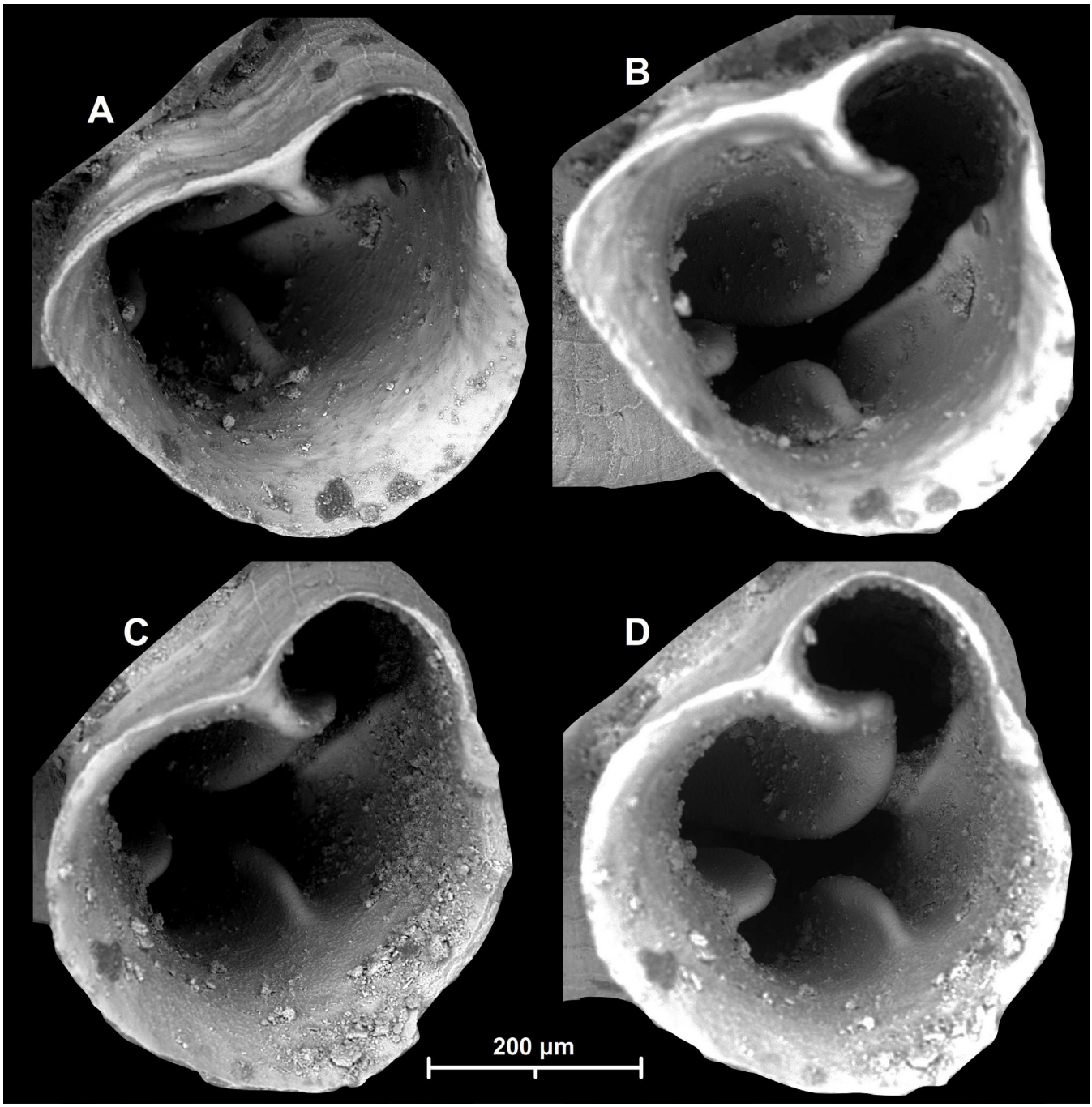

Fig. 16. *Clostophis lacrima* (Páll-Gergely & Hunyadi, 2015), from locality 2020/53. A, B, specimen 1; C, D, specimen 2.

Measurements. See holotype. Since the paratype has a broken apex, this measurement is not informative.

Differential diagnosis. Other *Clostophis* species with multiple apertural barriers (*C. socialis*, *C. lacrima*) have strongly elongated palatal and columellar folds.

Etymology. The specific epithet *obliquus* (oblique in Latin) refers to the oblique apertural barriers of this new species.

Clostophis socialis (Páll-Gergely & Hunyadi, 2015)

Hypselostoma socialis Páll-Gergely & Hunyadi, 2015 (in Páll-Gergely et al., 2015): 48, figs. 7, 8A–E.

Remarks. As with the preceding species, this species is also transferred to the genus *Clostophis*.

DISCUSSION

In the present paper we describe six new *Clostophis* species from Myanmar, Peninsular Malaysia, Vietnam, and the Chinese Guangxi Province.

Besides taxonomic remarks that are made under each taxon, one phenomenon deserves special mention. The last quarter whorl of some species of hypselostomatid genera, such as *Clostophis*, *Gyliotrachela* Tomlin, 1930, and *Hypselostoma* Benson, 1856, are detached from the

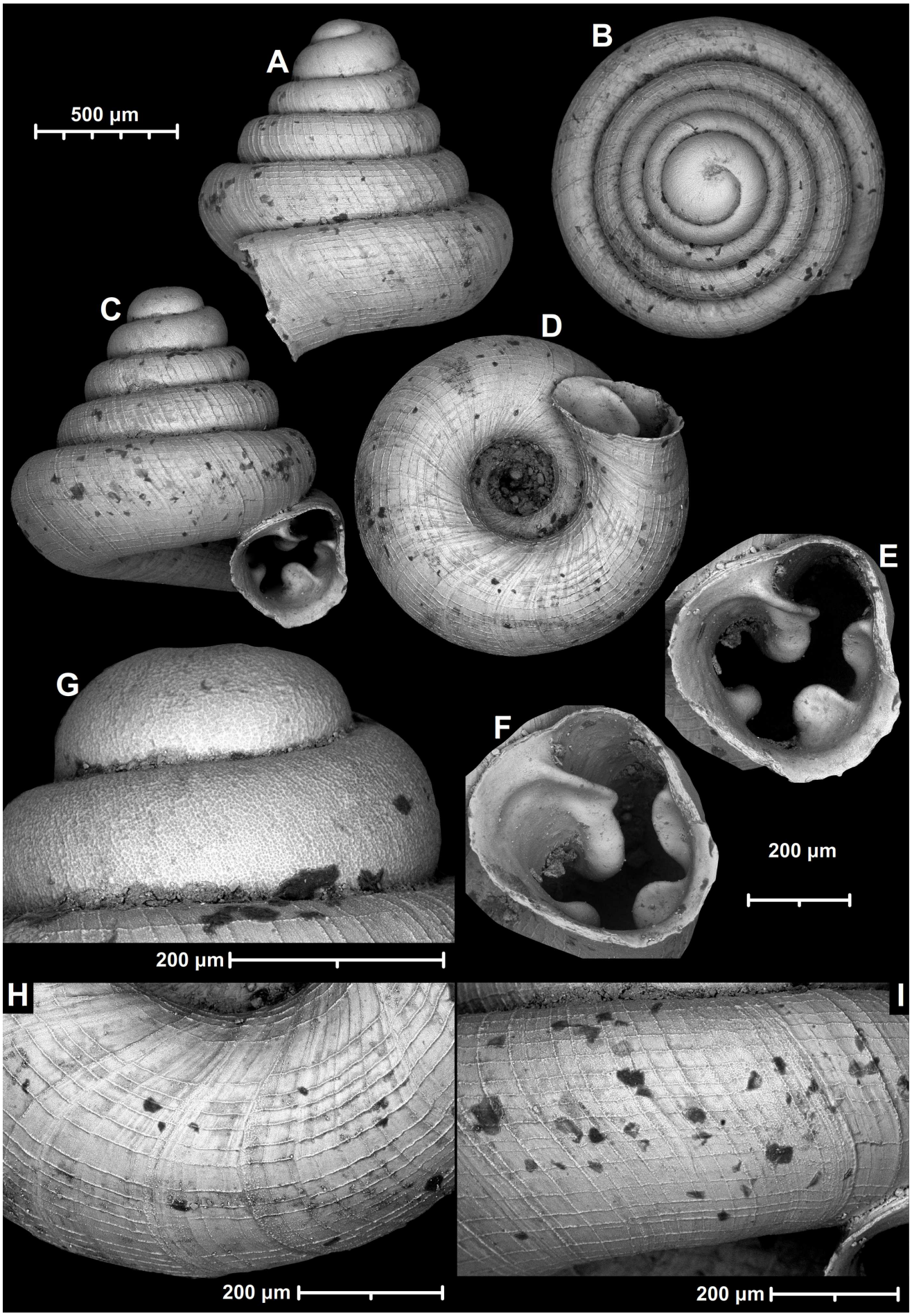

Fig. 17. *Clostophis obliquus*, new species (holotype, HNHM 105324).

penultimate whorl (Schileyko, 1998). This phenomenon is proportionally more common in terrestrial Caenogastropoda than in Stylommatophora (Chen et al., 2022). The reason behind this may be the fact that in most Caenogastropoda, the aperture is generally rounded (circular). As a result, the last and penultimate whorls do not overlap, or only do so slightly, and meet only at one point in a cross-sectional view. In contrast, the cross-sectional view of the stylommatophoran whorl is not circular but, to a variable degree, semilunar (Hutchinson, 2000). Therefore, a detached last whorl can evolve more frequently in groups where physical contact between the last and penultimate whorls is weaker (Chen et al., 2022). Within *Clostophis*, four species have such a detached last whorl. *Clostophis sankeyi* and *Clostophis candidus*, new species, are geographically adjacent to *C. proboscideus* and *C. yoga*, new species, respectively. This suggests that the detached last whorl has developed at least twice independently within the genus. Similar to the Urocoptidae with its detached aperture (Chen et al., 2022), independent, repeated acquisition of similar traits suggests that the trait may be adaptive, although its adaptive value is unknown.

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