

Clostophis Benson, 1860, is not a monotypic diplommatinid but a speciose hypselostomatid (Gastropoda: Eupulmonata), with descriptions of six new species

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Abstract. Examination of the holotype and newly collected specimens of *Clostophis sankeyi* Benson, 1860 (the only species of *Clostophis* Benson, 1860) from Myanmar revealed that it does not belong to the caenogastropod family Diplommatinidae, but to the “pulmonate” Hypselostomatidae. *Montapiculus proboscidea* Panha & Burch, 1999 from Thailand is a valid species, but the general shell shape and aperture formation of *Clostophis* and *Montapiculus* Panha & Burch, 1999, are so similar that the latter genus is considered to be a junior synonym of the former. The following new species are described from the re-diagnosed *Clostophis*: *C. multiformis* Páll-Gergely & A. Reischütz, new species (Laos), *C. obtusus* Páll-Gergely & Grego, new species (Laos), *C. infantilis* Páll-Gergely, new species (Laos), *C. platytrochus* Páll-Gergely & Hunyadi, new species (Vietnam), *C. koilobasis* Páll-Gergely & Vermeulen, new species (Vietnam), and *C. incurvus* Páll-Gergely & Vermeulen, new species (Vietnam). *Angustopila stochi* Páll-Gergely & Jochum, 2017, is moved to *Clostophis*.

Key words. microsnails, morphology, taxonomy, Laos, Vietnam

INTRODUCTION

Schileyko (1998), mostly based on the system of Zilch (1959–1960), listed the following genera as members of the Hypselostomatidae: *Acinolaemus* F. G. Thompson & Upatham, 1997, *Anauchen* Pilsbry, 1917 (described in Pilsbry, 1916–1918), *Aulacospira* Möllendorff, 1890, *Bensonella* Pilsbry & Vanatta, 1900, *Boysia* L. Pfeiffer, 1849, *Boysidia* Ancey, 1881 (with the subgenera *Paraboysidia* Pilsbry, 1917 [described in Pilsbry, 1916–1918] and *Dasypupa* F.G. Thompson & Dance, 1983), *Campolaemus* Pilsbry, 1892, *Gylotrachela* Tomlin, 1930, *Hypselostoma* Benson, 1856, and *Pseudostreptaxis* Möllendorff, 1890. A few additional genera were described subsequently, namely *Angustopila* Jochum, Slapnik & Páll-Gergely in Jochum, Slapnik, Kampschulte, Martels, Heneka & Páll-Gergely, 2014, *Antroapiculus* Panha & Burch, 1999 (in Panha & Burch, 1999a), *Dentisphaera*

Páll-Gergely & Jochum in Páll-Gergely, Jochum & Asami, 2017, *Krobylos* Panha & Burch, 1999 (in Panha & Burch, 1999a), *Montapiculus* Panha & Burch, 1999 (in Panha & Burch, 1999a), and *Tonkinospira* Jochum, Slapnik & Páll-Gergely in Jochum, Slapnik, Kampschulte, Martels, Heneka & Páll-Gergely, 2014. The last genus was proposed as a replacement name for *Systemostoma* Bavay & Dautzenberg, 1909 (non Marsson, 1887; Bryozoa), which was classified by Schileyko (1998) in Vertiginoidea without assigning it to any families. *Campolaemus*, based on characters of the apertural barriers and biogeographic information (endemic to Saint Helena Island of the South Atlantic Ocean), was recently excluded from the Pupilloidea and reclassified into the Streptaxidae (Páll-Gergely, 2020). Thus, all remaining hypselostomatid genera inhabit the Oriental Biogeographic Region, with some species reported from Australia, Japan, and central China (Schileyko, 1998).

The only molecular phylogenetic paper focusing on this group failed to resolve deep splits, and the analysis did not contain crucial genera, such as *Gastrocopta* Wollaston, 1878 (Tongkerd et al., 2004). Therefore, the systematics of the hypselostomatid genera is highly uncertain. These genera were included in various families by recent publications, i.e., in the Vertiginidae by Panha (1997) and Vermeulen et al. (2019), in the Pupillidae by Panha & Burch (1999b, 2005), and in the Hypselostomatidae by Páll-Gergely et al. (2015; 2017).

The genus *Clostophis* Benson, 1860, including the only species *C. sankeyi* Benson, 1860, has hitherto been classified

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into the Diplommatinidae (Benson, 1860; Kobelt, 1902; Egorov, 2013). The examination of the holotype and newly collected specimens of *C. sankeyi*, however, revealed that it is not a diplommatinid, and not even a caenogastropod, but a hypselostomatid, similar to *Montapiculus proboscidea* Panha & Burch, 1999. We concluded that *Montapiculus* is a junior synonym of *Clostophis* and that several other species, so far classified in other genera, belong to *Clostophis*. We also introduce some new species, which are characterised by colourless, small (max. 2 mm) shells, dense spiral striation, and few (0–2) teeth in the aperture.

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 (Miniscope TM-1000, Hitachi High-Technologies, Tokyo). Shell whorl number was counted to the nearest quarter whorl according to Kerney & Cameron (1979).

Measurements were taken using a VHX-5000 Keyence Digital microscope with a 20–200× objective.

Abbreviations.

HA: Collection András Hunyadi, Budapest, Hungary
 HNHM: Hungarian Natural History Museum, Budapest, Hungary
 JG: Collection Jozef Grego, Banská Bystrica, Slovakia
 JJV: Collection Jaap Vermeulen, Leiden, The Netherlands
 MNHN: Muséum National d'Histoire Naturelle, Paris, France
 MZUF: Natural History Museum University of Florence, Zoological Section “La Specola” Firenze, Florence, Italy
 NHM: The Natural History Museum, London, United Kingdom
 NHMUK: when citing specimens deposited in the NHM
 NHMW: Naturhistorisches Museum Wien, Vienna, Austria
 RE: Collection Reischütz, Horn, Austria
 SA: Collection Simon Aiken, York, United Kingdom
 SH: shell height
 SW: shell width (diameter)
 UMZC: University Museum of Zoology, Cambridge, United Kingdom

Taxon names. The new taxon names *Clostophis koilobasis* Páll-Gergely & Vermeulen, new species, and *Clostophis incurvus* Páll-Gergely & Vermeulen, new species, are the responsibility of Barna Páll-Gergely and Jaap Vermeulen. The authorship of the new taxon names should be cited as *Clostophis koilobasis* Páll-Gergely & Vermeulen in Páll-Gergely, Hunyadi, Grego, A. Reischütz, Buczkó & Vermeulen, 2020, and *Clostophis incurvus* Páll-Gergely & Vermeulen in Páll-Gergely, Hunyadi, Grego, A. Reischütz, Buczkó & Vermeulen, 2020.

The new taxon name *Clostophis multiformis* Páll-Gergely & A. Reischütz, new species, is the responsibility of Barna Páll-Gergely and Alexander Reischütz. The authorship of the new taxon name should be cited as *Clostophis multiformis*

Páll-Gergely & A. Reischütz in Páll-Gergely, Hunyadi, Grego, A. Reischütz, Buczkó & Vermeulen, 2020.

The new taxon name *Clostophis obtusus* Páll-Gergely & Grego, new species, is the responsibility of Barna Páll-Gergely and Jozef Grego. The authorship of the new taxon name should be cited as *Clostophis obtusus* Páll-Gergely & Grego in Páll-Gergely, Hunyadi, Grego, A. Reischütz, Buczkó & Vermeulen, 2020.

The new taxon name *Clostophis platytrochus* Páll-Gergely & Hunyadi, new species, is the responsibility of Barna Páll-Gergely and András Hunyadi. The authorship of the new taxon name should be cited as *Clostophis platytrochus* Páll-Gergely & Hunyadi in Páll-Gergely, Hunyadi, Grego, A. Reischütz, Buczkó & Vermeulen, 2020.

The new taxon name *Clostophis infantilis* Páll-Gergely, new species, is the responsibility of Barna Páll-Gergely. The authorship of the new taxon name should be cited as *Clostophis infantilis* Páll-Gergely in Páll-Gergely, Hunyadi, Grego, A. Reischütz, Buczkó & Vermeulen, 2020.

SYSTEMATICS

Family Hypselostomatidae Zilch, 1959

Clostophis Benson, 1860

Clostophis Benson, 1860: 95.

Montapiculus Panha & Burch, 1999a: 148. (new synonym)

Montapiculus — Panha & Burch, 2005: 38, 109.

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

Grammatical gender. Masculine.

Diagnosis. Shell minute, colourless (white), body whorl rounded or very slightly keeled or shouldered, detached from penultimate whorl forming a free tube, or normally attached to penultimate whorl; shell surface finely reticulated caused by the radial growth lines and stronger, dense spiral lines (usually at least 20 striae on the body whorl, counted from apertural view); aperture toothless, or with a short but often high parietal tooth, in some species with a palatal tooth.

Differential diagnosis. *Angustopila* shells are smaller, the body whorl is never detached from the penultimate whorl, and the spiral striation is less dense (up to 20 striae on the body whorl, counted from apertural view). Species assigned to *Tonkinospira* are mostly colourless and possess dense spiral striation, similar to *Clostophis*, but the aperture is toothless and the peristome is often not reflected. It is possible that *Clostophis* and *Tonkinospira* are not mutually monophyletic. *Acinolaemus* species have more apertural barriers, and at least the type species possesses a parietal and a separate angular tooth. Species assigned to *Acinolaemus* also need a generic revision. *Hypselostoma* (at least its type species) is large

(ca. 4 mm), has reduced spiral striation, and is brown in colour, not colourless like *Clostophis*. See also Discussion.

Included species. The genus *Clostophis* currently comprises ten species: *C. incurvus* Páll-Gergely & Vermeulen, new species; *C. infantilis* Páll-Gergely, new species; *C. koilobasis* Páll-Gergely & Vermeulen, new species; *C. multiformis* Páll-Gergely & A. Reischütz, new species; *C. neglectus* (van Benthem Jutting, 1961); *C. obtusus* Páll-Gergely & Grego, new species; *C. proboscideus* (Panha & Burch, 1999a); *C. platytrochus* Páll-Gergely & Hunyadi, new species; *C. sankeyi* Benson, 1860; and *C. stochi* (Páll-Gergely & Jochum in Páll-Gergely, Jochum & Asami, 2017) (Fig. 1).

Remarks. *Clostophis* was considered a diplommatinid genus (Benson, 1860; Kobelt, 1902; Egorov, 2013) although Benson (1860) had already mentioned that it might be related to *Hypselostoma*. After examining the holotype of *Clostophis sankeyi*, it became evident that the minute, white, finely reticulate shell with a descending aperture and the single parietal tooth is characteristic for the monotypic genus *Montapiculus* Panha & Burch, 1999 (type species: *Montapiculus proboscidea* Panha & Burch, 1999, by original designation). Thus, *Montapiculus* is a junior synonym of *Clostophis*. The two species, due to the considerable differences between them, are considered valid. The type locality of *C. proboscideus* is situated ca. 240 km in a straight line from that of *C. sankeyi* (Fig. 2).

Some additional species, for example *Hypselostoma edentata* (Panha & Burch, 1999), might also belong to *Clostophis* and will need to be confirmed by further study.

***Clostophis sankeyi* Benson, 1860**
(Fig. 3A)

Clostophis sankeyi Benson, 1860: 95.

Clostophis sankeyi — Kobelt, 1902: 484.

Clostophis sankeyi — Egorov, 2013: 24.

Type locality. “Prope Moulmein, ad cavernas “Farm Caves” dictas” [Farm Caves at 16°32'N 97°42.8'E].

Types examined. Holotype of *Clostophis sankeyi* (UMZCI.103320). Benson (1860) mentioned in the original description that only a single shell was available.

Additional material examined. 1 shell (coll. HA), Myanmar, Mon Province, Mawlamyine centre NEE ca. 26 km, Dhammasa Cave, 8 m a.s.l., 16°30.403'N, 97°48.646'E (locality codes 2018/49a and 20181011A), coll. A. Hunyadi, K. Okubo & J.U. Otani, 11 October 2018; 1 shell (coll. HA), 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 codes: 2018/50 and 20181011B), coll. A. Hunyadi, K. Okubo & J.U. Otani, 11 October 2018.

Diagnosis. A *Clostophis* species with detached and descending last quarter of the body whorl, a comparatively narrow umbilicus, and a weak parietal tooth.

Description. Shell conical, upper whorls growing regularly, and seemingly are sunken into the last whorl, i.e., last whorl coils around penultimate whorl more apically in position than it would be expected from the growth rate of initial whorls. Whorls rounded, showing a very slight indication of a blunt shoulder. Tuba (i.e., last quarter whorl) strongly detached from penultimate whorl. Protoconch consisting of 1.5 whorls, pitted and spirally striated. Entire shell with 4.5 whorls. Umbilicus oval due to the irregularly formed body whorl; occupies ca. one third of the shell width. Entire teleoconch with strong, elevated, rather equidistant spiral striae, and some weak, irregular radial growth lines. Some growth lines close to the suture on dorsal surface strong, almost rib-like. Aperture suboval. Sinulus wide. Parietal tooth weak and relatively short. Peristome expanded but not reflected.

Remarks. See under *C. proboscideus*.

***Clostophis incurvus* Páll-Gergely & Vermeulen, new species**
(Fig. 4)

Type material. Holotype (SH: 1.25 mm, SW: 1.08 mm) (NHMUK 20191125; original inv. number: JJV 6263), Vietnam, Quang Ninh Province, Halong Bay area, Dao Bo Hon, Song Sot Cave, 20°50.833'N, 107°5.667'E, drift material washed together over sinkhole in cave, coll. Vermeulen, J.J. & Whitten, A.J., 02 October 1998.

Diagnosis. A convexly conical *Clostophis* species with strong spiral striae, a well-developed parietal and a blunt palatal tooth.

Description. Shell triangular, convex, widest at its base. Whorls regularly increasing, bluntly shouldered. Protoconch consisting of ca. 1.5 whorls, no notable sculpture visible. Entire shell consisting of nearly five whorls, with fine, irregular radial growth lines and stronger, dense, equidistant spiral striae. Body whorl with ca. 17 spiral striae from apertural view. Umbilicus relatively narrow, occupies less than one third of the width. Aperture slightly oblique to shell axis, subcircular with blunt sinulus area. Parietal callus rather sharp, not smeared to penultimate whorl. Peristome relatively strongly thickened and expanded, not reflected. Parietal tooth moderately elevated, situated close to parietal callus. Parietal wall with a low, blunt, but strong tooth.

Differential diagnosis. *Clostophis stochi* has a weaker and denser spiral striation, a narrower umbilicus, and more rounded whorls. *Clostophis multiformis*, new species, possesses no or a weaker palatal tooth and a lower parietal tooth. See also under *C. koilobasis*, new species.

Etymology. The specific epithet means bent, curved in Latin, and refers to the last whorl, which is curved inwards in relation to the penultimate whorl.

Remarks. Although only a single shell is available, its shell characters clearly indicate that it differs from all congeners.

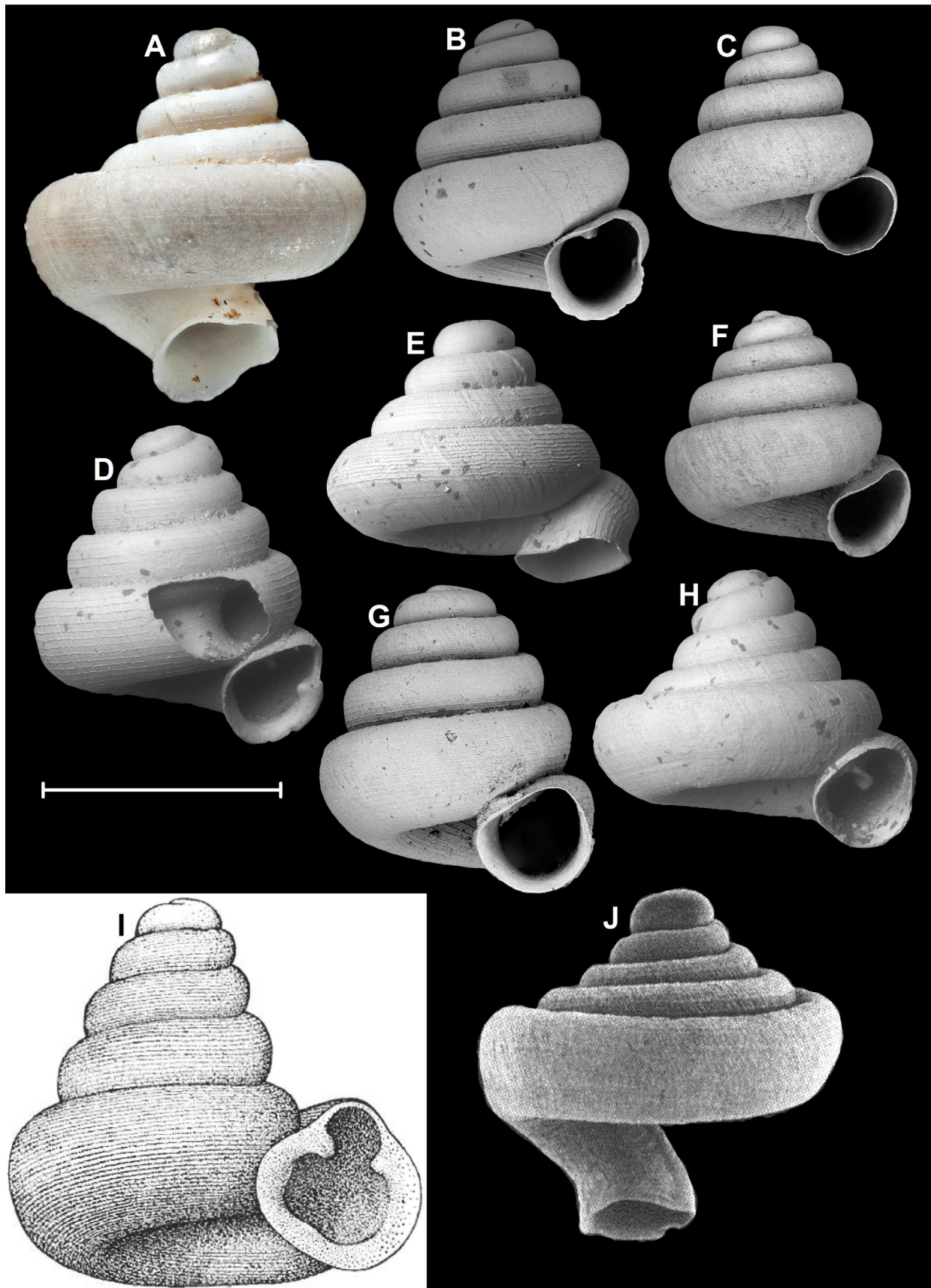


Fig. 1. Synoptic view of *Clostophis* species. A, *Clostophis sankeyi* (UMZCI.103320, holotype, copyright: The Trustees of the Natural History Museum, photo: Harry Taylor); B, *Clostophis stochi* (MZUF GC/49405, holotype, from the original description: Páll-Gergely & Jochum in Páll-Gergely et al., 2017); C, *Clostophis infantilis*, new species (MNHN-IM-2014-6401, holotype); D, *Clostophis incurvus*, new species (NHMUK 20191125, holotype); E, *Clostophis platytrochus*, new species (HNHM 104408, holotype); F, *Clostophis multiformis*, new species (NHMW 113273, holotype); G, *Clostophis obtusus*, new species (HNHM 104435, holotype); H, *Clostophis koilobasis*, new species (NHMUK 20191126, holotype); I, *Clostophis neglectus* (drawing from the original description: van Benthem Jutting, 1961); J, *Clostophis proboscideus* (holotype from the original description). Scale = 1 mm.

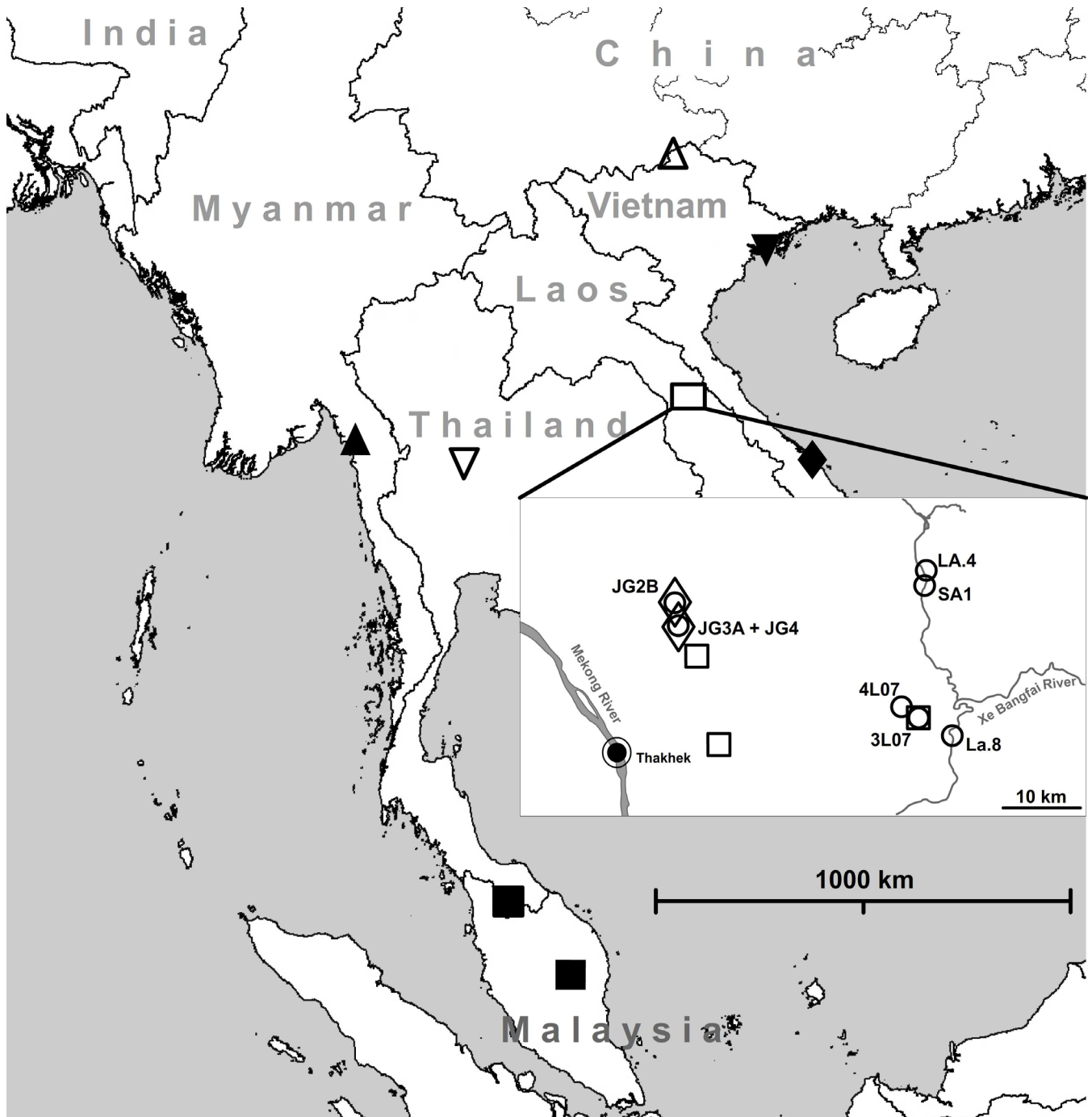


Fig. 2. Known distribution of *Clostophis* species. Empty triangle: *Clostophis stochi*; inverted empty triangle: *C. proboscideus*; filled triangle: *Clostophis sankeyi*; inverted filled triangle: *Clostophis koilobasis*, new species, and *Clostophis incurvus*, new species; filled square: *Clostophis neglectus*; filled diamond: *Clostophis platytrochus*, new species. Inset map shows the distribution of *Clostophis multiformis*, new species (circles with labels, see explanation in the text), *Clostophis obtusus*, new species (empty diamond), and *Clostophis infantilis*, new species (empty square), east of Thakhek.

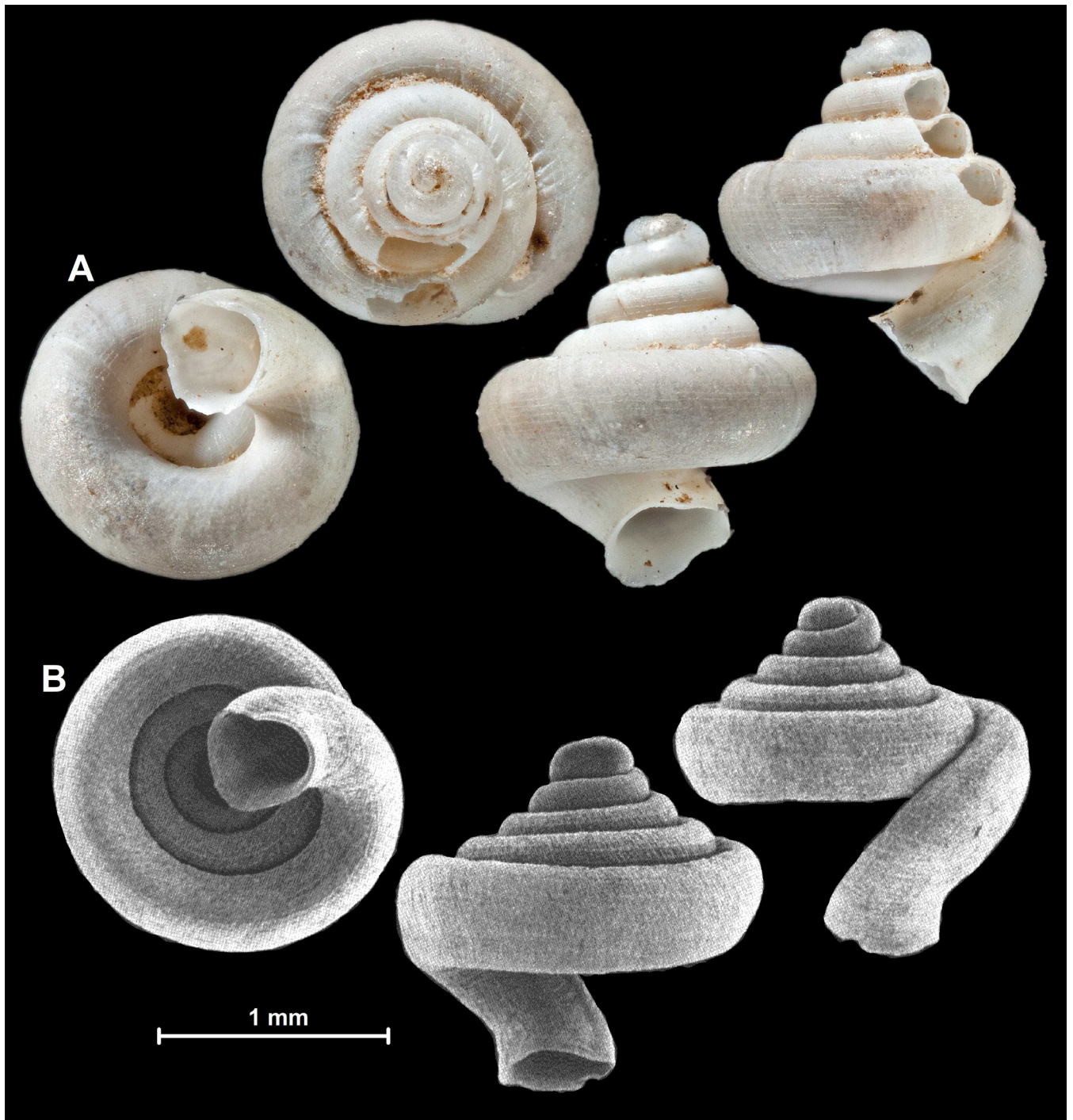


Fig. 3. Shells of *Clostophis* species. A, holotype of *Clostophis sankeyi* (UMZCI.103320, copyright: The Trustees of the Natural History Museum, photo: Harry Taylor); B, holotype of *Clostophis proboscideus* (from the original description).

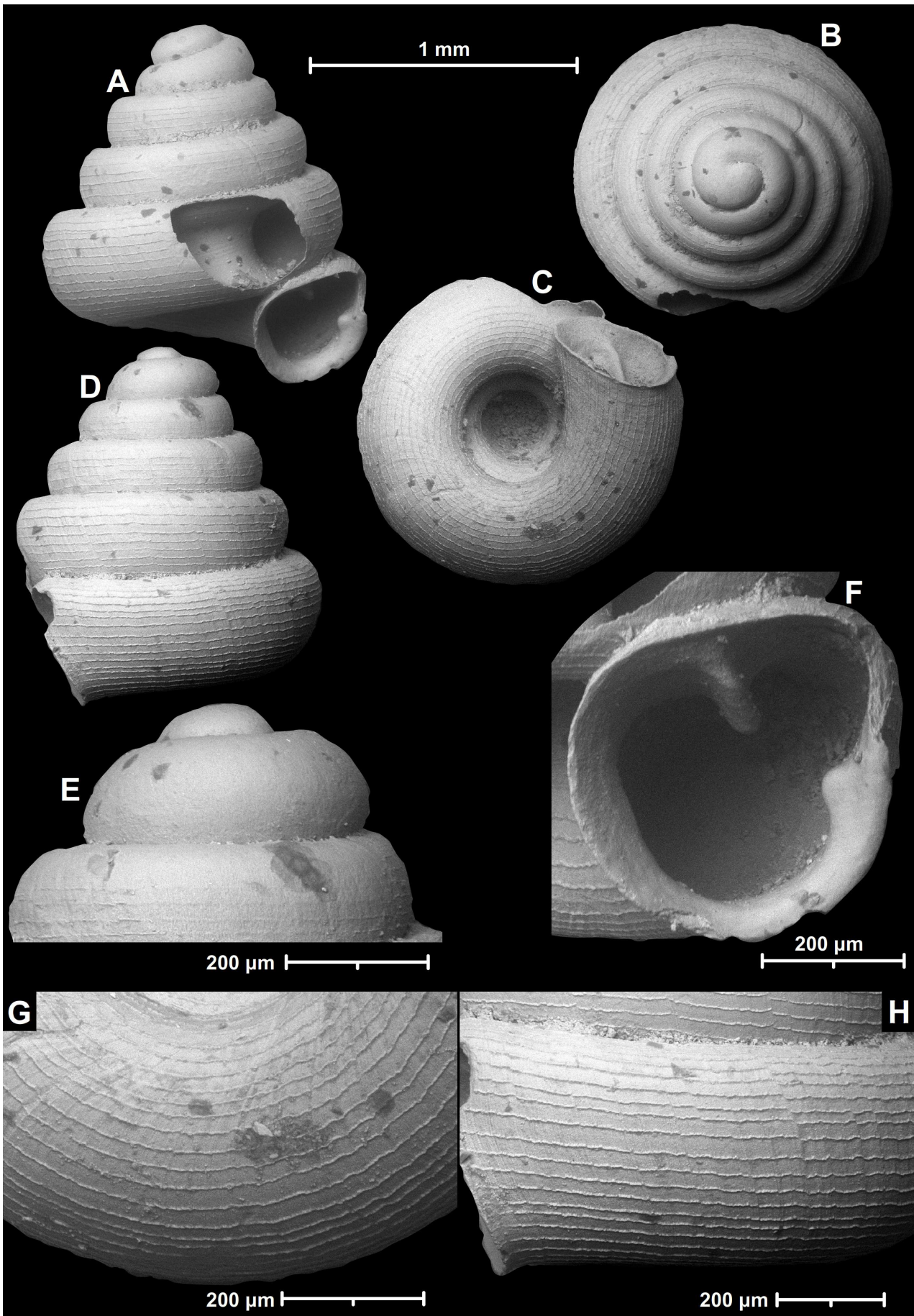


Fig. 4. *Clostophis incurvus* Páll-Gergely & Vermeulen, new species (NHMUK 20191125, holotype). A, apertural view; B, dorsal view; C, ventral view; D, lateral view; E, protoconch sculpture; F, aperture dentition; G, sculpture of the ventral side; H, sculpture of body whorl (lateral side is shown since the part from standard apertural view has been broken off).

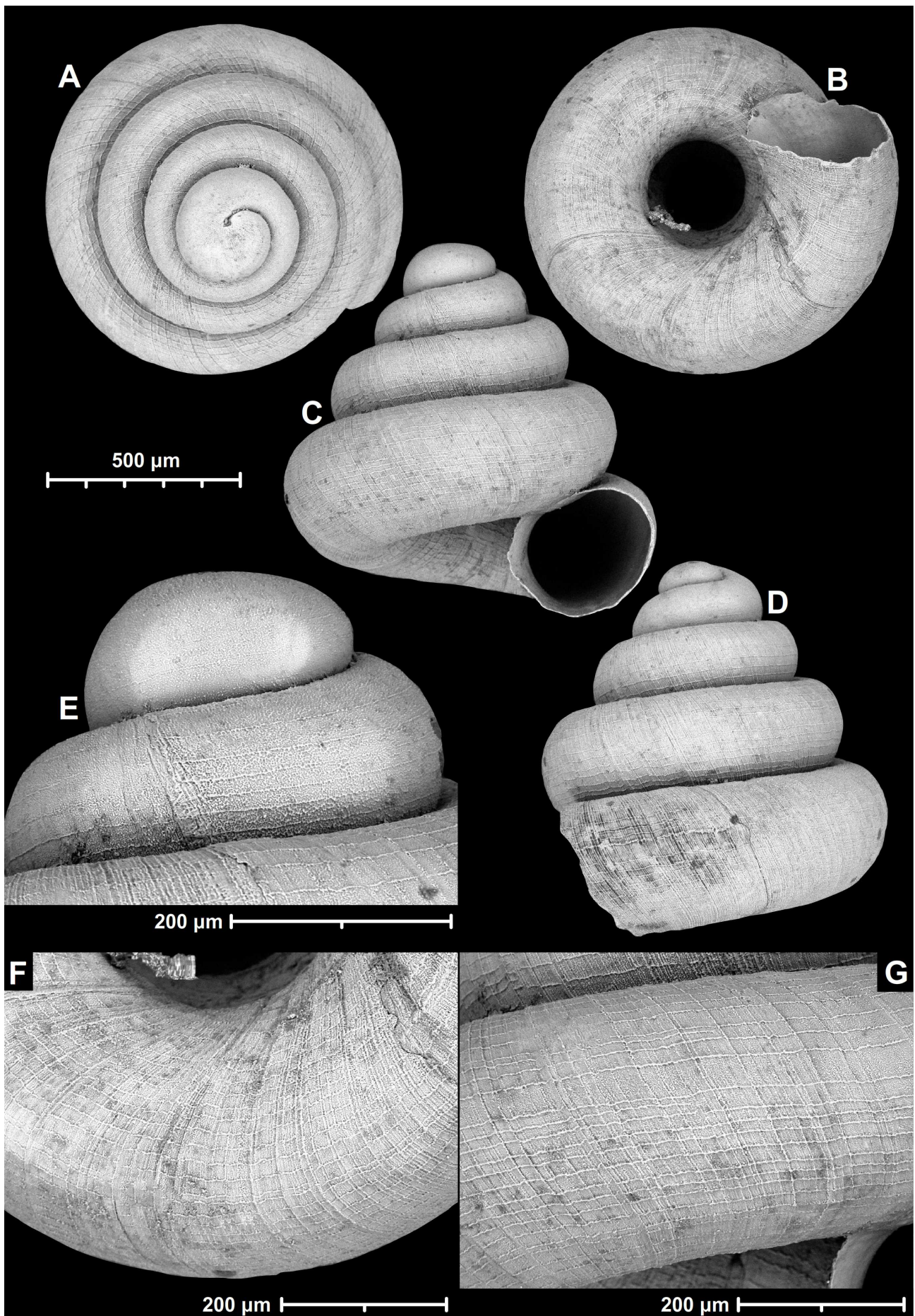


Fig. 5. *Clostophis infantilis* Páll-Gergely, new species (MNHN-IM-2014-6401, holotype). A, dorsal view; B, ventral view; C, apertural view; D, lateral view; E, protoconch sculpture; F, sculpture of the ventral side; G, sculpture of body whorl from standard apertural view

However, future efforts should focus on collecting more shells in order to reveal the intraspecific variability.

***Clostophis infantilis* Páll-Gergely, new species**
(Fig. 5)

Type material. Holotype (SH: 1.07 mm, SW: 1.02 mm) (MNHN-IM-2014-6401), South-Central Laos, Khammouan province, ca. 37 km ENE of Thakhek (Muang Khammouan), ca. 4.5 km WNW of Mahaxai, on and under rocks in dry secondary forest under E exposed cliff, 150 m a.s.l., 17°25.956'N, 105°09.669'E (locality code: 3L07), coll. A. Abdou & I.V. Muratov, 25 November 2007. Paratypes: 2 shells (MNHN-IM-2014-6402), same data as holotype; 3 shells (MNHN-IM-2014-6400), South-Central Laos, Khammouan province, ca. 10.5 km E of Thakhek (Muang Khammouan), on and under rocks, cave deposits, in secondary forest under entrance and in large cave on NE exposed steep slope, 160 m a.s.l., 17°24.340'N, 104°54.894'E (locality code: 25L07), leg. A. Abdou & I.V. Muratov, 09 December 2007; 4 shells (MNHN-IM-2014-6399), South-Central Laos, Khammouan province, ca. 15 km NE of Thakhek (Muang Khammouan), ca. 12.5 km SE of Ban Nase, on and under rocks in dry secondary forest near large flooded cave under W exposed cliff, 17°30.547'N, 104°53.444'E, alt. 127 m (locality code: 7L07), coll. A. Abdou & I.V. Muratov, 28 November 2007.

Diagnosis. A *Clostophis* species with pointed apex. The toothless aperture might be the result of insufficient sampling or the species' characteristics.

Description. Shell conical, slightly higher than wide, or in some specimens slightly wider than high. Apex pointed. Whorls rounded and very slightly shouldered. Tuba not detached from penultimate whorl. Protoconch consists of 1.25 whorls, pitted and spirally striated. Entire shell with 4 whorls. Umbilicus relatively narrow. Entire teleoconch with rather equidistant spiral striae, and some irregular radial growth lines of the same strength. Aperture subcircular, resembles that of juvenile specimens due to the lack of any teeth, and the sharp, not expanded peristome (see also Remarks). Aperture adnate to penultimate whorl.

Measurements (in mm). SH = 0.94–1.07, SW = 0.95–1.22 (n = 5).

Differential diagnosis. Shells of *Clostophis infantilis*, new species, can be distinguished from members of the genus *Angustopila* by the dense spiral striation of the shell. See under *C. multiformis*, new species.

Etymology. The specific epithet refers to the juvenile-looking shells of this species.

Remarks. Shells of *Clostophis infantilis*, new species, resemble juvenile shells of other *Clostophis* species due to the toothless aperture and the sharp, not expanded peristome. However, the shells of *C. infantilis*, new species, differ from all other *Clostophis* species in the region, and the relatively

high number of available shells suggests that this species does not develop apertural barriers. Moreover, *C. infantilis*, new species, and *C. multiformis*, new species, occur sympatrically. *Angustopila* species also inhabit this area and have less dense spiral striae (unpublished information).

***Clostophis koilobasis* Páll-Gergely & Vermeulen, new species**
(Fig. 6)

Type material. Holotype (SH: 1.06 mm, SW: 1.22 mm) (NHMUK 20191126; original inv. number: JJV 6230), Vietnam, Haiphong Prov., Cat Ba Isl., NE coast, 20°49.25'N 107°03.45'E, dry limestone scree slope with low woodland, in rock crevices, leg. J.J. Vermeulen & A.J. Whitten, 01 October 1998.

Diagnosis. A low conical shell with strongly widened body whorl, very wide umbilicus, and an elevated, distorted, short parietal lamella.

Description. Shell low triangular, wider than tall, with concave sides and strongly widened last whorl. Body whorl rounded, aperture not detached. Protoconch consisting of 1.25 whorls, with very finely raised threads arranged into hardly visible, widely-spaced spiral striae. Entire shell consisting of 4.75 whorls. Teleoconch with irregular, fine growth lines and dense (body whorl) and widely-spaced (previous whorls) spiral striation. Spiral striae ca. 22 on body whorl from lateral view (the holotype was strongly corroded, therefore the spiral striae were not counted from apertural view). Umbilicus very wide, occupies almost half of the shell width. Aperture subovate, peristome very slightly expanded, not reflected. Parietal tooth elevated, strong, but short, distorted internally (oblique to the growth axis of the body whorl).

Etymology. Combination of 'koilos' (= hollow in Greek) and 'basis' (= base in Greek), referring to the wide umbilicus as well as to the concave spire.

Differential diagnosis. *Clostophis incurvus*, new species, which is also known from the Halong Bay area, has a taller shell with narrower umbilicus and a strong parietal tooth. *Clostophis platytrochus*, new species, is somewhat similar in shell shape, but has a slightly keeled body whorl, a detached terminal part of the peristome, a strongly oblique aperture, and a strong palatal tooth. Some populations of *Clostophis multiformis*, new species, are similar to *C. koilobasis*, new species, in shell shape, but that species always has a low parietal tooth and narrower umbilicus.

***Clostophis multiformis* Páll-Gergely & A. Reischütz, new species**
(Figs. 7–9)

Type material. Holotype (SH: 1.09 mm, SW: 1.03 mm) (NHMW 113273, Fig. 7), Laos, Khammouane Prov., limestone hill in rice fields east of the road 1E, 300 m SE Gnommalat, NE Thakhek, at the base of rocks, 17°36.064'N, 105°10.356'E (locality code: La.4), coll. A. Reischütz,

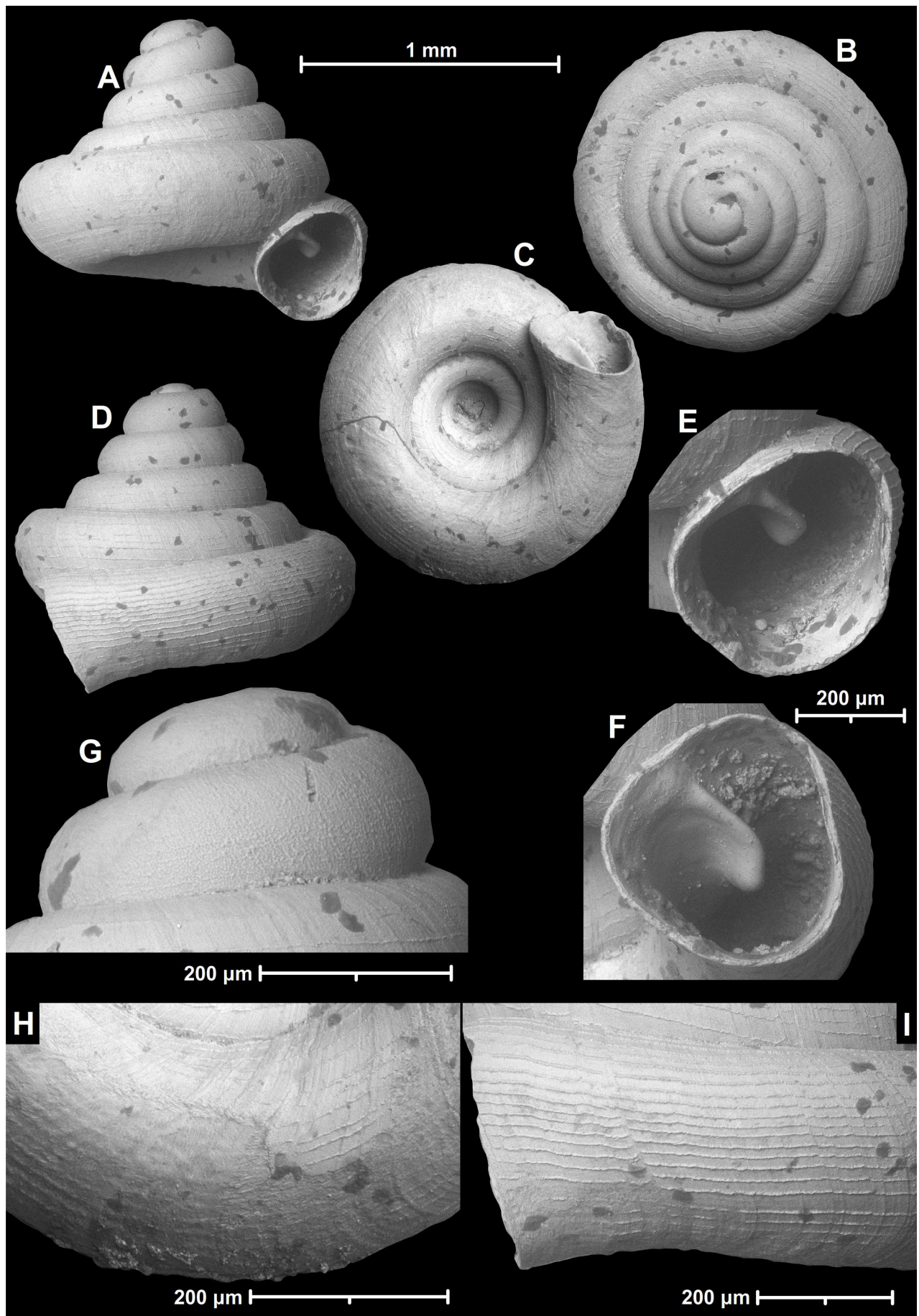


Fig. 6. *Clostophis koilobasis* Páll-Gergely & Vermeulen, new species (NHMUK 20191126, holotype). A, apertural view; B, dorsal view; C, ventral view; D, lateral view; E–F, apertural dentition; G, protoconch sculpture; H, sculpture of the ventral side; I, sculpture of body whorl (lateral side).

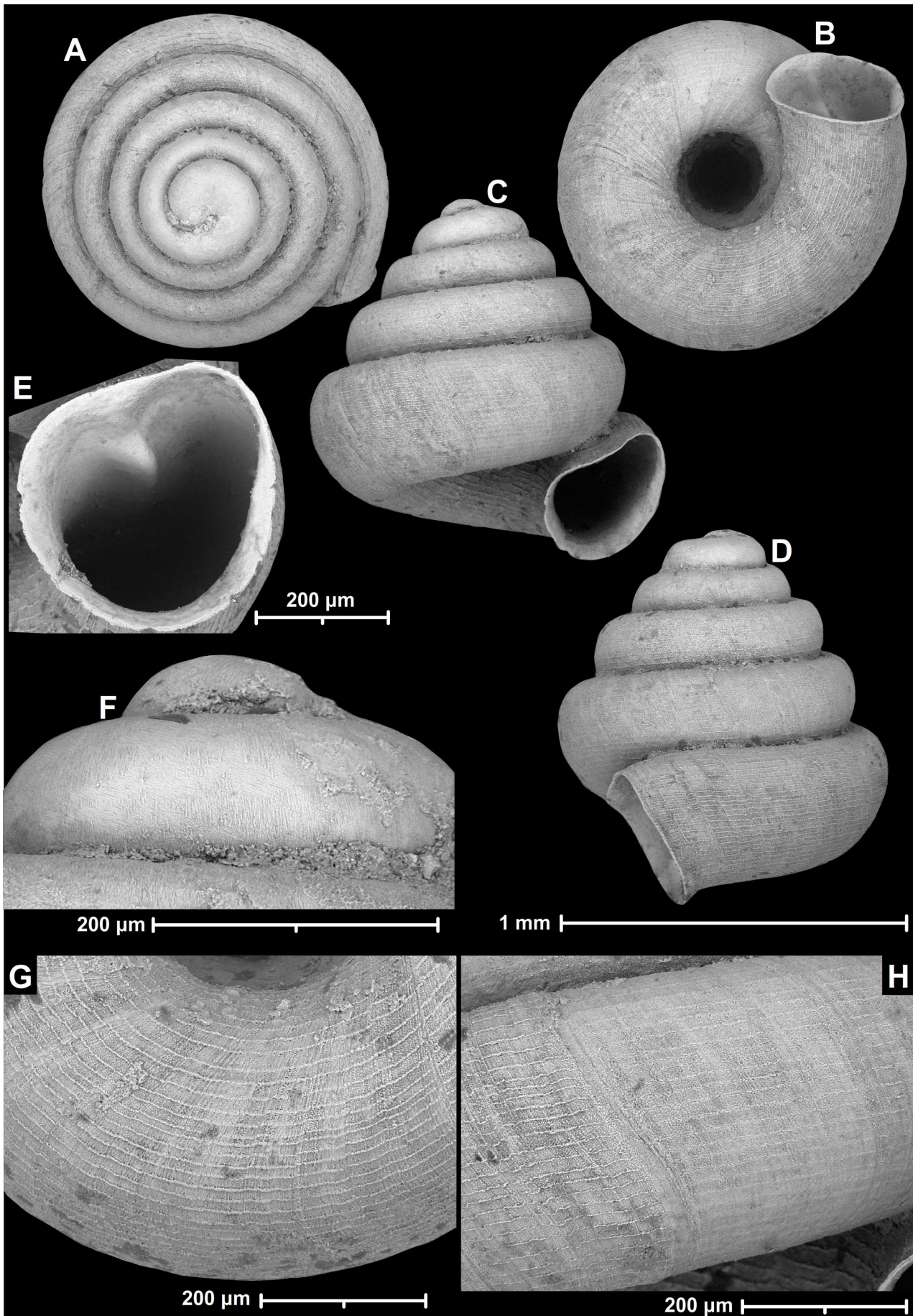


Fig. 7. *Clostophis multiformis* Páll-Gergely & A. Reischütz, new species (NHMW 113273, holotype). A, dorsal view; B, ventral view; C, apertural view; D, lateral view; E, aperture dentition; F, protoconch sculpture; G, sculpture of the ventral side; H, sculpture of body whorl from standard apertural view.

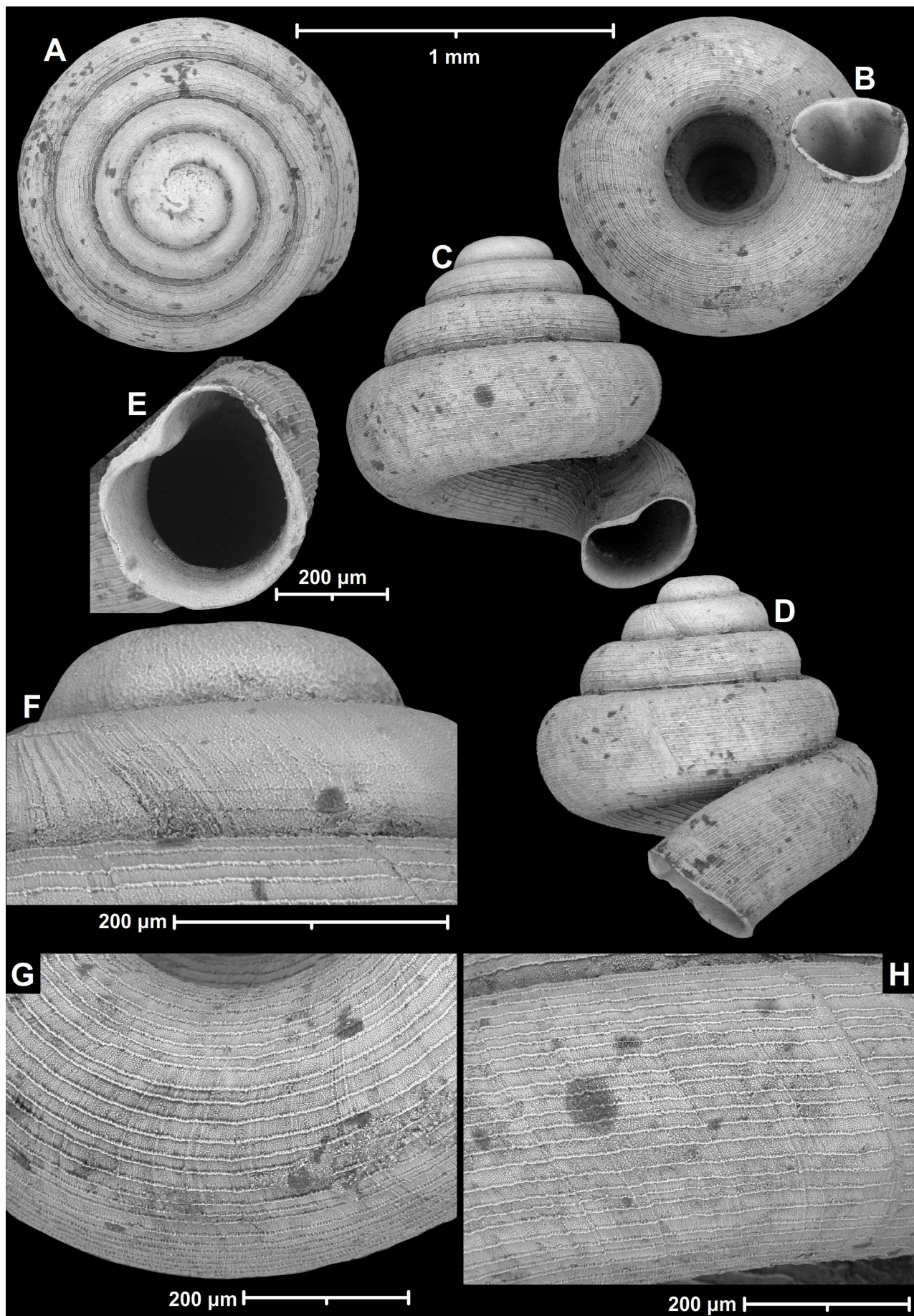


Fig. 8. *Clostophis multiformis* Páll-Gergely & A. Reischütz, new species (NHMW 113274, paratype). A, dorsal view; B, ventral view; C, apertural view; D, lateral view; E, aperture dentition; F, protoconch sculpture; G, sculpture of the ventral side; H, sculpture of body whorl from standard apertural view.

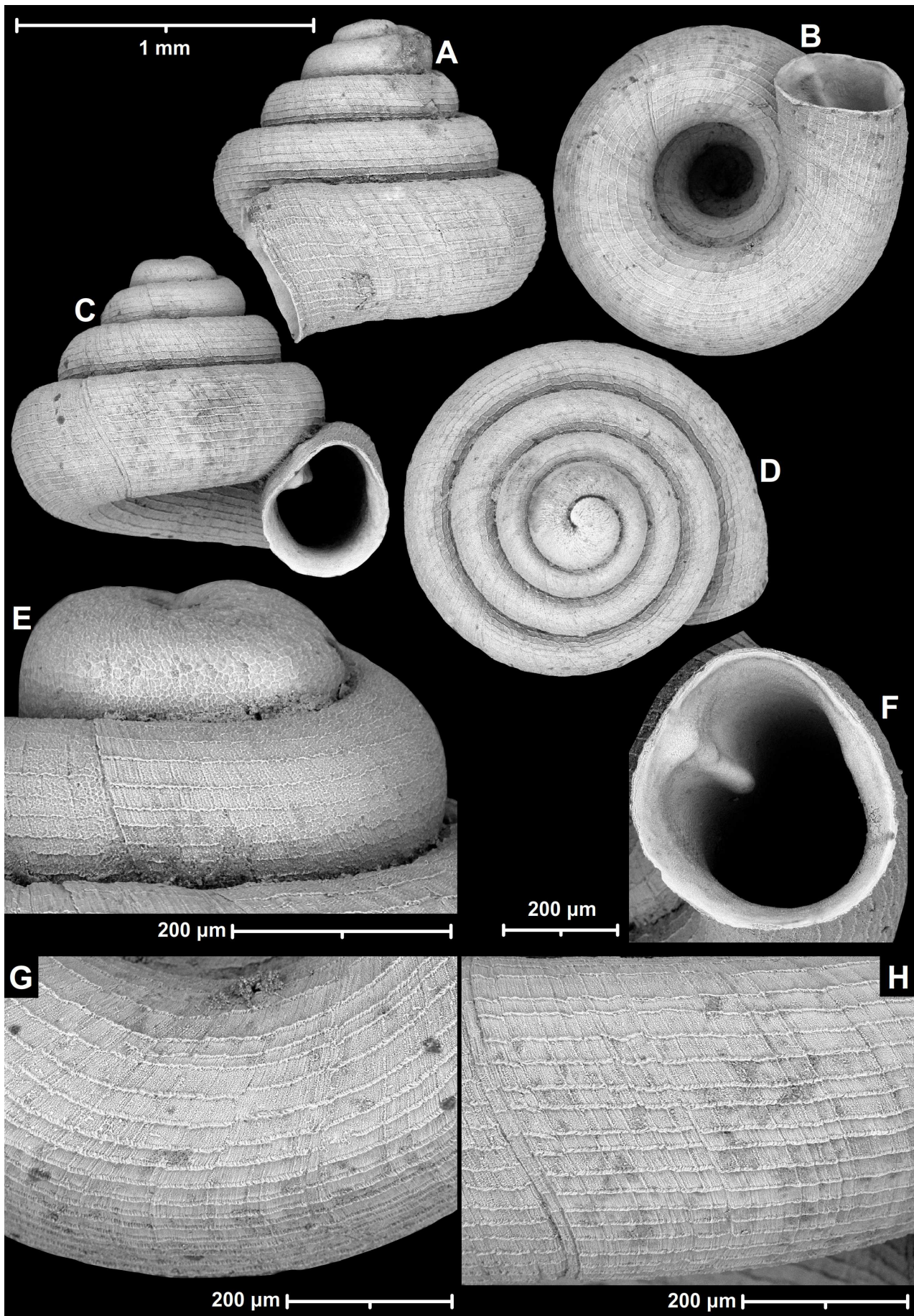


Fig. 9. *Clostophis multiformis* Páll-Gergely & A. Reischütz, new species (HNHM 104434, JG4). A, lateral view; B, ventral view; C, apertural view; D, dorsal view; E, protoconch sculpture; F, aperture dentition; G, sculpture of the ventral side; H, sculpture of body whorl from standard apertural view.

March 2010. Paratypes: 1 shell (NHMW 113274, Fig. 8), Laos, Khammouane Prov., limestone hill at the Xe Bangfai river city bridge from Mahaxay, E Thakhek, 17°24.608'N, 105°12.119'E (locality code: La.8), coll. A. Reischütz, March 2010; 2 shells (coll. RE), same data as preceding; 1 shell (coll. SA), Laos, Khammouane Province, 2 km N of Gnommalath, in dry soil on rock at foot of limestone hill, near the weir of powerplant channel, 17°34.859'N, 105°10.091'E (locality code: SA1), coll. S. Aiken, 19 July 2019; 3 shells (MNHN-IM-2014-6404), South-Central Laos, Khammouan province, ca. 37 km ENE of Thakhek (Muang Khammouan), ca. 4.5 km WNW of Mahaxai, on and under rocks in dry secondary forest under E exposed cliff, 150 m a.s.l., 17°25.956'N, 105°09.669'E (locality code: 3L07), coll. A. Abdou & I.V. Muratov, 25 November 2007; 1 shell (MNHN-IM-2014-6403), South-Central Laos, Khammouan province, ca. 35 km ENE of Thakhek (Muang Khammouan), ca. 7 km WNW of Mahaxai, on and under rocks in dry secondary forest under S exposed cliff, 169 m a.s.l., 17°26.736'N, 105°08.360'E (locality code: 4L07), coll. A. Abdou & I.V. Muratov, 25 November 2007.

Additional material. 2 shells (coll. JG), Laos, Khammouane Province, Tham Nam Dôn Cave, Earthquake Dome, sand sediments at bank of cave river, 160 m a.s.l., 17°33.815'N, 104°52.298'E (locality code: JG2B), coll. J. Grego, 11 February 2017; 1 shell (HNHM 104434, Fig. 9), Laos, Khammouane Province, cave at the NE foot of Mt. Pha Soung, caverns among slope boulders, 153 m a.s.l., 17°33.108'N, 104°52.301'E (locality code: JG4), coll. J. Grego, 08 February 2017; 2 shells (coll. JG), same data as preceding; 3 shells (coll. JG), Laos, Khammouane Prov., 2 km WNW of Ban Na village, Pha Soung Cave – Frog lake, 17°33.054'N, 104°52.414'E (locality code: JG3A), coll. Grego, J., 09 February 2017.

Diagnosis. This variable *Clostophis* species is characterised by a conical or ovoid-conical shell, a constricted, teardrop- or kidney-shaped aperture with a weak parietal tooth, and a rather wide umbilicus.

Description. Shell conical or ovoid, higher than wide to wider than high. Whorls rounded or very slightly shouldered. Tuba slightly (usually) or strongly (rarely) detached from penultimate whorl. Protoconch consisting of 1.25–1.5 whorls, pitted and spirally striated. Entire shell with 4.25–4.5 whorls. Umbilicus wide, occupies ca. one third of the shell width (see also Remarks). Entire teleoconch with strong, elevated, rather equidistant spiral striae (see also Remarks), and some weak, irregular radial growth lines. Aperture teardrop- or kidney-shaped. Sinulus wide. Parietal tooth weak and relatively short, in some shells reaches, in others does not reach peristome. In some shells there is a slight indication of a palatal tooth. Peristome expanded but not reflected.

Measurements (in mm). SH = 1.02–1.4, SW = 1.03–1.39 (n = 11, shells belonging to multiple populations).

Differential diagnosis. *Clostophis infantilis*, new species, has a smaller shell, a more pointed apex, stronger radial sculptural elements, and a narrower umbilicus. See also under *C. obtusus*, new species.

Etymology. This new species is named after the variability of its shell shape across populations.

Remarks. This is a variable species in terms of shape and size, and the density of spiral striae. Future investigations including more detailed sampling and larger sample sizes might reveal that the populations listed here belong to multiple species. The populations east of Thakhek (localities: 3L07, 4L07, La.4, La.8, SA1) are slightly smaller (SH: 1.09–1.21 mm, SW: 1.03–1.12 mm vs. SH: 1.14–1.4 mm, SW: 1.21–1.39 mm) and have a higher spire and a narrower umbilicus than the populations northeast of Thakhek (localities: JG2B, JG3A, JG4). The sculpture and the aperture dentition of the two groups are similar. We have no samples from the area between the two known areas, therefore, at the moment, we see no necessity of splitting this species into subspecies. The tube (terminal part of the body whorl) is slightly detached from the penultimate whorl, but in one population (locality: La.8) it was strongly detached. Nearly all examined shells have dense spiral striation (26–30 striae counted in the middle line of the body whorl from standard apertural view), whereas the single shell from population JG4 has only 20 striae. The shell and aperture shape are similar to the neighbouring population (locality: JG3A) and therefore, we consider it conspecific with the neighbouring population (locality: JG4). See Fig. 2.

***Clostophis neglectus* (van Benthem Jutting, 1961), new combination**
(Fig. 1)

Hypselostoma laidlawi — van Benthem Jutting, 1949: 19, fig. 9. (partim)

Paraboyssidia 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 (1949) as probably *Systemostoma* species) — Panha & Burch, 1999b: 125.

Diagnosis. A high conical *Clostophis* species with a strongly widened body whorl, a wide umbilicus, a strong parietal and a blunt palatal tooth.

Remarks. The small size, white shell, dense spiral striation and the presence of a parietal and a palatal tooth indicates that this species belongs to the genus *Clostophis*. *Paraboyssidia laidlawi* (Collinge, 1902) (originally described as *Hypselostoma*), the species which *C. neglectus* had been confused with, should probably be classified into *Acinolaemus* based on the basal and two palatal teeth, and the separate angular and parietal lamellae. The latter trait is characteristic for *Acinolaemus*.

***Clostophis obtusus* Páll-Gergely & Grego, new species**
(Fig. 10)

Material examined. Holotype (SH: 1.39 mm, SW: 1.22 mm) (HNHM 104435), Laos, Khammouane Province, Tham Nam Dôn Cave, Earthquake Dome, sand sediments at bank of cave river, 160 m a.s.l., 17°33.815'N, 104°52.298'E (locality code: JG2B), coll. J. Grego, 11 February 2017. Paratypes: 2 shells (coll. JG), same data as preceding; 1 shell (coll. JG), Laos, Khammouane Prov., 2 km WNW of Ban Na village, Pha Soung Cave – Frog lake, 17°33.054'N, 104°52.414'E (locality code: JG3A), leg. J. Grego, 09 February 2017.

Diagnosis. A relatively large, triangular *Clostophis* species with blunt apex, a relatively narrow umbilicus, and a parietal tooth that is only slightly indicated.

Description. Shell conical, higher than wide. Whorls rounded and very slightly shouldered. Tuba not detached from penultimate whorl. Protoconch nearly reaches 1.75 whorls, pitted and spirally striated. Entire shell with 4.5 whorls. Umbilicus narrow. Entire teleoconch with rather equidistant spiral striae, and some weak, irregular radial growth lines. Aperture subcircular with straight parietal part. Parietal tooth very weak, only slightly indicated, but as long as in *C. multiformis*, new species. Aperture not adnate to penultimate whorl. Peristome expanded but not reflected.

Measurements (in mm). SH = 1.17–1.39, SW = 1.07–1.24 (n = 4).

Etymology. The specific epithet “*obtusus*” (= obtuse, blunt in Latin) refers to the blunt apex of this new species.

Differential diagnosis. *Clostophis obtusus*, new species, differs from *C. multiformis*, new species (populations northeast of Thakhek), in the following traits: the shell of *C. obtusus* is larger, always triangular, not ovoid, apex blunter, umbilicus narrower, aperture never detached from penultimate whorl, parietal tooth weaker.

Remarks. We first considered this species to be fitting into the wide variability of *C. multiformis*, new species, but in fact, at one site (locality: JG2B) the two species occur sympatrically.

***Clostophis platytrochus* Páll-Gergely & Hunyadi, new species**
(Fig. 11)

Type material. Holotype (SH: 1.00 mm, SW: 1.19 mm) (HNHM 104408), Vietnam, Đà Nẵng, Ngũ Hành Sơn, Thái Sơn, environment of Chùa Quán Thế Âm, 7 m a.s.l., 15°59.944'N, 108°15.334'E (locality code: 2019/25a), coll. A. Hunyadi, 11 February 2019. Paratypes: 18 shells (coll. HA), same data as holotype.

Additional material. 5 juvenile shells, coll. HA, same data as holotype.

Diagnosis. A conical *Clostophis* species with detached terminal part of body whorl, dense spiral striation on the teleoconch except for largest part of ventral side, and a strongly descending aperture having a strong parietal and a palatal tooth.

Description. Shell white, triangular with flat base. Body whorl bluntly keeled. Terminal part of last whorl detached from penultimate whorl and strongly descending, resulting in a nearly horizontal aperture. Protoconch consisting of 1.25 whorls, with a few (ca. 6) widely-spaced spiral striae. Entire shell with 4.25–4.5 whorls. Dorsal part of teleoconch with irregular, fine radial lines, and stronger spiral striation. Spiral striae on the first whorl of teleoconch of similar density to that on the protoconch, and changes to a denser striation afterwards. Number of spiral striae 12–13 on body whorl above the keel in apertural view. Ventral side of shell with a few spiral striae near the keel, otherwise ornamented by irregular, fine, radial lines only. Umbilicus normally wide, occupies ca. one third of shell width. Aperture strongly oblique to the shell axis, nearly horizontal in lateral view. Peristome expanded but not reflected. Parietal tooth short, elevated, strong, situated in some distance from parietal callus. Palatal tooth blunt but strong, sits nearly on peristome.

Measurements (in mm). SH = 0.96–1.07, SW = 1.12–1.26 (n = 3).

Differential diagnosis. The unique shell shape, especially the slightly keeled body whorl and the sculpture (lack of spiral striae on the largest part of the ventral side) makes this species easy to recognise.

Etymology. The specific epithet is the combination of ‘*platus*’ (= wide in Greek) and ‘*trochus*’ (=wheel, Latinised Greek).

Remarks. This new species lives sympatrically with a new *Angustopila* species (unpublished information) and *Tonkinospira danangensis* Páll-Gergely & Hunyadi in Páll-Gergely, Grego, Vermeulen, Reischütz, Hunyadi & Jochum, 2019 (see Páll-Gergely et al., 2019).

***Clostophis proboscideus* (Panha & Burch, 1999), new combination**
(Fig. 3B)

Montapiculus proboscidea Panha & Burch, 1999a: 148, figs. 4–7.
Montapiculus proboscidea Panha & Burch, 2005: 109, fig. 94.

Type locality. “Teppratan mountain, Nakornsawan Province at 15°54'52"N, 99°53'63"E” [the last number is probably 53].

Diagnosis. A *Clostophis* species with detached and descending last quarter of the body whorl, a wide umbilicus, and a well-developed, deeply situated parietal tooth.

Remarks. *Clostophis proboscideus* differs from *C. sankeyi* by the more numerous and more tightly coiled whorls, the lower spire, and the wider umbilicus.

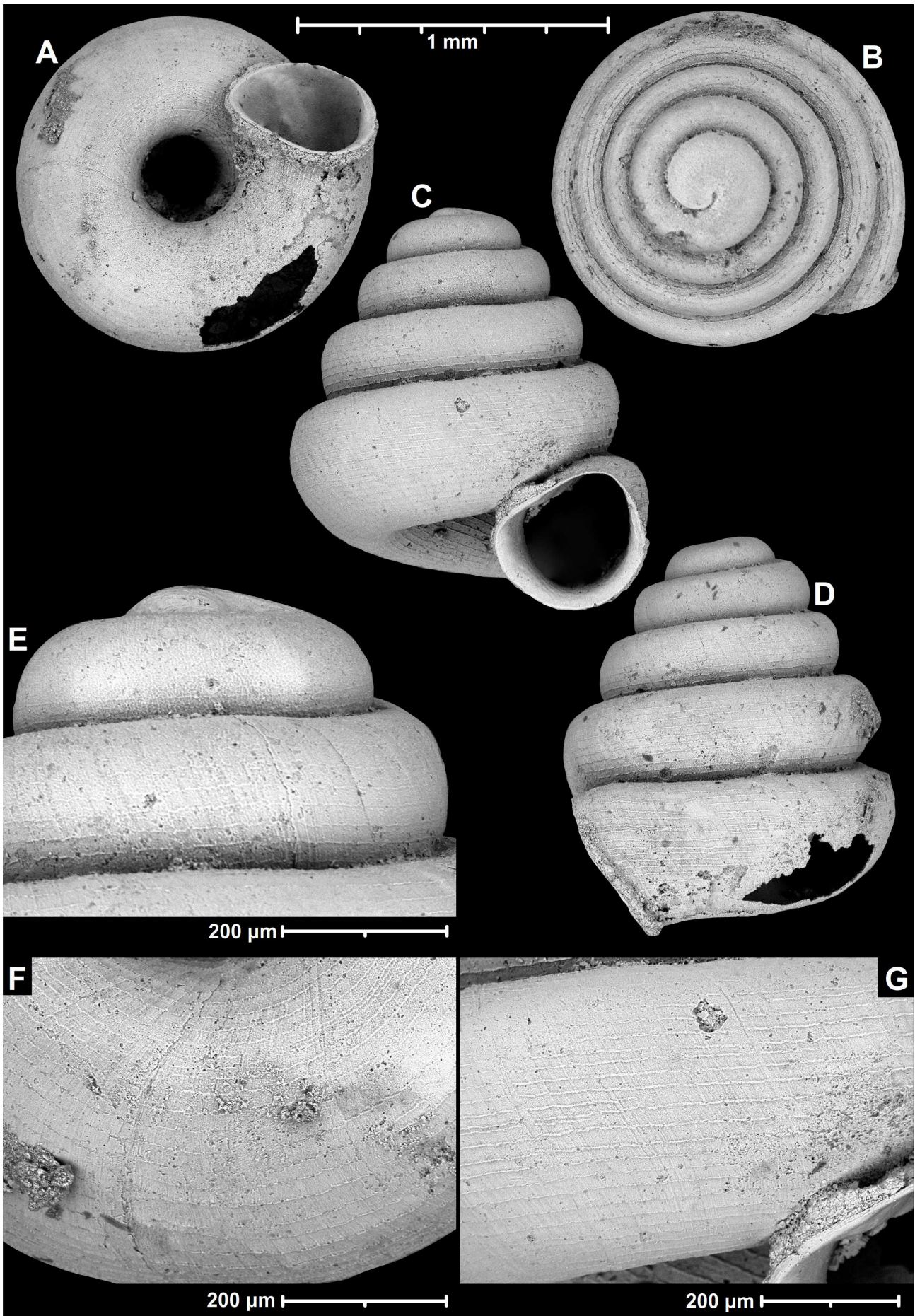


Fig. 10. *Clostophis obtusus* Páll-Gergely & Grego, new species (HNHM 104435, holotype). A, ventral view; B, dorsal view; C, apertural view; D, lateral view; E, protoconch sculpture; F, sculpture of the ventral side; G, sculpture of body whorl from standard apertural view.

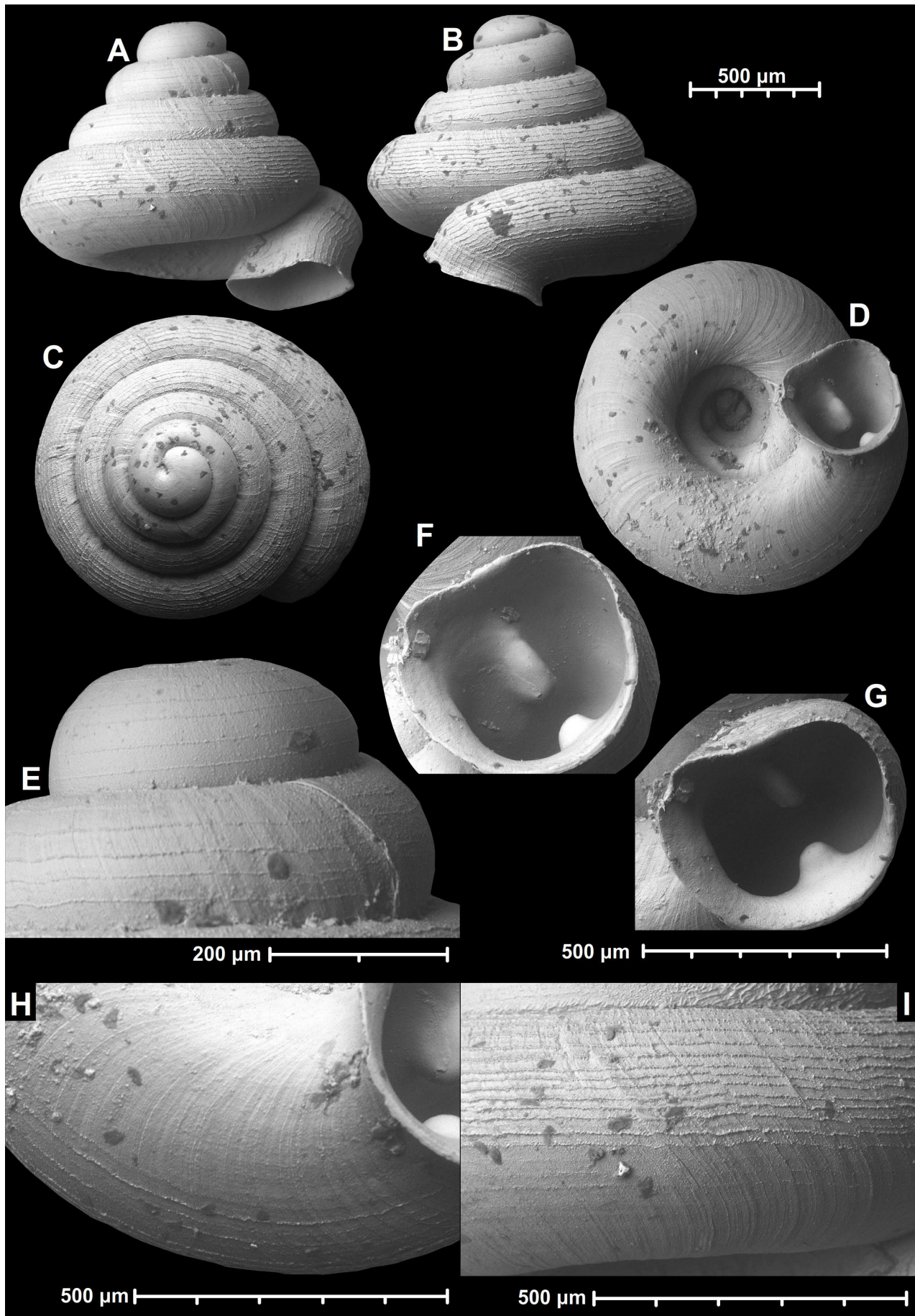


Fig. 11. *Clostophis platytrochus* Páll-Gergely & Hunyadi, new species (HNHM 104408, holotype). A, apertural view; B, lateral view; C, dorsal view; D, ventral view; E, protoconch sculpture; F, G, apertural dentition; H, sculpture of the ventral side; I, sculpture of body whorl from standard apertural view.

***Clostophis stochi* (Páll-Gergely & Jochum, 2017), new combination**
(Fig. 1)

Angustopila stochi Páll-Gergely & Jochum in Páll-Gergely et al., 2017: 329, figs. 1c, 3a–h.

Diagnosis. A convexly conic *Clostophis* species with an ovate-subquadrate aperture, a tuberculated parietal, and a low palatal denticle.

Remarks. Due to the larger shell and the dense spiral striation, this species is hereby moved to *Clostophis*.

DISCUSSION

The ten species assigned to the genus *Clostophis* inhabit an area in Southeast Asia from northern Vietnam to the Malay Peninsula (Fig. 2). Owing to uncertainties in the taxonomy of probably closely related, similarly tiny, and colourless hypselostomatid genera, many knowledge gaps remain, obscuring our understanding of the systematics of *Clostophis*.

The open questions which should be addressed in later publications are the following: (1) What is the relationship between *Tonkinospira* and *Clostophis*? Both are mostly between 1–2 mm, colourless, and mostly possess spiral striation. Species assigned to *Tonkinospira* show a relatively wide variability in terms of shell size, sculpture, and shape. It lacks apertural denticles, whereas *Clostophis* species (with the exception of *C. infantilis*, new species) possess some weak apertural barriers. Due to the lack of additional useful morphological characters, it is not possible to speculate further on the relationship of *Clostophis* and *Tonkinospira*. At the moment we find the distinction of the two genera useful. (2) Is *Acinolaemus* a “compact”, monophyletic group? The species assigned to the genus are variable in terms of apertural barriers. Some species have clearly separated angular and palatal teeth, whereas in others they form a single lamella (F. G. Thompson & Upatham, 1997). (3) Where do the two Chinese “*Hypselostoma*” species, *H. lacrima* Páll-Gergely & Hunyadi in Páll-Gergely, Hunyadi, Jochum & Asami, 2015, and *H. socialis* Páll-Gergely & Hunyadi in Páll-Gergely, Hunyadi, Jochum & Asami, 2015 belong? Both are small (1.1–1.4 mm), colourless, and densely spirally striated, similar to *Acinolaemus*, *Clostophis*, and *Tonkinospira*. They surely do not belong to *Hypselostoma* as its type species is a large (ca. 4 mm) brown species with reduced spiral striation.

Molecular phylogeny (Tongkerd et al., 2004) showed that shell shape and aperture dentition can be strikingly different between sister species, but shell sculpture is meaningful. Future research should focus on collecting living specimens for molecular phylogenetic study in order to test morphology-based preliminary classification.

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