

## New *Tonkinospira* Jochum, Slapnik & Pál-Gergely, 2014 species from Laos and Vietnam (Gastropoda: Pulmonata: Hypselostomatidae)

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**Abstract.** Five new species of *Tonkinospira* Jochum, Slapnik & Pál-Gergely, 2014 from Laos and Vietnam are described as follows: *T. crassicostata* Pál-Gergely & Grego, new species (Laos), *T. danangensis* Pál-Gergely & Hunyadi, new species (Vietnam), *T. raxajacki* Pál-Gergely & A. Reischütz, new species (Laos), *T. suturata* Pál-Gergely & Grego, new species (Laos) and *T. triangulata* Pál-Gergely & Vermeulen, new species (Vietnam). *Helix chytrophora* J. Mabille, 1887 is also revised and transferred to *Tonkinospira*.

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

### INTRODUCTION

Our knowledge on the microsnails of Southeast Asia (Cambodia, Thailand, Vietnam, Laos, Southern China) has increased considerably in the last two decades (Panha & Burch, 2005; Vermeulen et al., 2007, 2019; Inkhavilay et al., 2016; Pál-Gergely et al., 2015, 2017). All species are known based on shells only. Consequently, their systematic relationships are based on similarities of a few shell characters. Molecular phylogenetic studies of Thai species have revealed that striking conchologically different species can be closely related. For example, *Hypselostoma erawan* Panha & J. B. Burch, 2002 in Burch et al. (2002) has a typical “*Hypselostoma*-like” shell with a detached tuba and numerous apertural barriers. Its sister species, *H. panhai* J. B. Burch & Tongkerd, 2002 in Burch et al. (2002) has a regularly-coiled conical shell with three tiny apertural teeth (Tongkerd et al., 2004). Furthermore, the morphologically recognised genera could not be recovered as monophyletic groups, although this might be due to insufficient sequence data (Tongkerd et al., 2004).

Pupilloid microsnail genera such as *Hypselostoma* Benson, 1856 and *Boysidia* Ancey, 1881 have been classified in the family Pupillidae by Pilsbry (1917). Later, Zilch (1959) erected Hypselostomatinae Zilch, 1959 and Aulacospirinae Zilch, 1959 within Chondrinidae. Those subfamilies were synonymised with Gastrocoptinae by Gittenberger (1973). Schileyko (1998b) separated Hypselostomatidae as a distinct family, and treated Aulacospirinae as its synonym. Bouchet et al. (2017) treated Hypselostomatidae as a synonym of Gastrocoptidae Pilsbry, 1918, and noted that the relationships between these groups could not be solved by molecular phylogeny. In recent publications on *Hypselostoma* and other probably related microsnail genera were classified in various families such as Pupillidae Turton, 1831 (e.g., Panha & Burch, 1999), Vertiginidae Fitzinger, 1833 (e.g., Inkhavilay et al., 2019). We treat *Tonkinospira* and related genera as members of Hypselostomatidae (see Jochum et al., 2014; Pál-Gergely et al., 2015, 2017).

The genus *Systemostoma* Bavay & Dautzenberg, 1909 was diagnosed as a group of tiny snails with weak reticulated teleoconch sculpture and few (1–2) or no apertural teeth (Thompson & Upatham, 1997; Panha & Burch, 1999). Since *Systemostoma* is a junior homonym of Marsson, 1887 (Bryozoa), a new name, *Tonkinospira* Jochum, Slapnik & Pál-Gergely, 2014 in Jochum et al. (2014) was given to former species of *Systemostoma* Bavay & Dautzenberg, 1909 (Jochum et al., 2014). Based on the larger size, weaker peristome and lack of apertural barriers, *Tonkinospira* was distinguished from *Angustopila* Jochum, Slapnik & Pál-Gergely, 2014. *Tonkinospira* so far contains five species: *T. defixa* (Bavay & Dautzenberg, 1912), *T. depressa* (Jaeckel, 1950), *T. pauperrima* (Bavay & Dautzenberg, 1909), *T. pulverea* (Bavay & Dautzenberg, 1909), and *Tonkinospira tomasini* Pál-Gergely & Jochum, 2017 in Pál-Gergely et al. (2017). Here we describe five additional species of *Tonkinospira*, and move *Helix chytrophora* J. Mabille, 1887 also to this genus.

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## MATERIAL AND METHODS

Shells were manually brushed clean of mud using wet, fine, tapered brushes. The shells were viewed 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 20–200 objective.

### Abbreviations.

D: shell diameter

H: shell height

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

NHMUK: The Natural History Museum (London, UK)

NHMW: Naturhistorisches Museum Wien, Vienna, Austria

RBINS: Royal Belgian Institute of Natural Sciences, Brussels, Belgium

RE: Collection Reischütz, Horn, Austria

SMF: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

ZRC: Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore

The new taxon names *Tonkinospira crassicostata* Páll-Gergely & Grego, new species and *Tonkinospira suturata* Páll-Gergely & Grego, new species are the responsibility of Barna Páll-Gergely and Jozef Grego. The authorship of the new taxon name should be cited as *Tonkinospira crassicostata* Páll-Gergely & Grego, in Páll-Gergely, Grego, Vermeulen, Reischütz, Hunyadi & Jochum, 2019 and *Tonkinospira suturata* Páll-Gergely & Grego, in Páll-Gergely, Grego, Vermeulen, Reischütz, Hunyadi & Jochum, 2019.

The new taxon name *Tonkinospira danangensis* 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 *Tonkinospira danangensis* Páll-Gergely & Hunyadi, in Páll-Gergely, Grego, Vermeulen, Reischütz, Hunyadi & Jochum, 2019.

The new taxon name *Tonkinospira raxajacki* 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 *Tonkinospira raxajacki* Páll-Gergely & A. Reischütz, in Páll-Gergely, Grego, Vermeulen, Reischütz, Hunyadi & Jochum, 2019.

The new taxon name *Tonkinospira triangulata* Páll-Gergely & Vermeulen, new species is the responsibility of Barna Páll-Gergely and Jaap J. Vermeulen. The authorship of the new taxon name should be cited as *Tonkinospira triangulata*

Páll-Gergely & Vermeulen, in Páll-Gergely, Grego, Vermeulen, Reischütz, Hunyadi & Jochum, 2019.

## TAXONOMY AND SYSTEMATICS

Family Hypselostomatidae Zilch, 1959

**Genus *Tonkinospira* Jochum, Slapnik & Páll-Gergely, 2014 in Jochum et al. (2014)**

*Systemostoma* Bavay & Dautzenberg, 1909a: 243.

*Systemostoma* — Bavay & Dautzenberg, 1909b: 196.

*Tonkinospira* Jochum, Slapnik & Páll-Gergely in Jochum et al., 2014: 31 [replacement name].

**Type species.** *Helix (Systemostoma) pauperrima* Bavay & Dautzenberg, 1909 by subsequent designation (Pilsbry, 1917).

**Included species.** *Tonkinospira chytrophora* (J. Mabille, 1887), *Tonkinospira crassicostata* Páll-Gergely & Grego, new species, *T. danangensis* Páll-Gergely & Hunyadi, new species, *Tonkinospira defixa* (Bavay & Dautzenberg, 1912), *T. depressa* (Jaeckel, 1950), *T. raxajacki* Páll-Gergely & A. Reischütz, new species, *T. suturata* Páll-Gergely & Grego, new species, *T. pauperrima* (Bavay & Dautzenberg, 1909), *T. pulvrea* (Bavay & Dautzenberg, 1909), *T. triangulata* Páll-Gergely & Vermeulen, new species (Fig. 1).

**Distribution.** *Tonkinospira* species are so far only known from Northern and Central Vietnam and Central Laos (Páll-Gergely et al., 2015, 2017 and this study; Fig. 2).

***Tonkinospira chytrophora* (Mabille, 1887),  
new combination**  
(Fig. 3)

*Helix chytrophora* J. Mabille, 1887a: 4. (type locality: Tonkin [= northern Vietnam])

*Helix chytrophora* — J. Mabille, 1887b: 91–92.

**Types examined.** Lectotype, designated herein (H: 1.16 mm, D: 1.28 mm, Fig. 3) (MNHN-IM-2000-32862), Tonkin, coll. Balansa, 1887; 4 paralectotypes (MNHN-IM-2014-6407), same data as preceding. An additional label states “Anauchen, det. Schileyko”.

**Diagnosis.** A small *Tonkinospira* species with a depressed-globular shell, dense spiral striation, and a nearly adnate peristome.

**Description.** Shell small for the genus; depressed-globular with rounded body whorl; translucent when fresh; 4.5 whorls, regularly increasing; shell slightly wider than tall; protoconch consists of 1.25 whorls, rather roughly pitted, without spiral lines; teleoconch with irregular radial growth lines, and dense, regular spiral striation, ca. 30 in number in the middle shell line from apertural view; aperture strongly oblique to shell axis from lateral view; aperture subcircular; peristome expanded but not reflected; nearly adnate to penultimate whorl, although callus discernible; umbilicus

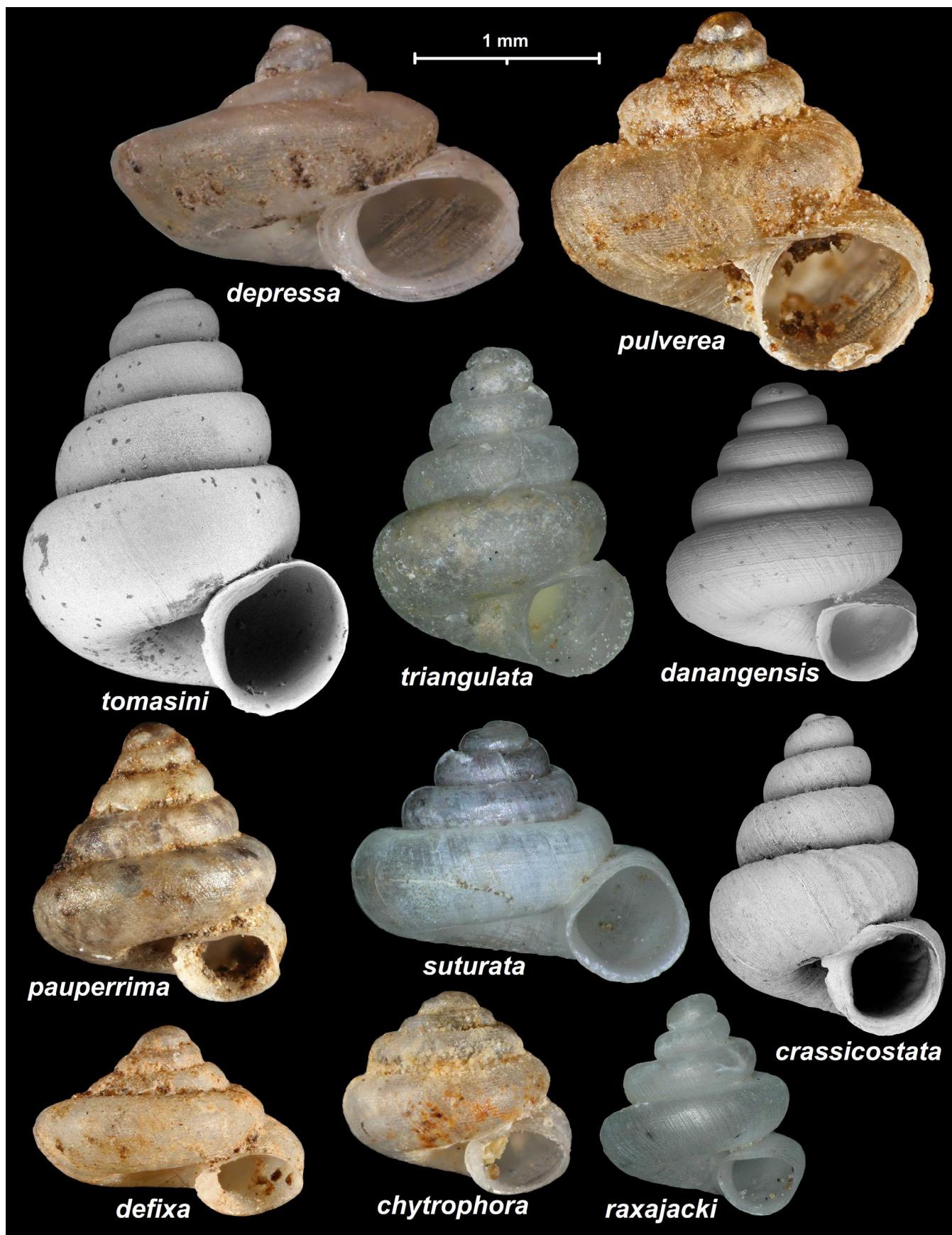


Fig. 1. Synoptic view of *Tonkinospira* species. *Tonkinospira chytrophora*: MNHN-IM-2000-32862 (lectotype); *T. crassicostata* new species, HNHM 104403 (holotype); *T. danangensis* new species, HNHM 104404 (holotype); *T. defixa*, MNHN-IM-2000-32866 (syntype); *T. depressa*, SMF 202927 (paratype); *T. pauperrima*, MNHN-IM-2000-32864 (syntype); *T. pulvrea*, MNHN-IM-2000-32863 (syntype); *T. raxajacki* new species, NHMW 113205 (holotype); *T. suturata*, new species, HNHM 104405 (holotype); *T. tomasini*, MZUF GC/49399 (holotype, from the original description, Páll-Gergely et al., 2017); *T. triangulata*, new species, (holotype). Scale bar represents 1 mm.

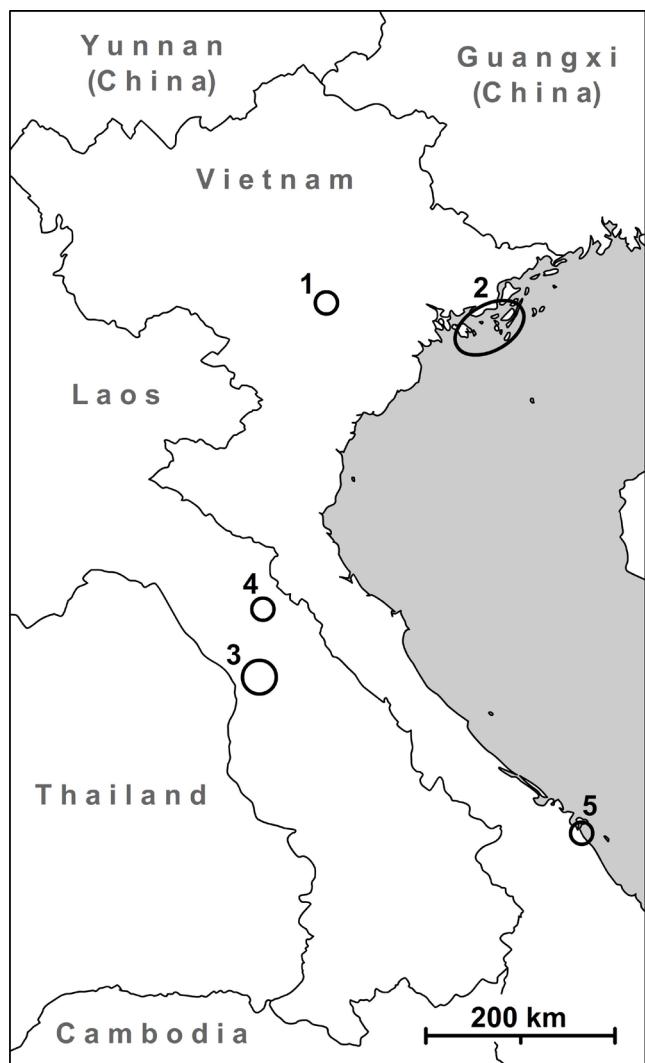


Fig. 2. Distribution of *Tonkinospira* Jochum, Slapnik & Páll-Gergely, 2014 species. 1, type locality of *Tonkinospira pauperrima* and *Tonkinospira pulvrea*; 2, Halong Bay area, locality of *Tonkinospira defixa*, *Tonkinospira* cf. *pauperrima*, *Tonkinospira triangulata* new species; 3, limestone area NE Thakhek, locality of *Tonkinospira crassicostata* new species, *Tonkinospira raxajacki* new species, *Tonkinospira suturata* new species; 4, additional locality of *Tonkinospira raxajacki* new species; 5, type locality of *Tonkinospira danangensis* new species.

very narrow, its edge covered by reflected peristome edge.

**Differential diagnosis.** *Tonkinospira chytrophora* can be distinguished from its congeners by the combination of the depressed globular shell, the adnate aperture and the rounded body whorl.

***Tonkinospira crassicostata* Páll-Gergely & Grego,  
new species  
(Fig. 4)**

**Type material.** Holotype (H: 1.84 mm, D: 1.37 mm, Fig. 4) (HNHM 104403), Laos, Khammouane Province, 500 m SE of village Ban Phondou, 17°31.763'N, 104°53.792'E, coll. J. Grego, 13 February 2017.

**Diagnosis.** A medium sized *Tonkinospira* species with a convexly conic shell, nearly absent spiral striation and strong, widely-spaced ribs, and an adnate peristome.

**Description.** Shell medium sized for the genus; convexly conic with rounded (slightly shouldered) body whorl; shell white, probably transparent when fresh; 4.5 whorls, regularly increasing; suture deep; protoconch finely rugose consisting of 1.25 whorls and spiral striation; teleoconch with rather regular, widely spaced ribs with fine wrinkles between ribs; aperture oblique to shell axis from lateral view; aperture subcircular with straight columellar and parietal part; slight knobby hint of an upper parietal barrier; peristome thickened, expanded only in direction of umbilicus, not reflected; aperture adnate to penultimate whorl; umbilicus narrow and deep, its edge covered by peristome.

**Differential diagnosis.** *Tonkinospira crassicostata* new species differs from all other *Tonkinospira* species by the strong ribs, the lack of spiral striation on the lower whorls, the knobby hint of an upper parietal barrier and the thickened peristome and adnate aperture. *Tonkinospira tomasini* is larger, has a less adnate peristome, weaker sculpture and a more sigmoid umbilicus. See also under *T. triangulata* new species.

**Etymology.** The specific epithet refers to the strong ribs of *Tonkinospira crassicostata* new species.

***Tonkinospira danangensis* Páll-Gergely & Hunyadi,  
new species  
(Fig. 5)**

**Type material.** Holotype (H: 1.56 mm, D: 1.26 mm, Fig. 5) (HNHM 104404), 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; 51 Paratypes + 13 broken shells (not paratypes), coll. HA, same data as preceding.

**Diagnosis.** A medium sized *Tonkinospira* species with a high conic shell, dense spiral striation, and a peristome that is not adnate to penultimate whorl.

**Description.** Shell medium sized for the genus; high conic with rounded body whorl; shell transparent, colourless; 5 whorls, regularly increasing; suture deep; penultimate whorl widest from standard apertural view; protoconch consists of 1.5 whorls, finely rugose, and densely, strongly spirally striated; teleoconch with irregular, rough radial growth lines, and dense, rather regular spiral striation creating a reticulate surface texture, ca. 22–23 in number in the middle shell line from apertural view; aperture strongly oblique to shell axis, turning downward in alignment with the penultimate whorl in lateral view; aperture ovate-subquadrate; peristome slightly expanded, not reflected; aperture not adnate to penultimate whorl; umbilicus narrow, not covered by peristome and is almost ½ the diameter of the base of the shell.

**Measurements (in mm).** H = 1.37–1.56, D = 1.2–1.36 (n = 3).

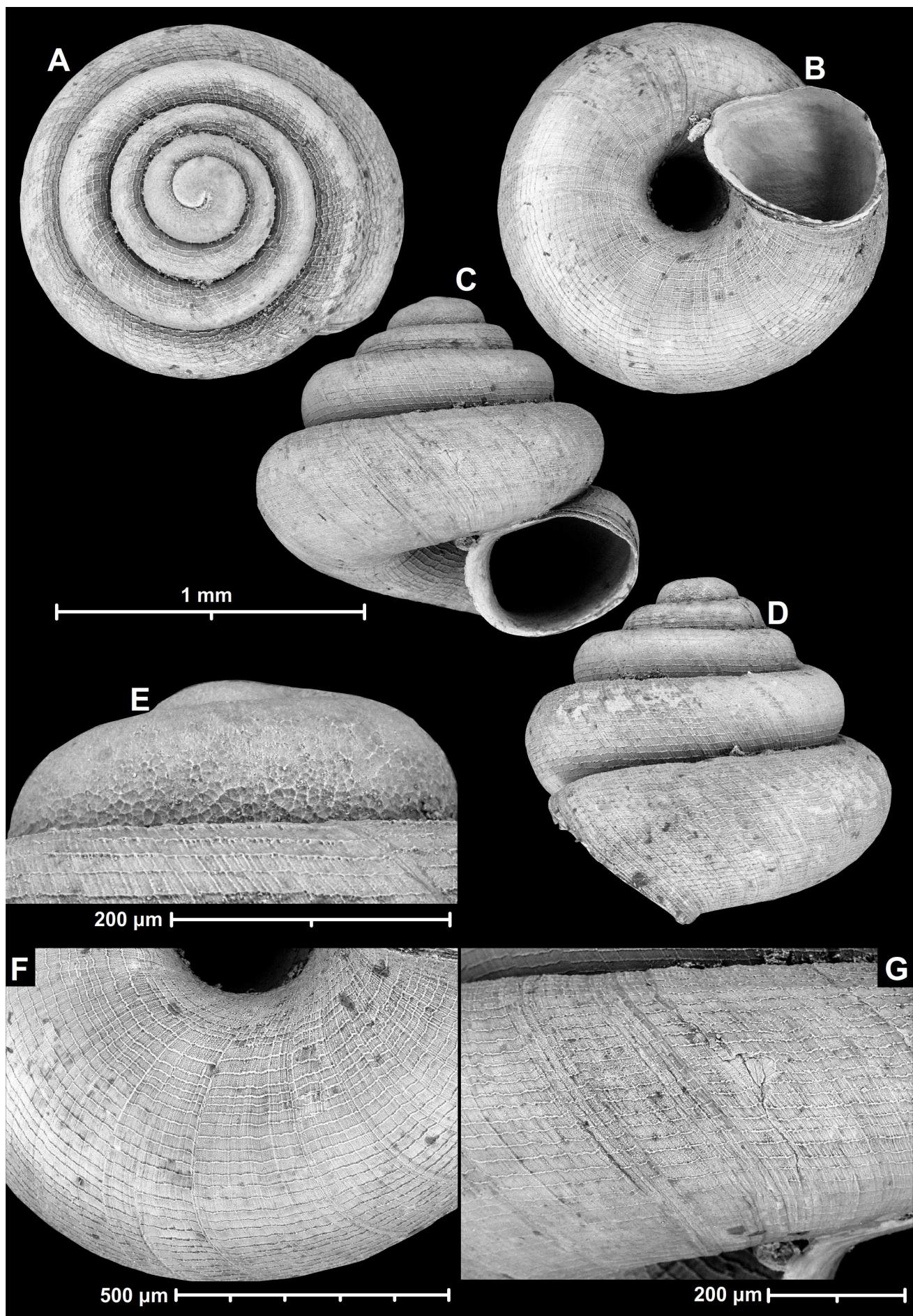


Fig. 3. *Tonkinospira chytrophora* (Mabille, 1887), MNHN-IM-2000-32862 (lectotype).

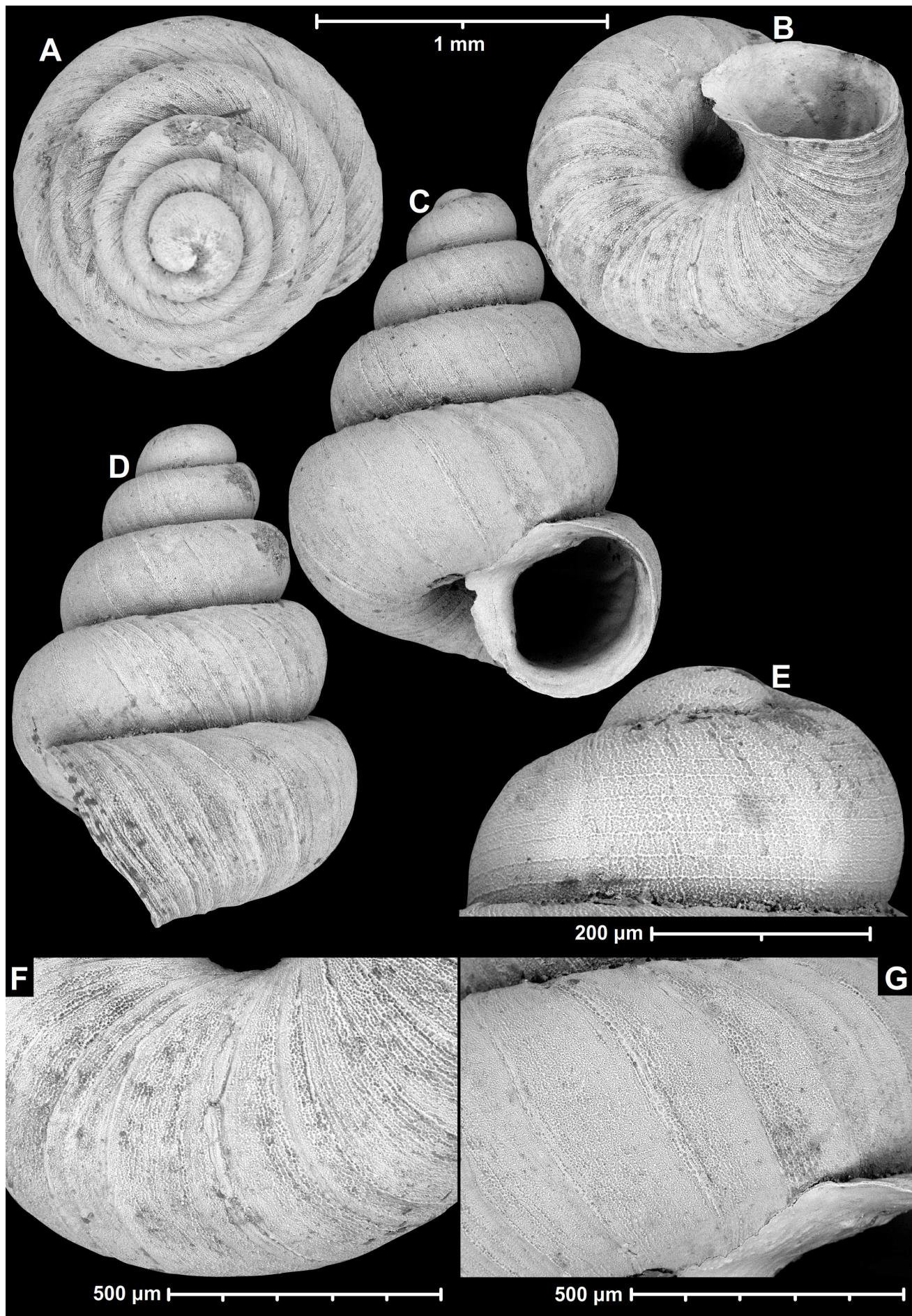


Fig. 4. *Tonkinospira crassicostata* Páll-Gergely & Grego, new species, HNHM 104403 (holotype).

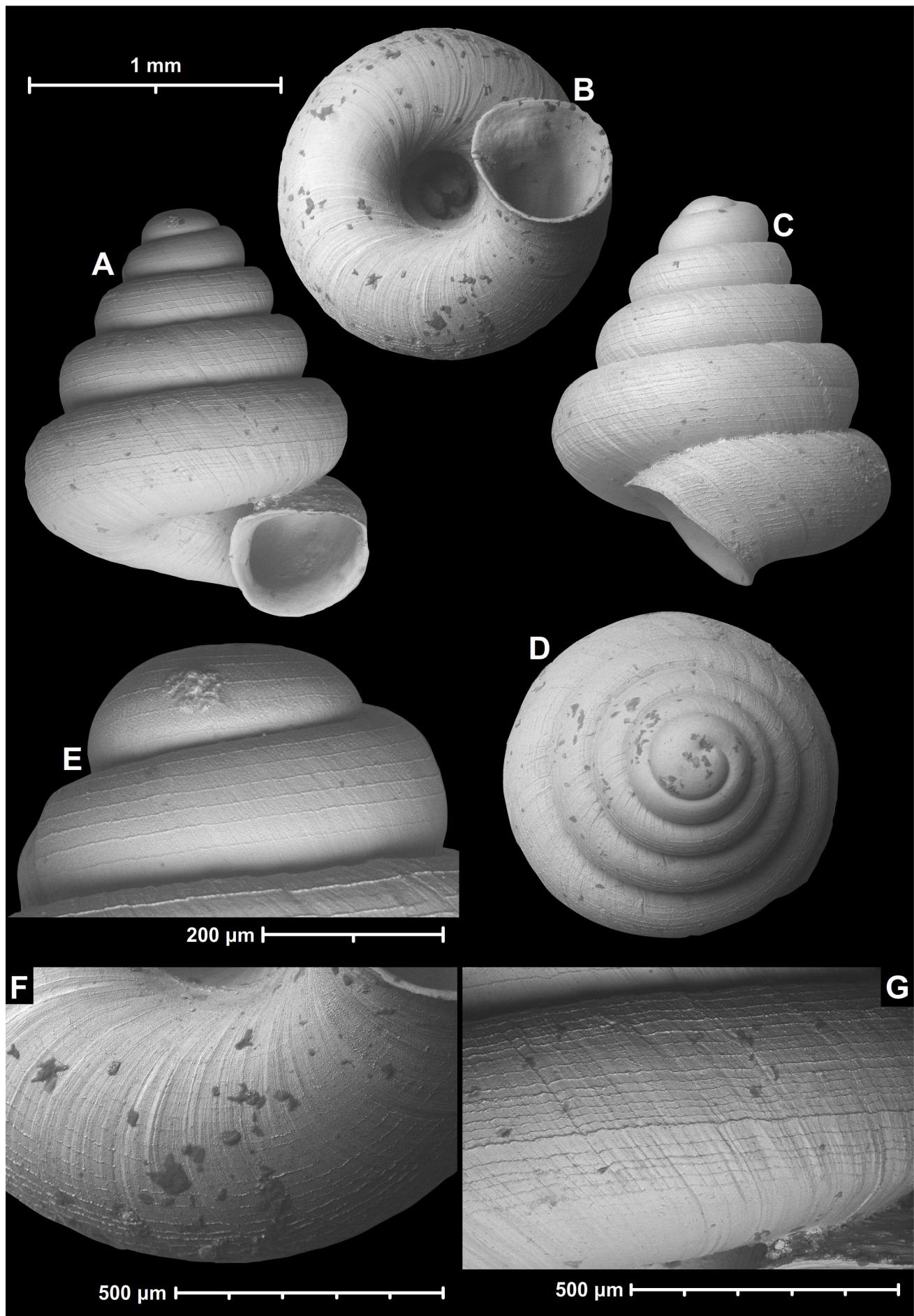


Fig. 5. *Tonkinospira danangensis* Páll-Gergely & Hunyadi, new species, HNHM 104404 (holotype).

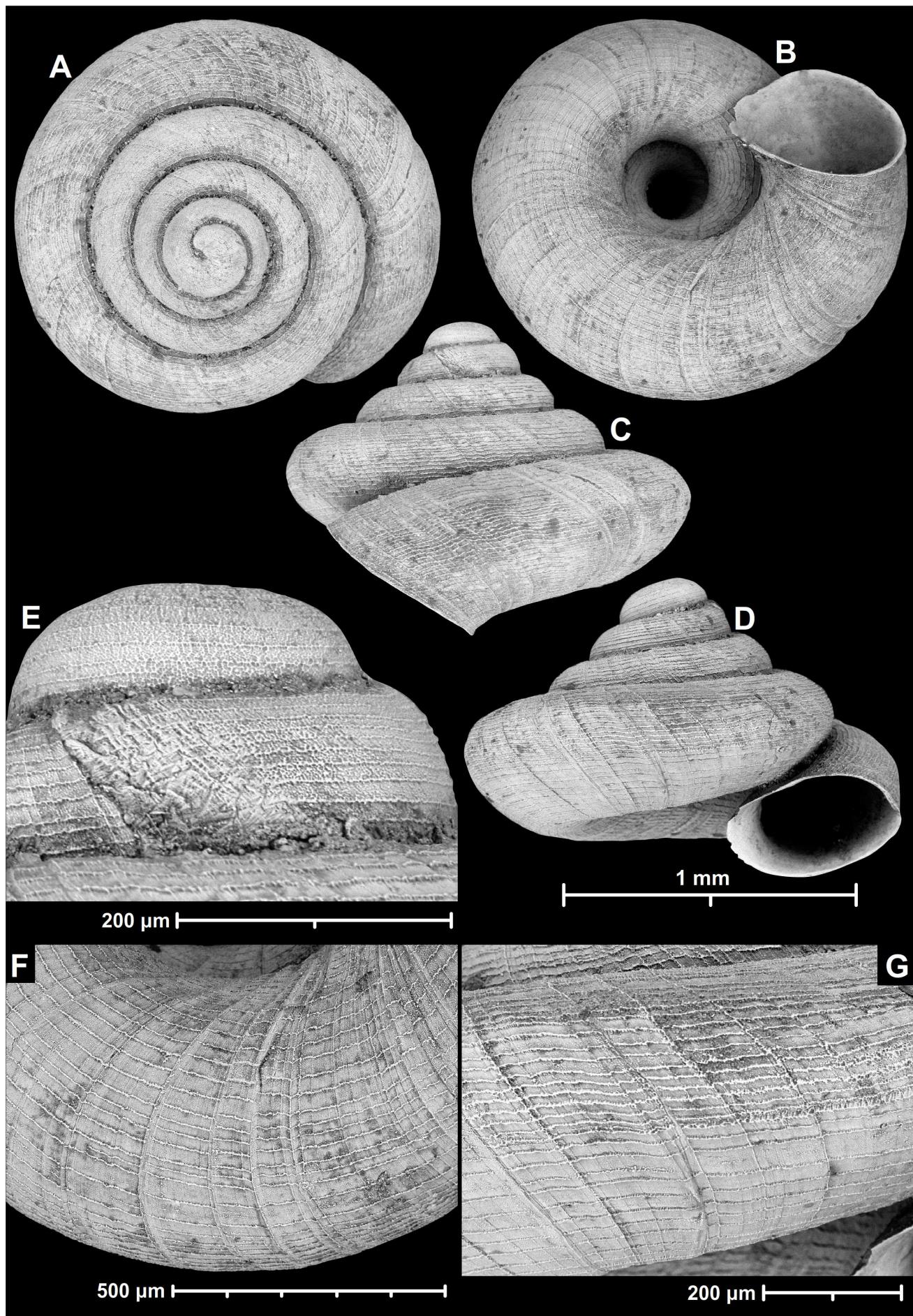


Fig. 6. *Tonkinospira defixa* (Bavay & Dautzenberg, 1912), MNHN-IM-2000-32866 (syntype).



Fig. 7. *Tonkinospira depressa* (Jaeckel, 1950), SMF 202927 (paratype). Scale bar represents 2 mm.

**Differential diagnosis.** *Tonkinospira danangensis* new species differs from *T. pauperrima* by the more accurately rounded whorls, shallower suture, and wider umbilicus. *Tonkinospira triangulata* new species has a comparatively larger aperture, more rapidly growing whorls and a narrower umbilicus.

**Etymology.** Named after the city of Đà Nẵng, where the type locality is located.

***Tonkinospira defixa* (Bavay & Dautzenberg, 1912)**  
(Fig. 6)

*Systemostoma defixa* Bavay & Dautzenberg, 1912: 22–23, pl. 1, figs 18–19. (type locality: Ile de la Table, baie d'Along [«Table Island» in the Halong Bay; the exact location of that island could not be located]).

*Systemostoma defixa* — Pilsbry, 1917: 226, pl. 38, figs 15–16.  
*Tonkinospira defixa* — Jochum et al., 2014: 32, fig. 1.

**Types examined.** 1 shell syntype (H: 1.09 mm, D: 1.57 mm, Fig. 6) (MNHN-IM-2000-32866), Île de la Table, Baie d'Along, coll. Demange.

**Other material examined.** Tonkin, coll. S.H. Jaeckel ex Rolle, SMF 202926/3; RBINS Dautzenberg Collection reg. nr. IG 10591 (tray 844), 2 shells (probably syntypes).

**Diagnosis.** A small *Tonkinospira* species with a strongly depressed shell, dense spiral striation, and a peristome that is not adnate to penultimate whorl.

**Description.** Shell small for the genus; strongly depressed with conical dorsal side and strongly widened body whorl; body whorl bluntly keeled; 4.25 whorls, regularly increasing except for the body whorl; protoconch consists of 1.25 whorls, finely pitted and with dense, regularly strong spiral striations; teleoconch with irregular, rough radial growth lines, and dense, regular spiral striation, ca. 28 in number in the middle shell line from apertural view; aperture strongly oblique to shell axis from lateral view; aperture ovate-oblong; peristome expanded but not reflected; aperture not adnate to penultimate whorl; umbilicus wide.

**Differential diagnosis.** This species is characterized by its depressed shell, keeled body whorl and wide umbilicus.

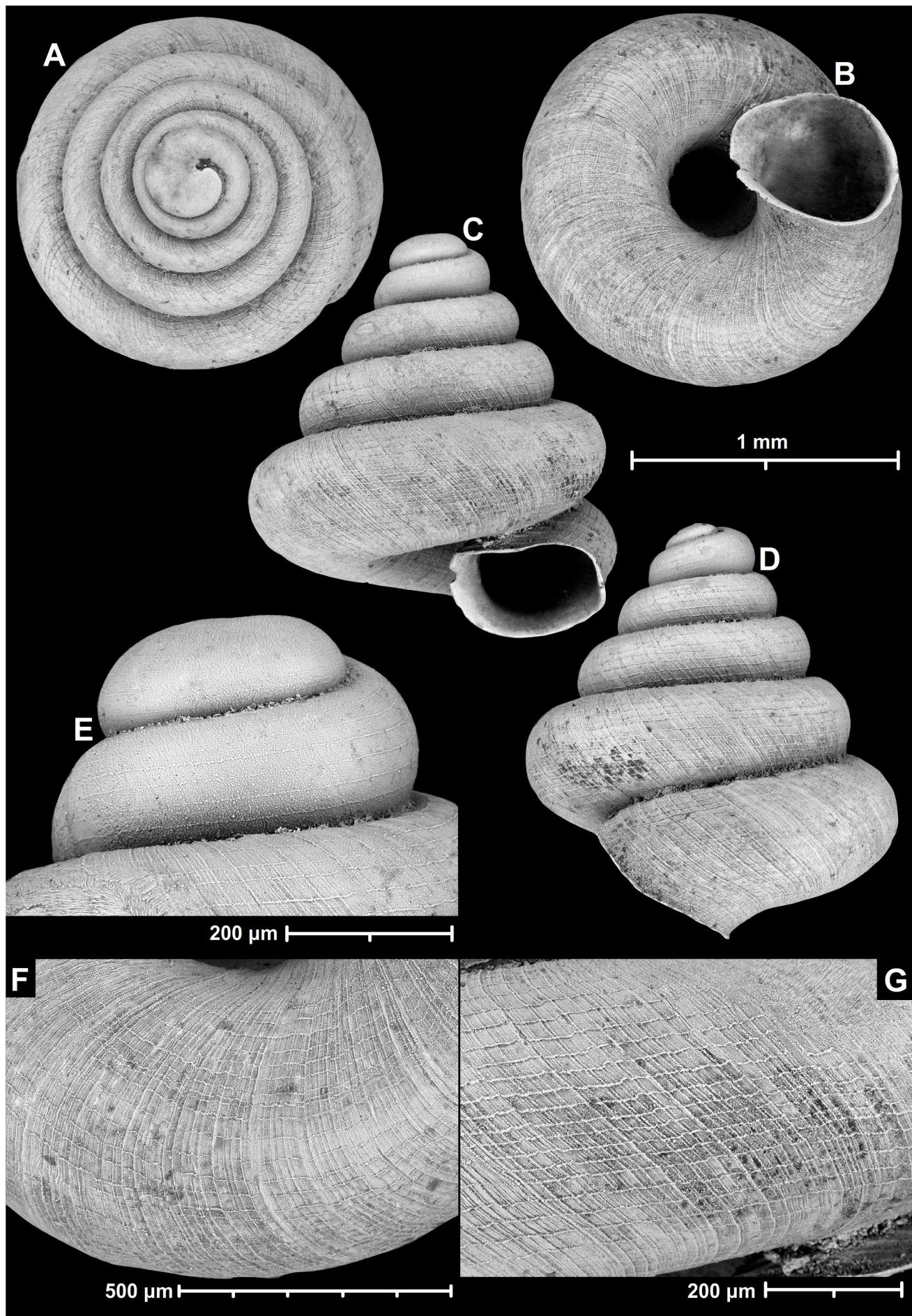


Fig. 8. *Tonkinospira pauperrima* (Bavay & Dautzenberg, 1909), MNHN-IM-2000-32864 (syntype).

***Tonkinospira depressa* (Jaeckel, 1950)**  
(Fig. 7)

*Systemostoma depressa* Jaeckel, 1950: 15–16, pl. 1, fig. 1. (type locality: Tonkin [northern Vietnam]).

*Aulacospira depressa* — Vermeulen et al., 2007: 91.  
*Tonkinospira depressa* — Jochum et al., 2014: 32.

**Types examined.** 33 paratypes (H = 1.6, D = 2.3, Fig. 7) (SMF 202927), Tonkin: Flußgenist (river debris), coll. S.H. Jaeckel ex coll. H. Rolle; 8 paratypes SMF 63875, Tonkin, Genist, coll. Zilch, ex coll. H. Rolle, ex coll. Jaeckel, 8 December 1949.

**Diagnosis.** A large *Tonkinospira* species with a strongly depressed shell, strongly angled body whorl, dense spiral striation, and a peristome that is more or less adnate to penultimate whorl.

**Description.** Shell large-sized for the genus; depressed conical with rapidly increasing whorls; body whorl strongly angled, keel not symmetrical, situated above mid line of body whorl, flattened above; keel not very sharp; whorls 3.75–4; suture moderately deep; protoconch consists of 1.25 whorls, roughly rugose and spirally striated; teleoconch with rather regular spiral striation and irregular, rough radial lines; aperture oblique to shell axis from lateral view; aperture ovate-oblong; peristome expanded especially in direction of the columella/umbilicus; aperture more or less adnate to penultimate whorl, but peristome continuous; umbilicus narrow, very slightly covered by peristome.

**Differential diagnosis.** The most similar species is *T. pulvrea*, which has a narrower umbilicus and a more rounded body whorl.

**Remarks.** *Tonkinospira depressa* is most similar to the Philippine members of the genus *Aulacospira*, and reflects this classification by Vermeulen et al. (2007). The most similar species is *Aulacospira hololoma* (Möllendorff, 1887), which has a regularly growing protoconch (tightly spired and projected above the teleoconch in *T. depressa*) and bears a columellar tooth (lacks in *T. depressa*). Moreover, the Philippine species typically have a prominent subsutural furrow on the body whorl, with the keel situated above the middle line of the body whorl (i.e., the keel is not symmetrical) (see Páll-Gergely et al., 2019). Although the similarity between *Tonkinospira* and *Aulacospira* is striking, the true phylogenetic relationships cannot be resolved based on conchological characters only. *Tonkinospira depressa* further differs from other *Tonkinospira* species in the brownish shell colour, which is colourless in the other species of this genus.

***Tonkinospira pauperrima* (Bavay & Dautzenberg, 1909)**  
(Fig. 8)

*Helix (Systemostoma) pauperrima* Bavay & Dautzenberg, 1909a:

243–244. (type locality: Phu-Quoc-Oai [see remarks])

*Helix (Systemostoma) pauperrima* — Bavay & Dautzenberg, 1909b: 195–196, pl. 8, figs 4–6.

*Systemostoma pauperrima* — Pilsbry, 1917: 225–226, pl. 38, figs 3–5.

*Systemostoma pauperrima* — Schileyko, 1998b: 165, fig. 202.

*Tonkinospira pauperrima* — Jochum et al., 2014: 32–36, fig. 2.

**Types examined.** 1 shell, syntype (H: 1.6 mm, D: 1.44 mm, Fig. 8.) (MNHN-IM-2000-32864), Phu-Quoc-Oai, coll. Demange.

**Additional material examined.** Vietnam, Quang Ninh Prov., Ha Long Bay, Cap La Cave, deposit of soil fallen in through roof in pristine cave, vegetation outside cave high and woody, 20°51.793'N, 107°13.541'E, leg. J.J. Vermeulen & K. Anker, 07 March 2018, JJV 17630/197 shells + 4 separated shells (identified as *Tonkinospira* cf. *pauperrima*).

**Diagnosis.** A medium sized *Tonkinospira* species with a high conic shell, rounded/parabolic body whorl, dense spiral striation, and a peristome that is not adnate to penultimate whorl.

**Description.** Shell medium sized for the genus; high conical with rounded (rather parabolic) body whorl; 5 whorls, regularly increasing; suture deep; penultimate whorl widest from standard apertural view; protoconch consists of almost 1.5 whorls, finely rugose, and densely, strongly spirally striated; teleoconch with irregular, rough radial growth lines, and dense, rather regular spiral striation creating a reticulate surface texture, ca. 24 in number in the middle shell line from apertural view; aperture strongly oblique to shell axis, turning downward in alignment with the penultimate whorl in lateral view; aperture ovate-subquadrate; peristome slightly expanded, not reflected; aperture not adnate to penultimate whorl; umbilicus narrow, partly covered by peristome and is almost ½ the diameter of the base of the shell.

**Differential diagnosis.** See under *Tonkinospira danangensis* and *T. raxajacki* new species.

**Remarks.** The type locality, “Phu-Quoc-Oai” (Quốc Oai; Phu is an old way to call a ward) is a district approximately 20 km west from the city centre of Hanoi. This must not be mistaken with Phú Quốc Island in southern Vietnam.

The newly-collected sample (JJV 17630) contains shells of variable shell characters such as shell height and shell width. Although the shells are generally smaller than the syntype of *T. pauperrima*, and the whorls are more accurately rounded, these differences are better explained as intraspecific variability.

***Tonkinospira pulvrea* (Bavay & Dautzenberg, 1909)**  
(Fig. 9)

*Helix (Systemostoma) pulvrea* Bavay & Dautzenberg, 1909a: 243. (type locality: Phu-Quoc-Oai [see remarks under *T. pauperrima*])

*Helix (Systemostoma) pulvrea* — Bavay & Dautzenberg, 1909b: 194–195, pl. 8, figs 7–9.

*Systemostoma pulvrea* — Pilsbry, 1917: 225, Plate 38, figs 10–12.

*Tonkinospira pulvrea* — Jochum et al., 2014: 36, fig. 3.

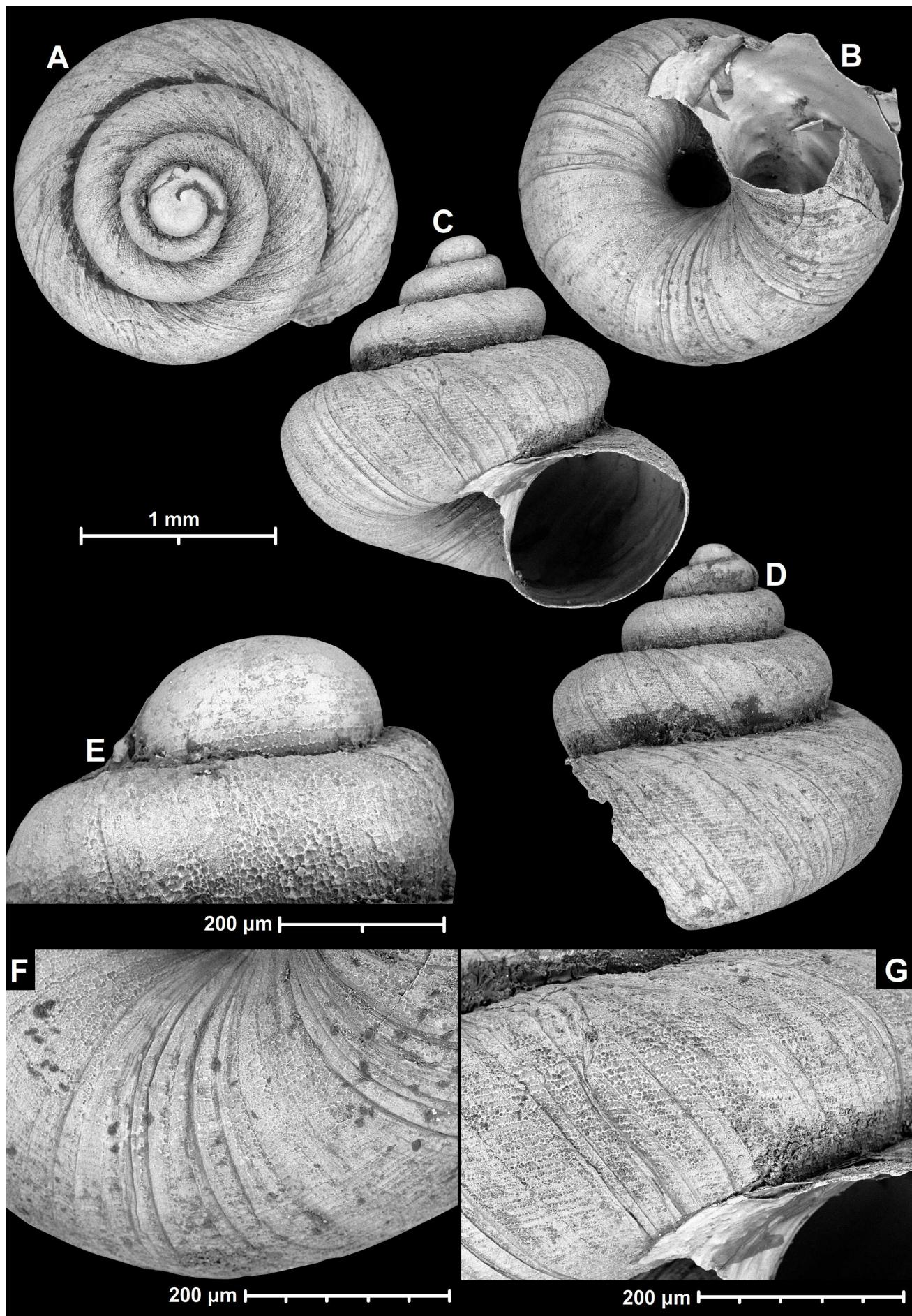


Fig. 9. *Tonkinospira pulvrea* (Bavay & Dautzenberg, 1909), MNHN-IM-2000-32863 (syntype).

**Types examined:** 1 shell, syntype (H: 2.05 mm, D: 2.15 mm, Fig. 9) (MNHN-IM-2000-32863), Phu-Quoc-Oaï, coll. Demange.

**Diagnosis.** A large *Tonkinospira* species with a depressed-conical shell, rounded body whorl, dense spiral striation, and a peristome that is adnate to penultimate whorl.

**Description.** Shell large for the genus; depressed-conical with very slightly, bluntly shouldered body whorl; whorls slightly more than 4, regularly increasing; suture deep; penultimate whorl widest from standard apertural view; protoconch consists of slightly more than one whorl, roughly rugose, and strongly spirally striated; teleoconch with very rough, irregular, radial growth lines, and dense, irregular spiral striation, ca. 36 in number in the middle shell line from apertural view; aperture oblique to shell axis and in alignment with the penultimate whorl from lateral view; aperture wide, circular; peristome not expanded and not reflected (although the holotype might be a subadult shell); aperture adnate to penultimate whorl; umbilicus narrow, partly covered by peristome.

**Differential diagnosis.** The most similar *Tonkinospira* species is *T. depressa* (for differences, see under that species). Otherwise, members of the genus *Krobylos* Panha & J.B. Burch, 1999 are similar in shell shape.

**Remarks.** For the type locality see *T. pauperrima*.

***Tonkinospira raxajacki* Pál-Gergely & A. Reischütz,  
new species**  
(Fig. 10)

**Type material.** Holotype (H: 1.2 mm, D: 1.09 mm, Fig. 10) (NHMW 113205), Laos, Khammouane Province, Tham Xienlab (cave), NE Thakhek, at the base of limestone rocks at the entrance of the cave, ca. 160 m a.s.l., approx. GPS coordinates: 17°27.213'N, 104°54.572'E (locality code: La.5), coll. Raxajack, S. & Reischütz, A., March 2010. Paratypes: 1 paratype (MNHN-IM-2014-6406), South-Central Laos, Khammouane Province, ca. 32 km ENE of Thakhek (Muang Khammouan), ca. 10 km WNW of Mahaxai, limestone, clay, black soil in limestone pockets, on and under rocks in dry secondary forest on steep N exposed slope under cliff, 180 m a.s.l., 17°26.957'N, 105°06.781'E (locality code: 1L07), coll. A. Abdou & I.V. Muratov, 24 November 2007; 1 paratype (coll. RE), Laos, Khammouane Province, Tham Pha Inh (cave), East of Thakhek, ca. 180 m a.s.l., 17°27.687'N, 104°54.951'E, (locality code: La.7), at the base of limestone rocks, coll. Raxajack, S. & Reischütz, A., March 2010; 10 paratypes (MNHN-IM-2014-6405), South-Central Laos, Khammouane 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, alt. 160 m, 17°24.340'N, 104°54.894'E (locality code: 25L07), coll. A. Abdou & I.V. Muratov, 09 December 2007; 1 paratype (coll. JG), Laos, Bolikhamsay Province, Nong Long 10 km SE of Lak Sao, Phou Phakô massif 2km E of the village, Spring and caves

at NW foot of the massif, in front of the quarry, 18°6.894'N, 105°3.092'E, coll. J. Grego, 17 February 2017.

**Diagnosis.** A small *Tonkinospira* species with an elongate-conic shell, rounded body whorl, irregularly growing whorls, conspicuously deep suture, dense spiral striation, and a peristome that is not adnate to penultimate whorl.

**Description.** Shell small for the genus; elongate-conic with rounded body whorl; 4.25–4.5 whorls, irregularly increasing; suture remarkably deep; protoconch consists of 1.25 whorls, finely rugose, and densely, strongly spirally striated; teleoconch reticulated with irregular, rough radial growth lines, and dense, rather regular spiral striation, ca. 30 in number in the middle shell line from apertural view; aperture oblique to shell axis from lateral view; aperture ovate-subquadrate; peristome not or very slightly expanded, not reflected; aperture not adnate to penultimate whorl and slightly separated (ventral view) from the body whorl; umbilicus deep, slightly smaller than 1/3 the diameter of the base and not covered by peristome.

**Measurements (in mm).** H = 1.14–1.22, D = 1.09–1.21 (n = 4).

**Differential diagnosis.** The most similar species is *Tonkinospira pauperrima*, which is larger, has a more oblique aperture to the shell axis, a narrower umbilicus (the peristome partly covers the umbilicus), and has more regularly growing whorls.

**Etymology.** We dedicate this species to Somsamay Raxajack for enduring A. Reischütz for seven weeks during a Southeast Asia trip and in gratitude for the outstanding hospitality of his family's native village Ban Pak Nam.

***Tonkinospira suturata* Pál-Gergely & Grego,  
new species**  
(Fig. 11)

**Type material.** Holotype (H: 1.41 mm, D: 1.84 mm, Fig. 11) (HNHM 104405), 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; 2 damaged paratypes (coll. JG), same data as preceding.

**Diagnosis.** A large *Tonkinospira* species with a depressed conical shell, rounded body whorl, fine radial growth lines and without spiral striation, a wide umbilicus, and a peristome that is not adnate to penultimate whorl.

**Description.** Shell large for the genus; depressed conical with rounded body whorl; shell wider than tall; 4.25 whorls, regularly increasing, separated by a very deep suture; whorls shouldered; protoconch consists of 1.5 whorls, with extremely fine radial growth lines and without spiral striation (on the first whorl of protoconch some spiral striae visible, but they are not regular, probably due to erosion of the shell surface); teleoconch overall weakly sculptured, with irregular, fine

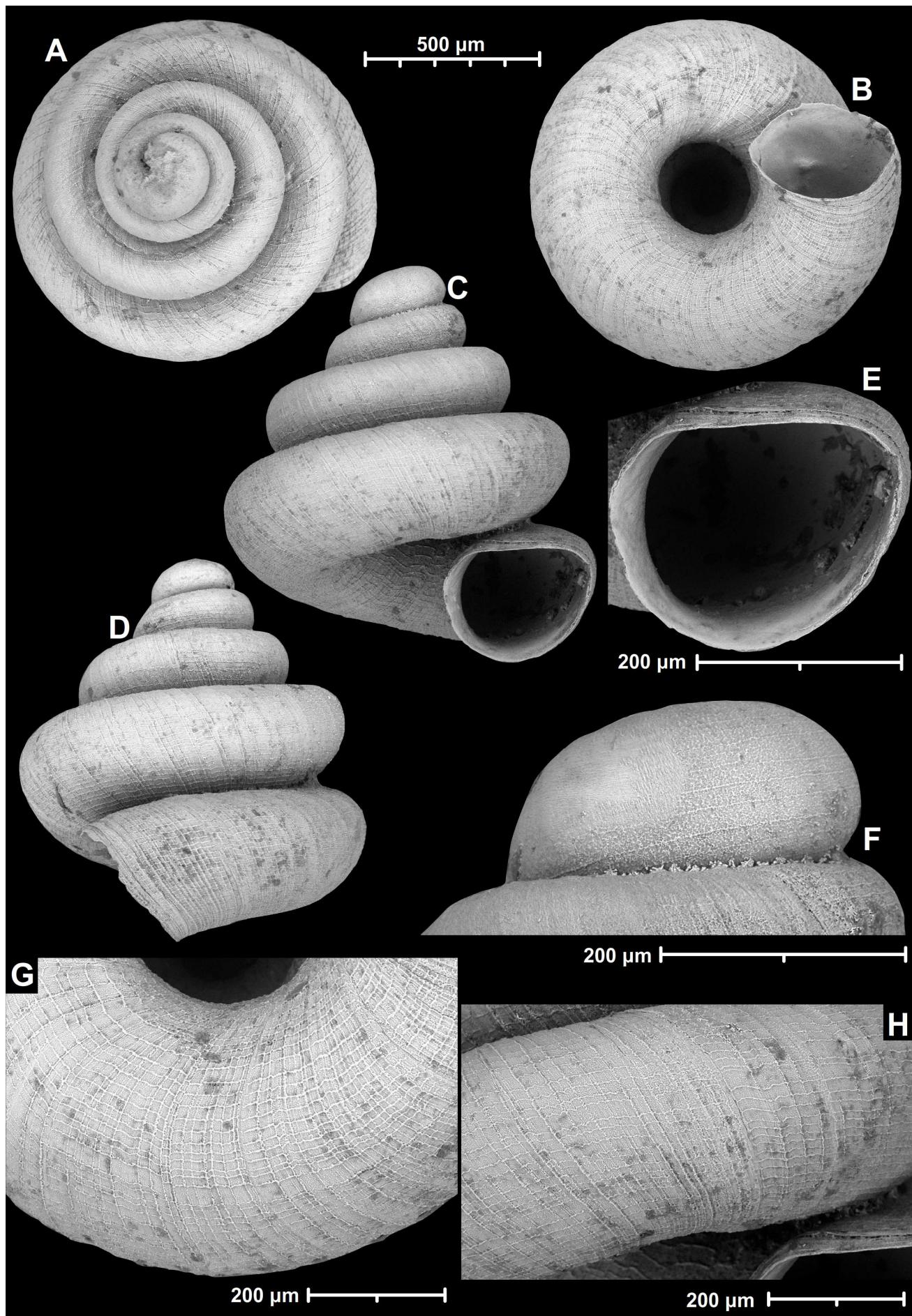


Fig. 10. *Tonkinospira raxajacki* Páll-Gergely & A. Reischütz new species, NHMW 113205 (holotype).

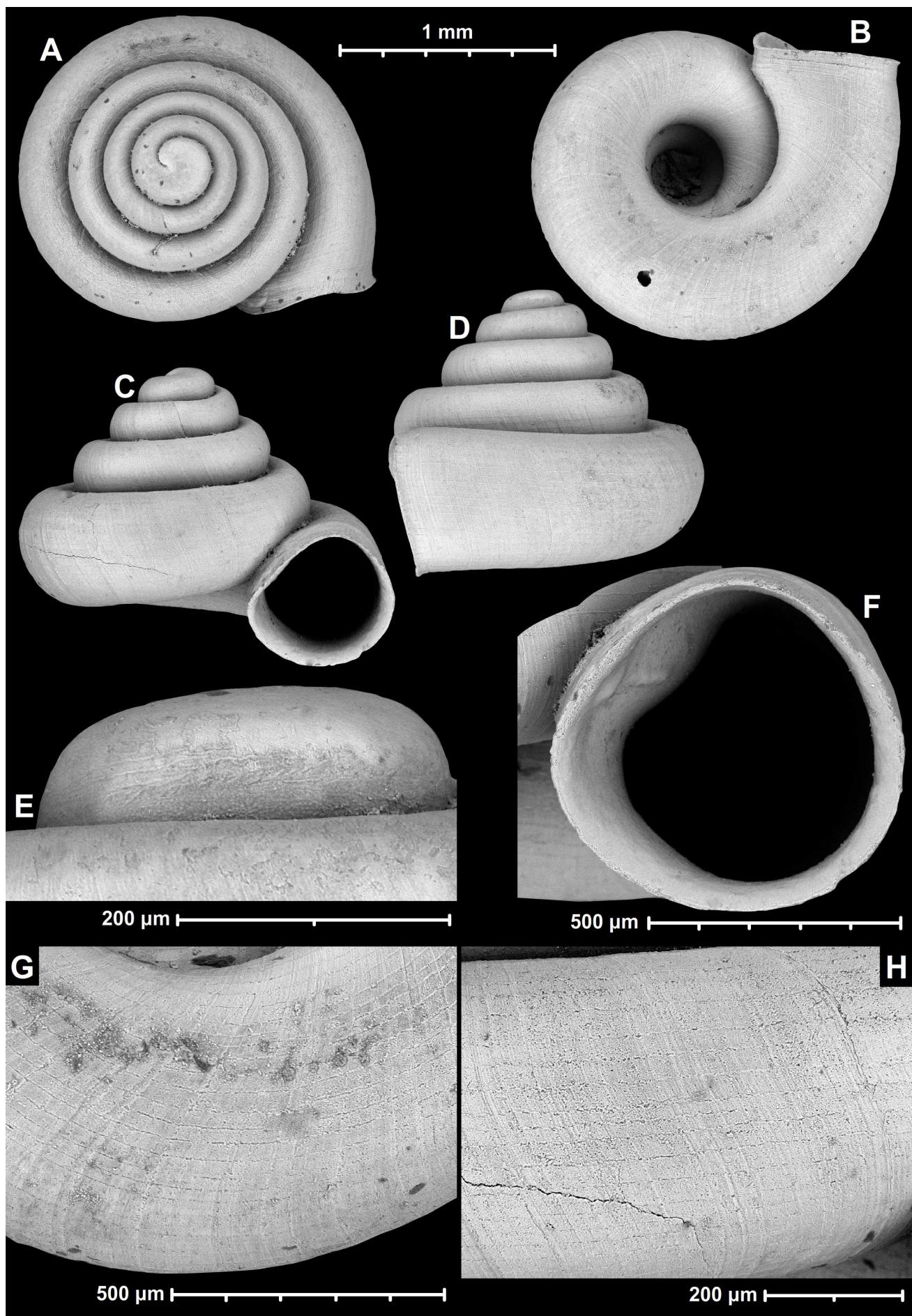


Fig. 11. *Tonkinospira suturata* Páll-Gergely & Grego, new species, HNM 104405 (holotype).

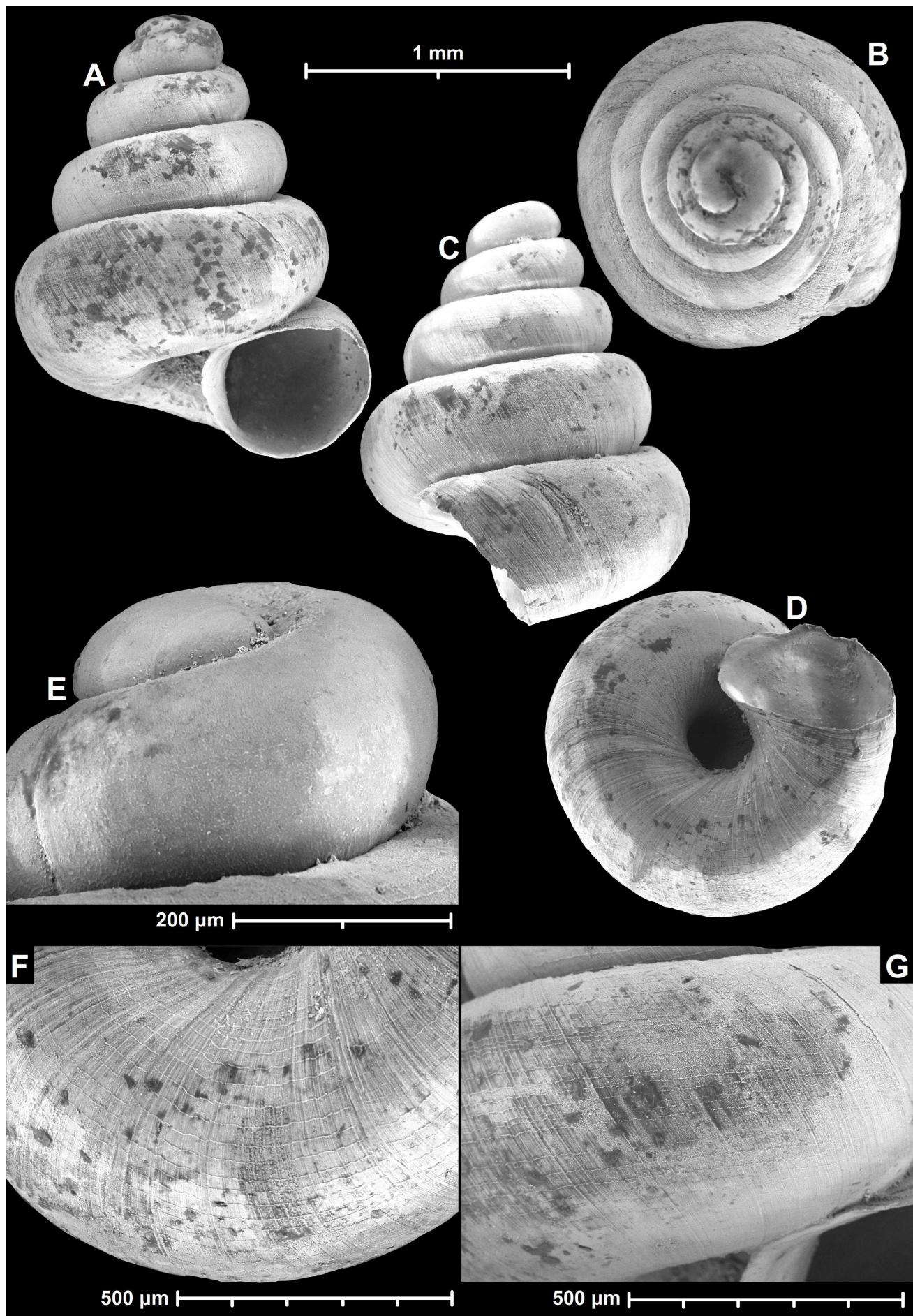


Fig. 12. *Tonkinospira triangulata* Páll-Gergely & Vermeulen, new species, NHMUK 20190687 (holotype).

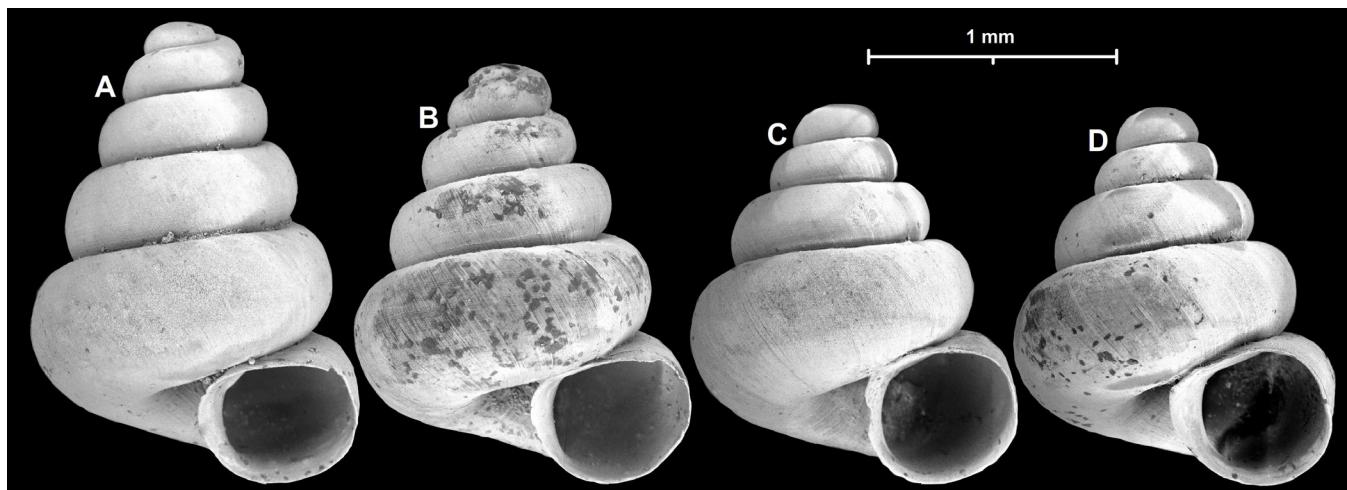


Fig. 13. Variability within *Tonkinospira triangulata* Páll-Gergely & Vermeulen, new species (JJV 6265).

radial growth lines, and relatively dense, regular, obscure spiral striation, ca. 22 in number in the middle shell line from apertural view; aperture almost in alignment with penultimate whorl and very slightly oblique to shell axis in lateral view; aperture rounded-ovate, slightly free from the preceding whorl along the parietal margin; peristome very slightly expanded, not reflected; aperture not adnate to penultimate whorl, protruding into a truncated tuba (best seen from umbilical perspective); two weak, very low suggestions of parietal barriers are discernible; umbilicus wider than narrow.

**Differential diagnosis.** The most similar species in terms of shell size and the weak sculpture is *T. tomasini*, which has a much more elevated spire, and adnate peristome and a more oblique aperture to the shell axis.

**Etymology.** The specific epithet *suturata* refers to the deep suture of the new species.

***Tonkinospira tomasini* Páll-Gergely & Jochum, 2017**  
(Fig. 1)

*Tonkinospira tomasini* Páll-Gergely & Jochum in Páll-Gergely et al., 2017: 337: figs 1a, 5, 6, 7a, b. (type locality: Northern Vietnam, Ha Giang Province, Quan Ba District, Tam Son, Cong Troi Cave, 980 m, 23°02'44.7"N, 104°59'23.9"E)

**Diagnosis.** A large *Tonkinospira* species with a conical shell, rounded body whorl, shallow sutures, weak growth lines and spiral striation, and a peristome that is adnate to penultimate whorl.

**Differential diagnosis.** See under *Tonkinospira suturata* new species, and *T. triangulata* new species.

***Tonkinospira triangulata* Páll-Gergely & Vermeulen, new species**  
(Figs. 12, 13)

**Type material.** Holotype (H: 1.83 mm, D: 1.42 mm, Fig. 12) (NHMUK 20190687), Vietnam, Quang Ninh Province,

Halong Bay area, Dao Bo Hon, Song Sot Cave, drift material washed together over sinkhole in cave, 20°50.833"N, 107°5.667"E, coll. Vermeulen, J.J. & Whitten, A.J., 02 October 1998; 3 cleaned paratypes (Fig. 13) + 96 non-cleaned paratypes + some fragments/juveniles (JJV 6265), same data as preceding; 84 paratypes (JJV 6244), same data as preceding; 5 paratypes (ZRC.MOL.015615), same data as preceding; 5 paratypes (HNHM 104433), same data as preceding.

**Diagnosis.** A medium sized *Tonkinospira* species with a convexly conic shell, rounded body whorl, dense spiral striation, and a peristome that is not adnate to penultimate whorl.

**Description.** Shell medium sized for the genus, convexly conic with pointed apex, greyish-white; protoconch consisting of 1–1.25 whorls, nearly smooth, at the last quarter whorl and near the suture granular with some elevated, serrated calcareous ridges that are partly arranged in a spiral line; entire shell consisting of 5.5–6 whorls, suture deep; teleoconch retiform with some faint, spiral threads; spaces between spiral striae variable in width on frontal view of body whorl, but striae are more equidistant on the umbilical side; aperture almost rounded, peristome very slightly expanded, especially in direction of umbilicus, not thickened, sharp; aperture slightly detached from body whorl in ventral view, turning slightly downwards at ca. 1/5 the diameter of the shell; umbilicus narrow and deep, only very slightly covered by reflected lip.

**Measurements (in mm).** H = 1.69–2.01, D = 1.42–1.46 (n = 4).

**Differential diagnosis.** *Tonkinospira triangulata* new species differs from *T. crassicostata* new species by the smoother shell and thinner peristome, from *T. pauperrima* by less bulging whorls and less oblique aperture, and *T. tomasini* by the smaller size and stronger sculpture and the horizontal alignment of the peristome to the body whorl versus the more oblique alignment in *T. tomasini*. See also under *T. danangensis* new species.

**Etymology.** This species is named after its triangular shell shape.

## DISCUSSION

The genus *Tonkinospira* is characterized by the absence of apertural barriers. Therefore, it is possible that the species included here are members of other genera with reduced dentition. The distinction between *Tonkinospira* and *Angustopila* is clear in that *Angustopila* consistently has a very tiny shell, an expanded peristome, and relatively widely-spaced spiral striation. In contrast, shell size is highly variable in *Tonkinospira*, which indicates that it is not a “compact” genus as is the case for *Angustopila*. Moreover, the dense spiral striation of *Tonkinospira* is similar to that of the genus *Hypselostoma* (Páll-Gergely et al., 2015). The placement of *T. chytrophora*, *T. danangensis* new species, *T. defixa*, *T. raxajacki* new species, *T. triangulata* new species is appropriate to *Tonkinospira* due to the similar size, shell shape and sculpture to the type species (*T. pauperrima*). On the other hand, the species with larger shells and/or different sculpture (*T. crassicosata* new species, *T. depressa*, *T. suturata* new species, *T. pulvereata*), are only tentatively placed in this genus, and their systematic position requires further confirmation.

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