

First record of subterranean rissoidean gastropod assemblages in Southeast Asia (Mollusca, Gastropoda, Pomatiopsidae)

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Abstract

In February 2017 we investigated several caves and karstic springs in Laos for the presence of underground freshwater gastropod species. We report previously unrecorded freshwater gastropod assemblages in the largest cave in Laos, Tham Khon Dôn, and in the third largest cave, Pha Soung, in Khammouane Province, with single finds in Na Li Cave (Khammouane Province), an unnamed cave near Vieng Thong (Bolikhamsay Province) and a small karst spring near Phonsavan (Xianghouan Province). All 15 species recorded and described herein are new to science. Four species are assigned to the new genus *Pseudoiglica*: *P. pseudoiglica* sp. n., *P. olsavskyi* sp. n., *P. kameniari* sp. n., and *P. phonsavanica* sp. n. Three species are assigned to the new genus *Thamkhondonia*: *T. moureti* sp. n., *T. vacquiei* sp. n., and *T. smidai* sp. n. Eight species are assigned to the genus *Tricula* Benson, 1843: *T. valenasi* sp. n., *T. davisi* sp. n., *T. spelaea* sp. n., *T. lenahani* sp. n., *T. reischuetzorum* sp. n., *T. phasoungensis* sp. n., *T. bannaensis* sp. n., and *T. viengthongensis* sp. n.

Keywords

Troglobiont, Stygobiont, Spring, Cave, Laos, Khammouane, Bolikhamsay, Xianghouan

Introduction

The subterranean freshwater molluscan fauna of South and East Asia is virtually unknown. Bole and Velkovrh (1986) mentioned only one subterranean species from South Asia that was recorded in Sri Lanka (*Srilankiella horanae* Bole & Velkovrh, 1986, *nomen nudum* according Kabat and Hershler 1993) and 12 probable pomatiopsid taxa from Japan belonging to the genera *Akiyoshia* Kuroda & Habe, 1954, *Cochliopopsis* Mori, 1938 and *Moria* Kuroda & Habe, 1958. Despite the recent increased interest in South and East Asian terrestrial micromolluscs (Maassen 2008, Culver 2012, Páll-Gergely 2014, Páll-Gergely et al. 2015, Inkhavilay et al. 2016, Páll-Gergely et al. 2016, Páll-Gergely et al. 2017), our knowledge of the stygobiont gastropod fauna of the region has not advanced significantly since 1986. Despite the extraordinary high radiation of surface freshwater Pomatiopsidae Bourguignat, 1863, species of the tribe Triculini Annandale, 1924 in the Mekong tributary (Deshayes and Jullien 1876; Crosse and Fischer 1879; Annandale 1919; Brandt 1968, 1970, 1974; Davis 1979, Temcharoen 1971; Brandt and Temcharoen 1974; Strong et al. 2007), the troglobiont and stygobiont species of the area remained unknown. Studies of this extraordinary high diversity in the Mekong Basin of over 90 taxa was driven primarily by parasitological studies of the trematode *Schistosoma mekongi* Voge, Bruckner & Bruce, 1978, the main intermediate hosts of which are some of the local Triculini species such as *Neotricula aperta* (Temcharoen, 1971). The assumption that the high diversity of surface Triculini species could extend into the underground stygobiont habitat was confirmed in the present study.

Materials and methods

The material studied was collected in Laos in February 2017 from the localities shown in Figs 1 and 2. Various cave streams, outflows and karstic springs were sampled using microhabitat preference and sampling methods as described by Grego et al. (2017).

Samples (fine sand) were screened under a stereomicroscope. They were first screened wet for live animals. Then they were dried and screened again for dry shells that might have been overlooked during the wet screening. Frontal and lateral view images were taken with a digital camera and ImageJ scientific image analysing software was used to take measurements, with additional direct measurements obtained using an eyepiece micrometer.

We followed the shell morphology nomenclature according Davis et al. (1992) and Hershler and Ponder (1998).

Abbreviations

NHMMUK Natural History Museum, London, UK

HNHM Hungarian Natural History Museum, Budapest, Hungary

OSUM Ohio State University Museum of Biological Diversity, Columbus, Ohio, USA

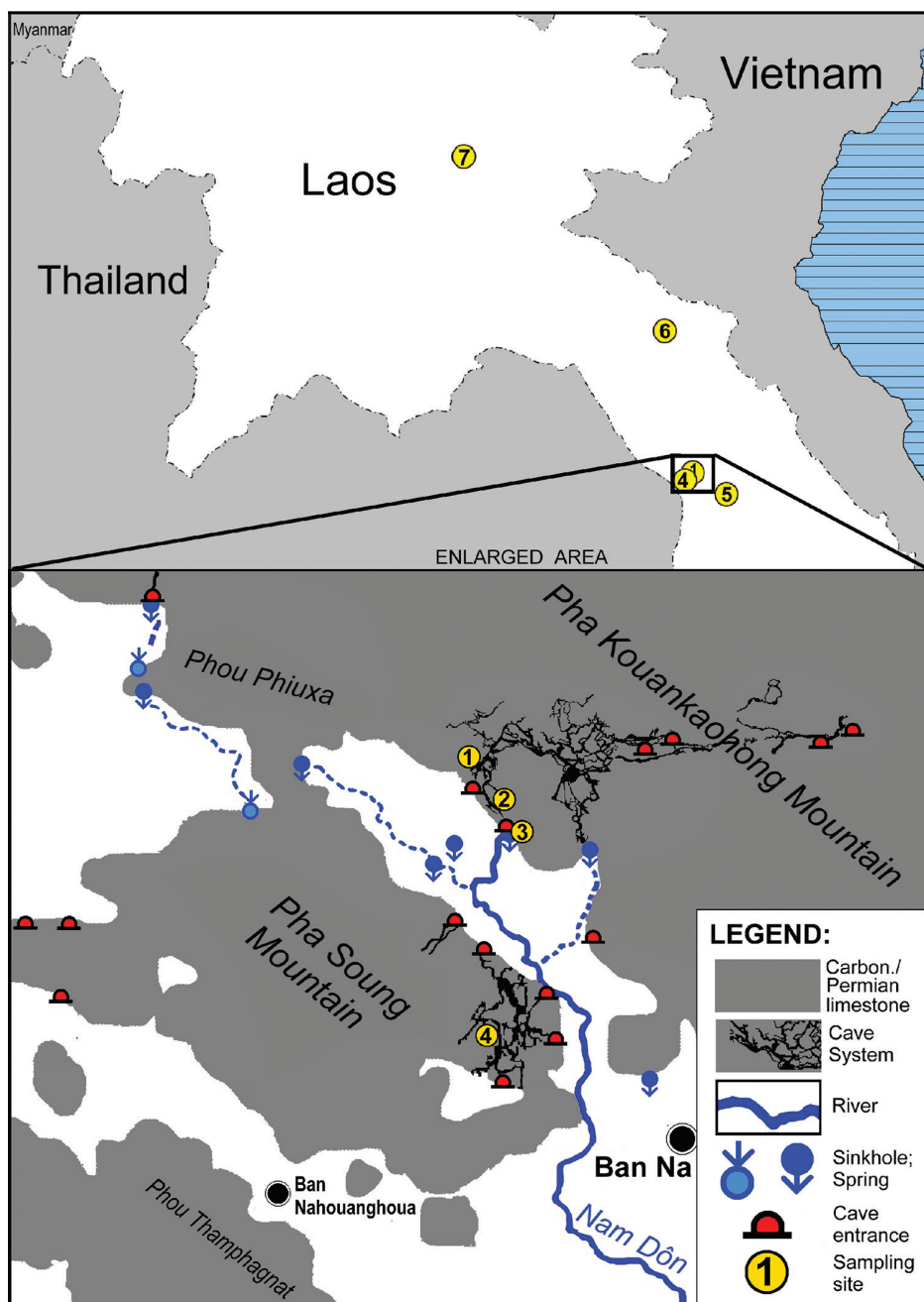


Figure 1. Map of sampling localities in Laos. **1–3** Khammouane: Tham Khon Dôn Cave **1** Earthquake Dome, Type locality (LT) of *Pseudoiglica pseudoiglica* gen. n., sp. n., *P. olsavskyi* n. sp., *P. kameniari* sp. n., *Thamkhondonia moureti* gen. n., sp. n., *T. vacquiei* sp. n., *T. smidai* sp. n., *Tricula valenasi* sp. n., *T. davisi* sp. n., *T. spelaea* sp. n., *T. lenahani* sp. n. and *T. bannaensis* sp. n. **2** Entrance passage **3** Source of Nam Dôn River **4** Khammouane: Tham Pha Soung Cave, Frog Lake, LT of *Tricula phasoungensis* sp. n. **5** Khammouane Cave Na Li, LT of *Tricula reischuetzorum* sp. n. **6** Bolikhamsay, 16 km W Vieng Thong, LT of *Tricula viengthongensis* sp. n. **7**, Xianghouan: Ban Nadom Village, LT of *Pseudoiglica phonsavanica* sp. n.

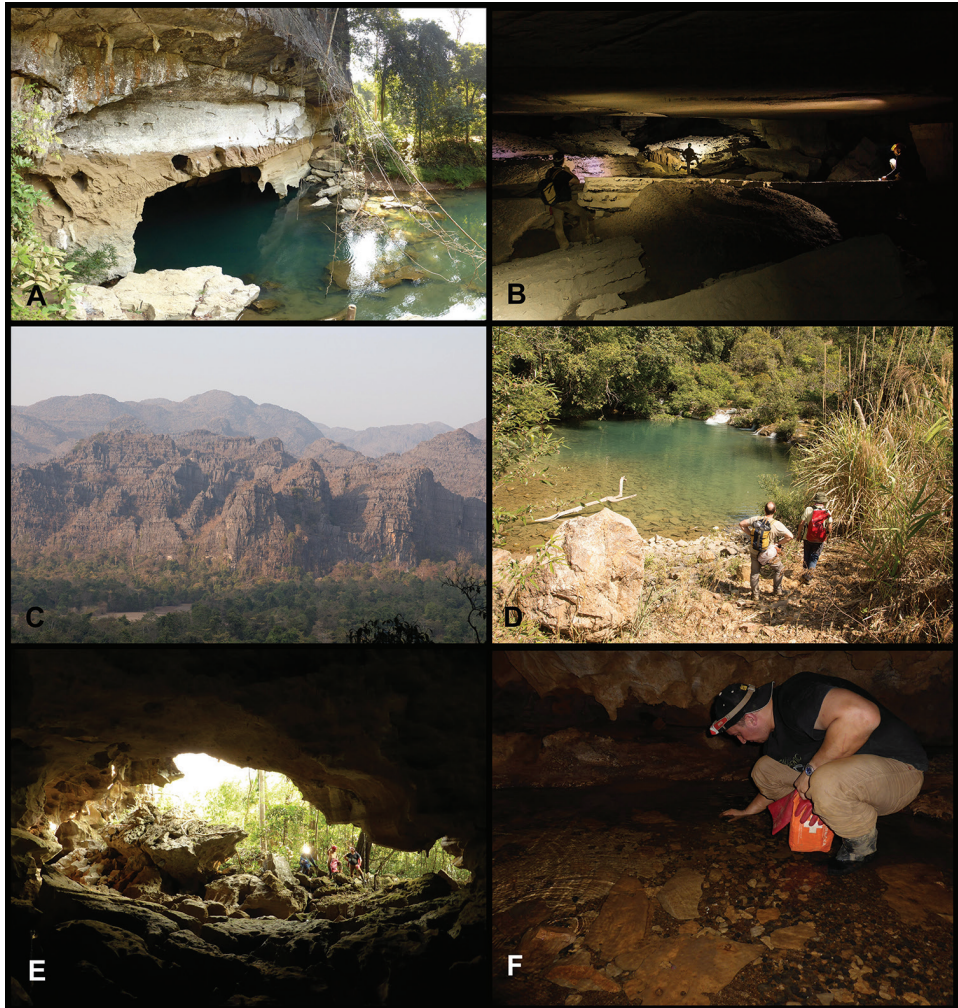


Figure 2. Photos of sites where subterranean gastropods were found. **A** Khammouane: main entrance of Tham Khon Dôn Cave with source of Nam Dôn River (2 in Fig. 1) **B** Earthquake Dome in cave Tham Khon Dôn (1 in Fig. 1) **C** Mount Pha Kouankaohong with entrance of Tham Khon Dôn cave at its foot **D** Bolikhamsay, travertine cascades below the LT of *Tricula viengthongensis* sp. n. (6 in Fig. 1) **E** Khammouane, one of the main entrances of Tham Pha Soung Cave **F** Tham Pha Soung Cave, sampling at Frog Lake (4 in Fig. 1). (Photos: Ondrej Kameniar, Mário Olšavský and Jozef Grego).

H	Shell height
W	Shell width
BH	Height of the body whorl
BW	Width of the body whorl
AH	Aperture height
AW	Aperture width
LT	Type locality
MY	Million years

Results

Many of the newly-recorded stygobiont Triculini have a convergent shell morphology superficially resembling to that of species of Moitessieriidae Bourguignat, 1863 and Hydrobiidae Troschel, 1857, known from other stygobiont habitats. All the present stygobiont specimens from the cave streams and spring outlets were empty shells collected during the dry season. As it is highly unlikely to find live specimens because of the inaccessibility of habitats during rainy seasons, the two new genera (*Pseudoiglica* gen. n. and *Thamkhondonia* gen. n.) were established based only on the shell morphology, without information on the soft parts and without molecular data. I assume, based on shell morphology that all the new species belong to the family Pomatiopsidae Bourguignat, 1863, tribe Triculini Annandale, 1924. The tribe is extremely diverse along the neighboring tributary of the Mekong River and represents the only known Gastropoda similar to the new taxa within the whole region.

Superfamily Truncatelloidea Gray, 1840

Family Pomatiopsidae Bourguignat, 1863

Tribe Triculini Annandale, 1924

Genus *Pseudoiglica* gen. n.

<http://zoobank.org/078DA479-6098-43ED-9357-D03815C8D782>

Diagnosis. The diagnostic features of the genus are the same as those of the type species, *Pseudoiglica pseudoiglica* sp. n. The elongated smooth shell shape with open umbilicus differs from all known genera of Pomatiopsidae in tributaries of the Mekong River.

Etymology. Named for the shell morphology, which is convergent with the subterranean moitessieriid genus *Iglica* Wagner, 1910 from the western Balkans.

Pseudoiglica pseudoiglica sp. n.

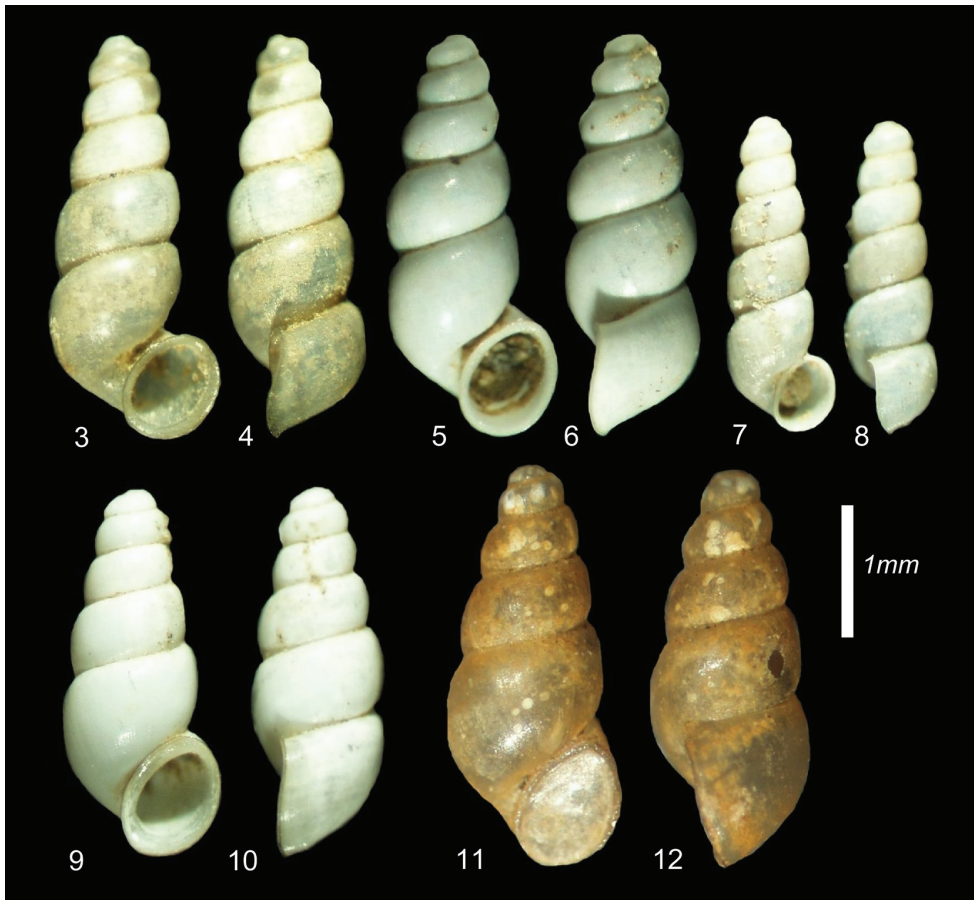
<http://zoobank.org/3D5A63D3-B516-4929-B002-DF41C10B23BA>

Figures 3–6

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments on bank of cave river (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180001).

Paratypes: type locality (NHMUK 20180016 – 1 specimen; HNHM 102769 – 1 specimen; coll. Grego F0871 – 6 specimens); Laos, Khammouane Province, Tham Nam Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., temporary side rivulet sediment at entrance passage 1.5 km from the main entrance, dry sand on the cave floor; J. Grego leg. 11 February 2017 (coll. Grego F0863 – 1 specimen).



Figures 3–12. Representatives of the genus *Pseudoiglica* gen. n. **3–6** *Pseudoiglica pseudoiglica* sp. n. (**3–4** holotype NHMUK 20180001 **5–6** paratype 1 coll. Grego F0871) **7–8** *P. olsavskyi* sp. n. (holotype NHMUK 20180003) **9–10** *P. kameniari* sp. n. (holotype NHMUK 20180002) **11–12** *P. phonsavanica* sp. n. (holotype NHMUK 20180004).

Other material. Laos, Khammouane Province, 2 km WNW of Ban Na village, Pha Soung Cave, Frog Lake, 155 m a.s.l., J. Grego leg. 09 February 2017, 17°33.052'N; 104°52.410'E (coll. Grego F0888).

Measurements. Holotype: H 3.08 mm; W 1.32 mm; BW 0.95 mm; BH 1.50 mm; AH 0.81 mm; AW 0.75 mm; H/W 2.33; AH/AW 1.08; W/BW 1.39; H/BH 2.05; H/AH 3.80; W/AW 1.76. Paratype 1: H 3.05 mm; W 1.31 mm; BH 1.00 mm; BW 1.55 mm; AH 0.87 mm; AW 0.75 mm; H/W 2.33; AH/AW 1.16; W/BW 1.31; H/BH 1.97; H/AH 3.51; W/AW 1.76.

Diagnosis. This new species is similar to the syntopic *Pseudoiglica kameniari* sp. n., from which it differs by its more slender, elongated shell with a more prominent umbilicus and less elongated aperture situated further to the right of the columellar axis.

It differs from syntopic *P. olsavskyi* sp. n. by its markedly larger and more conical shell shape and proportionally larger aperture. *Pseudoiglica phonsavanica* sp. n. (Xianghouan Province) has more a robust shell with more prominent body whorl and a differently shaped aperture.

Description. The milky yellowish silky shell has six tumid convex whorls with a deep suture and a blunt apex. The surface is smooth and shiny. The shell is elongated, almost cylindrical, slightly tapering towards a blunt apex, the umbilicus is tiny, open. In frontal view, the lateral aperture protrudes against the rest of the teleoconch. The aperture is ovoid, separated from the body whorl by a gap. The peristome margin is blunt, equally thick all the way around and slightly reflexed outwards. The outer lip is sinuous in lateral view and slightly scooped forward at its lower end.

Etymology. See the etymology of the genus *Pseudoiglica* gen. n.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as in the related source of the Nam Dôn River and from sediments in Tham Pha Soung Cave.

Ecology. Empty shells of the new species were extracted from the side stream sandy sediments of an underground river inside the cave Tham Khon Dôn about 3 km from the main entrance situated above the source of Nam Dôn River (Fig. 1A). The cave Tham Khon Dôn is situated under the massif of Mount Pha Kouankaohong (Fig. 2C) north of Ban Na Village. It represents the largest explored cave system in Laos, with a length of known passages of ca. 42 km. The cave is morphologically diverse with large domes and passages modeled by phreatic corrosion representing the cave multiple genetic horizons formed during the past 11 million years (since Late Miocene-Lower Pliocene) of its natural history possibly driven by a hydrothermal, H₂S speleogenesis (Mouret 2005). Despite the remarkable length of the cave system, its water passages are accessible only for a limited length near the entrance. The major part of the underground river comprises mostly unexplored submerged cave passages. The main sampling site was located at the bottom of Earthquake Dome (Fig. 2B), named after the sounds of the earthquake experienced here by the first explorers (Claude Mouret and Jean-Francois Vacquié pers. com.). The dome floor is covered by very large flat limestone slabs approx. 0.8–1.2 m thick fallen from the horizontally flat ceiling that reflects the horizontal beds of Carboniferous/Permian Khammouane Limestone. The fallen slabs fragmented the underground stream into several lakes and helped to create the sedimentation zones in which empty shells could be deposited during high water flows. A few shells were also found in the sand floor of the entrance passage approximately 1.5 km from the entrance close to the junction with a temporary side stream, as well as in the sand deposited directly at the cave entrance at the source of the Nam Dôn River (Fig. 1A). The character of the material deposited in the cave sediments and the freshwater shell assemblages suggested their autochthonous origin rather than the allochthonous influence of horizontal surface waters. The occurrence of tiny terrestrial gastropod shells of mainly soil and leaf litter dwelling families such as Vertiginidae Fitzinger, 1833 (*Hypselostoma* sp., *Angustopila*

sp., *Krobylos* sp., *Paraboysidia* sp.) and Diapheridae Panha & Naggs, 2010 (*Sinoennea* sp.) in the underground river sediments suggests a stronger influence of vertically circulating surface karst waters. The presence of the same species in the sediments of nearby Tham Pha Soung Cave indicates possible communication between the two caves through phreatic waters under Ban Na polje or during the rainy seasons. Surface Triculini species inhabiting the Nam Dôn River are larger, with a stronger periorostracum and different shell morphology. It appears that they are not penetrating deeply into the dark cave system, probably because of a lack of their main algal food. The new species probably inhabits the so far unexplored submerged cave passages of the Tham Khon Dôn system.

***Pseudoiglica olsavskyi* sp. n.**

<http://zoobank.org/3BB62BF8-DD8E-44F6-BD93-618321D7161F>

Figs 7–8

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments on cave river bank (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180003). Paratypes: type locality (NHMUK 20180149 – 1 specimen; coll. Grego F0872 – 3 specimens); Laos, Khammouane Province, Tham Nam Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., temporary side rivulet sediment at entrance passage 1.5 km from the main entrance, dry sand on the cave floor; J. Grego leg. 11 February 2017 (coll. Grego F0864 – 3 specimens); Laos, Khammouane Province, 3 km NW of Ban Na Village, sand on the bottom of Nam Dôn River source at 149 m a.s.l.; J. Grego leg. 07 February 2017, 17°33.20'N; 104°52.38'E (coll. Grego F0854 – 4 specimens) (Fig. 2A).

Measurements. Holotype: H 2.45 mm; W 0.85 mm; BW 0.52 mm; BH 1.00 mm; AH 0.61 mm; AW 0.45 mm; H/W 2.88; AH/AW 1.36; W/BW 1.63; H/BH 2.45; H/AH 4.02; W/AW 1.89

Diagnosis. The tiny, elongated cylindrical shell of *P. olsavskyi* sp. n. with a proportionally very small aperture distinguishes this species from all other known members of the genus, which all have larger shells.

Description. The tiny milky shell has six flattened convex whorls with a deep suture and a blunt apex. The surface is smooth and shiny. The shell is cylindrically elongated, slightly narrowing towards the apex. Umbilicus is slit-like. In frontal view, the aperture protrudes laterally from the shell periphery outline. Aperture is ovoid, separated from the body whorl by a weak furrow. The peristome margin is sharp, equally thick all the way around and very slightly reflexed outwards. The outer lip is sinuous in its lateral profile and its lower end scooped backward.

Etymology. Named after my friend Mario Olšovský, a geologist and speleologist from Banská Bystrica, Slovakia, who actively participated in sample collection in the cave Tham Khon Dôn.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as from the related source of Nam Dôn River

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.

***Pseudoiglica kameniari* sp. n.**

<http://zoobank.org/A529966B-65AD-404D-BCC6-552FF9832934>

Figures 9–10

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments on bank of cave river (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180002). Paratypes: type locality (NHMUK 20180017 – 1 specimen; HNHM 102770 – 1 specimen; OSUM 42383 – 1 specimen; coll. Grego F0873 – 11 specimens).

Measurements. Holotype: H 2.85 mm; W 1.21 mm; BW 0.85 mm; BH 1.50 mm; AH 0.95 mm; AW 0.75 mm; H/W 2.36; AH/AW 1.27; W/BW 1.42; H/BH 1.60; H/AH 3.00; W/AW 1.61.

Diagnosis. Similar to syntopic *Pseudoiglica pseudoiglica* sp. n., from which it differs by its smaller, more robust shell with a less prominent umbilicus and more elongated aperture situated more towards the columellar axis. It differs from the syntopic *P. olsavskyi* sp. n. by its larger and more conical shell shape and proportionally larger aperture. It differs from *P. phonsavanica* by its less robust shell, less prominent body whorl and the different shape of the aperture.

Description. The milky yellowish shell has five convex whorls with a deep suture and a blunt apex. The shell has a smooth and shiny surface and is elongated-conical. Umbilicus is slit-like. In frontal view, the aperture aligns with the shell periphery outline. Aperture is ovoid, attached to the body whorl by a very weak furrow. The peristome margin is a blunt callous, equally thick all the way around and slightly reflexed outwards. The outer lip is weakly sinuous in lateral profile.

Etymology. Named after Ondrej Kameniar, young speleologist and biologist, friend from Ľubochňa, Slovakia, who actively participated in our 2017 field trip to Laos.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as from the related source of Nam Dôn River.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.

***Pseudoiglica phonsavanica* sp. n.**

<http://zoobank.org/A659C91D-394C-42F4-9C29-8EE9FEFACB5F>

Figs 11–12

Type locality. Laos; Xianghouan Province, Ban Nadom Village, 18 km SE of Phonsavan, 3 km N of Ban Kaua cement factory at highway 1D (9 km ENE of Xiang

Khouang), small spring at eastern foot of limestone hill, 19°23.142'N; 103°17.630'E, 1196 m a.s.l., fine sand directly at spring zone.

Type material. Holotype: type locality: J. Grego leg. 22 February 2017 (NHMUK 20180004).

Measurements. Holotype: H 3.05 mm; W 1.30 mm; BW 1.00 mm; BH 1.71 mm; AH 0.93 mm; AW 0.79 mm; H/W 2.35; AH/AW 1.18; W/BW 1.30; H/BH 1.78; H/AH 3.28; W/AW 1.65.

Diagnosis. Similar to *Pseudoiglica kameniari* sp. n. (Khammouane Province), from which it differs by its more robust shell with a more prominent umbilicus and a proportionally smaller aperture. The robust shape differentiates the species from all other members of the genus.

Description. The light orange, silky shell has five tumid convex whorls with a weak suture and a blunt apex. The smooth shell surface is covered by sparse rusty incrustations. The shell is elongated conical, with a prominent body whorl. Umbilicus is slit-like. In frontal view, the aperture is aligned with the shell periphery outline. Aperture is ear-shaped, separated from the body whorl by a weak sulcus. The peristome margin is blunt, not reflexed and slightly callous internally. The labral lip has a straight profile in lateral view, scooped backward from the columellar axis. The elongate ellipsoidal spiral operculum is light yellowish corneous with submarginal nucleus.

Etymology. Named after the city of Phonsavan, Laos, capital of Xianghouan Province, which is the closest large city to the type locality.

Distribution. Only known from the type locality.

Ecology. The locality is a small karstic spring rising at the foot of a rounded cone-shaped limestone hill at the boundary between limestone beds and a sandy slate substrate just a few meters above the road. The spring is connected to a small waterworks to supply water to the nearby village Ban Nadom. The water supply seems to be permanent throughout all seasons.

Remarks. The body whorl of *P. phonsavanica* sp. n. is proportionally larger than that of all other species of the genus. The more teardrop-shaped aperture suggests that this geographically distant species could represent a new genus distinct from *Pseudoiglica* gen. n. Anatomical and molecular data are needed to confirm such a possible distinction.

Genus *Thamkhondonia* gen. n.

<http://zoobank.org/114E71B9-6D08-4028-A309-5EA7422D9CF5>

Diagnosis. The diagnostic features of the genus are the same as those of the type species, *Thamkhondonia moureti* sp. n. The elongated axially and radially sculptured shell with an ear-shaped aperture differs from that of any known genus of Pomatiopsidae from tributaries of the Mekong River. The shell shows some resemblance to those of species in the triculiniid genus *Paraprosothenia* Annandale, 1919 and the marine genus *Attenuata* Hedley, 1918, but differs from both by the characteristic shell sculpture consisting of spiral cords and axial ribs.

Etymology. Named after the type locality inside the Tham Khon Dôn Cave situated under the massif of Pha Kouankaohong near village Ban Na in Khammouane Province.

***Thamkhondonia moureti* sp. n.**

<http://zoobank.org/FC1E7A3C-3E20-4B42-BD32-669EB5A70E53>

Figs 13–14

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments on cave river banks (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180005). Paratypes: type locality (NHMUK 20180018 – 2 specimens; HNHM 102771 – 2 specimens; OSUM 42384 – 2 specimens; coll. Grego F0874 – 33 specimens); Laos, Khammouane Province, Tham Nam Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., temporary side rivulet sediment at entrance passage 1.5 km from the main entrance, dry sand on the cave floor; J. Grego leg. 11 February 2017 (coll. Grego F0865 – 2 specimens); Laos, Khammouane Province, 3 km NW of Ban Na Village, sand on the bottom of Nam Dôn River source at 149 m a.s.l.; J. Grego leg. 07 February 2017, 17°33.20'N; 104°52.38'E (coll. Grego F0855 – 1 specimen) (Fig. 2A).

Measurements. Holotype: H 4.48 mm; W 1.42 mm; BW 0.80 mm; BH 1.55 mm; AH 1.01 mm; AW 0.91 mm; H/W 3.15; AH/AW 1.11; W/BW 1.78 H/BH 2.89; H/AH 4.44; W/AW 1.56.

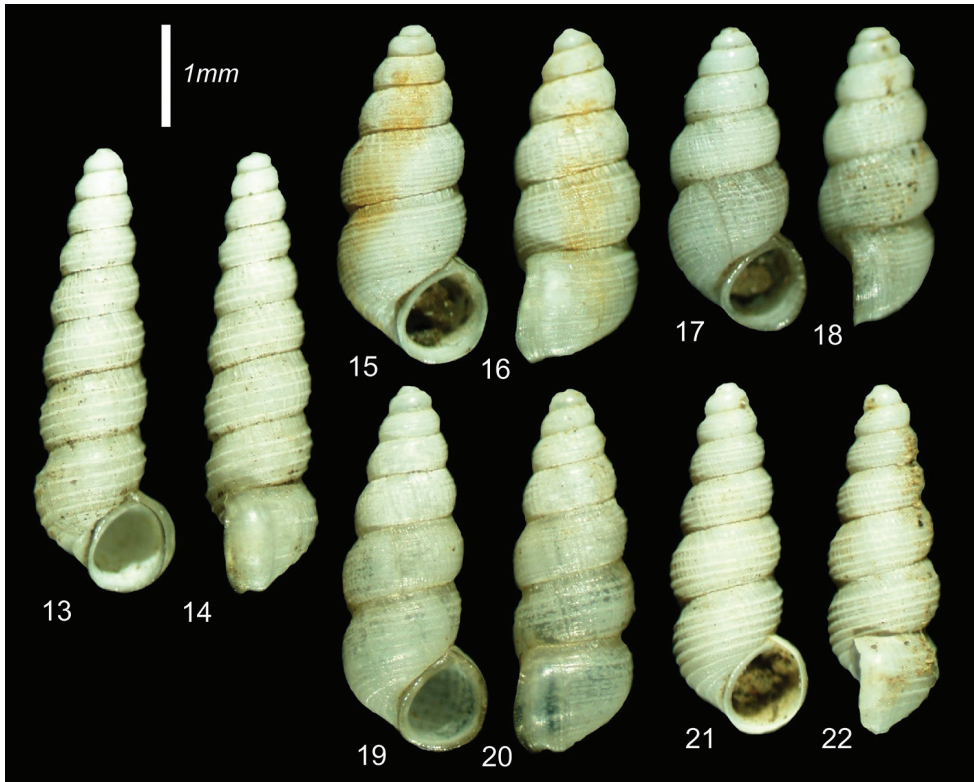
Diagnosis. Compared to the most closely related syntopic species, *Thamkhondonia vacquiei* sp. n. and *T. smidai* sp. n., *T. moureti* sp. n. has a much higher and more slender shell with much coarser spiral sculpture and a proportionally smaller aperture.

Description. The milky whitish, elongated turritiform shell has nine slightly convex whorls with a weak suture. The surface sculpture consists of 4–5 coarse spiral cords crossed by very fine axial ribs. The aperture is oval ear-shaped and extends beyond the shell periphery outline; the peristome is sharp and expands only at its columellar side. The lateral profile of the labral lip is straight and a characteristic axial varix is parallel to the labral lip. The umbilicus is closed.

Etymology. Named after my friend, a renowned French geologist and speleologist Claude Mouret (Magnac-Bourg, France), who in 2006 discovered and for the first time explored the Tham Khon Dôn cave system, the largest cave in Laos, and led annual expeditions to explore caves of Khammouane. Without his substantial help, the sampling of the type locality in cave Tham Khon Dôn would not have been possible.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as in the related source of Nam Dôn River.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.



Figures 13–22. Representatives of the genus *Thamkhondonia* gen. n. **13–14** *Thamkhondonia moureti* sp. n. (holotype NHMUK 20180005) **15–18** *T. vacquiei* sp. n. (**15–16** holotype NHMUK 20180006 **17–18** paratype 1 coll. Grego F0875) **19–22** *T. smidai* sp. n. (**19–20** holotype NHMUK 20180007 **21–22** paratype 1 coll. Grego F0876).

***Thamkhondonia vacquiei* sp. n.**

<http://zoobank.org/CF534C85-D526-43BF-95C0-02956FF6891D>

Figs 15–18

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek; Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments on cave river banks (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180006). Paratypes: type locality (NHMUK 20180019 – 5 specimens; HNHM102772 – 5 specimens; OSUM 42385 – 5 specimens; coll. Grego F0875 – 274 specimens); Laos, Khammouane Province, 3 km NW of Ban Na Village, sand on the bottom of Nam Dôn river source at 149 m a.s.l.; J. Grego leg. 07 February 2017, 17°33.20'N; 104°52.38'E (coll. Grego F0856 – 1 specimen) (Fig. 2A).

Measurements. Holotype: H 3.35 mm; W 1.51 mm; BW 1.25 mm; BH 1.65 mm; AH 0.95 mm; AW 0.90 mm; H/W 2.22; AH/AW 1.06; W/BW 1.21; H/BH 2.03;

H/AH 3.53; W/AW 1.68; Paratype 1: H 3.00 mm; W 1.40 mm; BH 1.20 mm; BW 1.55 mm; AH 0.90 mm; AW 0.85 mm; H/W 2.14; AH/AW 1.06; W/BW 1.17; H/BH 1.94; H/AH 3.33; W/AW 1.65.

Diagnosis. *Thamkhondonia vacquiei* sp. n. differs from the two syntopic species *T. moureti* sp. n. and *T. smidai* sp. n. by its shorter and more robust shell shape with a proportionally larger aperture and by its much finer and more numerous spiral sculpture.

Description. The whitish translucent, conical shell has six convex whorls with a weak slightly wavy suture. The surface sculpture consists of 11–12 weak spiral cords crossed by fine axial ribs. The aperture is oval ear-shaped with an indication of a posterior canal that extends slightly beyond the shell periphery outline. The peristome is sharp and expands only on the columellar side. The lateral edge of the labral lip is sinuous and a weak axial varix is present parallel to the labral edge. The umbilicus is slit-like.

Etymology. Named after my friend Jean-Francois Vacquié (Castelnau d'Estretfonds, France), a French speleologist who participated in the explorations of Tham Khon Dôn Cave and supported our activities during the 2017 field trip.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as in the related source of Nam Dôn River.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.

Thamkhondonia smidai sp. n.

<http://zoobank.org/62043A71-D01B-4BA3-8EE5-1C65D5B1EF62>

Figs 19–22

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments at cave river bank (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180007). Paratypes: type locality (NHMUK 20180020 – 2 specimens; HNHM 102773 – 2 specimens; OSUM 42383 – 2 specimens; coll. Grego F0876 – 34 specimens); Laos, Khammouane Province, 3 km NW of Ban Na Village, sand on the bottom of Nam Dôn river source at 149 m a.s.l.; J. Grego leg. 07 February 2017, 17°33.20'N; 104°52.38'E (coll. Grego F0902 – 2 specimens) (Fig. 2A).

Measurements. Holotype: H 3.62 mm; W 1.45 mm; BW 1.15 mm; BH 1.45 mm; AH 1.05 mm; AW 0.75 mm; H/W 2.50; AH/AW 1.15; W/BW 0.36; H/BH 2.16; H/AH 3.45; W/AW 1.59. Paratype 1: H 3.45 mm; W 1.38 mm; BH 1.10 mm; BW 1.50; AH 1.00 mm; AW 0.87 mm; H/W 2.50; AH/AW 1.15; W/BW 0.36; H/BH 2.18; H/AH 3.45; W/AW 1.59.

Diagnosis. *Thamkhondonia smidai* sp. n. differs from syntopic *T. moureti* sp. n. by its smaller shell with less coarse and more numerous spiral sculpture and from *T. vacquiei* sp. n. (syntopic) by its longer and more slender shell shape with coarser spiral cords.

Description. The whitish translucent, elongate shell has seven convex whorls with a weakly wavy suture. The shell surface sculptured by 5–6 spiral cords crossed by very

fine axial ribs. The oval ear-shaped aperture has a weak posterior canal and extends slightly beyond the shell periphery outline; the peristome is blunt and reflexed at the columellar side. The lateral edge of the labral lip is weakly sinuated and an axial varix is present parallel to the labral lip. The umbilicus is closed.

Etymology. Named after the famous Slovak speleologist Branislav Šmída, Bratislava, Slovakia, who actively participated in our 2017 biospeleology survey of Laos.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as in the related source of Nam Dôn River.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.

Remark. The shell morphology of *T. smidai* sp. n. is an intermediate between that of *T. moureti* sp. n. and *T. vacquiei* sp. n.

Genus *Tricula* Benson, 1843

Nore. Based on their shell morphology the species described below are provisionally placed in the genus *Tricula* until anatomical and molecular data can be obtained.

Tricula valenasi sp. n.

<http://zoobank.org/D6866F52-BB80-40F1-8B16-8F79C53CEAC0>

Figs 23–24

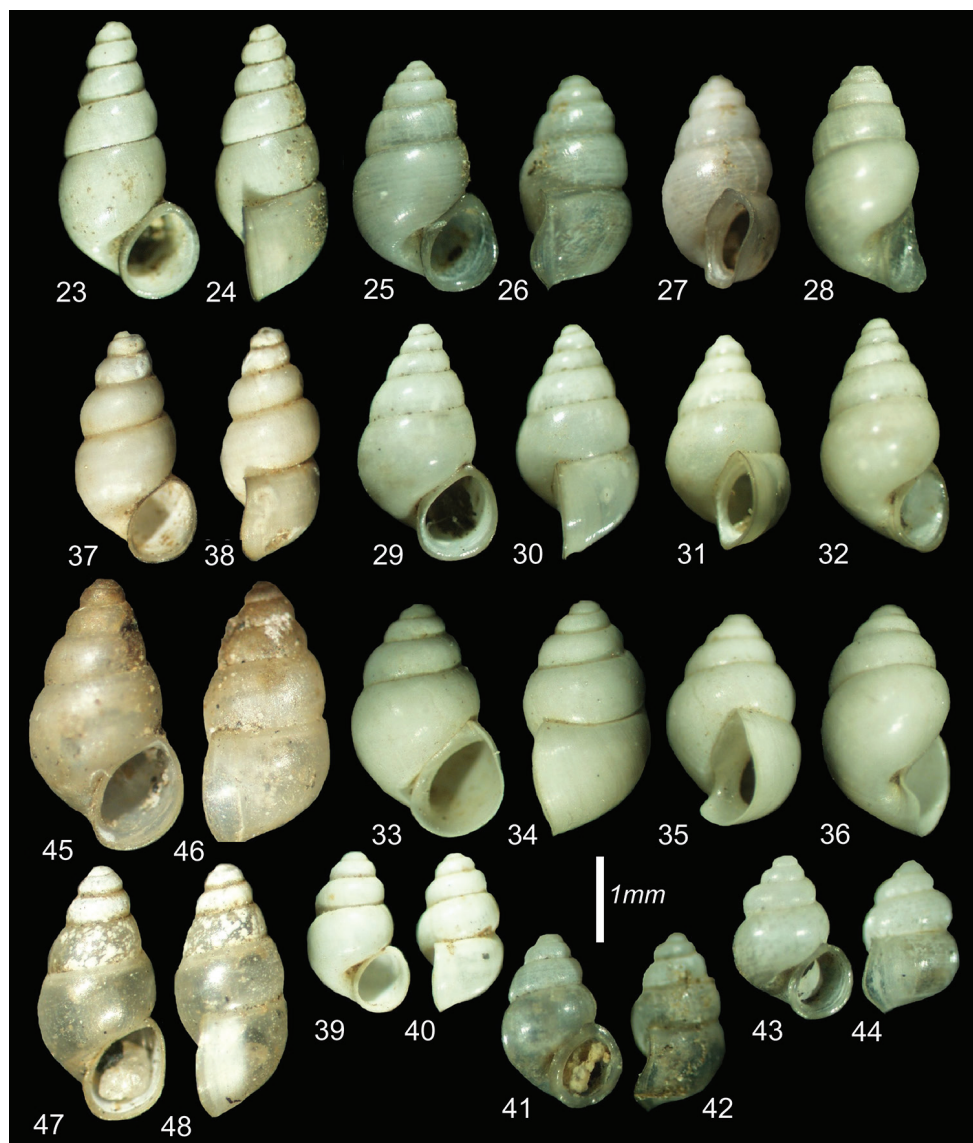
Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments at cave river banks (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšavský leg. 11–12 February 2017 (NHMUK 20180008). Paratypes: type locality (coll. Grego F0877 – 3 specimens).

Measurements. Holotype: H 3.25 mm; W 1.65 mm; BW 1.05 mm; BH 1.25 mm; AH 1.15 mm; AW 0.95 mm; H/W 1.97; AH/AW 1.2; W/BW 1.57; H/BH 2.60; H/AH 2.83; W/AW 1.74.

Diagnosis. *Tricula valenasi* sp. n. is similar to syntopic *T. lenahani* sp. n., from which it differs by its elongate shell with a less open umbilicus and an aperture more prominent at the shell periphery outline. It differs significantly from syntopic *T. davisi* sp. n. by its longer, more elongated shell shape, its more inflated whorls and its proportionally smaller aperture with a straight columellar margin rather than the columellar sinuation characteristic of *T. davisi* sp. n. From *T. bollingi* Davis, 1968 it differs by the aperture shape, which extends beyond the shell periphery outline and by its more open umbilicus and more blunt apex. It can be distinguished from *T. burchi* Davis, 1968, by its more slender and more conical shape with a smaller aperture, a more prominent umbilicus and a less blunt apex.

Description. The whitish shell has five rounded convex whorls with a semi-deep suture and a blunt apex. The surface is smooth and shiny. The shell is narrow-coni-



Figures 23–48. Representatives of the genus *Tricula*, Benson, 1843. **23–24** *Tricula valenasi* sp. n. (holotype NHMUK 20180008) **25–28** *T. lenahani* sp. n. (holotype NHMUK 201800010) **29–32** *T. spelaea* sp. n. (holotype NHMUK 20180011) **33–36** *T. davisi* sp. n. (holotype NHMUK 20180009) **37–38** *T. reischuetzorum* sp. n. (holotype NHMUK 20180012) **39–42** *T. phasoungensis* sp. n. (**39–40** holotype NHMUK 20180013 **41–42** paratype 2 coll. Grego F0881) **43–44** *T. bannaensis* sp. n. (holotype NHMUK 20180014) **45–48** *T. viengthongensis* sp. n. (**45–46** holotype NHMUK 20180015 **47–48** paratype 1 coll. Grego F0904).

cal with prominent body whorl. Umbilicus is tiny opened. In frontal view, the outer part of the aperture protrudes from the shell periphery outline. Aperture is ovoid ear-shaped, separated from the body whorl by a very weak furrow and an adapical gap. The

peristome margin is blunt, slightly reflexed outwards. The outer lip is slightly callous and has a straight lateral profile.

Etymology. Named after my friend Liviu Valenas (Nuremberg, Germany), an avid speleologist born in Romania, who spent 10 years exploring the cave system Pha Soung, which, with its currently documented 20.4 km, is the third largest cave system in Laos.

Distribution. Only known from the type locality.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.

***Tricula lenahani* sp. n.**

<http://zoobank.org/3FE20728-0E33-4D26-B964-0E38B9C93F06>

Figs 25–28

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments of cave river banks (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 201800010). Paratypes: type locality (NHMUK 20180021 – 5 specimens; HNHM 102774 – 5 specimens; OSUM 42391 – 5 specimens; coll. Grego F0879 – 103 specimens); Laos, Khammouane Province, Tham Nam Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., temporary side rivulet sediment at entrance passage 1.5 km from the main entrance, dry sand on the cave floor; J. Grego leg. 11 February 2017 (coll. Grego F0868 – 1 specimen); Laos, Khammouane Province, 3 km NW of Ban Na Village, sand on the bottom of Nam Dôn River source at 149 m a.s.l.; J. Grego leg. 07 February 2017. 17°33.20'N; 104°52.38'E (coll. Grego – 6 specimens) (Fig. 2A).

Measurements. Holotype: H 2.72 mm; W 1.71 mm; BW 0.96 mm; BH 1.70 mm; AH 1.15 mm; AW 0.93 mm; H/W 1.59; AH/AW 1.24; W/BW 1.78; H/BH 1.60 H/AH 2.37; W/AW 1.84.

Diagnosis. This species is similar to the syntopic *Tricula valenasi* sp. n., but differs from it by its more robust, shorter shell with a more open umbilicus as well as by its sinuated labral margin profile. It differs from syntopic *T. spelaea* sp. n. by its more inflated shell shape, and a different arrangement of the whorls, a larger umbilicus and a different shape of the aperture. It can be distinguished from syntopic *T. davisi* sp. n. by its more slender, less inflated shell and the shape of the columellar peristome. From *T. bollingi* Davis, 1968 it differs by its general shell shape and the position of the aperture, and by its more open umbilicus and blunter apex.

Description. The whitish, semi-translucent shell has five convex whorls with a deep suture. The surface is smooth with fine, whitish, inconsistent axial bands. The shell is ovate-conical with whorls smoothly tapering towards the apex. The aperture is ear-shaped; the peristome expands outwards especially at the columellar side. The lateral edge of the labral lip is characteristically sinuated, as well a weak sinuation is pre-

sent at apical inner peristome. The umbilicus is open, partly obscured by the reflected columellar margin.

Etymology. This species is named after my ever helpful friend Peter Lenahan, an avid caver from New York City, USA, for his great support during the field trip and for his indispensable help to Ban Na village by supporting construction of a new well and tap water supply for the villagers.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as in the related source of Nam Dôn River.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n..

***Tricula davisi* sp. n.**

<http://zoobank.org/0BB6C9B6-08D5-411A-BCC8-9818E0BCF4EC>

Figs 29–32

Type locality. Laos; Khammouane Province; Ban Na village 20 km NNE of Thakhek; Tham Khon Dôn Cave, 161 m a.s.l.; 17°33.82'N; 104°52.30'E; Earthquake Dome 3 km from the south entrance, sand sediments at cave river banks (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180009). Paratypes: type locality (NHMUK 20180022 – 3 specimens; HNHM 102775 – 3 specimens; OSUM 42387 – 3 specimens; coll. Grego F0878 – 76 specimens); Laos, Khammouane Province, 3 km NW of Ban Na Village, sand on the bottom of Nam Dôn River source at 149 m a.s.l.; J. Grego leg. 07 February 2017, 17°33.20'N; 104°52.38'E (coll. Grego F0858 – 6 specimens) (Fig. 2A).

Measurements. Holotype: H 2.72 mm; W 1.81 mm; BW 1.23 mm; BH 1.88 mm; AH 1.5 mm; AW 1.05 mm; H/W 1.50; AH/AW 1.29; W/BW 1.47; H/BH 1.45; H/AH 2.01; W/AW 1.72.

Diagnosis. This new species is similar to syntopic *Tricula lenahani* sp. n., from which it differs by its more oval, inflated shell with more inflated whorls, a closed umbilicus and the shape of the aperture. The aperture of *T. davisi* sp. n. has a characteristic sinuation at the columellar peristome and a straight labral peristome, distinguishing it from *T. lenahani* sp. n., which has a sinuated labral peristome and a different columellar peristome, as well from the syntopic *T. spelaea* sp. n., the peristome of which lacks significant sinuation on both sides. From *T. bollingi* Davis, 1968 and *T. burchi* Davis, 1968 it differs by its shell and aperture shapes.

Description. The shell is rounded oval-conical with four slightly inflated whorls with elevated spire and a deeper suture. The surface is milky whitish and smooth with faint growth lines. The aperture is oval ear-shaped, the peristome slightly callous attached to the body whorl and expanding only towards the columella. The labral lip lateral profile is straight, while a characteristic deep sinuation is present at the apical inner lip. The last whorl is broadening towards the aperture and from lateral view is curved upward. The umbilicus is closed.

Etymology. Named after George M. Davis, (Washington D.C., USA) who contributed much to the molecular phylogeny and taxonomy of the Mekong River Pomatiopsidae.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as from the related source of Nam Dôn River.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.

***Tricula spelaea* sp. n.**

<http://zoobank.org/2665A01E-E4EA-4D7E-BEC2-A91FFF12085C>

Figs 33–36

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments on cave river bank (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180011). Paratypes: type locality (Grego F0880 – 3 specimens); Laos, Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Pha Soung Cave, 17°33.052'N; 104°52.410'E, 155 m a.s.l., sandy sediment on the bottom of Frog Lake at central part of the cave (coll. Grego F0886 – 2 specimens).

Measurements. Holotype: H 2.80 mm; W 1.65 mm; BW 1.05 mm; BH 1.80 mm; AH 1.10 mm; AW 0.95 mm; H/W 1.70; AH/AW 1.16; W/BW 1.57; H/BH 1.56; H/AH 2.55; W/AW 1.74.

Diagnosis. This new species is similar to syntopic *Tricula lenahani* sp. n., from which it differs by its more conical shell with less inflated whorls, a closed umbilicus and the different shape of the aperture. It differs significantly from syntopic *T. valenasi* sp. n. by its shorter, more inflated shell shape, more flattened whorls, straight lateral labral profile and closed umbilicus. From the *T. bollingi* Davis, 1968 it differs by its shell and aperture shape, position of the aperture and a more blunt apex. From *T. burchi* Davis, 1968, it differs by its more conical shape with a smaller aperture. The labral lateral profile of *T. spelaea* sp. n. is straight, and no sinuation is present on its columellar side.

Description. The shell shape is conical with five somewhat flattened but still convex whorls with a weak suture and blunt apex. The surface is milky whitish and smooth. The aperture is oval tear-shaped; the peristome slightly callous expanding outwards. The labral lip lateral profile is straight, and no sinuation is present at the apical inner lip. The umbilicus is closed.

Etymology. Named after its type locality inside the Cave Tham Khon Dôn in Khammouane.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well from the related source of Nam Dôn River.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.

***Tricula reischuetzorum* sp. n.**

<http://zoobank.org/A23FADBE-1D6C-42A8-876D-0D0AFCB313B8>

Figs 37–38

Type locality. Laos; Khammouane Province, Cave Tham Na Li 8 km E of Thakhek on road AH131, bottom of cave river Nam Xiangliap, 17°27.20'N; 104°54.54'E.

Type material. Holotype: type locality: J. Grego leg. 16 February 2017 (NHMUK 20180012).

Measurements. Holotype: H 2.68 mm; W 1.29 mm; BW 0.86 mm; BH 1.61 mm; AH 0.93 mm; AW 0.79 mm; H/W 2.08; AH/AW 1.18; W/BW 1.50; H/BH 1.66; H/AH 2.88; W/AW 1.63.

Diagnosis. The shell is similar to that of *Tricula valenasi* sp. n. (Tham Khon Dôn Cave), from which it differs by being smaller, less elongate and with more inflated whorls, a more closed umbilicus and a more elongated aperture situated more towards the columella. It differs significantly from *T. lenahani* sp. n. (Tham Khon Dôn Cave) by its overall shell shape, the position of aperture and the closed umbilicus. From *T. bollingi* and *T. burchi* it differs by general shell and aperture shape and the position of the aperture.

Description. The milky white, narrow oval-conical shell with four convex whorls and deep suture has a blunt apex. The shell surface is smooth and shiny. The shell is narrow-conical. Aperture is ovoid elongated and its lower part slightly angled towards the columella. The aperture is attached to the body whorl by a weak furrow. The peristome margin is sharp, somewhat darker stained. The outer lip is slightly sinuated laterally. Umbilicus is closed.

Etymology. Named after active researchers of the Balkan stygobiont gastropod fauna, Peter L. and Alexander Reischütz (Horn, Austria), who brought our attention to the Na Li cave.

Distribution. Only known from the type locality.

Ecology. The shells were found in the sandy sediment inside the cave Tham Na Li close to the river outlet. The about 300m long cave passage was formed by the river Nam Xiangliap under the limestone hill, and thus the cave habitat has a direct contact with surface waters.

***Tricula phasoungensis* sp. n.**

<http://zoobank.org/FD3FC3E5-702E-4796-A928-9064C91A5E52>

Figs 39–42

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Pha Soung Cave, 33.052°N; 104°52.410'E, 155 m a.s.l., sandy sediment on the bottom of Frog Lake at central part of the cave (Fig. 2F).

Type material. Holotype: type locality: J. Grego leg. 09 February 2017 (NHMUK 20180013).

Paratypes: type locality (Grego F0887 – 1 specimen); Laos, Khammouane Province; Ban Na village 20 km NNE of Thakhek; Tham Khon Dôn Cave, 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the S entrance, sand sedi-

ments on cave river banks (NHMUK 20180023 – 3 specimens; HNHM 102776 – 3 specimens; OSUM 42388 – 3 specimens; coll. Grego F0881 – 60 specimens).

Measurements. Holotype: H 1.91 mm; W 1.20 mm; BW 0.70 mm; BH 1.25 mm; AH 0.82 mm; AW 0.65 mm; H/W 1.59; AH/AW 1.26; W/BW 1.71; H/BH 1.53; H/AH 2.33; W/AW 1.85; Paratype 2: H 2.05 mm; W 1.43 mm; BH 0.75 mm; BW 1.35 mm; AH 1.06 mm; AW 0.84 mm; H/W 1.43; AH/AW 1.26; W/BW 1.91; H/BH 1.52; H/AH 1.93; W/AW 1.70.

Diagnosis. With its small hydrobioid shell it is similar to *T. bannaensis* sp. n., but differs from it by its more slender shell, its less inflated whorls, its more closed umbilicus and the shape of the aperture. The similar but larger *T. lenahani* sp. n. differs by having less inflated whorls, different shell and aperture shapes and a narrower umbilicus. *Tricula reischuetzorum* sp. n. has a more elongate shell with more inflated whorls, a smaller umbilicus and a different shape of the aperture.

Description. The milky whitish shell has four convex whorls with a deep suture and a smooth, shiny surface. The bythinelloid-shaped shell is oval sub-conical with a blunt apex. The aperture is oval; the peristome is slightly callused and outwardly expanded and connected to the body whorl. The lateral edge of the labral lip is very slightly sinuated. The umbilicus is open and conspicuous.

Etymology. Named after the type locality inside the Pha Soung Cave system, which is 20.4 km long and the third longest cave in Laos.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as in the related source of Nam Dôn River.

Ecology. Shells were found in the sandy sediment of a small and shallow “Frog Lake” (Fig. 2F) in the central part of the Pha Soung Cave system. The site is a shallow 20–30 cm deep pond at the lowest part of a cave meander passage, which holds the remains of water after seasonal water crossflow. Green-black streaked frogs *Rana chloranata* (Günther, 1876) washed from the surface inhabit the pond. The Pha Soung cave system (fig. 2E) is 20.4 km long and is situated under the massif of Mount Pha Soung near village Ban Na in SW Khammouane. The cave consists of several floors of old corrosive and phreatic passages developed during the past 11 MY of speleogenesis in the Khammouane limestone of Carboniferous/Permian age. During the rainy season it drains the Ban Na polje towards a closed flat bottom karstic depression in the southern part of the Pha Soung Mountain and then downwards to the Mekong basin. Many of the entrances act not only as sinkholes, but seasonally also as large springs, which indicate a connection to the deep karst phreatic zone also situated under the Ban Na polje.

Tricula bannaensis sp. n.

<http://zoobank.org/C27849D1-8078-44EE-ADB7-BDDF40E06F18>

Figs 43–44

Type locality. Laos; Khammouane Province, Ban Na village 20 km NNE of Thakhek, Tham Khon Dôn Cave, 17°33.82'N; 104°52.30'E, 161 m a.s.l., Earthquake Dome 3 km from the south entrance, sand sediments on cave river banks (Fig. 2B).

Type material. Holotype: type locality: J. Grego and M. Olšovský leg. 11–12 February 2017 (NHMUK 20180014). Paratypes: type locality (NHMUK 20180024 – 5 specimens; HNHM 102777 – 5 specimens; OSUM 42389 – 5 specimens; Grego F0904 – 277 specimens).

Measurements. Holotype: H 1.90 mm; W 1.41 mm; BW 0.75 mm; BH 1.15 mm; AH 0.92 mm; AW 0.76 mm; H/W 1.35; AH/AW 1.21; W/BW 1.88; H/BH 1.65; H/AH 2.07; W/AW 1.86.

Diagnosis. The small hydrobioid shell is similar to that of *T. phasoungensis* sp. n., from which it differs by being more robust and with more inflated whorls, and by its larger umbilicus and larger aperture. *Tricula lenahani* sp. n. has a larger shell with less inflated whorls and a different shape of the aperture.

Description. The whitish, translucent shell has four inflated convex whorls with a deep suture. The shell is inflated ovoid-conical with an oval aperture and slightly outward reflexed margins. Its inner side is attached to the body whorl by a marginal callus. The labral lip is typically sinuated at its lateral profile. The umbilicus is open and conspicuous.

Etymology. Named after the village Ban Na, where the team enjoyed the hospitality of villagers in our base camp in the local Buddhist temple.

Distribution. Only known from the type locality and nearby sites in Tham Khon Dôn Cave as well as in the related source of Nam Dôn River.

Ecology. The same as *Pseudoiglica pseudoiglica* sp. n.

Tricula viengthongensis sp. n.

<http://zoobank.org/4169E1A2-FE23-470A-9B52-D00F67AED790>

Figs 45–48

Type locality. Laos; Bolikhamsay Province, 16 km West of Vieng Thong, 500 m North of the road from Vieng Thong to Ban Samsok Noy (and Sôp Sang), unnamed cave with entrance above large karst spring with travertine cascades (Fig. 2D), 18°34.080'N; 104°31.79'E, sand sediments on the bottom of cave rivulet.

Type material. Holotype: type locality: J. Grego and B. Šmída leg. 19 February 2017 (NHMUK 20180015) Paratypes: , type locality (coll. Grego F0904 – 3 specimens).

Measurements. Holotype: H 2.64mm; W 1.64mm; BW 0.93mm; BH 1.71mm; AH 1.14mm; AW 1.00mm; H/W 1.6; AH/AW 1.14; W/BW 1.76; H/BH 1.54; H/AH 2.32; W/AW 1.64.

Diagnosis. The small conical shell is similar to that of *T. valenasi* sp. n. (Khammouane Province) from which it differs by its smaller size and its more blunt apex. From *T. lenahani* sp. n. (Khammouane Province) it differs by having a smaller shell with a weaker suture and a closed umbilicus. *Tricula phasoungensis* sp. n. and *T. bannaensis* sp. n. have a more robust and rounded shell with more convex whorls and an open umbilicus.

Description. The shell of *Tricula viengthongensis* sp. n. is whitish, semi-translucent with four slightly flattened convex whorls and a weak suture. The shape of the shell

is conical with a blunt apex and an oval ear shaped aperture. The marginal lips with a slight callosity are not reflexed and laterally have a straight profile without any sinuation. The umbilicus is closed.

Etymology. Named after the city of Vieng Thong (Bolikhamsay Province), the larger settlement closest to the type locality.

Distribution. Only known from the type locality.

Ecology. The unnamed cave is situated immediately above a large karstic spring with travertine cascades (fig. 2D), and drains a limestone ridge NW of the main water outlet. The cave entrance is a 15m vertical abyss continuing upstream the underground river to a siphon lake. The total length is approximately 400 m with several parallel draining passages. The specimens were collected from sandy sediment at the bottom of a cave stream about 40 m upstream from the entrance.

Discussion

The present study indicates that the underground freshwater gastropod species are more widely distributed in the Southeast Asian habitats than was hitherto supposed. The wide diversity of karstic and cave habitats in the region (Culver 2012) together with the extraordinary high diversity of the surface and troglobiont gastropod species (Culver 2012) indirectly predicted rich stygobiont malacocenoses. We believe the habitat preferences and the factors driving their diversity are the same as we assumed for the stygobiont habitats of the Balkans (Grego et al. 2017) and subsequent SE Asian studies could prove their presence also in the local non-karstic springs, wells and adjacent groundwater systems. Additionally, the natural history of the area had not been influenced by the dramatic climate changes over the Late Cenozoic and Holocene and this may have facilitated uninterrupted diversification through evolutionary adaptation towards a very rich subterranean diversity.

The shell shape evolutionary convergence between the studied SE Asian species and stygobiont species from other parts of the world is remarkable. This indirectly confirms our theory (Grego et al. 2017), that the slender elongated shape could be evolved in the species preferably inhabiting habitats with permanently higher water velocity within the small caverns of gravel and cracklings. The shell shape of *Iglica* Wagner, 1910, *Pseudoiglica* gen. n. and *Thamkhondonia* gen. n. species provides lower frontal hydrodynamic resistance by turning the shell in the flow direction avoiding the shear stress caused by turbulences and thus preventing dislodging from the substrate. Gastropods with globose shell would have a problem to stay attached at high water velocity as also the adaptive evolution of gastropod mucus adhesion to the substrate has some limitations. Small species living interstitially among smaller gravel or sand have still elongated but proportionally shorter shells (*Paladilhiopsis* Pavlović, 1913, *Thamkhondonia smidai* sp. n., *Tricula reischuetzorum* sp. n.) to enable movement under the limitation by the smaller space. The species adapted to calmer waters within larger cavi-

ties such as cave lakes tend to have more globose shapes (*Dabriana* Radoman, 1974, *Horatia* Bourguignat, 1887, *Pontohoratia* Vinarsky et al., 2014, *Motsametia* Vinarsky et al., 2014, *Tricula* Benson, 1843). The species living in habitats with alternating water velocities (calm waters with frequent occasional floods and temporary very high water velocity) have developed their survival strategy by the globose, but more robust shell shape with more thick shell walls, additionally with broadening apertures (sometimes up to a limpet like shape). The expanded aperture has frequently folds and reflexions along the margin to help attachment of the animal on the rocky substrate during the interim periods with high water velocity. (*Plagigeyria* Tomlin, 1930, *Tricula davisi* sp. n., *Tricula lenahani* sp. n., *Pseudotricula eberhardi* Ponder, 1992)

As in the other well-known hotspots of stygobiont gastropod biodiversity (Pyrenees, Dinarides) (Darwall et al. 2014) the hidden, hardly accessible subterranean habitats only seldom allow researchers to obtain live specimens for anatomical and molecular studies (Glöer and Grego 2015). This hidden habitat was the main reason why the underground species had been overlooked for such a long time.

However, Laos as well as other SE Asian countries are facing the same ecological threats as most tropical countries worldwide: deforestation, drought, erosion and environmental pollution, together with artificial dam construction, which floods valleys and basins with stagnant water. These negative anthropogenic influences could negatively impact the more stable underground aquatic habitats and all of the sensitive stygobiont/troglobiont species could rapidly vanish prior to the scientists having a chance to fully understand their biology and role in the subterranean ecosystem.

Conclusions

This study confirmed the presence of underground freshwater gastropod species in Laos. Species inhabiting similar habitats were mainly known only from North and South America, North Africa, Europe and the Balkans through Turkey and the Caucasus to Central Asia (Bole and Velkovrh 1986, Kabat and Hershler 1993). The localities from Laos are situated between the single so far known locality in Sri Lanka (wells in the village of Pokonwita, south of Horana) and the few localities hitherto known throughout the Japanese Archipelago (Mori 1938; Kuroda and Habe 1957; Habe 1965; Kuroda 1963; Matsumoto 1976; Bole and Velkovrh 1986). The new finds partly fill the zoogeographical gap and also suggest their probable presence in a much wider area than hitherto supposed: from Naga Hills and Arunachal-Pradesh in India through Myanmar, Thailand, Laos and Vietnam to South China (Yunnan and Guangxi) and likely northward to the central and east mainland of China and Korea. I hope this study will encourage all people involved in local biospeleological investigation throughout SE Asia to focus more towards the so far underestimated diversity of subterranean Mollusca and thus gather more knowledge about their biology, anatomy and phylogeny in the near future.

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