

## First record of the microsnail genus *Clostophis* Benson, 1860 (Eupulmonata: Pupilloidea) from Cambodia, with description of a new species

CHIRASAK SUTCHARIT<sup>1</sup>, SOTHEAREN THI<sup>2</sup>, NASAK CHANTHA<sup>2</sup>, PHYROUM CHOURN<sup>2</sup>, CHHIN SOPHEA<sup>3</sup>,  
EKGACHAI JERATHITIKUL<sup>4</sup>, ARTHIT PHOLYOTHA<sup>1</sup>, WARUT SIRIWUT<sup>4</sup>, RUTTAPON SRISONCHAI<sup>5</sup> & SOMSAK PANHA<sup>1,6</sup>

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

2 *Fauna & Flora Cambodia Programme, 19 Street 360, Phnom Penh, Cambodia*

3 *Department of Biodiversity, General Directorate of Policy and Strategy, Ministry of Environment, Phnom Penh, Cambodia*

4 *Animal Systematics and Molecular Ecology Laboratory, Department of Biology, Faculty of Science, Mahidol University, Bangkok 10400, Thailand*

5 *Department of Biology, Faculty of Science, Khon Kaen University, Khon Kaen 40002, Thailand*

6 *Academy of Science, The Royal Society of Thailand, Bangkok 10300, Thailand*

Corresponding author: Somsak Panha ([somsak.pan@chula.ac.th](mailto:somsak.pan@chula.ac.th))

**Abstract.** Specimens of a new species of hypselostomatid microsnail, *Clostophis udayaditinus* Sutcharit & Panha, n. sp., were collected from the limestone hills area in Battambang Province, western Cambodia. Besides being a species new to science, this discovery represents a new country record for the genus. The new species differs from all other congeners by its concave-conical shell, with apertural dentition four in number, and hooked parietal and columellar lamellae. Living snails were found crawling on the walls in a cave, and the snails have a colourless, semitransparent soft body.

**Key words.** Angkor Kingdom, endemic species, limestone, pulmonates, taxonomy

**ZooBank identifier.** urn:lsid:zoobank.org:pub:4625ED08-AECA-4E8B-863C-A96EE085898C

**DOI.** <https://doi.org/10.61733/jconch/4538>

### INTRODUCTION

*Clostophis* Benson, 1860 is a genus of pulmonate microsnails characterised by small (usually <2 mm) colourless shells with prominent spiral striations and possessing no dentition or several apertural lamellae/plicae. The genus was recently transferred from the diplommatinids to the stylommatophoran Hypselostomatidae Zilch, 1959 (Páll-Gergely *et al.* 2020). Shortly thereafter, Páll-Gergely & Hunyadi (2022) revised 19 species, providing a collocation of the type and authenticated specimens, together with detailed illustrations of shell sculpture and apertural dentition. This fine piece of revisionary work has become a very useful reference for subsequent scholars. Among the recognised species are four species from Peninsular Malaysia and Thailand, two species from Myanmar, three species from Laos, seven species from Vietnam, and three species from Guangxi Province of China (Benson 1860; Collinge 1902; van Benthem

Jutting 1961; Panha & Burch 2002; Páll-Gergely *et al.* 2015, 2020; Páll-Gergely & Hunyadi 2022).

The terrestrial malacofauna of the limestone karst areas in Cambodia have recently been studied, and 13 species belonging to five hypselostomatid genera, *Acinolaemus* Thompson & Upatham, 1997, *Anauchen* Pilsbry, 1917, *Aulacospira* von Möllendorff, 1890, *Gyliotrachela* Tomlin, 1930 and *Hypselostoma* Benson, 1856, have been reported (Vermeulen *et al.* 2007, 2019; Sutcharit *et al.* 2020, 2023), but unreported from Cambodia was the genus *Clostophis*. Our recent land-snail survey explored the Sisophon-Battambang limestone hills in western Cambodia, one of three limestone hill areas in the country. This area is densely covered by deciduous vegetation, and due to weathering of the steep mountain slopes, the habitat includes vertical cliffs and caves (Day & Urich 2000; Mouret 2004; Laumanns 2009; Kiernan 2010; Sophady *et al.* 2016). These unique topographies and diverse landscapes are favourable for a high

diversity of habitat-specialist plants and animals (Schilthuizen *et al.* 2005; Clements *et al.* 2006, 2008; Nicolas *et al.* 2012), especially hypselostomatid microsnails which are highly restricted to limestone and which we collected during our survey. When comparing our specimens with all known hypselostomatid species, they clearly differ in their shell form, sculpture, and apertural dentition. In the present paper, we report the first record of the genus *Clostophis* and a new species based on shell morphology. Living snails are reported and described for the first time.

## MATERIALS AND METHODS

The field survey was conducted in July–August 2024 under the auspices of the Biodiversity Conservation to Mitigate the risks of emerging infectious diseases (BCOMING) project of the Terrestrial Conservation Programme, Fauna & Flora of Cambodia. Snails were hand-collected from a limestone wall in the Sisophon-Battambang limestone hills area. Living specimens were photographed and euthanised by the two-step method (AVMA 2020) before preservation; this protocol was approved by Chulalongkorn University Animal Care and Use Committee (CU-ACUC-1723018). Shell specimens were first soaked in a Petri dish with water and detergent and were then physically brushed and cleaned of mud and dirt using fine paintbrushes. The cleaned shells were air-dried and examined under an Olympus SZX7 stereomicroscope. For morphological descriptions, representative shells were carefully examined and imaged using a Leica M205C microscope with a fusion optics stereomicroscope and the Leica Application Suite Image System. Additional specimens were photographed under a scanning electron microscope (SEM; JEOL, JSM-6610 LV). Specimens were identified based on Páll-Gergely *et al.* (2020) and by comparison with the illustrations of the type materials in Páll-Gergely and Hunyadi (2022).

The number of shell whorls was counted to the nearest quarter (Kerney & Cameron 1979). Measurements of shell height and width were made from images taken by Leica M205C, Leica DMC5400, Digital Camera, and LAS X software. The terminology used to describe the apertural dentition follows Pilsbry (1918, 1948), Páll-Gergely & White (2023), Páll-Gergely *et al.* (2020, 2023), Páll-Gergely & Hunyadi (2022), and Sutcharit *et al.* (2023).

**Institutional abbreviation.** CUMZ, Chulalongkorn University Museum of Zoology, Bangkok, Thailand.

**Authorship of the new name.** Description of this new species has been attributed to the first and last authors. The

complete citation of this new species is *Clostophis udayaditinus* Sutcharit & Panha in Sutcharit *et al.*

## SYSTEMATICS

### Family Hypselostomatidae Zilch, 1959

#### *Clostophis* Benson, 1860

*Clostophis* Benson 1860: 95—Páll-Gergely *et al.* 2020: 351, 352. Páll-Gergely & Hunyadi 2022: 419. Preece *et al.* 2022: 156.

*Montapiculus* Panha & Burch 2002 [1999]: 148 (type species: *Montapiculus proboscidea* Panha & Burch, 2002 [1999])—Panha & Burch 2005: 38, 109. Jirapatrasilp *et al.* 2023: 26, 27.

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

**Remarks.** Until now, the genus *Clostophis* has been known to be widely distributed from Peninsular Malaysia to Myanmar, mainland Indochina, and southern China (Páll-Gergely *et al.* 2020; Páll-Gergely & Hunyadi 2022; MolluscaBase Eds 2024). There are 20 species known from Cambodia, including the new species, described here.

#### *Clostophis udayaditinus* Sutcharit & Panha, n. sp.

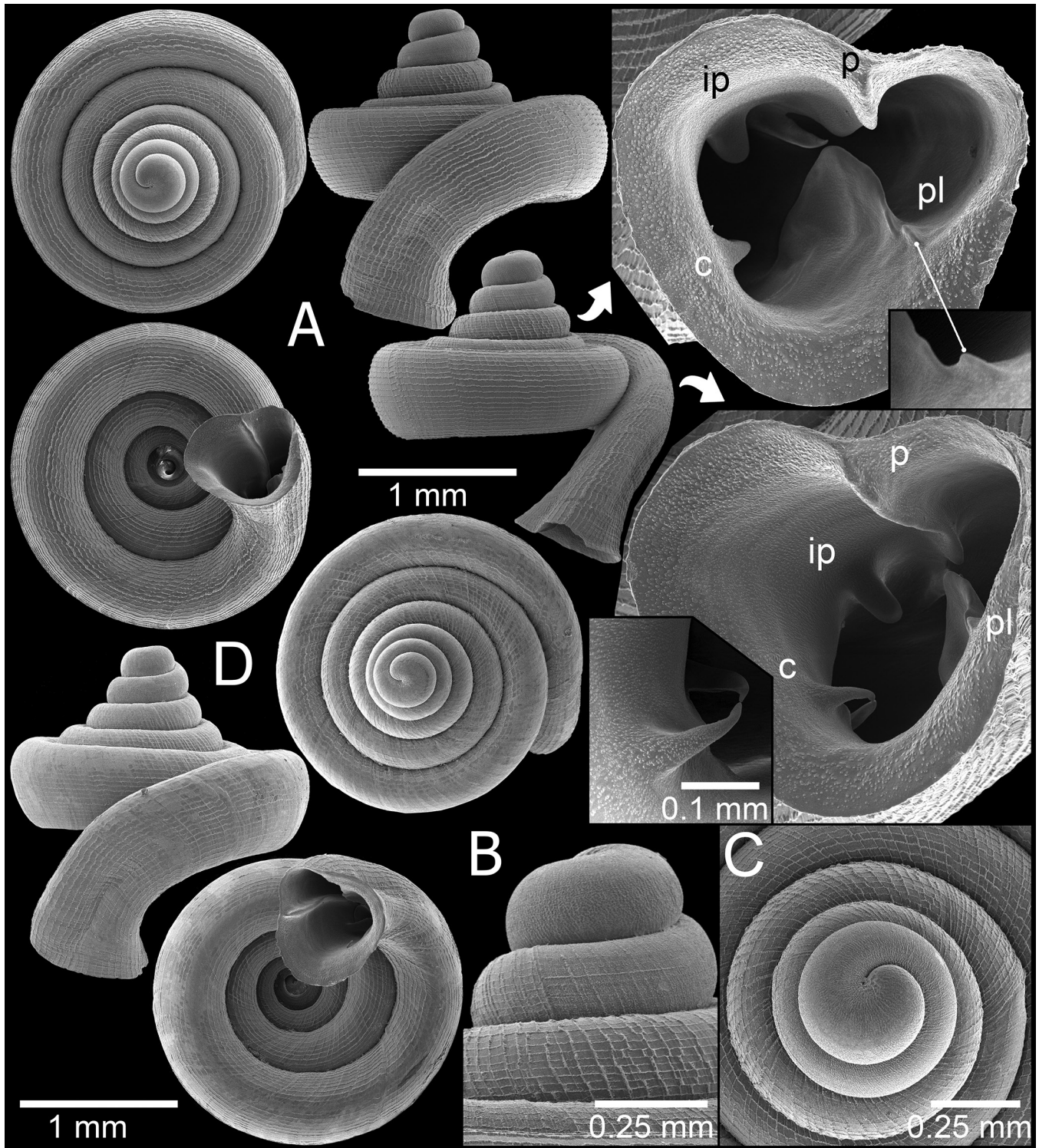
Figures 1, 2

**ZooBank identifier.** urn:lsid:zoobank.org:act:CA5FA502-35FB-42B7-9B0C-4AB9FE662134

**Type material.** Holotype CUMZ 14441 (height including tuba 2.0 mm, width 1.9 mm; Fig. 1A, B) from La Ang Kang Keb Pagoda, Sneung Communes, Banan District, Battambang Province, Cambodia, rock wall of mountain crevices around 100 m from cave entrance, 40 m a.s.l., 12°57'21.4"N 103°05'40.8"E (locality code: CM-102). Paratypes CUMZ 14466 (5 shells; Fig. 1C, 2D), CUMZ 14467 (15 adults + 7 juveniles in ethanol; Fig. 2A–C); all have same data as the holotype.

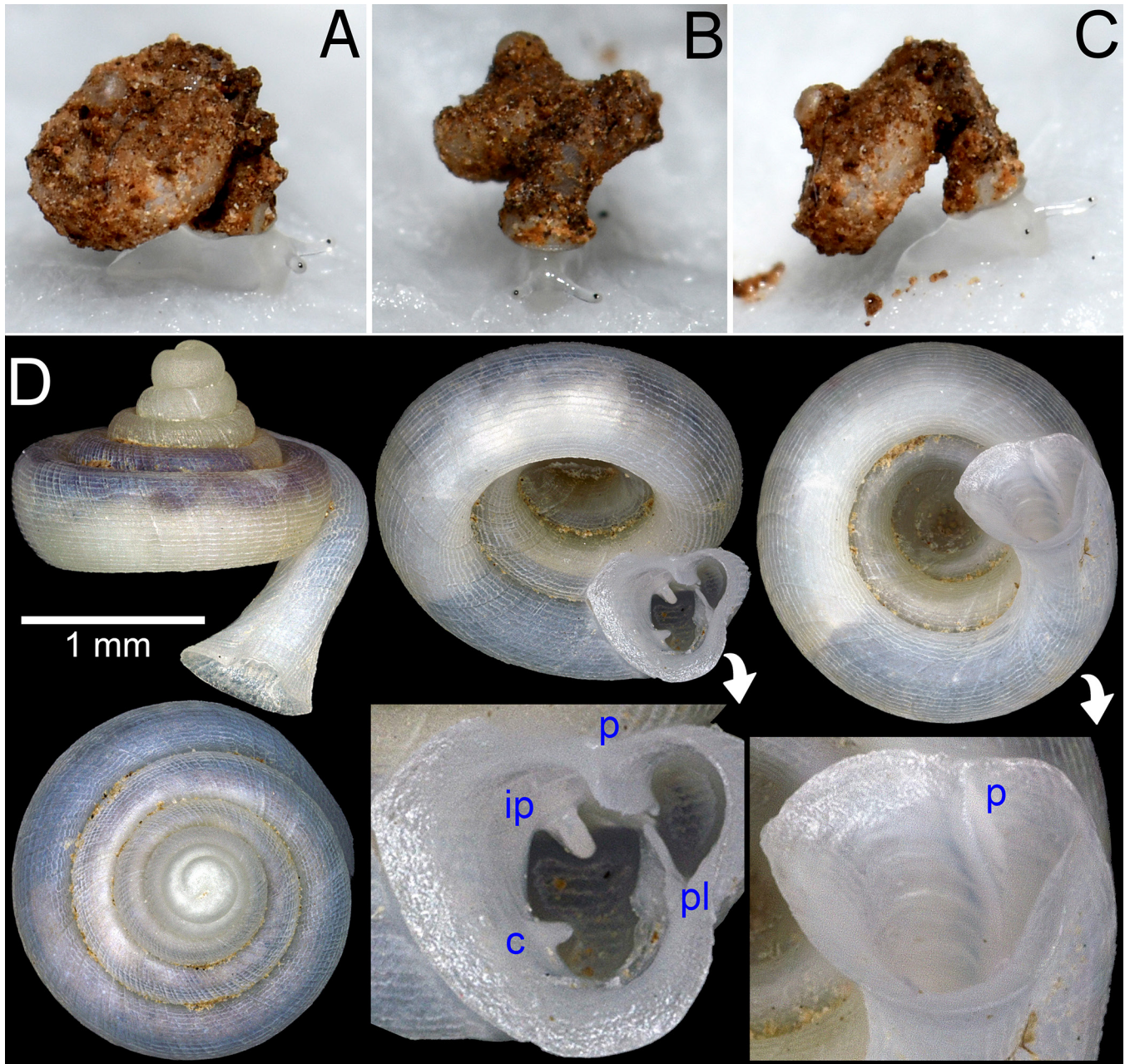
**Diagnosis.** Shell concave-conical, with long, descending tuba and expanded peristome. Apertural dentition four: consisting of one hooked parietal lamella, one small infraparietal lamella, one large, strong palatal plica, and one hooked columellar lamella. Umbilicus wide.

**Description.** Shell concave-conical, pale whitish or colourless; spire conical and growing regularly; last whorl expanded. Shell height, including tuba, 1.9–2.1 mm, and shell width 1.8–1.9 mm. Apex large and rounded; protoconch *c.* 2 whorls and sculptured with thin, pitted spiral striations. Whorls *c.* 5 (excluding tuba), rounded, and convex; suture



**Figure 1.** *Clostophis udayaditinus* n. sp. from Battambang, Cambodia. **A**, holotype CUMZ 14441 with enlarged aperture at different angles, and enlarged columellar lamella and palatal plica, and **B**, **C**, protoconch. **D**, paratype CUMZ 14446 from the type locality. Abbreviations: c = columellar lamella, ip = infraparietal lamella, p = parietal lamella, pl = palatal plica.





**Figure 2.** *Clostophis udayaditinus* n. sp. from the type locality. **A–C**, paratype CUMZ 14466 of living snails crawling on wet tissue paper (three snails at different angles; all shell widths about 1.3 mm). **D**, light microscope image of paratype CUMZ 14467 with enlarged aperture at different angles. Abbreviations: c = columellar lamella, ip = infraparietal lamella, p = parietal lamella, pl = palatal plica.

wide and deep; penultimate whorl sunken. Shell surface with strong, equidistant spiral striae (20–22 on body whorl in frontal view); growth lines somewhat strong and rib-like on earlier whorls, then weak and not prominent on penultimate and last whorls. Last whorl much expanded, with blunt shoulder; tuba long, about  $\frac{1}{4}$  whorl, strongly descending and curving; shallow longitudinal furrows behind apertural lip correspond to palatal plica. Aperture subovate or heart-

shaped, open ventrally to subventrally; peristome slightly thickened, expanded, and surface granulated; prominent depression area present on parietal side corresponding to parietal lamella. Apertural dentition four: parietal lamella divided into two parts: inner part strongly hooked and pointed outside aperture; outer part strong, S-like, curved, blunt, and reaching expanded peristome edge; infraparietal lamella strong, conical, and deep inside aperture; palatal

plica very strong and prominent, pointed in middle, leaning upwards (not perpendicular to palatal wall), very high, and nearly reaching parietal lamella and thus almost enclosing sinulus; a small notch closer to the peristome sometime present; columellar lamella low and divided into two parts: an outer hooked part pointing inside aperture, and an inner hooked part and pointing outside aperture; hooked ends almost merging and resembling a bridge arch. Umbilicus widely opened, occupying c.  $\frac{2}{3}$  of shell width and showing all preceding whorls.

**Etymology.** The species name *udayaditinus* is from “udayadit-”, and the suffix “-inus”, meaning possession or belonging to. This name is a memorial to King Udayadityavarman II, who ruled the Angkor Kingdom around 1100 A.D. He also ordered the building of the Bannan Temple (Higham 2014), which became the name of the hill—the type locality of this new species.

**Distribution and habitat.** The new species is currently known only from the type locality, where we found living snails crawling on wet rock walls in the twilight zone of the cave, about 100 m from the entrance. The cave’s roof is open in the middle, caused by the natural collapse of a large block of limestone. The limestone wall and outcrop near the cave were occupied by individuals of *Gyliotrachela khmeriana* Sutcharit & Panha, 2023 and *G. torticollis* van Benthem Jutting, 1962.

Banan hill is located southeast of Battambang town. The hill is about 7 km long, 2 km wide, and aligned east–west. The hill is at a low elevation, with scattered, exposed limestone rocks, cliffs, and caves. The hill range is covered with low, dry deciduous forest and is surrounded by agricultural areas. The type locality is at the west end of the hill.

**Differential diagnosis.** *Clostophis udayaditinus* n. sp. has a concave-conical shell and a long, descending tuba similar to *C. candidus* Páll-Gergely & Hunyadi, 2022, *C. proboscideus* (Panha & Burch, 2002), *C. sankeyi* Benson, 1860, and *C. yoga* Páll-Gergely & Hunyadi, 2022. It differs from these four species in having the dentition well developed and four in number: one hooked parietal, one infraparietal, one palatal, and one hooked columella. In comparison, *C. candidus* and *C. yoga* from Vietnam lack dentition, and in *C. proboscideus* from Thailand and *C. sankeyi* from Myanmar the dentition consists of one parietal and a weak palatal (Panha & Burch 2002; Páll-Gergely et al. 2020; Páll-Gergely & Hunyadi 2022).

*Clostophis bactrianus* Páll-Gergely & Hunyadi, 2022, *C. lacrima* (Páll-Gergely & Hunyadi, 2015), *C. obliquus* Páll-Gergely & Hunyadi, 2022, and *C. socialis* Páll-Gergely &

Hunyadi, 2022 are similar to the new species in their dentition. While *C. udayaditinus* n. sp. has a strong, hooked parietal lamella and a small infraparietal lamella on the parietal wall, one strong palatal plica, and one small and hooked columellar lamella, lamellae in the other four species are not hooked (Páll-Gergely et al. 2015; Páll-Gergely & Hunyadi 2022). Moreover, *C. bactrianus* from Malaysia has a strong parietal lamella, a strong palatal plica, and weak basal plica and columellar lamella; *C. obliquus* from China has a parietal, two palatals, and a columellar, all very strong and curved. Meanwhile, *C. lacrima* and *C. socialis* from China have a parietal, two palatals, and a basal, all long, as well as palatal and basal plicae which are deeper inside the aperture. In *C. lacrima* the spiral striations are weaker than in the new species.

*Clostophis udayaditinus* n. sp., differs from *Acinolaemus pyramidalis* and *A. rectus* in having a long tuba, the penultimate whorl sunken into the last whorl, a strongly concave-conical shell, an aperture that opens ventrally, and apertural dentition four in number (two parietals, one palatal, and a columellar). In comparison, these two species possess a short tuba, a not sunken (regularly coiled) penultimate whorl, a concave-conical shell, an aperture that opens laterally or sublaterally, and dentition numbering four or five (two on parietal wall, two palatals, and a very inconspicuous columellar sometimes present) (Vermeulen et al. 2007, 2019). In addition, *C. udayaditinus* n. sp. differs from *A. carcharodon* in having a long tuba, conical spire, hooked columellar lamella, and no basal plica, while *A. carcharodon* possesses a short tuba, depressed conical spire, no columellar lamella, and hooked basal plica (Vermeulen et al. 2007).

For further comparison with the new species, *C. laidlawi* (Collinge, 1902) and *C. multiformis* Páll-Gergely & Reischütz, 2020 have a tuba which varies from short to long. The new species differs from these in having a concave-conical shell with a strongly concave side, dentition four in number (one each of parietal, infraparietal, palatal, and columellar), a long, descending tuba, and an aperture that opens ventrally. In comparison, *C. laidlawi* from Malay Peninsula has an elongate-conical shell, apertural dentition five in number (one parietal, one angular, two palatals, and one columellar), a long, slightly descending tuba, and an aperture opening sublaterally. In contrast, *C. multiformis* from Laos possesses a depressed-conical shell, apertural dentition consisting of a weak parietal and/or very weak palatal, a short, slightly descending tuba, and an aperture opening sublaterally (Collinge 1902; van Benthem Jutting 1961; Páll-Gergely et al. 2020; Páll-Gergely & Hunyadi 2022).

**Remarks.** The new species is typical for a stylommato-phoran, with two pairs of tentacles present; the tentacles of the upper pair are long, stout, cylindrical tubes with dark eye spots on their tips (Fig. 2A–C). The lower pair is very short to knob-shaped (rarely seen in live snails), and most visible in preserved snails. The body is colourless to semi-translucent. The snails tend to decorate their shells with soil and dirt in star-shaped patterns. This encrustation presumably serves as a humidity reservoir or camouflage (Allgaier 2007; Yanes et al. 2010, 2011; Páll-Gergely et al. 2022).

## DISCUSSION

We describe *Clostophis udayaditinus* n. sp. from the Sisophon-Battambang limestone hills in Cambodia, and thus expand the distribution of the genus to Cambodia. The conservation status of the new species is of interest. The forest habitat of this karst is likely undisturbed and currently protected by its association with the monastery, but habitat modification caused by development for tourism around the temple is a potentially significant threat to the species. Since *Clostophis* has not been recorded from Cambodia in the literature (Vermeulen et al. 2007, 2019; Sutcharit et al. 2020, 2023), this new find is especially significant. The absence of *Clostophis* in previous surveys in Cambodia might be explained by the small area of the collection site and insufficient surveys. Most land snails known from Cambodia, as in other South-east Asian countries, were much reported during the period of European colonisation; only after the mid-20th century have a few new species been described (Inkhavilay et al. 2019; Sutcharit et al. 2020; Man et al. 2022, 2023, 2024; Tongkerd et al. 2024). So far, three hypselostomatid species from the Kampot limestone hills have been assigned to the *Acinolaemus* Thompson & Upatham, 1997: *A. pyramidalis* (Vermeulen, Phung & Truong, 2007), *A. rectus* Vermeulen, Luu, Keum & Anker, 2019, and *A. carcharodon* Vermeulen, Phung & Truong, 2007. These three species possess shell characters intermediate to *Clostophis*: for example, a colourless shell, prominent spiral striations, and a slightly descending tuba. However, further evidence and more specimens from the Kampot limestone hills are needed to elucidate the relationship between *Clostophis* and *Acinolaemus* species.

## ACKNOWLEDGEMENTS

We thank Uy Vanna (Forestry Administration Battambang Cantonment) and Soeung Somony (Fauna & Flora Cambodia) for their participating and assisting in data collection

during the fieldwork. This work was sanctioned under Ministry of Environment permit number 3988/23 and Battambang Provincial Administration permit number 2810/23, issued on 28 December 2023 and 7 November 2023, respectively. This research was funded by the European Union through the BCOMING project, Horizon Europe Project 101059483. This study was partially supported by the Center of Excellence on Biodiversity, Thailand [BDC-PG2-160012] and the National Research Council of Thailand (grant numbers NRCT-N35E660138 and NRCT-N34E670115). We also thank D.J. Anderson for his initial linguistic help in the original manuscript. We also express our gratitude for the comments from B. Páll-Gergely and an anonymous reviewer, which greatly improved the manuscript.

## REFERENCES

- BENSON WH. 1856. Description of *Tanystoma tubiferum*, a Burmese form related to the genus *Anostoma* of Lamarck. *Annals and Magazine of Natural History, Series 2* **17** (98): 129–131. doi: 10.1080/00222935608697483
- BENSON WH. 1860. On *Clostophis* and *Rhiostoma*, new Burmese genera of land-shells. *Annals and Magazine of Natural History, Series 3* **5** (26): 95–97. doi: 10.1080/00222936008697183
- CLEMENTS R, NG PKL, LU XX, AMBU S, SCHILTHUIZEN M, BRADSHAW CJA. 2008. Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts. *Biological Conservation* **141**: 2751–2764. doi: 10.1016/j.biocon.2008.08.011
- CLEMENTS R, SODHI NS, SCHILTHUIZEN M, NG PKL. 2006. Limestone karsts of Southeast Asia: imperiled arks of biodiversity. *BioScience* **56**: 733–742. doi: 10.1641/0006-3568(2006)56[733:lkosai]2.0.co;2
- COLLINGE WE. 1902. On the non-operculated land- and freshwater molluscs collected by the members of the “Skeat Expedition” in the Malay Peninsula, 1899–1900. *Journal of Malacology* **9**: 71–95. <https://biodiversitylibrary.org/page/28220889>
- DAY MJ, URICH PB. 2000. An assessment of protected karst landscapes in Southeast Asia. *Cave and Karst Science* **27**: 61–70.
- HIGHAM C. 2014. *Early Mainland in Southeast Asia: from First Humans to Angkor*. River Books Press, Bangkok, 477 pp.
- INKHAVILAY K, SUTCHARIT C, BANTAOWONG U, CHANABUN R, SIRIWUT W, SRISONCHAI R, PHOLYOTHA A, JIRAPATRASILP P, PANHA S. 2019. Annotated checklist of the terrestrial molluscs from Laos (Mollusca, Gastropoda). *ZooKeys* **834**: 1–166. doi: 10.3897/zookeys.834.28800
- JIRAPATRASILP P, TONGKERD P, SUTCHARIT C. 2023. Somsak Panha and his contribution to Southeast Asian biodiversity research. *Tropical Natural History, Supplement 7*: 1–30.
- KERNEY MP, CAMERON RAD. 1979. *A Field Guide to the Land*



- Snails of Britain and North-West Europe*. Collins, London, 288 pp.
- KIERNAN K. 2010. Environmental degradation in karst areas of Cambodia: a legacy of war? *Land Degradation & Development* **21**: 503–519. doi: 10.1002/ldr.988
- LAUMANN M. 2009. *International Speleological Project to Cambodia 2008 (Battambang Area)*. *Berliner Höhlenkundliche Berichte* 34. Selbstverlag des Speläoclub Berlin, Berlin.
- MAN NS, ABLETT JD, LWIN N, SUTCHARIT C, PANHA S. 2024. Contributions on a small collection of the former Subulinidae Fischer & Crosse, 1877 (Eupulmonata, Achatinoidea) with catalogue of the *Glessula* and *Rishetia* species recorded from Myanmar. *ZooKeys* **1208**: 173–239. doi: 10.3897/zookeys.1208.116083
- MAN NS, LWIN N, SUTCHARIT C, PANHA S. 2023. Further notes on the taxonomy of the land snail family Clausiliidae Gray, 1855 (Stylommatophora, Helicina) from Myanmar with description of two new species. *ZooKeys* **1160**: 1–59. doi: 10.3897/zookeys.1159.98022
- MAN NS, SIRIBOON T, LIN A, SUTCHARIT C, PANHA S. 2022. Revision of the carnivorous land snail family Streptaxidae (Stylommatophora, Achatinina) in Myanmar, with description of four new species. *ZooKeys* **1110**: 39–102. doi: 10.3897/zookeys.1110.85399
- MÖLLENDORFF OF VON. 1890. Die Landschnecken-Fauna der Insel Cebu. *Bericht über die Senckenbergische Naturforschende Gesellschaft* **1890**: 189–292. <https://biodiversitylibrary.org/page/9003882>
- MOLLUSCABASE EDS. (2024). MolluscaBase. Accessed at <https://www.molluscabase.org> on 2024-11-06. doi:10.14284/448
- MOURET C. 2004. Asia, Southeast. Pp. 210–217 in Gunn J (Ed.) *Encyclopedia of Caves and Karst Science*. New York: Fitzroy Dearborn.
- NICOLAS V, HERBRETEAU V, COULOUX A, KEOVICHIT K, DOUANGBOUPHA B, HUGOT JP. 2012. A remarkable case of micro-endemism in *Laonastes aenigmamus* (Diatomyidae, Rodentia) revealed by nuclear and mitochondrial DNA sequence data. *PLoS ONE* **7**: e48145. doi: 10.1371/journal.pone.0048145
- PÁLL-GERGELY B, HUNYADI A. 2022. New and little-known species of *Clostophis* Benson, 1860 from Southeast Asia (Gastropoda: Eupulmonata: Hypselostomatidae). *Raffles Bulletin of Zoology* **70**: 417–439. doi: 10.26107/rbz-2022-0023
- PÁLL-GERGELY B, HUNYADI A, GREGO J, REISCHÜTZ A, BUCZKÓ K, VERMEULEN JJ. 2020. *Clostophis* Benson, 1860, is not a monotypic diplommatinid but a speciose hypselostomatid (Gastropoda: Eupulmonata), with descriptions of six new species. *Raffles Bulletin of Zoology* **68**: 350–368. doi: 10.26107/rbz-2020-0052
- PÁLL-GERGELY B, HUNYADI A, JOCHUM A., ASAMI T. 2015. Seven new hypselostomatid species from China, including some of the world's smallest land snails (Gastropoda, Pulmonata, Orthurethra). *ZooKeys* **523**: 31–64. doi: 10.3897/zookeys.523.6114
- PÁLL-GERGELY B, HUNYADI A, VERMEULEN JJ, GREGO J, SUTCHARIT C, REISCHÜTZ A, DUMRONGROJWATTANA P, BOTTA-DUKÁT Z, ÖRSTAN A, FEKETE J, JOCHUM A. 2023. Five times over: 42 new *Angustopila* species highlight Southeast Asia's rich biodiversity (Gastropoda, Stylommatophora, Hypselostomatidae). *ZooKeys* **1147**: 1–177. doi: 10.3897/zookeys.1147.93824
- PÁLL-GERGELY B, JOCHUM A, VERMEULEN JJ, ANKER K, HUNYADI A, ÖRSTAN A, SZABÓ Á, DÁNYI L, SCHILTHUIZEN M. 2022. The world's tiniest land snails from Laos and Vietnam (Gastropoda, Pulmonata, Hypselostomatidae). *Contributions to Zoology* **91**: 62–78. doi: 10.1163/18759866-bja10025
- PÁLL-GERGELY B, WHITE TS. 2023. Solving the mystery of the misunderstood *Bensonella plicidens* (Benson, 1849) (Gastropoda: Stylommatophora: Hypselostomatidae). *Journal of Natural History* **56** (45–48): 2011–2029. doi: 10.1080/00222933.2022.2152750
- PANHA S, BURCH JB. 2002. Two new genera of pupillid land snails from Thailand (Pulmonata: Pupillidae: Gastrocoptinae). *Malacological Review* **32** [1998–1999] (2): 143–153.
- PANHA S, BURCH JB. 2005. An introduction to the microsnailes of Thailand. *Malacological Review* **37/38** [2004–2005]: i–iv, 1–155.
- PILSBRY HA. 1917, 1918. Pupillidae (Gastrocoptinae). *Manual of Conchology. Second Series, Volume 24*. The Academy of Natural Sciences of Philadelphia, Philadelphia. 380 pp. [pp. 1–112, pls 1–13 (1916); pp. 113–256, pls 14–38 (1917); pp. 257–380, pls 39–49 (1918)]. <https://www.biodiversitylibrary.org/page/1295231>
- PILSBRY HA. 1948. *Land Mollusca of North America (north of Mexico)*. Volume II, Part 2. The Academy of Natural Sciences of Philadelphia, Philadelphia, pp. 521–1113.
- PREECE RC, WHITE TS, RAHEEM DC, KETCHUM H, ABLETT J, TAYLOR H, WEBB K, NAGGS F. 2022. William Benson and the origins of the golden age of malacology in British India: Biography, illustrated catalogue and evaluation of his molluscan types. *Tropical Natural History*, Supplement **6**: 1–434.
- SCHILTHUIZEN M, LIEW T-S, BIN ELAHAN B, LACKMAN-ANCRENAZ I. 2005. Effects of karst forest degradation on pulmonate and prosobranch land snail communities in Sabah, Malaysian Borneo. *Conservation Biology* **19**: 949–954. doi: 10.1111/j.1523-1739.2005.00209.x
- SOPHADY H, FORESTIER H, ZEITOUN V, PUAUD S, FRÉRE S, CELIBERTI V, WESTAWAY K, MOURER R, MOURER-CHAUVIRÉ C, THAN H, BILLAULT L, TECH S. 2016. Laang Spean cave (Battambang province): a tale of occupation in Cambodia from the Late Upper Pleistocene to Holocene. *Quaternary International* **416**: 162–176. doi: 10.1016/j.quaint.2015.07.049
- SUTCHARIT C, NGOR PB, PÁLL-GERGELY B, JERATTHITIKUL E, SIRIWUT W, SRISONCHAI R, NG TH, JIRAPATRASILP P, PANHA S. 2023. Notes on the hypselostomatid snails (Gastropoda: Heterobranchia) from limestone hills in Western Cambodia with a new record and a new species. *Journal of*

- Natural History* **57** (25–28): 1287–1303. doi: 10.1080/00222933.2023.2223386
- SUTCHARIT C, THACH P, CHHUOY S, NGOR PB, JERATHITIKUL E, SIRIWUT W, SRISONCHAI R, NG TH, PHOLYOTHA A, JIRAPATRASILP P, PANHA S. 2020. Annotated checklist of the land snail fauna from southern Cambodia (Mollusca, Gastropoda). *ZooKeys* **948**: 1–46. doi: 10.3897/zookeys.948.51671
- THOMPSON FG, UPATHAM S. 1997. Vertiginid land snails from Thailand (Gastropoda, Pulmonata, Pupilloidea). *Bulletin of the Florida Museum of Natural History* **39** (7): 221–245. <http://ufdc.ufl.edu/UF00095785/00001>
- TOMLIN JR. le B. 1930. Some preoccupied generic names.—II. *Proceedings of the Malacological Society of London* **19** (1): 22–24.
- TONGKerd P, LWIN N, PÁLL-GERGELY B, CHANABUN R, PHOLYOTHA A, PRASANKOK P, SEESAMUT T, SIRIWUT W, SRISONCHAI R, SUTCHARIT C, PANHA S. 2024. Contributions of a small collection of terrestrial microsnailed (Pupilloidea, Hypselostomatidae) from Myanmar with description of three new species. *ZooKeys* **1195**: 157–197. doi: 10.3897/zookeys.1195.112112
- VAN BENTHEM JUTTING WSS. 1961. Additional new species and new localities of the family Vertiginidae and the genera *Oophana* and *Opisthostoma* from Malaya. *Bulletin of the Raffles Museum* **26**: 34–48.
- VAN BENTHEM JUTTING WSS. 1962. Coquilles terrestres nouvelles de quelques collines calcaires du Cambodge et du Sud Vietnam. *Journal de Conchyliologie* **102** (1): 3–15.
- VERMEULEN JJ, PHUNG CL, TRUONG QT. 2007. New species of terrestrial molluscs (Caenogastropoda, Pupinidae & Pulmonata: Vertiginidae) of the Hon Chong–Ha Tien limestone hills, Southern Vietnam. *Basteria* **71**: 81–92.
- VERMEULEN JJ, LUU HT, KEUM T, ANKER K. 2019. New species of land snails (Mollusca: Gastropoda: Caenogastropoda and Pulmonata) of the Mekong Delta Limestone Hills (Cambodia, Vietnam). *Folia Malacologica* **27** (1): 7–41. doi: 10.12657/folmal.027.001
- YANES Y, MARTÍN J, DELGAD JD, ALONSO MR, IBÁÑEZ M. 2010. Active disguise in land snails: *Napaeus badius* (Gastropoda, Pulmonata, Enidae) from the Canary Islands. *Journal of Conchology* **40** (2): 143–148.
- YANES Y, MARTÍN J, SANTANA J, HOLYOAK GA, HOLYOAK DT, ARTILES M, DENIZ F, ALONSO MR, IBÁÑEZ M. 2011. Four new *Napaeus* species (Gastropoda: Pulmonata: Enidae) from La Gomera (Canary Islands). *Journal of Conchology* **40** (4): 393–407.
- ZILCH A. 1959. Gastropoda. Teil 2. Euthyneura. In: Schindewolf OH (Ed.) *Handbuch der Paläozoologie, Band 6*. Borntraeger, Berlin. Lfg. 1–2, pp. 1–400.

Manuscript received: 28 January 2025

Revised manuscript accepted: 14 February 2025

Editor: Robert Forsyth