# The first record of an operculate micro land snail from the Alycaeinae (Caenogastropoda, Cyclophoridae) in Cambodia, with description of a new species of *Chamalycaeus* von Möllendorff, 1897

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**ABSTRACT.** This study reports the first record of the operculate micro land snail from the Alycaeinae, *Chamalycaeus aduncus* Jirapatrasilp sp. nov., also the first new species of the genus in Cambodia, based on a recent survey in Battambang. This new species is similar to *Chamalycaeus excisus* (Möllendorff, 1887) and *C. excisus sublimus* Páll-Gergely et Auffenberg, 2019 from the Philippines, in shell size and shape, and the strongly downwards coiling of R3, but differs in having a shorter R2 without any blunt keel, a round aperture without any incision, and a beak- or hook-like basal edge of the outer peristome.

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Первая находка микроскопической наземной улитки подсемейства Alycaeinae (Caenogastropoda, Cyclophoridae) в Камбодже, с описанием нового вида рода *Chamalycaeus* von Möllendorff, 1897

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**РЕЗЮМЕ.** В данном исследовании сообщается о первой находке микроскопической наземной улитки с крышечкой из подсемейства Alycaeinae, *Chamalycaeus aduncus* Jirapatrasilp sp. nov., а также о первом новом виде этого рода в Камбодже, основанном на недавнем исследовании в Баттамбанге. Новый вид похож на *Chamalycaeus excisus* (Möllendorff, 1887) и *C. excisus sublimus* Páll-Gergely et Auffenberg, 2019 с Филиппин по размеру и форме раковины, а также по сильно загнутой вниз R3, но отличается более короткой R2 без притупленного киля, округлым устьем без выемки и основанием наружного перистома в форме клюва или крючка.

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### Introduction

Micro land snails with an adult size not exceeding 5–7 mm, are fascinating land snail groups with an elaborate shell sculpture, apertural barriers and configuration of tuba [Panha, Burch, 2005; Dumrongrojwattana, Wongkamhaeng, 2024]. Micro land snails can be separated into two main groups: (i) one with an operculum in the families Hydrocenidae, Diplommatinidae, and Cyclophoridae, and (ii) another one without an operculum or the pulmonated land snails in several families, but most speciose in the Hypselostomatidae [Panha, Burch, 2005; Páll-Gergely et al., 2023]. In the past few years, a number of new species of both hypselostomatid [Vermeulen et al., 2019b; Sutcharit et al., 2023] and operculated micro land snails have been reported from Cambodia [Vermeulen et al., 2007, 2019a, b; Sutcharit et al., 2020], all of which were from limestone hills in southern Cambodia (Table 1). However, no new species of operculated micro land snails from the subfamily Alycaeinae has yet been reported from Cambodia.

The subfamily Alycaeinae Blanford, 1864 of the Cyclophoridae Gray, 1847 is distinct in having a sutural tube that connects to numerous perpendicular microtunnels and these microtunnels open near the umbilicus [Páll-Gergely et al., 2016, 2024]. Several taxa from this subfamily have been newly discovered and revised from mainland Southeast Asia, e.g., Laos and Vietnam [Páll-Gergely et al., 2017; Do, Nguyen, 2022; Páll-Gergely, 2023], Myanmar and Thailand [Páll-Gergely, Hunyadi, 2018, 2022; Jirapatrasilp et al., 2021; Páll-Gergely et al., 2021], and Peninsular Malaysia [Foon, Liew, 2017]. Currently, this subfamily contains a total of 368 species from eight genera, and its distribution ranges from western India to East Asia, and down to Indonesia in the south [Gittenberger et al., 2024; Páll-Gergely et al., 2024]. In this study, based on a recent survey in Battambang, Cambodia, we report the first record of an operculate micro land snail from the Alycaeinae, Chamalycaeus aduncus Jirapatrasilp sp. nov., which is also the first new species of the genus Chamalycaeus von Möllendorff, 1897 from Cambodia.

### Material and methods

This study is based on material recently collected from Battambang, Cambodia, 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. Empty shells were hand-collected from the forest floor around limestone outcrops. Latitude, longitude, and elevation were obtained with a Garmin GPSMAP 60 CSx. Shells were photographed and measured under light microscopy using a Leica M205C microscope with a fusion optics

stereo microscope and the Leica Application Suite Image System, and by scanning electron microscopy (SEM; JEOL, JSM-6610 LV) at Chulalongkorn University, Thailand. The counting of the shell whorls to the nearest quarter follows Kerney, Cameron [1979]. The nomenclature of external alycaeid shell features and the three-part division of the teleoconch namely R1 (the beginning of the teleoconch to the beginning of the differently ribbed region along the suture), R2 (the differently ribbed area to the constriction), and R3 (the constriction to the peristome) follow Páll-Gergely *et al.* [2017] and Jirapatrasilp *et al.* [2021].

Institutional abbreviations. CUMZ, Chulalong-korn University Museum of Zoology, Bangkok; NHM, The Natural History Museum, London; NHMUK, when citing specimen lots deposited in the NHM; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main.

Other abbreviations. SH, shell height; SW, shell width.

Description of this new species has been attributed to the first author. The complete citation of this new species is *Chamalycaeus aduncus* Jirapatrasilp in Jirapatrasilp *et al*.

### **Taxonomy**

Family Cyclophoridae Gray, 1847 Subfamily Alycaeidae Blanford, 1864 *Chamalycaeus* von Möllendorff, 1897

Alycaeus (Chamalycaeus) von Möllendorff, 1897: 93. Kobelt, von Möllendorff, 1897: 148. Kobelt, 1902: 352. Gude, 1921: 223.

Chamalycaeus (Chamalycaeus) – Thiele, 1929: 107–108. Wenz, 1938: 477–478. Egorov, 2013: 35.

Chamalycaeus – Páll-Gergely et al., 2020: 34–36. Páll-Gergely et al., 2021: 5.

**Type species.** *Alycaeus (Chamalycaeus) fruh-storferi* von Möllendorff, 1897 [Páll-Gergely *et al.*, 2020: fig. 6b] by monotypy.

Remarks: This genus is diagnosed by having a spirally-striated teleoconch, a protoconch without spiral striae, and a wide umbilicus. At present, there is a total of 31 species and two subspecies of *Chamalycaeus* known from the southeastern Himalaya Region, Myanmar, Thailand, down to the Malay Peninsula, Sumatra, Java, Borneo, Sulawesi, including the Philippine Palawan Island [Páll-Gergely *et al.*, 2020, 2021; Vermeulen, Liew, 2022]. See Páll-Gergely *et al.* [2020] for extended diagnosis and taxonomic remarks.

Chamalycaeus aduncus Jirapatrasilp sp. nov. (Figs 1–3)

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Table 1. List of all operculated micro land snail species recorded from Cambodia. References: 1 = Sutcharit *et al.* [2020], 2 = Vermeulen, Aiken [2020], 3 = Foon *et al.* [2017], 4 = Vermeulen *et al.* [2019b], 5 = Vermeulen *et al.* [2007], 6 = Vermeulen *et al.* [2019a], 7 = van Benthem Jutting [1962], and 8 = Dautzenberg, Fischer [1906].

Species	Type locality	Distribution	References
Family Hydrocenidae			
Georissa carinata Sutcharit et Jirapatrasilp, 2020	Phnom Kampong Trach Cave Temple, Kampong Trach District, Kampot Province, Cambodia (10°34'43.06"N, 104°28'17.67"E)	Southern Cambodia and southern Vietnam	1, 2
Georissa monterosatiana Godwin-Austen et Neville, 1879	Perak, Malaysia	Southern Cambodia, southern Thailand and Malaysia	1, 3
Family Cyclophoridae			
Subfamily Cyclophorina	ne		
Speleocyclotus laangensis Vermeulen et al., 2019	Cave with shrine at its entrance, first chamber with collapsed roof, Phnom La'Ang, Kampot area, Kampot Province, Cambodia (10°42'25.84"N, 104°21'09.55"E)	Southern Cambodia	4
Speleocyclotus microcoryphe Vermeulen et al., 2019	Phnom Koun Sat, Banteay Meas area, Kampot Province, Cambodia (10°39'53.01"N, 104°32'16.24"E)	Southern Cambodia and southern Vietnam	4
Subfamily Alycaeinae			
Chamalycaeus aduncus Jirapatrasilp, sp. nov.	Temple in Kantueu Pir (Kantueu Hill), Banan, Battambang, Cambodia (12°54'15.7"N 103°07'13.1"E)	Eastern Cambodia	This study
Family Diplommatinidae			
Diplommatina decapitata Vermeulen et al., 2019	Phnom Chhngauk, Kampot area, Kampot Province, Cambodia (10°38'33.82"N, 104°16'17.42"E)	Southern Cambodia	4
Notharinia attenuata Vermeulen et al., 2007	Nui Chua Hang (= Pagoda Hill), north flank of hill and west end, slopes bordering temple complex, Kien Luong, Kien Giang Province, Vietnam (10°08'22.83"N, 104°38'35.80"E)	Southern Cambodia and southern Vietnam	5, 6
Notharinia brevior Vermeulen et al., 2007	Thach Dong Hill, Ha Tien, Kien Giang Province, Vietnam (10°24'38.33"N, 104°28'29.98"E)	Southern Cambodia and southern Vietnam	5, 6
Notharinia constricta Vermeulen et al., 2019	Phnom Chhngauk, Kampot area, Kampot Province, Cambodia (10°38'33.82"N, 104°16'17.42"E)	Southern Cambodia	6
Notharinia crassilabris Vermeulen et al., 2007	Thach Dong Hill, Ha Tien, Kien Giang Province, Vietnam (10°24'38.33"N, 104°28'29.98"E)	Southern Cambodia and southern Vietnam	5, 6
Notharinia lyostoma Vermeulen et al., 2019	Phnom Kampong Trach, Kampong Trach area, Kampot Province, Cambodia (10°34'43.06"N, 104°28'17.67"E)	Southern Cambodia	6
Notharinia soluta Vermeulen et al., 2019	Phnom Koun Sat, Banteay Meas area, Kampot Province, Cambodia (10°39'53.01"N, 104°32'16.24"E)	Southern Cambodia	6
Notharinia stenobasis Vermeulen et al., 2019	Southeast-end, Phnom La'Ang, Kampot area, Kampot Province, Cambodia (10°42'25.84"N, 104°21'09.55"E)	Southern Cambodia	6
Opisthostoma supinum Benthem Jutting, 1962	Phnom Totong, à 4 km au NO. de Tuk Méas, Cambodia	Southern Cambodia and southern Vietnam	4, 7
Plectostoma lavillei (Dautzenberg et Fischer, 1906) (syn. Plectostoma haplohelix Vermeulen et al., 2019)	Pnom-Roang, Cambodia	Southern Cambodia	4, 6, 8
Plectostoma tonkinianum (Dautzenberg et Fischer, 1906)	Tonkin	Southern Cambodia and southern Vietnam	4, 8

**Type material:** Holotype CUMZ 14461 (Fig. 1), paratypes CUMZ 14462 (25 shells; Fig. 2), NHMUK 20250001 (3 shells) and SMF 380296 (3 shells) from Locality C110, Temple in Kantueu Pir (Kantueu Hill), Banan, Battambang, Cambodia, 12°54'15.7"N, 103°07'13.1"E (Fig. 3), 2 Aug 2024, coll. W. Siriwut, C. Sutcharit.

**Diagnosis:** SH up to 2.0 mm, SW up to 2.7 mm, depressed-conical. Spire ca. 1/4 of shell height. Spiral striation with 11–13 spiral striae at apical view. R1 ca. 1<sup>1</sup>/<sub>4</sub> whorls with regular ribs; R2 ca. 1/5 whorl and nearly as long as R3; R2 with ca. 22 ribs. R3 strongly coils downwards, being highly oblique to the shell's horizontal axis, expanding near the end of the aperture. Aperture round. Inner peristome sharp, protruding. Outer peristome thickened, multilayered expanded; palatal to basal edge expanded, columellar to parietal edge not expanded, basal edge triangular and bending inwards, appearing beak- or hook-like. Umbilicus round.

**Description:** SH up to 2.0 mm, SW up to 2.7 mm, depressed-conical, solid, translucent, yellowish to pale crimson. Shell outline oval in apical view, spire ca. 1/4 of shell height. Whorls ca. 3<sup>3</sup>/<sub>4</sub>–4. Protoconch low, ca. two whorls, glossy, smooth, without spiral striation. Spiral striation starts from R1, continuing to the end of aperture, with 11–13 spiral striae at apical view, spiral striation weaker than radial ribs in R1 and R2. R1 ca. 11/4 whorls, with fine, regular ribs; with ca. 13 ribs in \( \frac{1}{4} \) whorl adjoining R2. Boundary between R1 and R2 distinct as R2 contains more close-set and thicker ribs than R1; R2 with ca. 22 ribs that are curved towards aperture, ribs less thickened at the beginning and the end of R2; R2 ca. 1/5 whorl and nearly as long as R3. Boundary between R2 and R3 distinct due to very shallow constriction; R3 with indistinct growth lines, strongly coils downwards being highly oblique to the shell's horizontal axis, expanding near the end of the aperture. Last whorl with bluntly shouldered and ended around the beginning of R3. Aperture round; opening obliquely downwards. Peristome double with prominent outer peristome. Inner peristome sharp, protruding. Outer peristome thickened, multilayered (visible in lateral view); palatal to basal edge expanded, columellar to parietal edge not expanded, basal edge triangular and bending inwards, appearing beak- or hook-like. Umbilicus round, open, approximately one third of shell width, and with weakly blunt-periumbilical ridge that ended around the beginning of R3. Operculum unknown.

**Etymology:** The specific epithet is derived from the Latin word 'uncus' meaning 'hook, barb or bent'. The epithet *aduncus* refers to the basal edge of the outer lip bending inwards and appearing beak- or hook-like.

**Distribution and habitat:** Known only from the type locality in Kantueu Hill, Battambang, Cambo-

dia. The Kantueu Hill is an isolated limestone outcrop located south of Battambang town. The hill is about 400 m wide and surrounded by agricultural areas and temple buildings. The vegetation of this hill is a deciduous forest with moderate disturbance by clearing or mowing of low vegetation and with evidence of fire. The specimens examined herein are empty shells, which were collected from the topsoil under the leaf litter near rock base or crevices.

Remarks: Among all *Chamalycaeus* species, there are only three taxa where the R3 strongly coils downwards, being highly oblique to the shell's horizontal axis. They are *Chamalycaeus aduncus* sp. nov., *C. excisus excisus* (von Möllendorff, 1887) and *C. excisus sublimus* Páll-Gergely et Auffenberg, 2019; the latter two being from the Philippines [Páll-Gergely, Auffenberg, 2019]. These three species are also similar in shell size and depressed-conical shell shape. However, this new species differs from both *C. excisus excisus* and *C. excisus sublimus* in having a shorter R2 without any blunt keel, a round aperture without any incision, and a beak- or hook-like basal edge of the outer peristome (Fig. 1B).

The aperture of *Chamalycaeus aduncus* sp. nov. is also similar to *C. serratus* Páll-Gergely et Auffenberg, 2021 and *C. krabiensis* Páll-Gergely et A. Reischütz, 2021 from Thailand [Páll-Gergely et al., 2021]. However, the basal edge of the outer peristome in this new species is triangular and highly bending inwards, appearing beak- or hook-like. Moreover, the new species has a shorter R2 with less ribs, and a more bluntly shouldered last whorl.

Five shells out of the 32 examined specimens had a scraping hole. It is possible that these specimens were predated by the carnivorous micro land snail *Diaphera saurini* Benthem Jutting, 1962, as they were found abundant at this locality.

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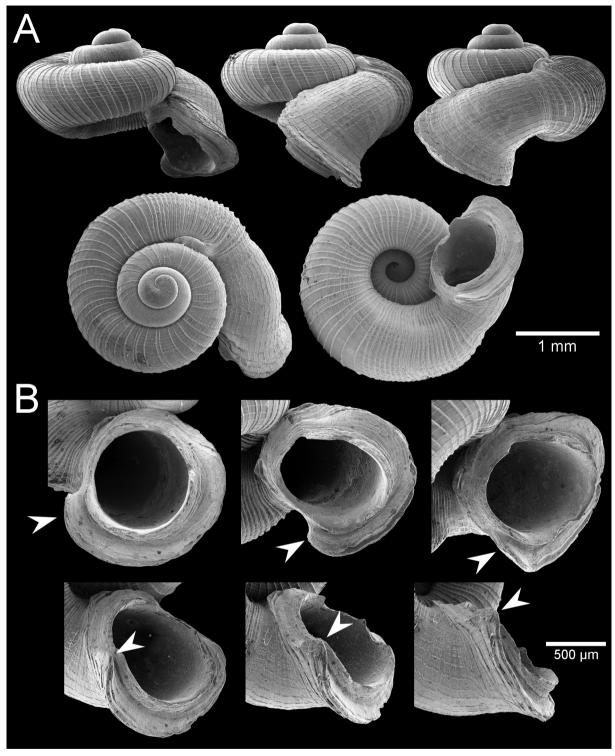


FIG. 1. Representative SEM images of *Chamalycaeus aduncus* sp. nov., holotype CUMZ 14461 **A** whole shell in different positions, and **B** Close-up images of the aperture; white arrows pointing to the beak- or hook-like basal edge of the outer peristome.

# References

Dautzenberg P., Fischer H. 1906. Liste des mollusques récoltés par M.H. Mansuy en Indo-Chine et au Yunnan et description d'espèces nouvelles. *Journal de Conchyliologie*, 53[1905]: 343–471.

Conchyliologie, 53[1905]: 343–471.

Do D.S., Nguyen T.S. 2022. The land snail genus *Pincerna* Preston, 1907 (Gastropoda: Alycaeidae)

from Vietnam and Laos, with description of a new species. *Raffles Bulltein of Zoology*, 70: 364–375. Dumrongrojwattana P., Wongkamhaeng K. 2024. Two decades of microsnails (Gastropoda: Prosobranchia:

Pulmonata) study in Thailand and ongoing research. In: Claude J., Kitana N. (Eds) *On the edge of the Sixth Mass Extinction in biodiversity hotspots: facts, needs, solutions and opportunities in Thailand* 

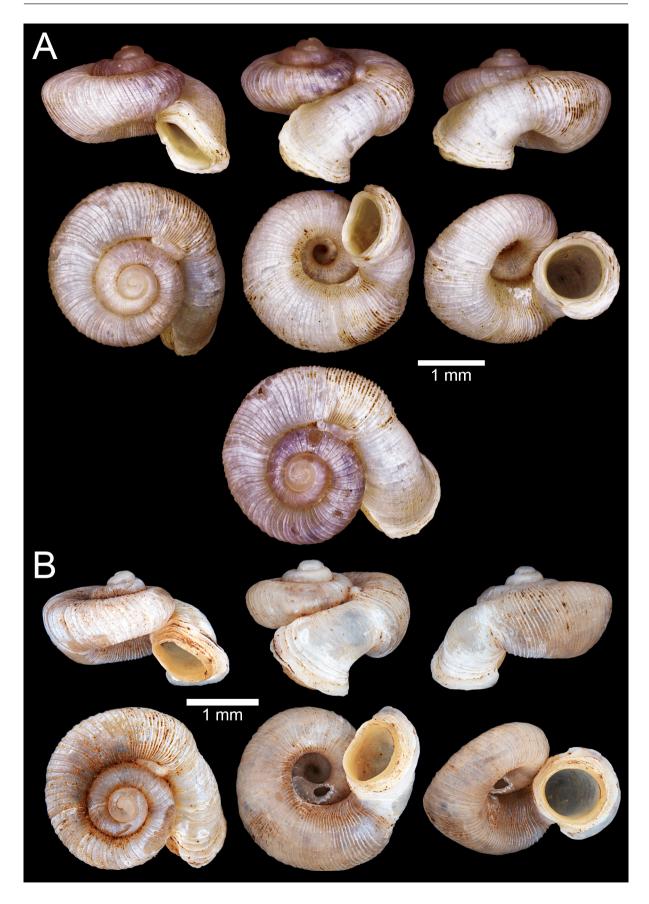


FIG. 2. *Chamalycaeus aduncus* sp. nov. **A** paratype CUMZ 14462/1, and **B** paratype CUMZ 14462/2, showing a scraping hole at the umbilical side.

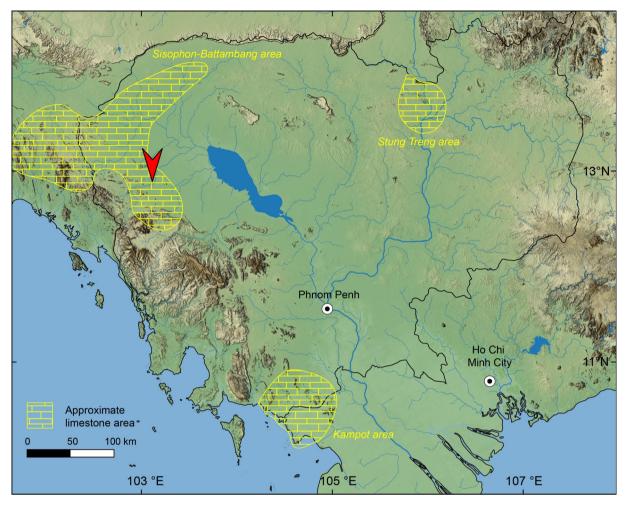


FIG. 3. Geographical position of the type locality of *Chamalycaeus aduncus* sp. nov. (red arrow) in Battambang, Cambodia. The approximate location of limestone areas (yellow rectangular pattern) in Cambodia (Sisophon-Battambang, Stung Treng, and Kampot areas) is modified from Mouret [2004].

*and adjacent countries*. Chulalongkorn University Press, Bangkok: 313–336.

Egorov R.V. 2013. A review of the genera of the terrestrial pectinibranch molluses (synopsis mainly based on published data). Littoriniformes: Liareidae, Pupinidae, Diplommatinidae, Alycaeidae, Cochlostomidae. *Treasure of Russian Shells*, Supplement 3 (Part 3): 1–62.

Foon J.K., Clements G.R., Liew T.-S. 2017. Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. *ZooKeys*, 682: 1–94. doi: 10.3897/zookevs.682.12999

Foon J.K., Liew T.-S. 2017. A review of the land snail genus *Alycaeus* (Gastropoda, Alycaeidae) in Peninsular Malaysia. *ZooKeys*, 692: 1–81. doi: 10.3897/zookeys.692.14706

Gittenberger E., Gyeltshen C., Tobgay K., Sherub S. 2024. The genera *Metalycaeus* and *Dicharax* (Caenogastropoda, Cyclophoroidea, Alycaeidae) in Bhutan, with the description of 16 new species. *Basteria*, 88(2): 187–219.

Gude G.K. 1921. The fauna of British India including

Ceylon and Burma. Mollusca - III. Land operculates. Taylor and Francis, London, 386 p.

Jirapatrasilp P., Páll-Gergely B., Sutcharit C., Tongkerd P. 2021. The operculate micro land snail genus *Dicharax* Kobelt & Möllendorff, 1900 (Caenogastropoda, Alycaeidae) in Thailand, with description of new species. *Zoosystematics and Evolution*, 97(1): 1–20. doi: 10.3897/zse.97.59143

Kerney M.P., Cameron R.A.D. 1979. A field guide to the land snails of Britain and north-west Europe. Collins, London, 288 p.

Kobelt W. 1902. *Cyclophoridae*. *Das Tierreich*. R. Friedländer und Sohn, Berlin, 662 p.

Kobelt W., von Möllendorff O.F. 1897. Catalog der gegenwärtig lebend bekannten Pneumonopomen. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 29: 73–88, 105–120, 137–152.

Mouret C. 2004. Asia, Southeast. In: Gunn J. (Ed.) *Encyclopedia of Caves and Karst science*. Fitzroy Dearborn, New York: 210–217.

Páll-Gergely B. 2023. Revision of the Alycaeidae of China, Laos and Vietnam (Gastropoda: Cyclophoroidea) II: The genera Alycaeus and Pincerna.

- *Zootaxa*, 5249(2): 253–276. doi: 10.11646/zootaxa.5249.2.4
- Páll-Gergely B., Auffenberg K. 2019. A review of the Alycaeidae of the Philippines with descriptions of new species and subspecies (Gastropoda: Caenogastropoda: Cyclophoroidea). *Molluscan Research*, 39(4): 377–389. doi: 10.1080/13235818.2019.1638541
- Páll-Gergely B., Hunyadi A. 2018. Four new cyclophoroid species from Thailand and Laos (Gastropoda: Caenogastropoda: Alycaeidae, Diplommatinidae, Pupinidae). *Zoosystema*, 40(3): 59–66. doi: 10.5252/zoosystema2018v40a3
- Páll-Gergely B., Hunyadi A. 2022. Two new species of *Dicharax* Kobelt & Möllendorff, 1900 from Myanmar and one from Thailand (Gastropoda: Caenogastropoda: Alycaeidae). *Acta Phytopathologica et Entomologica Hungarica*, 57(2): 94–105. doi: 10.1556/038.2022.00165
- Páll-Gergely B., Hunyadi A., Do D.S., Naggs F., Asami T. 2017. Revision of the Alycaeidae of China, Laos and Vietnam (Gastropoda: Cyclophoroidea) I: The genera *Dicharax* and *Metalycaeus. Zootaxa*, 4331(1): 1–124. doi: 10.11646/zootaxa.4331.1.1
- Páll-Gergely B., Hunyadi A., Grego J., Reischütz A., Auffenberg K. 2021. Nineteen new species of Alycaeidae from Myanmar and Thailand (Gastropoda: Caenogastropoda: Cyclophoroidea). *Zootaxa*, 4973(1): 1–61. doi: 10.11646/zootaxa.4973.1.1
- Páll-Gergely B., Hunyadi A., Vermeulen J.J., 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., Naggs F., Asami T. 2016. Novel shell device for gas exchange in an operculate land snail. *Biology Letters*, 12(7): 20160151. doi: 10.1098/ rsbl.2016.0151
- Páll-Gergely B., Ruthensteiner B., Harl J., Magonyi N.M., Asami T., Krizsik K., Schwaha T., Fehér Z. 2024. Recurrent evolution of breathing microtunnel system in terrestrial operculate snails (Gastropoda: Caenogastropoda: Cyclophoroidea). *Zoological Journal of the Linnean Society*, 202(4): zlae158. doi: 10.1093/zoolinnean/zlae158
- Páll-Gergely B., Sajan S., Tripathy B., Meng K., Takahiro A., Ablett J. 2020. Genus-level revision of the Alycaeidae, with a catalog of the species (Gastropoda: Cyclophoroidea). *ZooKeys*, 981: 1–220. doi: 10.3897/zookeys.981.53583
- Panha S., Burch J.B. 2005. An introduction to the microsnails of Thailand. *Malacological Review*, 37/38[2004–2005]: 1–155.

- Sutcharit C., Ngor P.B., Páll-Gergely B., Jeratthitikul E., Siriwut W., Srisonchai R., Ng T.H., 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 P.B., Jeratthitikul E., Siriwut W., Srisonchai R., Ng T.H., 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
- Thiele J. 1929. *Handbuch der systematischen Weichtierkunde, Teil 1*. Verlag von Gustav Fischer, Jena, 376 p.
- van Benthem Jutting W.S.S. 1962. Coquilles terrestres nouvelles de quelques collines calcaires du Cambodge et du Sud Vietnam. *Journal de Conchyliologie*, 102: 3–15.
- Vermeulen J.J., Aiken S. 2020. Two land snail species of the Mekong Delta limestone hills (Cambodia, Vietnam): *Aulacospira furtiva* (Eupulmonata: Vertiginidae) and *Georissa carinata* (Neritimorpha: Hydrocenidae). *Folia Malacologica*, 28: 235–241. doi: 10.12657/folmal.028.020
- Vermeulen J.J., Liew T.-S. 2022. *Land snails and slugs of Sabah and Labuan (Malaysia)*. Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia, x, 432 p.
- Vermeulen J.J., Luu H.T., Keum T., Anker K. 2019a. Land snail fauna of the Mekong Delta limestone hills (Cambodia, Vietnam): *Notharinia* Vermeulen, Phung et Truong, 2007, and a note on *Plectostoma* A. Adams, 1865 (Mollusca: Gastropoda: Caenogastropoda: Diplommatinidae). *Folia Malacologica*, 27: 167–177. doi: 10.12657/folmal.027.015
- Vermeulen J.J., Luu H.T., Keum T., Anker K. 2019b. New species of land snails (Mollusca: Gastropoda: Caenogastropoda and Pulmonata) of the Mekong Delta Limestone Hills (Cambodia, Vietnam). Folia Malacologica, 27: 7–41. doi: 10.12657/ folmal.027.001
- Vermeulen J.J., Phung C.L., Truong Q.T. 2007. New species of terrestrial molluscs (Caenogastropoda, Pupinidae & Pulmonata: Vertiginidae) of the Hon Chong Ha Tien limestone hills, Southern Vietnam. *Basteria*, 71: 81–92.
- von Möllendorff O. 1897. Neue Landschnecken von Java. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 29: 89–97.
- Wenz W. 1938. Gastropoda I. Allgemeiner Teil und Prosobranchia. In: Schindewolf O.H. (Ed.) Handbuch der Paläozoologie. Bd. 6(1). Gastropoda. Borntraeger, Berlin: 1639.