RAFFLES BULLETIN OF ZOOLOGY **74**: 483–496
Date of publication: 3 June 2026
DOI: 10.26107/RBZ-2026-0032
https://zoobank.org/urn:lsid:zoobank.org:pub:EE7D69D3-C7B2-4CC1-9D98-0195AE49BA88

A new *Bensonella* species, and redescription of *Hypselostoma loei* Panha & Prateepasen, 2005 (Eupulmonata: Hypselostomatidae) from central Laos

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Abstract. This study examined a small collection of hypselostomatids from limestone karsts in Feuang District, Vientiane Province, central Laos, comprising two species. A new species, *Bensonella hunlaman*, is described. It differs from all congeners by its white translucent shell, elongated upper palatal plica, and infrapalatal knob. Additionally, *Hypselostoma loei* Panha & Prateepasen, 2005, previously recorded only from northeastern Thailand, was collected and redescribed based on comparison with the topotypic specimens. The cytochrome c oxidase subunit I (COI) sequences of both species are reported herein for the first time. Molecular phylogenetic analysis confirmed the validity of a new species by recovering it as a monophyletic group, and supported the new record of *H. loei*, which broadens its known distribution from Thailand into Laos.

Key words. barcoding, limestone, microsnail, taxonomy

INTRODUCTION

Limestone karsts are globally significant for biodiversity, particularly in Southeast Asia, where they form isolated habitats resembling islands that support exceptional levels of endemism (Clements et al., 2006; Sutcharit et al., 2023). These habitats promote speciation in microsnails, particularly limestone-obligate snails, including members of the family Hypselostomatidae Zilch, 1959, which comprises 13 genera that vary considerably in size. The smallest representatives belong to the genus *Angustopila* Jochum, Slapnik & Páll-Gergely, 2014, with adults measuring less than one millimetre (Páll-Gergely et al., 2015, 2022, 2023; Dumrongrojwattana et al., 2021). The other genera are typically greater than 1 mm and up to 5 mm in size (Panha & Burch, 2005; Gojšina et al., 2025). These microsnails are usually attached to the limestone walls, and some taxa even occupy the dark environments of caves (Panha & Burch, 2005; Clements et al., 2006; Gojšina et al., 2025). Laos is one of the countries in mainland Indochina with extensive limestone karst formations (Inkhavilay & Sutcharit, 2024). A recent revision by Gojšina et al. (2025) added several new species of hypselostomatids combined with new species from Do et al. (2026) increasing the known diversity in Laos to eight genera and 34 species (Table 1). Among these, *Bensonella* Pilsbry & Vanatta, 1900, the second most species-rich genus in Laos, includes nine species. In contrast, *Hypselostoma* Benson, 1856, the most diverse genus in the family, is represented by only one species in Laos.

To date, taxonomic work on the limestone-obligate microsnails in this family has relied primarily on conchological features, such as shell shape, teleoconch and protoconch sculptures, and the apertural barriers, which are by far the most significant characters. Due to their distribution across isolated limestone hills, variation in some diagnostic characters is expected, particularly in taxa such as *Bensonella*, where differences in apertural dentition and shell sculpture are often ambiguous (Páll-Gergely & White, 2022; Gojšina et al., 2025). For this reason, application of molecular data has begun to overcome these limitations, and assess the reliability of these diagnostic characters, as it provides a greater number of independent characters than morphology alone. Therefore, the integration of morphological and molecular data facilitates the identification or recognition of cryptic species and the resolution of synonymies (Dayrat, 2005). Nevertheless, the molecular information for this microsnail family still remains very limited. For example, Schilthuizen et al. (1999) first sequenced ITS1 in this family, then Tongkerd et al. (2004)

Accepted by: Fred E. Wells

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ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

Table 1. Updated list of all hypselostomatid species recorded from Laos, including a new species. References: 1 = Morlet (1886, 1887), 2 = Bavay & Dautzenberg (1912), 3 = Saurin (1953), 4 = Thompson & Upatham (1997), 5 = Panha et al. (2003), 6 = Maassen (2008), 7 = Schileyko (2011), 8 = Páll-Gergely et al. (2015), 9 = Inkhavilay et al. (2016), 10 = Páll-Gergely et al. (2019), 11 = Páll-Gergely et al. (2020), 12 = Páll-Gergely et al. (2022), 13 = Páll-Gergely & White (2022), 14 = Páll-Gergely (2023), 15 = Páll-Gergely et al. (2023), 16 = Inkhavilay & Sutcharit (2024), 17 = Gojšina et al. (2025), 18 = Do et al. (2026)

Species	**Type locality in province [recorded in LAOS]**	**References**
Anauchen grandiportus Gojšina, Grego & Páll-Gergely, 2025	Khammouane, Laos	17
Anauchen kozari Páll-Gergely, 2023	Khammouane, Laos	14
Angustopila bathyodon Páll-Gergely & Hunyadi, 2023	Khammouane, Laos	15
Angustopila bidentata Páll-Gergely & Jochum, 2023	Khammouane, Laos	15
Angustopila cavicola Páll-Gergely & Dumrongrojwattana, 2023	Loei, Thailand [Oudomxay, Laos]	15
Angustopila coprologos uninodus Páll-Gergely & Grego, 2023	Bolikhamsai, Laos	15
Angustopila coprologos coprologos Páll-Gergely et al., 2022	Bolikhamsai, Laos	12
Angustopila elevata (Thompson & Upatham, 1997),	Chiangmai, Thailand [Khammouane, Luang Namtha, Luang Prabang, Oudomxay and Vientiane, Laos]	4, 15
Angustopila fabella Páll-Gergely & Hunyadi, 2015	Guangxi, China [Bolikhamsai, Houaphanh, Luang Namtha, Luang Prabang, Oudomxay, Vientiane and Xiangkhouang, Laos]	8, 9, 15
Angustopila gracilis Páll-Gergely & Hunyadi, 2023	Bolikhamsai, Laos	15
Angustopila margaritarion Páll-Gergely & Hunyadi, 2023	Luang Namtha, Laos	15
Angustopila pusilla Páll-Gergely & Hunyadi, 2023	Vientiane, Laos	15
Angustopila steffeki Páll-Gergely & Grego, 2023	Bolikhamsai, Laos	15
Angustopila szekeresi Páll-Gergely & Hunyadi, 2015	Guangxi, China [Luang Prabang and Oudomxay, Laos]	8, 15
Bensonella cardiostoma Gojšina, Vermeulen & Páll-Gergely, 2025	Vientiane, Laos	17
Bensonella expansa Do, Nguyen & Dao, 2026	Xieng Khouang, Laos	18
Bensonella hunlaman, new species	Vientiane, Laos	this study
Bensonella gittenbergeri (Maassen, 2008),	Luang Namtha, Laos	6
Bensonella mitochondria Gojšina, Vermeulen & Páll-Gergely, 2025	Khammouane, Laos	17
Bensonella novemdentata (Saurin, 1953),	Xaisomboun, Laos	3, 16
Bensonella paralella (Inkhavilay & Panha, 2016),	Luang Namtha, Laos	9
Bensonella paviei (Bavay & Dautzenberg, 1912),	probably in Son La and Lao Cai, Vietnam [No specific locality in Laos]	2, 7, 9, 13
Bensonella perfecta Gojšina & Páll-Gergely, 2025	Xieng Khouang, Laos	17
Bensonella wangviangensis (Panha & Tongkerd, 2003),	Vientiane, Laos	5
Boysidia houaphanica (Inkhavilay & Sutcharit, 2024),	Houaphanh, Laos	16
Boysidia pahpetensis Saurin, 1953	probably in Xaisomboun, Laos	3
Clostophis infantilis Páll-Gergely, 2020	Khammouane, Laos	11
Clostophis multiformis Páll-Gergely & Reischütz, 2020	Khammouane, Laos	11
Clostophis obtusus Páll-Gergely & Grego, 2020	Khammouane, Laos	11
Hypselostoma loei Panha and Prateepasen, 2005	Vientiane, Laos	this study
Hypselostoma crossei Morlet, 1886	Houaphanh, Laos	1, 9, 17

Species	Type locality in province [recorded in LAOS]	References
Krobylos clerxi Maassen, 2008	Luang Namtha, Laos	6
Krobylos laosensis (Saurin, 1953),	probably in Xaisomboun, Laos	3, 16
Tonkinospira crassicostata Páll-Gergely & Grego, 2019	Khammouane, Laos	10
Tonkinospira raxajacki Páll-Gergely & Reischütz, 2019	Khammouane, Laos	10
Tonkinospira suturata Páll-Gergely & Grego, 2019	Khammouane, Laos	10

employed a multilocus phylogenetic analysis using 16S and 28S. After that, Hoekstra & Schilthuizen (2011) used COI and ITS1 as molecular markers, and more recently, Tongkerd et al. (2025) used only COI.

In this study, a rapid survey was undertaken on several limestone karsts in Feuang District of Vientiane Province, in Central Laos, under a Memorandum of Agreement (MOA) between the National University of Laos and the Center of Excellence in Biodiversity (Thailand). Two hypselostomatid species were collected during this survey. The first is a previously undescribed *Bensonella* species, which is described herein. The second is *Hypselostoma loei* Panha & Prateepasen, 2005, which was originally described from Thailand; it is also newly recorded, and is redescribed herein to assess geographical variation in shell morphology. In addition, DNA barcoding of the COI gene was conducted for both species to provide the first genetic data for the genus *Bensonella*, serving as a baseline for more comprehensive molecular phylogenetic studies of Hypselostomatidae in the future.

MATERIAL AND METHODS

Specimen sampling and identification. The snails were hand-collected from limestone surfaces of karst habitats. Their localities are illustrated in Fig. 1. The snails were euthanised in accordance with the guidelines of the American Veterinary Medical Association (AVMA, 2020). Then specimens were preserved in 95% ethanol for long-term storage and molecular analyses. Shells were examined under a microscope for morphological study, then soaked with water and cleaned using paintbrushes to remove any remaining dirt or clay. After that, shells were examined and imaged using a scanning electron microscope (SEM; JEOL, JSM-6610 LV) and Leica M205C microscope.

The specimens were identified by comparison with type specimens or images of the types, and authenticated specimens published in Gojšina et al. (2025). The terminology used for shell sculpture and apertural dentition followed Pilsbry (1917), Páll-Gergely & White (2022), and Gojšina et al. (2025). All specimens were deposited in the CUMZ, Chulalongkorn University Museum of Zoology, Bangkok, Thailand.

DNA extraction and PCR method. Total genomic DNA was extracted from the whole-body using G-spin™ Genomic DNA Extraction Kit. A fragment of 654 bp of the protein-coding Cytochrome c oxidase subunit I (COI) was used to provide genetic markers in this study. The set of primers used in PCR was LCO1490 forward primer (5′- GGT CAA CAA ATC ATA AAG ATA TTG G -3′) and HCO2198 reverse primer (5′- TAA ACT TCA GGG TGA CCA AAA AAT CA -3′) (Folmer et al., 1994). The final volume of PCR reaction was 30 µl, including 15 µl of EmeraldAmp PCR Master Mix (TAKARA BIO INC.), 1.5 µl of each of the forward and reverse primers, 9 µl of distilled water, and 3 µl of the template DNA. The PCR cycling profile was as follows: pre-denaturation for 3 min at 94°C, then 35 cycles of denaturation for 45s at 94°C, annealing for 45s at 45.4–46.0°C, elongation for 1 min at 72°C, and post-elongation for 5 min at 72°C. The PCR products were purified by using the DNA-spin™ Plasmid DNA Purification Kit, then were sequenced in both directions at Bioneer Corporation in South Korea. Sequences were edited by using MEGA11 v. 11.0.13 (Tamura et al., 2021). The new sequences obtained in this study were submitted to the GenBank database under the accession numbers PX895006–PX895019 (Table 2).

Phylogenetic analyses. The dataset for phylogenetic analyses consisted of 34 sequences (Table 2). Of these, 13 sequences were newly generated in this study, comprising four sequences from Laos and nine sequences from Thailand. An additional 11 sequences of *Hypselostoma* species from Hoekstra & Schilthuizen (2011), and seven sequences representing four *Acinolaemus* species and two *Clostophis* species from Tongkerd et al. (2025) were employed herein. These sequences were retrieved from the GenBank database and used to infer the evolutionary relationships within the Hypselostomatidae, including the placement of the unidentified species. Moreover, three sequences from the pupilloid genera, *Pupilla* Fleming, 1828 (Pupillidae) and *Gastrocopta* Wollaston, 1878 (Gastrocoptidae) were used as the outgroup. One of these, namely *Gastrocopta pellucida* (Pfeiffer, 1841), was newly sequenced in this study.

Alignments were performed by the MUSCLE algorithm using MEGA11. Two phylogenetic tree reconstruction methods, Bayesian inference (BI) and maximum likelihood (ML), were performed through the online server CIPRES Science Gateway (Miller et al., 2010). The optimal nucleotide substitution model was identified using PartitionFinder2 v. 2.3.4 (Lanfear et al., 2017). The best nucleotide substitution models suggested by the program were GTR+G, F81+I, and HKY+G for each COI codon position, respectively. These nucleotide substitution models were used in the subsequent

Table 2. List of samples used in phylogenetic analyses, with specimen vouchers and GenBank accession numbers. References: 1 = Hoekstra & Schilthuizen (2011), 2 = Tongkerd et al. (2025), 3 = Nekola et al. (2015), 4 = Whisson & Köhler (2013).

Taxon	Locality	Voucher ID	COI	Reference
Ingroup				
Hypselostomatidae Zilch, 1959				
Bensonella hunlaman, new species	Feuang, Vientiane, Laos	PUP064	PX895007	This study
Bensonella hunlaman, new species	Feuang, Vientiane, Laos	PUP064-3	PX895006	This study
Bensonella fracta	Limestone mountains near Pha Fai Cave, Nong Hin, Loei, Thailand	ES010-2	PX895014	This study
Hypselostoma loei	Feuang, Vientiane, Laos	PUP063-2	PX895009	This study
Hypselostoma loei	Feuang, Vientiane, Laos	PUP063-4	PX895008	This study
Hypselostoma loei	Wat Tham Phraya Chang Phueak, Khon San, Chaiyaphum, Thailand	ES001	PX895019	This study
Hypselostoma loei	Wat Tham Huang Po, Khon San, Chaiyaphum, Thailand	ES002	PX895018	This study
Hypselostoma loei	Wat Tham Phra Wanaram, Phu Pha Man, Khon Kaen, Thailand	ES003	PX895017	This study
Hypselostoma loei	Wat Thep Udom Wanaram, Chum Phae, Khon Kaen, Thailand	ES005	PX895016	This study
Hypselostoma loei	Limestone mountains near Pha Fai Cave, Nong Hin, Loei, Thailand	ES009	PX895015	This study
Hypselostoma loei	Pha Fai Cave, Nong Hin, Loei, Thailand	ES011	PX895013	This study
Hypselostoma loei	Wat Tham Pha Wiang, Na Wang, Nong Bua Lam Phu, Thailand	ES013-2	PX895012	This study
Hypselostoma loei	Wat Tham Saeng Tham, Si Chomphu, Khon Kaen, Thailand	ES017-2	PX895011	This study
Hypselostoma hungerfordianum	Perlis, Malaysia	HM240395.1	HM240395	1
Hypselostoma hungerfordianum	Perlis, Malaysia	HM240396.1	HM240396	1
Hypselostoma hungerfordianum	Perlis, Malaysia	HM240397.1	HM240397	1
Hypselostoma hungerfordianum	Perlis, Malaysia	HM240398.1	HM240398	1
Hypselostoma salpinx	Raub, Pahang, Malaysia	HM240407.1	HM240407	1
Hypselostoma salpinx	Raub, Pahang, Malaysia	HM240408.1	HM240408	1
Hypselostoma serpa	Langkawi, Kedah, Malaysia	HM240411.1	HM240411	1
Hypselostoma serpa	Langkawi, Kedah, Malaysia	HM240412.1	HM240412	1
Hypselostoma serpa	Langkawi, Kedah, Malaysia	HM240413.1	HM240413	1
Hypselostoma transitans	Langkawi, Kedah, Malaysia	HM240405.1	HM240405	1
Hypselostoma transitans	Langkawi, Kedah, Malaysia	HM240406.1	HM240406	1
Acinolaemus rhamphodontis	Tak, Thailand	HC025-1	PV698334	2
Acinolaemus rhamphodontis	Tak, Thailand	HC025-2	PV698335	2
Acinolaemus mueangonensis	Tak, Thailand	HC026	PV698336	2
Acinolaemus colpodon	Chon Buri, Thailand	HE022-2	PV698337	2
Acinolaemus rhamphodon	Chon Buri, Thailand	HE025-2	PV698338	2
Clostophis rhynchotes	Nakhon Sawan, Thailand	HC016-2	PV698339	2
Clostophis udayaditinus	Battambang, Cambodia	PUP020	PV698440	2

Taxon	Locality	Voucher ID	COI	Reference
Outgroup				
Pupillidae Turton, 1831				
Pupilla muscorum	Czech Republic, Brno,Moravia	KM518583.1	KM518583	3
Gastrocoptidae Pilsbry, 1918				
Gastrocopta mussoni	Pilbara, Australia	KC143991.1	KC143991	4
Gastrocopta pellucida	Wihan Luang Pho Dam, Sattahip, Chonburi, Thailand	HE032	PX895010	This study

phylogenetic analyses. The ML trees were executed in IQ-Tree v. 2.1.2 (Nguyen et al., 2015), with 1,000 bootstrap replications. The BI analyses were conducted in MrBayes v. 3.2.6 (Ronquist et al., 2012), using 10,000,000 generations of Metropolis-coupled Markov chain Monte Carlo (MCMC), with the first 25% obtained trees discarded as burn-in. Nodes with ≥ 70% bootstrap values (BS) from the ML analysis and/or ≥ 0.95 Bayesian posterior probabilities (BPP) were considered as significantly supported, while nodes receiving lower values were considered as weakly or not supported (Tongkerd et al., 2025). Both trees were illustrated and modified in Figtree v. 1.4.4 (Rambaut, 2018).

Abbreviations.

a	angular
ap	angulo-parietal
b	basal
c	columellar
ifpl	infrapalatal
ifr	infraparietal
itpl	interpalatal
lpl	lower palatal
p	parietal
pl	palatal
sc	subcolumellar
spl	suprapalatal
upl	upper palatal

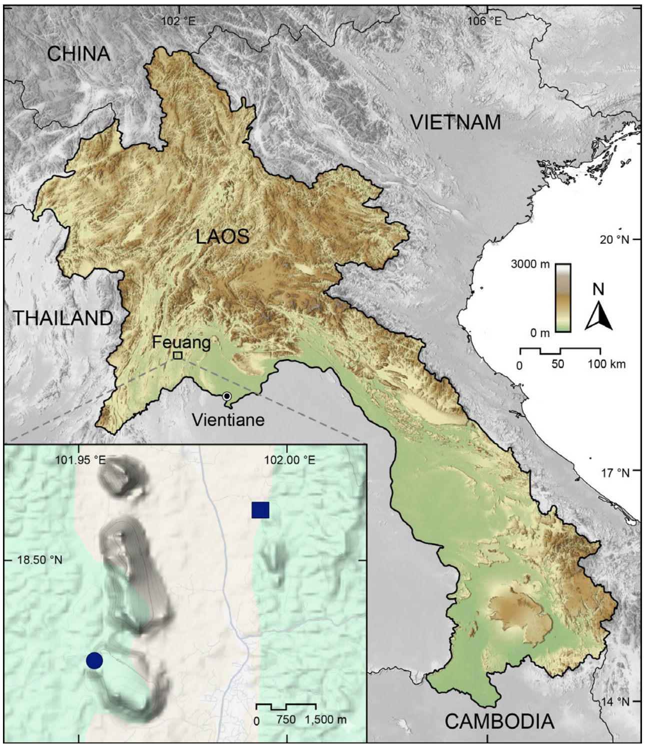

Fig. 1. Map illustrating locations of the type locality of a new species, and additional examined specimens of *H. loei* in Laos. Circle indicates limestone karsts in Ban Pha Sung, collection locality of *H. loei* in Laos. Square indicates limestone karsts in Ban Na Dan, the type locality of *Bensonella hunlaman*, new species.

RESULTS

Molecular phylogenetic tree and genetic distance analyses. The final COI alignment comprised a total length of 654 bp, including 264 variable sites (240 parsimony-informative sites and 24 singleton sites). The phylogenetic trees inferred from BI and ML analyses were similar, therefore only the topology from the ML is presented in Fig. 2. The deep node showed significant support value (BPP = 0.97, BS = 79%), indicating a well-supported ingroup clade for the family Hypselostomatidae. *Bensonella* formed a strongly supported monophyletic group under both methods (BPP = 1, BS = 100%). Interestingly, two sequences of unidentified *Bensonella* specimens from Laos grouped together with high support (BPP = 1, BS = 100%). This clade was recovered as a sister taxon to a topotype sequence of *B. fracta*, and with distinct COI p-distance of 6.7% (Table 3). Although this genetic divergence level is lower than typical interspecific distances for *Hypselostoma* (12.2–16.6%), *Acinolaemus* (14.2–18.2%), and *Clostophis* (15.9%), it still exceeds intraspecific variation (0.3%). Combined with unique morphological characters, these results support the recognition of the two specimens as a new species, herein described as *B. hunlaman*, new species.

The same was true for *Hypselostoma*, although the ML analysis returned only moderate support (BPP = 1, BS = 84%), the inclusion of a limited number of species resulted in poor resolution within the genus *Hypselostoma* (BPP < 0.95, BS < 50–70%). Nevertheless, all examined species were recovered as monophyletic and with high nodal support (BPP = 0.98–1, BS = 90–100%), confirming their validity. Among these, *Hypselostoma* specimens from Laos were nested with *H. loei* specimens (including a topotype sequence from Thailand)

Table 3. Intraspecific (in bold) and interspecific *p*-distances from COI in the Hypselostomatidae.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. *H. loei* from Thailand (*n* = 8)	**0.059**													
2. *H. loei* from Laos (*n* = 2)	0.052	**0.000**												
3. *H. hungerfordianum* (*n* = 4)	0.133	0.134	**0.031**											
4. *H. transitans* (*n* = 2)	0.151	0.145	0.144	**0.029**										
5. *H. salpinx* (*n* = 2)	0.133	0.122	0.144	0.166	**0.000**									
6. *H. serpa* (*n* = 3)	0.141	0.133	0.138	0.136	0.146	**0.002**								
7. *A. colpodon* (*n* = 1)	0.167	0.171	0.164	0.181	0.168	0.163	**n/c**							
8. *A. mueangonensis* (*n* = 1)	0.190	0.192	0.182	0.195	0.207	0.189	0.178	**n/c**						
9. *A. rhamphodon* (*n* = 1)	0.190	0.187	0.180	0.186	0.191	0.172	0.142	0.181	**n/c**					
10. *A. rhamphodontis* (*n* = 2)	0.209	0.208	0.179	0.209	0.202	0.172	0.165	0.156	0.182	**0.002**				
11. *C. rhynchotes* (*n* = 1)	0.175	0.185	0.171	0.190	0.183	0.163	0.133	0.174	0.164	0.188	**n/c**			
12. *C. udayaditinus* (*n* = 1)	0.189	0.187	0.186	0.199	0.199	0.176	0.133	0.183	0.135	0.177	0.159	**n/c**		
13. *B. hunlaman*, new species (*n* = 2)	0.170	0.168	0.161	0.170	0.182	0.159	0.167	0.167	0.154	0.174	0.174	0.168	**0.003**	
14. *B. fracta* (*n* = 1)	0.169	0.162	0.179	0.183	0.188	0.166	0.171	0.197	0.171	0.187	0.179	0.180	0.067	**n/c**

with high support (BPP = 0.98, BS = 90%). These specimens can thus be confidently identified as *H. loei*, supporting the morphology-based identification and representing a new country record for Laos. Among *Hypselostoma* species, the interspecific COI p-distances ranged from 12.2% to 16.6%, whereas the intraspecific p-distances within *Hypselostoma* ranged from 0% to 5.9% (Table 3).

Lastly, the genera *Acinolaemus* Thompson & Upatham, 1997 and *Clostophis* Benson, 1860 exhibit an ambiguous evolutionary relationship, as reported by Tongkerd et al. (2025). Although a sister-group relationship between *A. rhamphodontis* Tongkerd & Panha in Tongkerd et al., 2025 and *A. mueangonensis* Changlom, Chan-ard & Dumrongrojwattana, 2019 is well supported, other clades which are mixture of both genera are not supported. Overall, the relationship between *Acinolaemus* and *Clostophis* remains unclear, however, these genera are clearly distinct from *Bensonella* and *Hypselostoma* with a well-supported value.

TAXONOMY AND SYSTEMATICS

Family Hypselostomatidae Zilch, 1959

Bensonella Pilsbry & Vanatta, 1900

Bifidaria (*Bensonella*) Pilsbry & Vanatta, 1900: 591.
Boysidia (*Paraboysidia*) Pilsbry, 1917: 174, 201.
Boysidia (*Bensonella*) – Pilsbry, 1917: 198.
Bensonella – Zilch, 1959: 164.

Type species. *Pupa plicidens* Benson, 1849, by original designation.

Remarks. The genus is characterised by shell shape, distinct palatal tubercle on the peristome, and the number and position of apertural barriers, particularly on the parietal wall. In the recent revision, Gojšina et al. (2025) recognised 36 nominal species, which are widely distributed ranging from eastern India to Southeast Asia, as well as Japan, southern China, and Taiwan. In Laos, eight species have been recorded from the limestone karsts in the northern and central regions of the country (Inkhavilay & Sutcharit, 2024; Gojšina et al., 2025).

Bensonella hunlaman, new species
(Fig. 3)

Type material. Holotype (CUMZ 15429), from the limestone hills in Ban Na Dan, Feuang District, Vientiane Province, Laos, 18°30′38.8″N, 101°59′16.4″E, coll. T. Janjai & K. Inkhavilay, 8 October 2024 (Fig. 3A–F; height 1.50 mm, width 1.68 mm, 4¼ whorls). 9 paratypes (8 shells + 1 immature; Fig. 3G–I) (CUMZ 15430), all other information same as holotype.

Etymology. The specific name '*hunlaman*' is derived from the Lao word 'Hunlaman' or 'ຫນຸລະມານ'. It is a principal character in the Laos national epic 'Phra Lak Phra Ram', an adaptation of the Indian epic Ramayana. 'Hunlaman' is

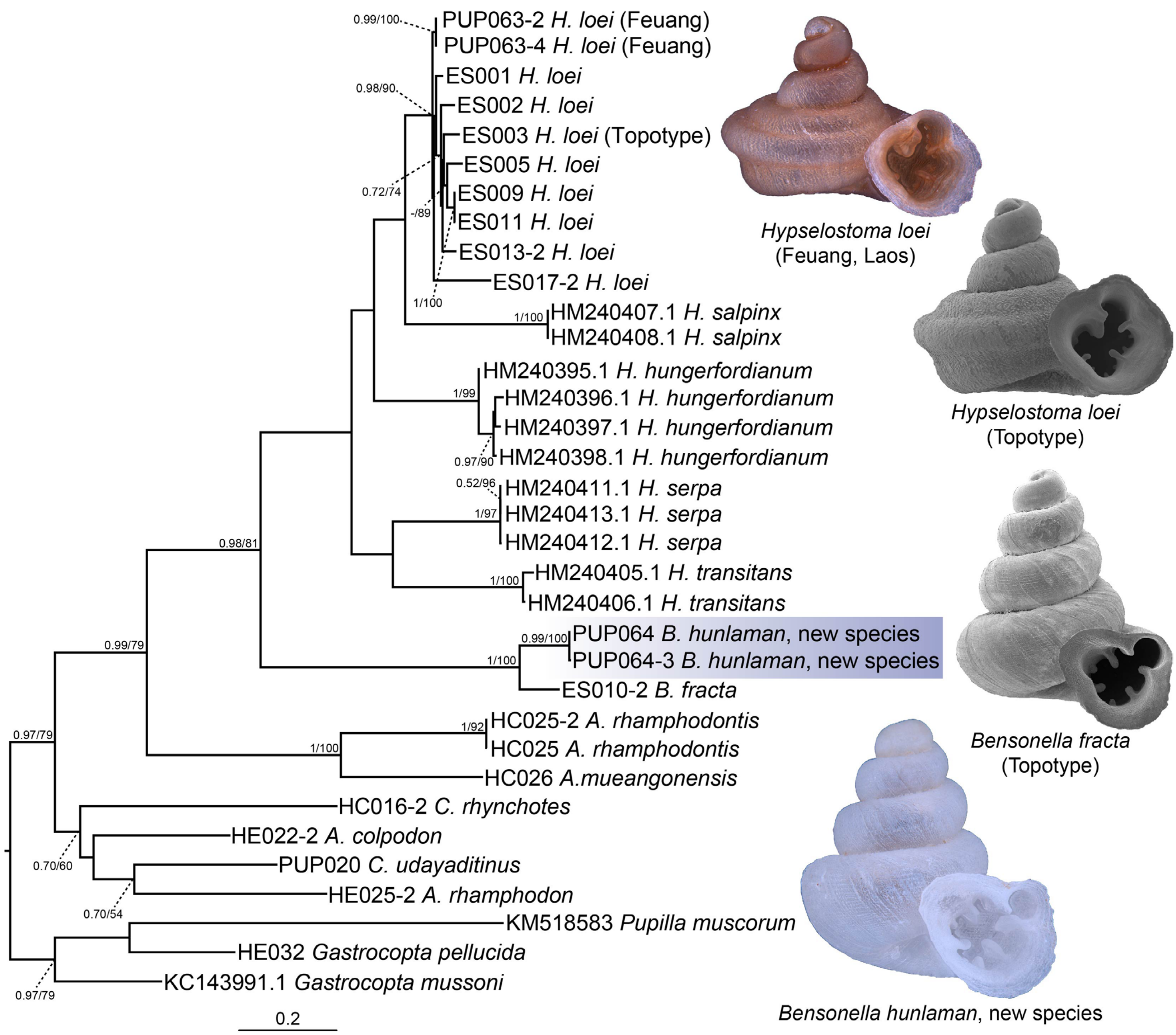

Fig. 2. Phylogenetic tree of *Bensonella* and *Hypselostoma* recovered from maximum likelihood analysis of 654-bp COI gene. Numbers on nodes show only high support values, which are Bayesian posterior probabilities and bootstrap values of maximum likelihood analysis, respectively. Scale bar indicates substitutions per site. Shells of some representative taxa are shown. Shells not to scale.

depicted as a white monkey with sharp canines, which is similar to the pale colouration and strong angular lamella of this species.

Diagnosis. Shell conical, white translucent; shell surface sculptured with fine spiral striae crossed by irregular growth lines; peristome with rough or granulated surface. Last whorl round-shouldered. Apertural dentition of eight: three on parietal wall (infraparietal, parietal, and angular), two on palatal wall (upper- and lower-), one basal plica, and two on columellar wall (subcolumellar and columellar). Palatal tubercle inconspicuous.

Description. Shell small (height 1.50–1.70 mm, width 1.62–1.82 mm), white translucent, low-conical to high conical. Protoconch ca 1¼ whorls, with thin spiral striations. Whorls 4–4¼, rounded; suture wide and deeply impressed. Shell surface sculptured with irregular growth lines that are superimposed with fine and prominent spiral striae throughout. Last whorl round-shouldered, straight to slightly ascending near peristome. Peristome expanded, adnate to penultimate whorl, and with rough granulated surface. Apertural dentition of eight, generally strong, finely granulated surface (without spines), and sinulous conspicuous. Parietal wall with three lamellae: infraparietal lamella small, low knob shape, situated slightly deep inside aperture; parietal lamella tall with blunt ridge; angular lamella tall with sharp ridge, extending to expanded lip. Palatal tubercle undifferentiated from upper palatal plica, situated near expanded lip. Palatal wall with two plicae: upper palatal plica tall, with sharp ridge, then long inside into aperture; lower palatal plica tall with blunt ridge. Basal plica somewhat low, short, with blunt ridge. Columellar wall with two lamellae: columellar lamella tall with blunt ridge; subcolumellar lamella small, similar in shape and size to basal plica. Umbilicus narrow, deep, covering ca ⅛ of shell width.

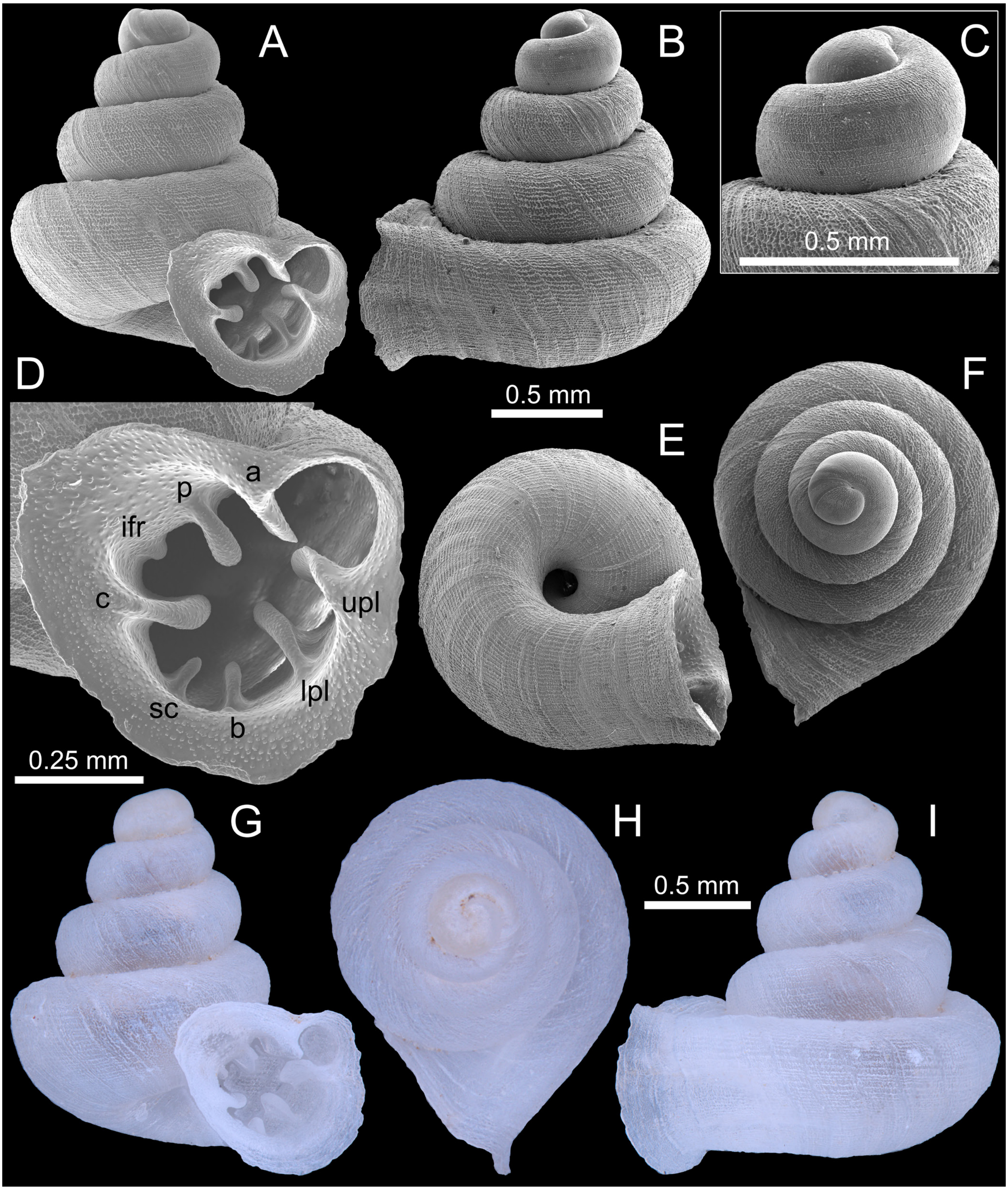

Fig. 3. *Bensonella hunlaman*, new species. A–F, holotype CUMZ 15429; C, protoconch and earlier whorl sculptures; D, enlarged aperture; G–I, paratypes CUMZ 15430. All from the type locality at Ban Na Dan, Feuang District, Vientiane Province, Laos.

Distribution. This species is known only from its type locality, sloping limestone outcrops surrounded with paddy fields and lime orchards. This area has low moisture and is covered with dense tree vegetation that shades the limestone surface from direct sunlight. The snails were attached to the limestone walls, with some individuals aestivating within cracks and crevices along the rock face.

Differential diagnosis: *Bensonella hunlaman*, new species, can be placed within the *B. wangviangensis* species group based on the indistinguishable palatal tubercle and palatal plicae (Gojšina et al., 2025). However, it differs from other species in this group in having very dense spiral striation and closely situated angular lamella and palatal tubercle, which clearly separated the sinulus from the rest of the aperture.

This new species differs from *B. cardiostoma* Gojšina, Hunyadi & Páll-Gergely, 2025, and *B. mitochondria* Gojšina, Vermeulen & Páll-Gergely, 2025, in having a larger shell (height ~1.7 mm / ~1.1/1.3 mm), and greater number of whorls (4 whorls / 3½ whorls). In addition, this new species has the apertural dentitions reaching the peristome edge and can be observed easily from the aperture, whereas the other two species have apertural dentitions situated deeper inside the aperture. Furthermore, the shell sculpture of the new species has an irregular pattern of growth lines, in contrast to the roughly sculptured surface in *B. cardiostoma*, and the strongly raised spiral striae with some radial growth lines in *B. mitochondria* (Gojšina et al., 2025).

Bensonella hunlaman, new species, differs from *B. wangviangensis* (Panha & Tongkerd in Panha et al., 2003), by having a low conical shell shape while *B. wangviangensis* exhibits a conical-ovoid shape. In terms of dentition, the new species lacks spikes on the apertural barriers, and all dentitions are generally robust. In contrast, *B. wangviangensis* possesses outwardly directed spines on the dentition surface, with dentitions that are generally short and blunt (Panha et al., 2003; Gojšina et al., 2025).

Bensonella hunlaman, new species, has shell shape and shell sculpture similar to *B. fracta* Gojšina, Hunyadi & Páll-Gergely, 2025, from Thailand. It also was nested as a sister group in our phylogenetic tree. However, it differs in several key characters: the new species has no tuba, peristome is adnate to the preceding whorl, and it has a small subcolumellar lamella. In comparison, *B. fracta* possesses a short tuba, an elevated peristome, and is without a subcolumellar lamella (Gojšina et al., 2025). Furthermore, they were genetically distinct on the phylogenetic tree and were separated by a considerably high p-distance value of 6.7% based on the COI gene (Table 3).

Hypselostoma Benson, 1856

Tanystoma (*Hypselostoma*) Benson, 1856a: 129–131.
Hypselostoma – Benson, 1856b: 342.

Type species. *Tanystoma tubiferum* Benson, 1856, by monotypy.

Remarks. The genus is characterised by having a conical shell, expanded peristome and tuba either short to long and may be adnate to detached from the penultimate whorl (Panha & Burch, 2005; Gojšina et al., 2025). Within the family, *Hypselostoma* is the most speciose genus, comprising 87 nominal species with a wide distribution ranging from southern China and Taiwan through Indochina and the Malay Peninsula to Indonesia (Maassen, 1999; Guo et al., 2006; Hwang, 2014; Gojšina et al., 2025; Tanmuangpak et al., 2025). The recent systematic revision has subdivided the genus into four species groups, of which only one species, *H. crossei* Morlet, 1886, belonging to the *H. tubiferum* species group has been recorded from Laos (Gojšina et al., 2025). A second species, *H. loei*, belonging to the *H. hungerfordianum* species group, represents a new record from Laos and is redescribed herein.

Hypselostoma loei Panha & Prateepasen, 2005
(Fig. 4)

Hypselostoma loei Panha & Prateepasen, 2005: 99–102, fig. 2. Type locality: Loei Province, Thailand. Panha & Burch, 2005: 94, 95, fig. 80. Gojšina et al., 2025: 253–256, figs 186h, 203, 223.

Type material. Holotype CUMZ 15349 (=Ver 024) from Loei Province (16°45′47″N 101°59′8″E). Paratypes CUMZ 15350 (= Ver 026) (6 shells) all other information same as holotype.

Material examined. LAOS • 94 shells (CUMZ 15431), Vientiane Province, Feuang District, Limestone hills in Ban Pha Sung, 18°28′47.2″N 101°57′12.0″E, coll. T. Janjai & C. Sutcharit, 8 October 2024 (Fig. 4A–E). **THAILAND** • 21 shells (CUMZ 15432), Nong Bua Lam Phu Province, Na Wang District, Wat Tham Pha Wiang, 17°25′42.1″N 102°05′10.1″E, coll. T. Janjai & C. Sutcharit, 20 May 2025; 91 shells (CUMZ 15433), Loei Province, Nong Hin District, Pha Fai Cave, 17°02′35.0″N 101°44′09.6″E, coll. T. Janjai & C. Sutcharit, 19 May 2025; 78 shells (CUMZ 15434), Loei Province, Nong Hin District, Limestone mountains near Pha Fai cave, 17°02′28.2″N 101°43′38.4″E, coll. T. Janjai & C. Sutcharitt, 19 May 2025; 316 shells (CUMZ 15435), Khon Kaen Province, Si Chomphu District, Wat Tham Saeng Tham, 16°50′34.1″N 102°03′57.5″E, coll. T. Janjai & C. Sutcharit, 20 May 2025; 56 shells (CUMZ 15436), Khon Kaen Province, Chum Phae District, Wat Thep Udom Wanaram, 16°45′27.3″N 101°57′54.1″E, coll. T. Janjai & C. Sutcharit,19 May 2025; 44 shells (CUMZ 15437), Khon Kaen Province, Phu Pha Man District, Wat Tham Phra Wanaram, 16°39′53.0″N 101°53′47.0″E, coll. T. Janjai & C. Sutcharit, 18 May 2025 (Fig. 4F–J); 29 shells (CUMZ 15438), Chaiyaphum Province, Khon San District, Wat Tham Huang Po, 16°35′01.5″N 101°49′43.2″E, coll. T. Janjai & C. Sutcharit, 18 May 2025; 44 shells (CUMZ 15439), Chaiyaphum Province, Khon San District, Wat Tham Phraya Chang Phueak, 16°33′45.3″N 101°51′40.0″E, coll. T. Janjai & C. Sutcharit, 18 May 2025.

Diagnosis. Shell concave-conical, raised tuba, strong ridge on last whorl, surface granulated. Peristome expanded; apertural dentition well-developed: two on parietal wall (infraparietal, concrescence angulo-parietal), four on palatal wall (supra-, upper-, inter-, and lower-), one basal plica, and two on columellar wall (subcolumellar and columellar).

Re-description. Shell small (height 2.33–2.50 mm, width 3.10–3.28 mm), brownish to yellowish-brown, concave-conical. Protoconch ca 1½ whorls with roughly pitted sculpture. Whorls 4–4½, rounded; suture wide and deep. Shell surface with irregular growth lines and sculptured with granulated surface. Last whorl enlarged, with prominent rounded peripheral keel; tuba short, slightly ascending. Peristome expanded, not reflected, sharp edges, smooth

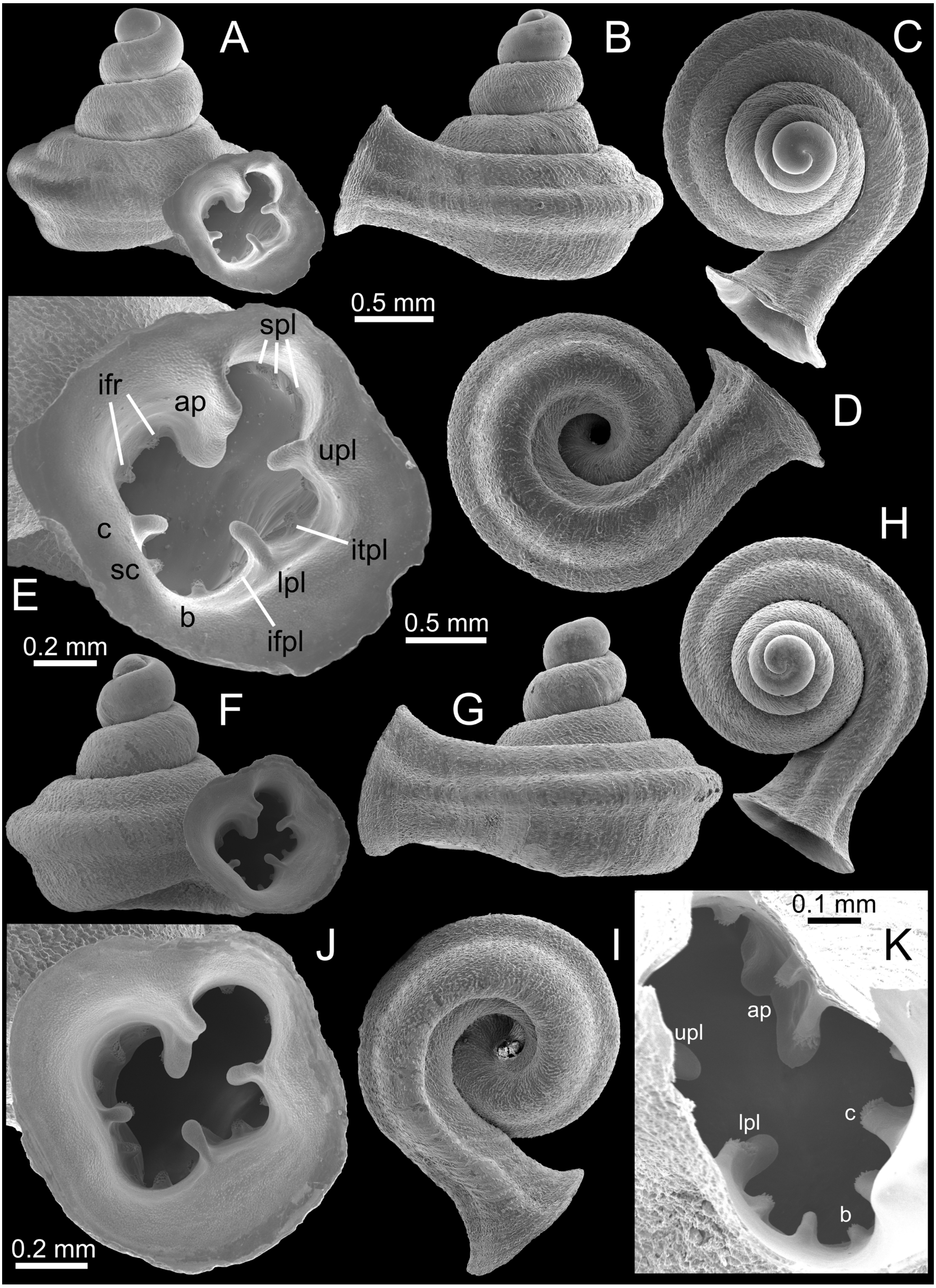

Fig. 4. *Hypselostoma loei* from Laos and Thailand. A–E, specimen CUMZ 15431 from Ban Pha Sung, Feuang District, Vientiane Province, Laos; D, enlarged aperture showing small barriers and spike-surfaces; F–J, CUMZ 15437 from Loei Province, Thailand (topotype); J, enlarged aperture of the topotypic specimen; K, apertural barriers from inside looking out direction showing the spike-surface on inner half of the main barriers.

surface. Aperture equipped with four main barriers (angulo-parietal, upper palatal, lower palatal, and columellar) and several smaller barriers located between main barriers. Surface of all barriers decorated with fine spikes on inner halves of main barriers, obvious when viewed from inside the aperture looking outward, and other barriers with spikes on surface (Fig. 4K). Parietal wall: angulo-parietal lamella very tall, strong, blunt, slightly sinuous, reaching expanded peristome, and long deeply inside aperture; two smaller infraparietal lamellae present. Palatal wall with two main plicae: upper palatal plica tall, strong, blunt ridge; lower palatal plica tall, blunt ridge. Sinulus rounded, with three or four smaller barriers in suprapalatal position, and two smaller barriers in interpalatal position. Basal plica small, low rise, knob shaped, with one smaller barrier situated between basal and lower palatal plicae. Columellar wall with one main barrier: columellar lamella tall, strong, with blunt ridge, and one smaller subcolumellar. Umbilicus narrow, covering ca ⅓ of shell width, deep, with strong periumbilical groove.

Distribution. This species appears to be widely distributed in northeastern Thailand, including the provinces of Loei, Nong Bua Lam Phu, Khon Kaen, and Chaiyaphum, as well as in Phitsanulok in central Thailand (Panha & Prateepasen, 2005; Gojšina et al., 2025). In this study, it is recorded from Vientiane Province in central Laos. This collection site is located on a limestone karst slope adjacent to a road in the countryside. The snails were observed attached to the limestone walls, high above the ground (approximately 2 to 5 m), living among patches of mosses and lichens.

Differential diagnosis. Recently, Gojšina et al. (2025) placed this species into the *H. hungerfordianum* species group. For comparison, *H. loei* can be distinguished from *H. hungerfordianum* Möllendorff, 1891, by having concrescence on the angulo-parietal lamella, small barriers in the interpalatal position, and four main dentitions that are generally covered with spikes on their inner surfaces. In contrast, *H. hungerfordianum* possesses separate angular and parietal lamellae, interpalatal lamellae forming a low knob, and all apertural barriers covered with spikes across their surfaces. In addition, *H. loei* is primarily distributed in northeastern Thailand, with a recent new record from central Laos, whereas *H. hungerfordianum* occurs in southern Thailand and Peninsular Malaysia (Gojšina et al., 2025).

Although *H. loei* has a shell shape superficially similar to *H. sichang* (Panha & Burch, 2002), from Thailand and *H. vesovici* Gojšina & Páll-Gergely, 2025, from Malaysia, it differs by having a concrescence on the angulo-parietal lamella, a low spire, and shell that is curved above the peripheral keel. In contrast, the two latter species possess separate angular and parietal lamellae, a high spire, and shell that is truncate above the peripheral keel (Panha & Burch, 2002; Gojšina et al., 2025).

Remarks. This species possesses a concrescence angulo-parietal lamellae, and spike-covered surfaces are present across all dentitions. However, these spike-surfaces are clearly visible from inside the aperture looking out (Fig. 4K) on approximately half on the main barriers and are fully developed on the small barriers.

The specimens from Laos tended to differ from the other populations in Thailand, which are located about 300 km to the south, by having a longer, less ascending tuba and a more curved angulo-parietal lamella. However, our phylogenetic analyses grouped them together as monophyletic with high nodal support (BPP = 0.99, BS = 94%), suggesting that these morphological differences are forms of intraspecific variation. In addition, intraspecific p-distance values among *H. loei* populations were relatively low (0.0%–5.9%; Table 3), which further support them as conspecific.

DISCUSSION

This study reports the discovery of a new species of *Bensonella* and provides additional molecular data for the species in Laos, and an updated list of hypselostomatid species recorded from Laos is presented in Table 1. This checklist shows that these microsnails are widely distributed across many provinces in Laos; however, no records have previously been reported from central Laos, particularly in the genus *Bensonella* (Bavay & Dautzenberg, 1912; Saurin, 1953; Panha et al., 2003; Maassen, 2008; Inkhavilay et al., 2016; Páll-Gergely & White, 2022; Inkhavilay & Sutcharit, 2024; Gojšina et al., 2025; Do et al., 2026). Phylogenetic analyses strongly support *B. hunlaman*, new species, as a distinct species, with *B. fracta* identified as its sister taxon within the same species group. The COI p-distances for intraspecific variation in the new species and interspecific variation within the species group are 0.3% and 6.7%, respectively. Furthermore, the genus *Bensonella* is clearly separated from *Hypselostoma* with high support values and forms a monophyletic clade, at least for the *B. wangviangensis* species group. Meanwhile, these genera are clearly distinct from *Acinolaemus* and *Clostophis*, though the relationship between the latter two genera remains unclear (Tongkerd et al., 2025). Conchological comparisons separated the new species from other members of this group by the presence of a strong angular lamella and a blunt subcolumellar lamella. Therefore, this study increases the total number of *Bensonella* species recorded in Laos to ten.

Previous records show that *H. loei* is widely distributed in provinces bordering central Laos (Panha & Prateepasen, 2005; Gojšina et al., 2025). Specimens from central Laos can be defined as *H. loei*, based on molecular results and conchological examination. The COI p-distance within the genus *Hypselostoma* shows intraspecific variation ranging from 0.0% to 5.9%, which is lower than that reported for *H. hungerfordianum* clades, for which Hoekstra & Schilthuizen (2011) reported up to 9%. Therefore, although some morphological differences exist between the Thai and Laos specimens, these differences are not significant enough to recognise them as distinct species. In the latest revision of the genus, only a single species, *H. crossei*, was recorded from Laos. This study provides a record of the second species in Laos and suggests that *H. loei* has a broader distribution than previously recognised.

To examine conchological characters in detail, the usage of the Scanning Electron Microscope (SEM) remains the most effective method for determination of species, and to minimise the risk of morphological misidentification. The SEM images of *H. loei* reveal that the small apertural barriers possess spike-like projections on their surfaces, while the main barriers are robust, with spiked surfaces visible only from posterior angles (inside out). However, this technique has limitations for visualising characters of some deep apertural barriers, as observed in *H. loei* in this study. Observation of these characters requires breaking the shell, which causes damage to the specimen.

Finally, molecular analysis should be considered essential evidence for evaluating new species. In this study, a phylogenetic tree of these microsnails was constructed using the COI gene, in contrast to Schilthuizen et al. (1999) and Tongkerd et al. (2004), who used ITS1 or both16S and 28S markers, respectively. This result shows that the *B. wangviangensis* species group is currently distinct from other *Hypselostoma* species. However, support values at some deep nodes remain low and controversial. Further studies should incorporate more specimens and molecular data to improve our understanding of the evolutionary relationships among these microsnail genera within the Hypselostomatidae.

ACKNOWLEDGEMENTS

We are grateful to the Research and Academic Service Office of the National University of Laos and to members of the Department of Biology, National University of Laos (NUOL), for their assistance in preparing permission documents, facilitating data collection, and providing support during fieldwork in Laos. We also thank all members of the Animal Systematics Research Unit (ASRU), Chulalongkorn University, for their kind assistance during field trips. We sincerely thank the reviewers, T.-S. Liew, B. Páll-Gergely, and F. Wells, for their careful evaluation and insightful comments, which greatly improved the clarity of this manuscript. The experimental protocol was approved by the Animal Care and Use Committee of the Faculty of Science, Chulalongkorn University (Protocol Review No. 2523009). This study was funded by the Thailand Science Research and Innovation Fund, Chulalongkorn University (DIS-FF-69-149-2300-037); the NSRF via the Program Management Unit for Human Resources & Institutional Development, Research and Innovation (B42G670038); the Second Century Fund (C2F), Chulalongkorn University, and the National Research Council of Thailand (NRCT-N35E660138, NRCT-N34E670115).

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