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Research Article

Hidden Diversity of Cave Millipedes From Mainland Southeast Asia Revealed by Species Delimitation and Phylogenetic Analysis, With a Description of a New Genus (Spirostreptida: Cambalopsidae)

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Southeast Asia's karst landscapes host a remarkable yet understudied diversity of cave-dwelling fauna, where morphological conservatism often masks true species boundaries. Using an integrative taxonomic framework, we investigated the systematics of the millipede family Cambalopsidae Cook, 1895 inhabiting caves across Thailand, Laos, Myanmar, and Cambodia, combining morphological evidence with mitochondrial cytochrome *c* oxidase subunit I (COI) sequences. Analyses of 213 specimens revealed the polyphyletic relationships of the two largest genera, *Glyphiulus* Gervais, 1847 and *Plusioglyphiulus* Silvestri, 1923, necessitating major taxonomic revision. Consequently, we erect *Somsakiulus* Seesamut & Likhitrakarn, gen. nov. to accommodate a distinct clade formerly classified within *Plusioglyphiulus*, and resurrect *Cambalomorpha* Pocock, 1895 stat. resurr. from synonymy within *Glyphiulus*. Species delimitation analyses using four single-locus methods (ASAP, GMYC, bPTP, and mPTP) consistently uncovered extensive cryptic diversity, with molecular data identifying substantially more putative species (molecular operational taxonomic units [MOTUs]) than morphology, most notably within the *Trachyjulus unciger* species complex (46–54 MOTUs vs. 25 morphospecies). This work underscores the limitations of relying on traditional gonopod-based taxonomy alone, elevates the diagnostic importance of peripheral characters, such as the male first legs, and collum and mid-body carinotaxy, and provides a robust systematic framework essential for future evolutionary studies and conservation planning within these vulnerable cave ecosystems.

Keywords: cryptic species; gonopod; peripheral characters; phylogeny

1. Introduction

Cave millipedes represent a group of specialized terrestrial invertebrates with extreme local endemism and limited ecological distributions in and around caves and limestone karst ecosystems. Most cave millipedes are trogophilic, meaning that they are adapted to cave environments without being obligate cave-dwellers. However, they remain strongly associated with dark, enclosed habitats and have developed several morphological and physiological adaptations to address the challenges of subterranean existence. These adaptations that occur in cave millipedes involve reduced or entirely absent eyes, depigmented cuticles, elongated appendages and in some cases, dependance on guano as a primary food source [1, 2].

In the Oriental region, particularly in East and Southeast Asia, cave millipedes are commonly encountered and often form dominant components of cave arthropod communities [3–5]. However, the cave systems across this region remain vastly understudied despite being extensive and diverse, especially within the large karst landscapes of Thailand, Laos, Myanmar, and Cambodia [6–8]. As cave millipedes exhibit a high degree of ecological sensitivity and micro-endemism [9, 10], comprehensive taxonomic knowledge of these organisms throughout the region is therefore essential for biodiversity assessments and conservation planning.

In the past decades, cave millipedes from the family Cambalopsidae Cook, 1895 have been the subject of taxonomic studies in mainland Southeast Asia, with new species being discovered and described periodically (e.g., [11–13]). To date, a total of 64 cambalopsid species have been described from type localities recorded from this region. Twenty-four of these species are from Thailand [11], 14 from Vietnam [14–19], 12 from Laos [13, 20], five from Myanmar [21, 22], five from Peninsular Malaysia [23, 24], and four from Cambodia [12, 25]. Many of these cambalopsid taxa are narrow endemics and exhibit highly restricted distributions, particularly those adapted to cave environments (e.g., [13]).

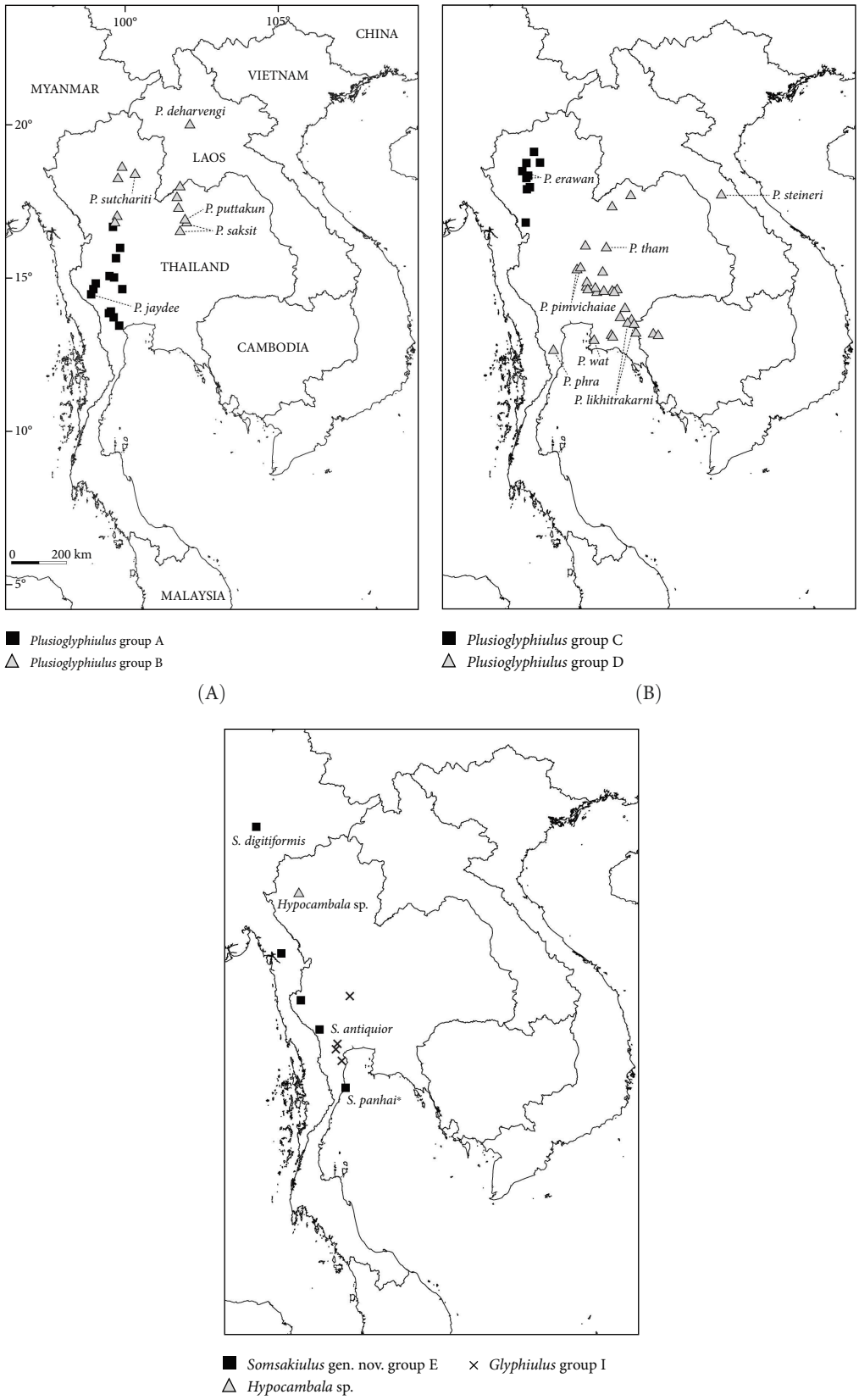
At present, cave millipede species of the Cambalopsidae from mainland Southeast Asia belong to five genera. The oldest and largest genus, *Glyphiulus* Gervais, 1847 contains 79 species distributed across China and mainland Southeast Asia, but not beyond the Isthmus of Kra, with two disjunct occurrences, one in Borneo and one in Java [13, 26, 27]. *Trachyjulus* Peters, 1864 presently includes 31 species and one subspecies, spanning from India in the west through Vietnam in the east, and southward to Indonesia with one record in the Bismarck Archipelago [28]. *Hypocambala* Silvestri, 1895 is notably widespread, currently containing 15 species scattered throughout Southeast Asia and several islands in the Pacific and Indian Oceans [19, 29]. *Podoglyphiulus* Attems, 1909 is a small genus containing only seven species and two subspecies, narrowly distributed in India, Sri Lanka, and Myanmar [23]. *Plusioglyphiulus* Silvestri, 1923 comprises 30 species distributed from northern Thailand, Myanmar, and Laos, and southward through Malaysia to Borneo [12].

Species delimitation in cambalopsid cave millipedes has been based primarily on morphological characteristics, including the gonopod structure, the carinotaxic patterns of the metaterga and collum, the structure of the first three pairs of male legs, and the number and length of body rings (e.g., [30, 31]). The differentiation of these characters is sufficiently informative to support recognizing these species as distinct and valid, and this species-level differentiation highly correlates with their geographical isolation (e.g., [30–32]). Nevertheless, such morphology-based approaches, especially when applied to troglophilic taxa, often encounter significant limitations, due to convergent evolution and limited morphological differentiation [21, 33]. Relying only on morphological characters could possibly complicate species identification and obscure species boundaries, especially for those species containing populations inhabiting geographically adjacent caves, where external morphological traits are nearly indistinguishable. Traditionally, these closely related populations have been grouped into a single species displaying subtle morphological variation [21, 27]. However, the question of whether these populations should be identified as different distinct species or as variations of a single species remains unresolved. To help circumvent these problems, an approach of integrative taxonomy [34], combining DNA sequence data, especially the DNA barcode region of mitochondrial cytochrome *c* oxidase subunit I (COI) gene fragment with morphological data, holds promise to clarify the ambiguity of species boundaries among closely related cambalopsid taxa. This approach has already been applied in some cambalopsid cave millipedes in East and Southeast Asia, yielding a high level of accuracy in species delimitation (e.g., [13, 28, 35, 36]).

During several cave surveys in the past few years, a number of cave millipede specimens were collected from more than 200 localities within and around limestone caves in mainland Southeast Asia, especially throughout Thailand. Some of these specimens represent unique morphotypes not observed in any previously described taxa. However, the extent of morphological variation and exact species boundaries of these cave millipedes remain to be investigated. Therefore, we applied integrative taxonomic framework applying both morphological and molecular data (COI barcode) to delimit cave millipede species within the genera *Glyphiulus*, *Trachyjulus*, *Plusioglyphiulus*, and *Hypocambala* from Thailand, Laos, Myanmar, and Cambodia. In addition, by combining available data of southern Chinese species, preliminary phylogenetic relationships, as well as prospective taxonomic classification of East Asian and mainland Southeast Asian cave millipedes will be inferred.

2. Materials and Methods

2.1. Specimen Collection, Preparation, and Morphological Species Delimitation. Voucher specimens of the Cambalopsidae collected from sites throughout Thailand and some areas in Laos, Cambodia, and Myanmar (Figure 1) during 2010–2011, and 2016–2024 were acquired from collections at Chulalongkorn University Museum of Zoology (CUMZ), Bangkok, and Forschungsinstitut und Naturmuseum Senckenberg (SMF), Frankfurt am Main (Supporting Information: Table S1). Some specimens collected in Laos during 2014 and 2016 were part of the biodiversity exploration for the Northern Lao-European Cave Project 2014 and the Hin Nam No Project, respectively. Geographic coordinates and elevations of collection sites were recorded using a Garmin GPSMAP 60CSx and verified with Google Earth. Live specimens were photographed using a Nikon 700D digital camera with a Nikon AF-S VR 105 mm macro lens (Figure 2). Euthanasia followed a two-step protocol suggested by the AVMA [37] Guidelines for the Euthanasia of Animals. Specimens were preserved in 95% ethanol for morphological and molecular analyses, with ethanol replaced after 24 h to minimize degradation from defensive compounds. The handling of animals in this study was approved by Chulalongkorn University Animal Care and Use Committee (CU-ACUC) under the approval numbers 1723018 and 2523009.



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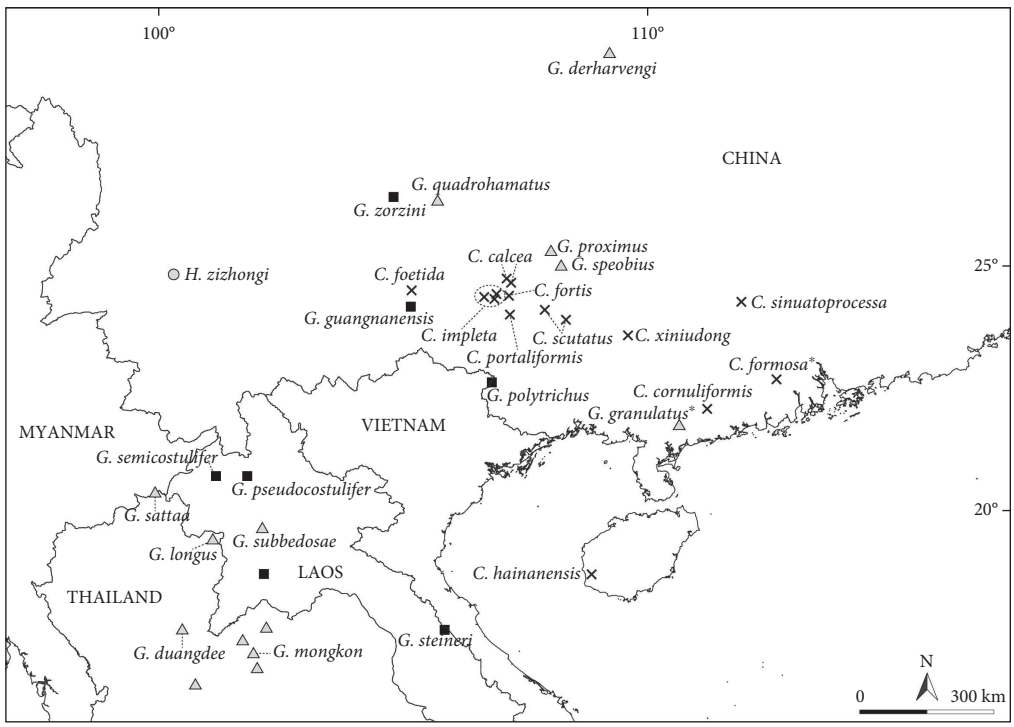

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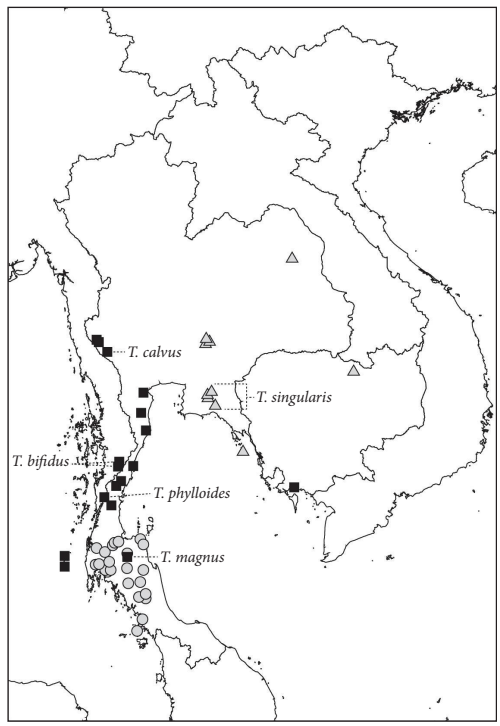

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Figure 1: Distribution maps of cave millipede species of the family Cambalopsidae, according to the phylogenetic groups (A–L) identified in this study. (A) *Plusioglyphiulus* group A, black square; *Plusioglyphiulus* group B, gray triangle. (B) *Plusioglyphiulus* group C, black square; group D, gray triangle. (C) *Somsakiulus* gen. nov. group E, black square; *Hypocambala* sp., gray triangle; *Glyphiulus* group I, X mark. (D) *H. zizhongi*, gray circle; *Glyphiulus* group G, black square; *Glyphiulus* group H, gray triangle; *Cambalomorpha* group J, X mark. (E) *Trachyjulus* group K except *T. unciger* species complex, black square; *T. unciger* species complex group K, gray circle; *Trachyjulus* group L, gray triangle.

Species identification, generic assignment, and morphological examination of the head, the male first legs, the carinotaxy of collum and mid-body, and the anterior and posterior gonopods followed the literature of each cambalopsid genus: (1) *Glyphiulus* [15, 17, 18, 30, 32, 38], (2) *Hypocambala* [19, 29], (3) *Plusioglyphiulus* [12, 16, 21, 39], and (4) *Trachyjulus* [21, 24, 28]. Specimens were compared with the relevant type specimens if possible. Morphological data of Chinese cambalopsids were also retrieved from several sources [29, 31, 35, 36, 40, 41]. The morphological terminology and the carinotaxic formulae used follow those in previous taxonomic papers [15–18, 38]. Distinct undescribed morphospecies were delimited by the unique combination of non-overlapping morphological characters.

2.2. DNA Extraction, PCR Amplification, and DNA Sequencing. Total genomic DNA was extracted from the dissected midbody ring tissues using a DNA extraction kit (G-Spin Total DNA Extraction Mini Kit; iNtRON Biotechnology, Korea), following the standard procedure of the manual. Amplification of the mitochondrial COI gene was performed using LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) [42] and hco-outout (5′-GTAAATATATGRTGDGCTC-3′) [43], or using the degenerate primer pair LCO-JJ (5′-CHACWAAYCA TAAAGATATYGG-3′) and HCO-JJ (5′-CHACWAAYCAT AAAGATATYGG-3′) [44]. PCR reactions were carried out in a total volume of 30 μL, comprising 2 μL of genomic DNA, 1.25 μL each of forward and reverse primers, 15 μL of 2xTaq Master Mix (Dye Plus) (Nanjing Vazyme Biotech, China), and 10.5 μL of nuclease-free water. Thermal cycling was conducted using a BIO RAD T100 Thermo Cycler (Bio-Rad, United States) with a gradient temperature function. PCR conditions included an initial denaturation at 94°C for 5 min, followed by 36 cycles of denaturation at 94°C for 30 s, annealing at 42°C for 60 s (LCO1490/hco-outout) and 55°C for 60 s (LCO-JJ/HCO-JJ), and extension at 72°C for 60 s. A final extension step was performed at 72°C for 5 min. PCR products were resolved by 1% agarose gel electrophoresis stained with NEOGREEN, DNA Gel Staining reagent (NeoScience, Korea), and visualized under B-BOX Blue Light LED epi-illuminator (SMOBIO, Taiwan). The purifying and sequencing of PCR products (in both directions) were done commercially by Macrogen Inc. (Japan). The collecting localities and submission codes of each specimen are listed in Supporting Information: Table S1.

2.3. Sequence Editing, Alignment, and Phylogenetic Analyses. To identify and verify the amplified sequences, the obtained sequences were compared against those in the GenBank database using the BLASTn algorithm via the NCBI platform (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and BOLDSYSTEMS platform (https://id.boldsystems.org/). All sequences were subsequently reassembled, edited, and aligned using the MUSCLE algorithm [45] in MEGA X [46] with default settings, followed by manual inspection for accuracy. No sequencing artifacts, ambiguous base calls or misreads were detected. The accession numbers of newly generated sequences deposited in the GenBank database, as well as other relevant sequences of Chinese cambalopsid species (Figure 1) retrieved from GenBank that were used in subsequent analyses are given in Supporting Information: Table S1. Two sets of outgroups were also incorporated into the dataset: (1) outgroup taxa within the suborder Cambalidea, to which the Cambalopsidae also belongs [47], including the families Cambalidae Bollman, 1893 (one species) and Pericambalidae Silvestri, 1909 (five species) and (2) outgroup taxa outside the Cambalidea, but still within the order Spirostreptida, represented by two species of *Thyropygus* Pocock, 1894 from the Harpagophoridae Attems, 1909 (Supporting Information: Table S1).

The maximum likelihood (ML) analysis was performed using the IQ-TREE webserver (see http://iqtree.cibiv.univie.ac.at), with the integrated ModelFinder function [48–50]. Branch support was estimated using 10,000 ultra-fast bootstrap replicates [51], the Shimodaira and Hasegawa-approximate likelihood-ratio (SH-aLRT) test and the approximate Bayes (aBayes) test [52]. The Bayesian inference (BI) analysis was also performed with the best-fitting models of each codon position of COI as retrieved from Kakusan4 [53], including a symmetrical model (SYM) + gamma (G) for the 1st codon position, a generalized time reversible (GTR) + G for the 2nd and 3rd codon positions, using MrBayes on XSEDE v.3.2.6 [54] in the CIPRES Science Gateway [55]. Two independent analyses were run simultaneously and consisted of four chains of five million generations, sampling every 500th generations and discarding the first 50% of samples as burn-in. Convergence of the two runs was achieved if the average standard deviation of split frequencies was $\leq$0.01, and Markov chain Monte Carlo (MCMC) samples from the posterior probability (PP) distributions were assessed as adequate if potential scale reduction factor (PSRF) values of each parameter approached 1.0 [54]. A clade was considered to be well-supported if the SH-aLRT support values were $\geq$80%, aBayes support values were $\geq$0.95, the ultra-fast bootstrap support (BS) values were $\geq$95%, and the Bayesian PP values were $\geq$0.95 [51, 52, 56]. All trees were rooted with the family Harpagophoridae. Uncorrected pairwise genetic distances (*p*-distances) among different genera and among different taxa or OTUs within each genus based on the COI sequences were calculated in MEGA X using partial deletion with a cut-off value of 95%.

2.4. Species Delimitation Based on DNA Sequence Data. Molecular species delimitation based on COI sequences was conducted using four complementary methods: assemble species by automatic partitioning (ASAP) [57], Bayesian implementation of Poisson tree processes (bPTP) [58], multi-rate Poisson tree processes (mPTP) [59], and the generalized mixed Yule coalescent model (GMYC) [60]. ASAP was performed via the ASAP web server (https://bioinfo.mnhn.fr/abi/public/asap/asapold.html, accessed on May 9, 2025) under the Kimura (K80) model. The output with the lowest ASAP score was selected to represent the ASAP result [61]. The bPTP analysis was performed on an online web server (https://species.h-its.org, accessed on May 9, 2025), setting the reversible Markov chain number to 100,000, and with other parameters set to default. The mPTP analysis was conducted via the online server (http://mptp.h-its.org, accessed on May 27, 2025), using an input tree in the Newick format generated from MrBayes.

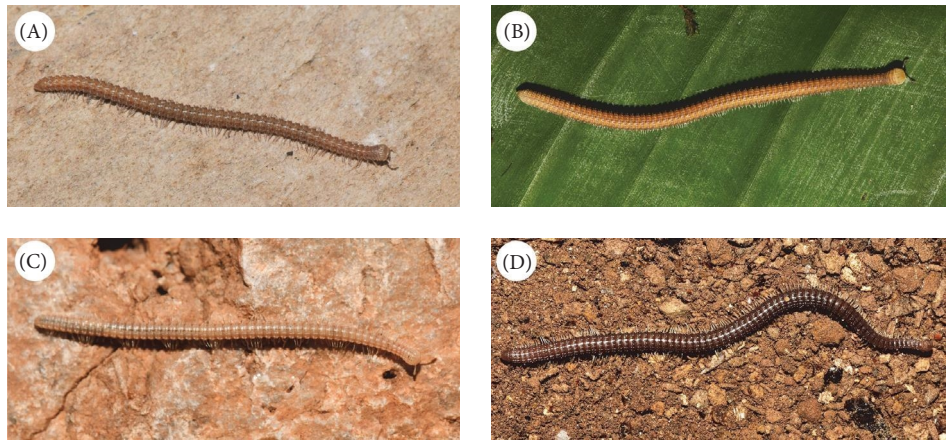

Figure 2: Live specimen of (A) *Glyphiulus* sp. H4. (B) *Plusioglyphiulus likhitrakarni* Golovatch et al., 2011. (C) Somsakiulus antiquior (Golovatch et al., 2011). (D) Trachyjulus magnus Likhitrakarn et al., 2020. All not to scale.

The GMYC analysis was conducted using the online platform (https://species.h-its.org/gmyc/, accessed on May 27, 2025), employing the single-threshold method. The input dataset consisted of an ultrametric Bayesian guide tree generated with BEAST2 on ACCESS v.2.6.7-2.7.7 [62] via CIPRES Science Gateway. The analysis assumed a Yule speciation process with a relaxed uncorrelated clock and a GTR evolutionary model, while all other parameters were kept at their default settings. MCMC sampling was conducted with 10 million generations, sampled every 1000 generations, with the first 10% discarded as burn-in. LogCombiner v. 2.7 [63] was used to resample the tree files every 5000 generations, while assessing the effective sample size (ESS) values for all parameters to be above 200 and the convergence in Tracer v. 1.7.2 [64]. TreeAnnotator v. 2.7.7 [63] was used to construct the maximum clade credibility tree using median heights as node heights, after discarding the first 10% of the trees as burn-in.

2.5. Taxonomy. In the taxonomy sections, D stands for the original description and/or subsequent descriptive notes, K for the appearance in a key, L for the appearance in a species list, R for a new subsequent record, and M for a mere mention. A reference to the original description is always given.

3. Results

3.1. Categorization of Morphological Characters and Morphology-Based Species Identification and Delimitation. Six morphological characters were identified in this study: (1) the male first legs, (2) the anterior gonopod, (3) the posterior gonopod, (4) the expansion of the head, (5) collum carinotaxy, and (6) mid-body carinotaxy (Figure 3 and Supporting Information: Table S1). See below for the recognition of the genera *Cambalomorpha* and *Somsakiulus* gen. nov. The male first legs could be categorized into 10 character states, in which the number of character states for each genus is as follows: two for *Trachyjulus* (T1, T2), one for *Cambalomorpha* (G3), three for *Glyphiulus* (G1, G2, G4), one for *Hypocambala* (H1), two for *Somsakiulus* gen. nov. (P2, P3), and two for *Plusioglyphiulus* (P1, P2). The anterior gonopod could be categorized into 12 character states: five for *Trachyjulus* (T1–T5), one for *Cambalomorpha* (G1), four for *Glyphiulus* (G1–G4), one for *Hypocambala* (G1), one for *Somsakiulus* gen. nov. (P1), and two for *Plusioglyphiulus* (P2, P3). The posterior gonopod could be categorized into 13 character states: five for *Trachyjulus* (T1–T5), one for *Cambalomorpha* (G2), four for *Glyphiulus* (G1–G4), one for *Hypocambala* (G2), one for *Somsakiulus* gen. nov. (P1; see below), and three for *Plusioglyphiulus* (P2–P4). Details of each character state of the male first legs, the anterior and posterior gonopods are given in Table 1, whereas the character states of the expansion of the head, collum, and mid-body carinotaxies are given in Supporting Information: Table S1.

Based on this morphological category and the unique combination of non-overlapping morphological characters, the number of morphospecies of each cambalopsid genus is as follows: 11 *Cambalomorpha* morphospecies (11 named species), 25 *Glyphiulus* morphospecies (16 named species and 9 unidentified species), two *Hypocambala* morphospecies (one named species and one unidentified species), 60 *Plusioglyphiulus* morphospecies (12 named species and 48 unidentified species), four *Somsakiulus* gen. nov. morphospecies (three named species and one unidentified species), and 25 *Trachyjulus* morphospecies (6 named and 19 unidentified species). This results in a total of 127 morphospecies retrieved from this study. Among *Trachyjulus* morphospecies, a number of specimens were assigned to the non-monophyletic *T. unciger* species complex, due to the combination of these characters: the male first legs type T2, the collum carinotaxy of 1+2a+3a, the mid-body carinotaxy of 6-8/6-8+I/i+5/5+I/i+6-8/6-8, the anterior gonopod type T4, and the posterior gonopod type T3 (Supporting Information: Table S1).

3.2. Phylogenetic Analyses and Genus-Level Relationships. The final alignment of 221 sequences (213 ingroup and 8 outgroup sequences) had a length of 669 bp, including 372 (55.6%) variable sites. Considering only the ingroup taxa, there were 359 (53.7%) variable sites. Closest identification of all sequences analyzed in this study via BOLDSYSTEMS is given in Supporting Information: Table S1. The phylogenetic analyses gave largely consistent topologies between ML and BI analyses for both strongly supported and less supported

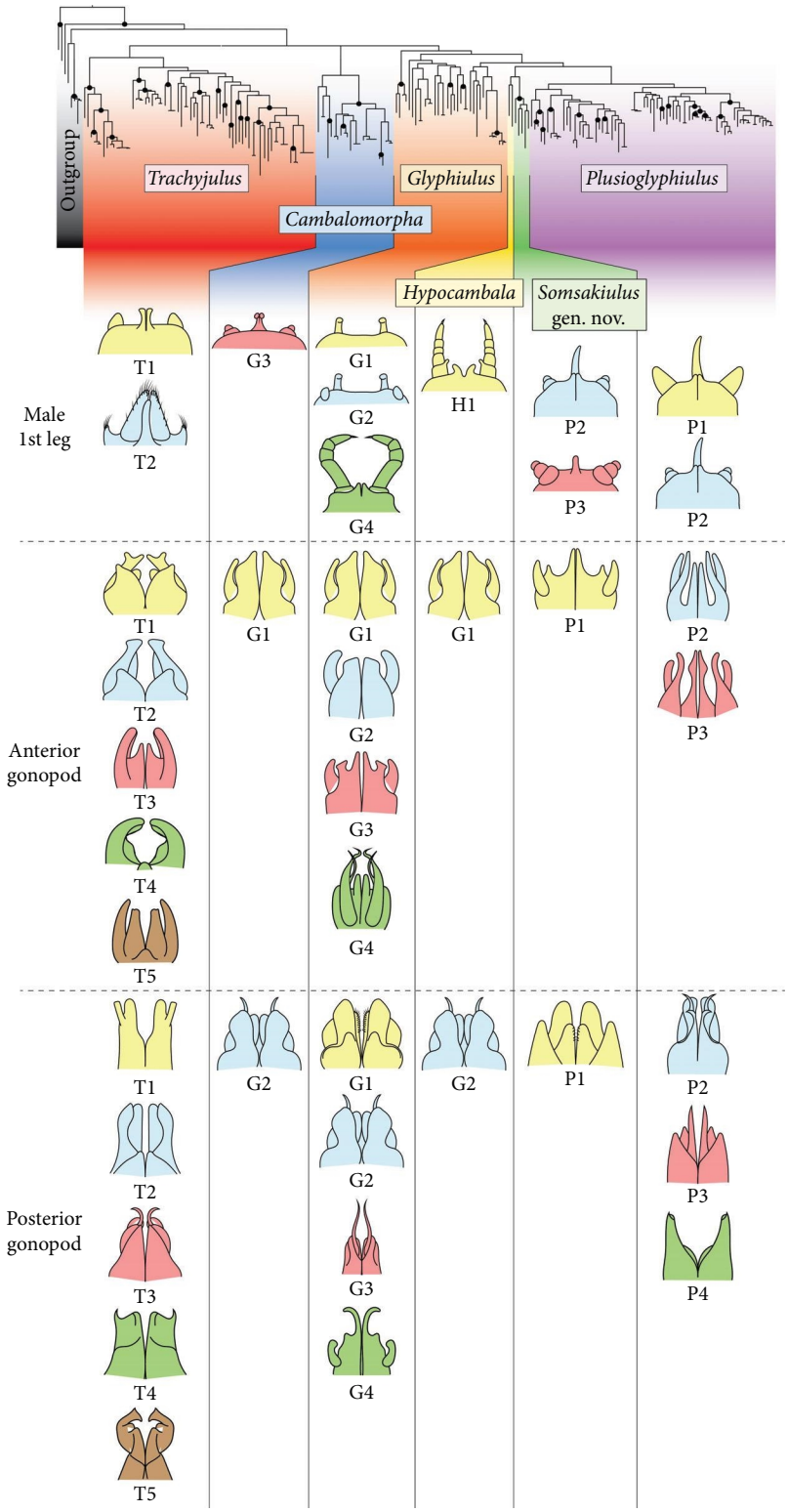

FIGURE 3: Maximum likelihood tree of the family Cambalopsidae showing the relationships among different genera in this study, with drawings showing different types of male first legs, anterior and posterior gonopods of each genus. A black circle on a node indicates a clade with all well-supported values. Character codes correspond to Table 1.

nodes (Figures 3–6, showing ML topology). All taxa in the family Cambalopsidae were retrieved together as monophyletic, although the intergeneric relationship was still not resolved. The family Pericambalidae was retrieved as a sister clade to the Cambalopsidae, supported by ML aBayes and Bayesian PP values. *Cambala annulata* (Say,

Table 1: Details of each character state of male first legs, anterior gonopod, and posterior gonopod of cambalopsid genera in this study.

Character	Character state	Details
Male first legs	P1	Strongly reduced to 2-segmented telopodites; coxosternum with a single, long, strong, median, unciform process, clearly surpassing the telopodites in height
	P2	Strongly reduced to 2-segmented telopodites; coxosternum with a single, median unciform process not surpassing the telopodites or equal to the height of the telopodites
	P3	Strongly reduced to 3-segmented telopodites; coxosternum with a short, medial hook
	G1	Strongly reduced, telopodite absent or vestigial; coxosternal processes represented by a pair of widely separated and strongly curved prongs
	G2	Strongly reduced to 1- or 2-segmented telopodites; coxosternal processes represented by a pair of widely separated and strongly curved prongs
	G3	Strongly reduced to 2- or 3-segmented telopodites; coxosternal processes paired, hooked, in medial contact
	G4	Sub-normal, 4- or 5-segmented telopodites, coxal processes medially contiguous but not fused
	H1	Slightly reduced, 5-segmented telopodites, coxosternum with a pair of subdigitiform processes medially; prefemur likewise with a process
	T1	Strongly reduced to a broad transverse coxosternum, which supports a pair of central, hook-shaped coxal processes flanked by small, rudimentary, 1-segmented telopodites
	T2	Strongly reduced to a central, high, hook-shaped and densely setose syncoxite, flanked by strong, high, sac-shaped, densely setose, 1-segmented telopodites, each bearing a modest, lateral, tuberculiform and setose bulge
Anterior gonopod (AG)	P1	Plate-like coxosternum with notch separating high apicomesal and lower basolateral processes; telopodite 1-segmented
	P2	Complex, bearing a paramedian pair of high and suberect anterior and posterior coxosternal processes; telopodite 1-segmented
	P3	Complex, bearing a paramedian pair of suberect anterior coxosternal processes and a posterior pair evidently expanded laterally; telopodite 1-segmented
	G1	Coxosternum shield-like; apicomesal process higher than or subequal to 1-segmented telopodite
	G2	Coxosternum shield-like, with or without an apicomesal process; telopodite 1-segmented, clearly surpassing the coxosternum in height
	G3	Coxosternum shield-like, with an evident mesal process a lateral subsecuriform process and a 1-segmented telopodite
	G4	Coxosternum shield-like, with a long mesal process; telopodite very long, 1-segmented and flagelliform
	T1	Simple, with stout, bipartite telopodites consisting of two widely separated and curved, digitiform processes; lateral coxosternal process shorter than or subequal in height to the medial one
	T2	Simple, with stout, apically expanded telopodites; lateral coxosternal process slender, flanking the telopodites, and higher than the medial one
	T3	Anterior gonopods simple, with stout telopodites; lateral coxosternal process slender, flanking the telopodites, and higher than the medial one, the latter being slender and nearly contiguous
	T4	Simple with subtrapezoid medial coxosternal processes; telopodites club-shaped, curved, nearly as high as slender, long lateral coxosternal process, placed basal to telopodites
	T5	Simple, with elongated medial coxosternal processes and long, slender telopodites; lateral coxosternal processes missing
Posterior gonopod (PG)	P1	Compressed, coxal process elongate, ending in flagellum or fovea; telopodite 1-segmented, erect
	P2	Compressed, coxal process elongate, ending in flagellum or fovea; telopodites absent
	P3	Compressed, with a high, blade-shaped middle process caudally; telopodites absent
	P4	Simple, with sac-shaped, membranous; telopodites absent
	G1	Compressed and broadly subquadrate, apically without any process
	G2	Compressed and broadly subquadrate, apically with a small process
	G3	Compressed and broadly subquadrate, bearing a very long, stout and medially densely setose flagellum
	G4	Coxosternum shield-like; apicomesal process clearly surpassing the 1-segmented telopodite
	T1	Simple, membranous and elongated, apically bipartite
	T2	Simple, membranous and elongated, evidently bipartite, with the division extending nearly to the base
	T3	Compressed and broadly subquadrate, with a flagellum
	T4	Compressed and broadly subrectangular; apex usually bipartite
	T5	Complex, elongated and membranous distally; telopodites membranous, strongly curved mesad and strongly expanded distally

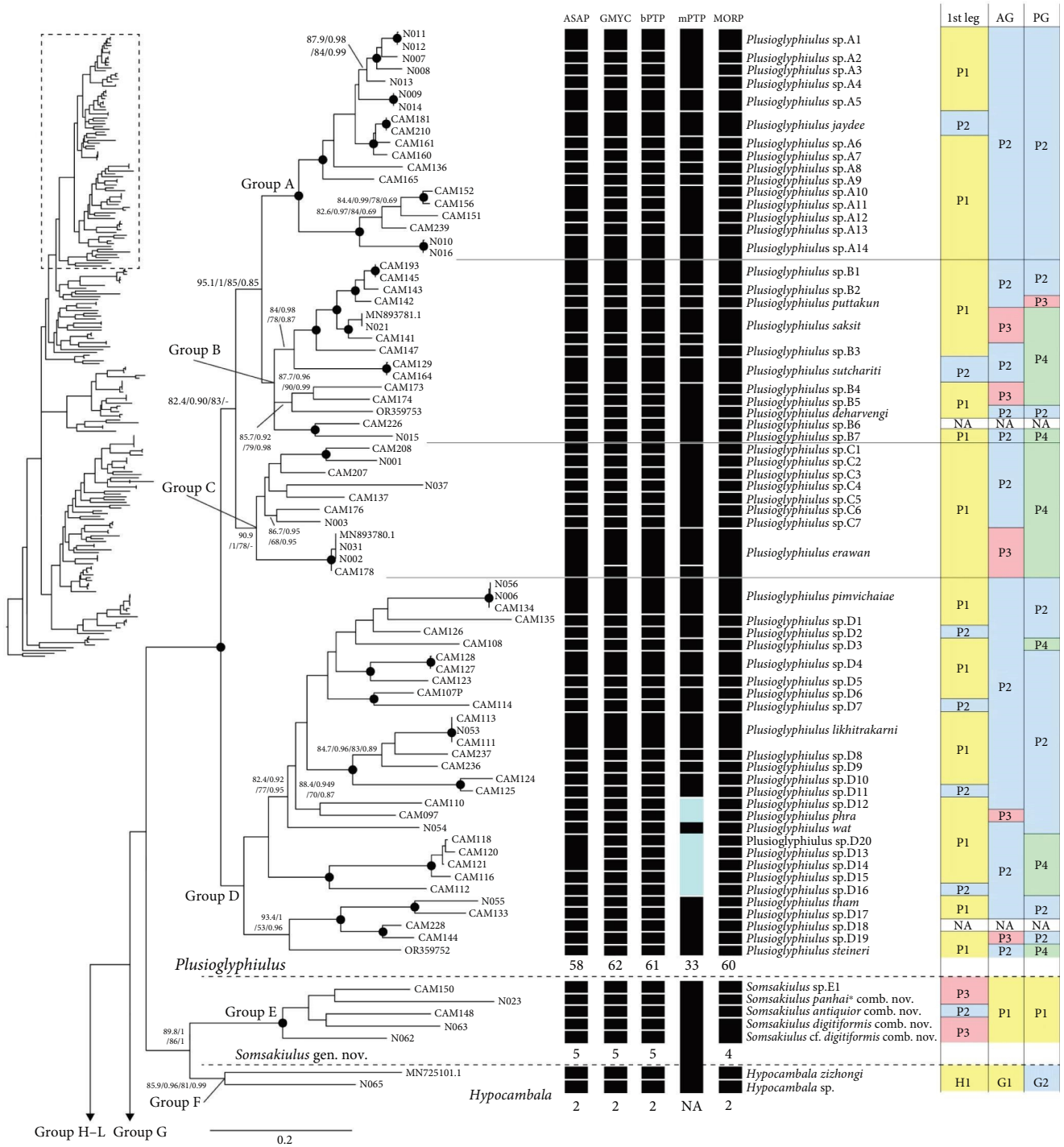

FIGURE 4: Maximum likelihood tree of the family Cambalopsidae indicating clade support level, species delimitation clustering results, and character states of male first legs, anterior (AG) and posterior gonopods (PG), featuring the genera *Plusioglyphiulus*, *Somsakiulus* gen. nov., and *Hypocambala*. Nodal support values are given as SH-aLRT/aBayes/ultra-fast bootstrap (IQ-TREE, ML)/posterior probability (MrBayes, BI). A black circle on a node indicates a clade with all well-supported values (SH-aLRT ≥ 80%, aBayes ≥ 0.95, BS ≥ 95%, PP ≥ 0.95). Abbreviations used on the figure are as follows: ASAP, assemble species by automatic partitioning; bPTP, Bayesian Poisson tree processes; GMYC, generalized mixed Yule coalescent model; MORP, morphological identification; mPTP, multi-rate Poisson tree processes. Blue box color indicates lumped MOTUs recognized by mPTP. An asterisk (*) indicates the type species of *Somsakiulus* gen. nov. Codes and colors of character states correspond to those in Figure 3 and Table 1.

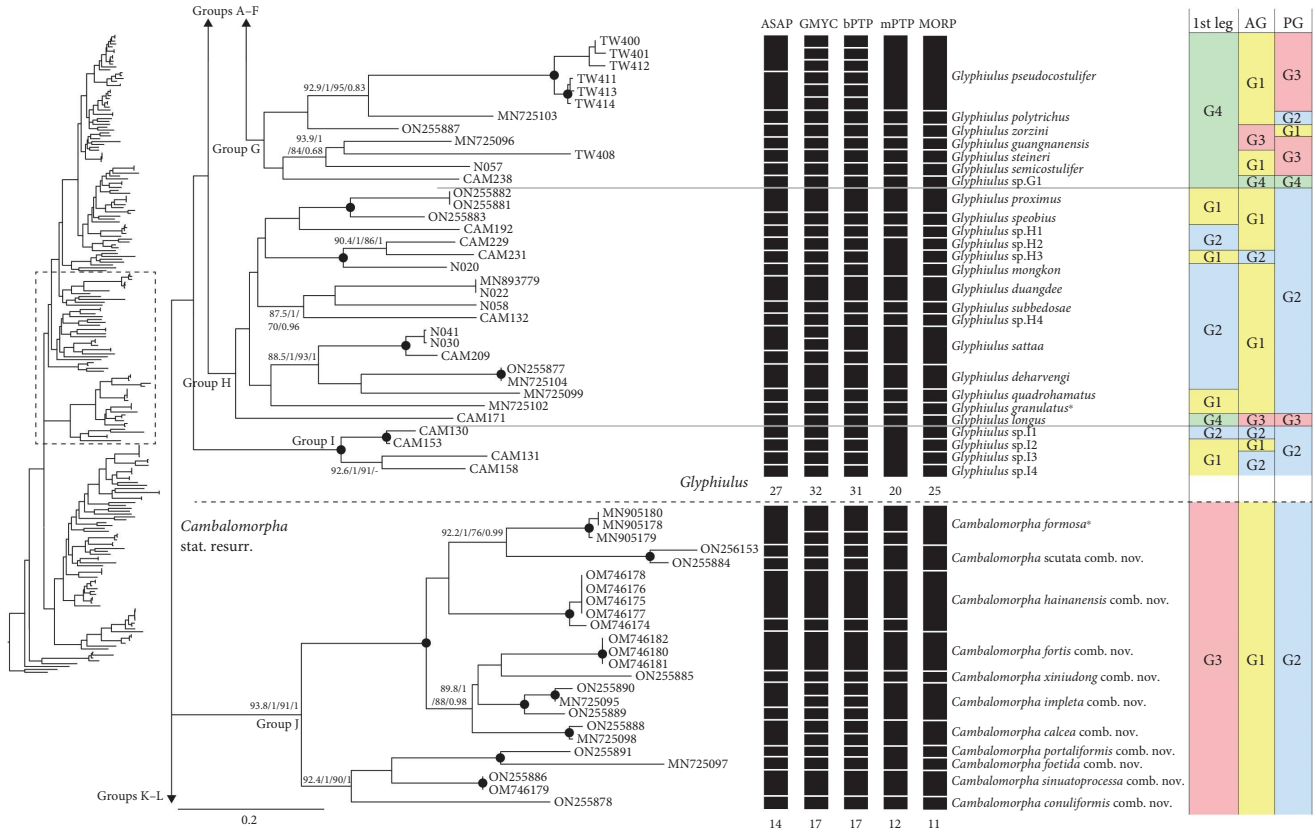

FIGURE 5: Maximum likelihood tree of the family Cambalopsidae indicating clade support level, species delimitation clustering results, and character states of male first legs, anterior (AG), and posterior gonopods (PG), featuring the genera *Glyphiulus* and *Cambalomorpha*. For abbreviations used on the tree, see Figure 4. Codes and colors of character states correspond to those in Figure 3 and Table 1. Asterisks (*) indicate the type species of the respective genus.

1821) of the family Cambalidae is a sister taxon to the clade Cambalopsidae + Pericambalidae.

All cambalopsid taxa in the phylogenetic analyses could be separated into 12 groups (A–L) within six genera (see below), in which the distribution of members within each phylogenetic group is shown in Figure 1. The uncorrected intrageneric and pairwise intergeneric distances for COI ranged between 14.50% and 18.92% and between 18.13% and 22.23%, respectively (Table 2). Percentage ranges of uncorrected pairwise interspecific and intraspecific distances for the partial COI gene fragments among taxa or OTUs in each cambalopsid genus in this study are given in Table 3.

The genus *Plusioglyphiulus* was separated into five groups: the first four groups (Groups A–D) were retrieved together as monophyletic, all with well-supported values, whereas the last group (E) was retrieved as a sister clade to the supported *Hypocambala* clade. As the clade of *Plusioglyphiulus* group E has a distinct set of morphological characters and was not closely phylogenetically related to the remaining *Plusioglyphiulus* taxa (Figures 3, 4), this clade is herein established as the new genus *Somsakiulus* (see below). The introduction of *Somsakiulus* gen. nov. resolves the polyphyletic nature of *Plusioglyphiulus*, rendering it monophyletic. Groups A and B of *Plusioglyphiulus* were each retrieved as monophyletic with mostly to all well-supported values, whereas groups C and D were not (Figure 4). The validity of *Somsakiulus* gen. nov. is also corroborated by the higher value of the intergeneric distance between *Plusioglyphiulus* and *Somsakiulus* gen. nov. (19.83%; Table 2) than the intrageneric distances of both *Plusioglyphiulus* (15.61%) and *Somsakiulus* gen. nov. (14.50%).

Glyphiulus was separated into four groups (Groups G–J), and they were not retrieved together as monophyletic. Only groups I and J were each retrieved as monophyletic with mostly to all well-supported values, whereas groups G and H were not (Figure 5). Most *Glyphiulus* species in group G belong to the *G. sinensis* (Meng & Zhang, 1993) subgroup of the *G. javanicus* Carl, 1911 species group. *Glyphiulus* group H belongs to the *G. granulatus* (Gervais, 1847) species group, except for *G. longus* Likhitrakarn et al., 2021 [30] which belongs to the *G. javanicus* species group. *Glyphiulus* group I belongs to the *G. granulatus* species group, whereas *Glyphiulus* group J belongs to the *G. formosus* (Pocock, 1895) subgroup of the *G. javanicus* species group (Supporting Information: Table S1). As the clade of *Glyphiulus* group J has a distinct set of morphological characters and is not closely phylogenetically related to the remaining *Glyphiulus* taxa (Figures 3, 5), a distinct genus is justified for this clade. The clade of group J contains *G. formosus*, the type species of *Cambalomorpha* Pocock, 1895, which is currently a junior synonym of *Glyphiulus* (synyonymized by Mauriès [65]). Therefore, this clade was

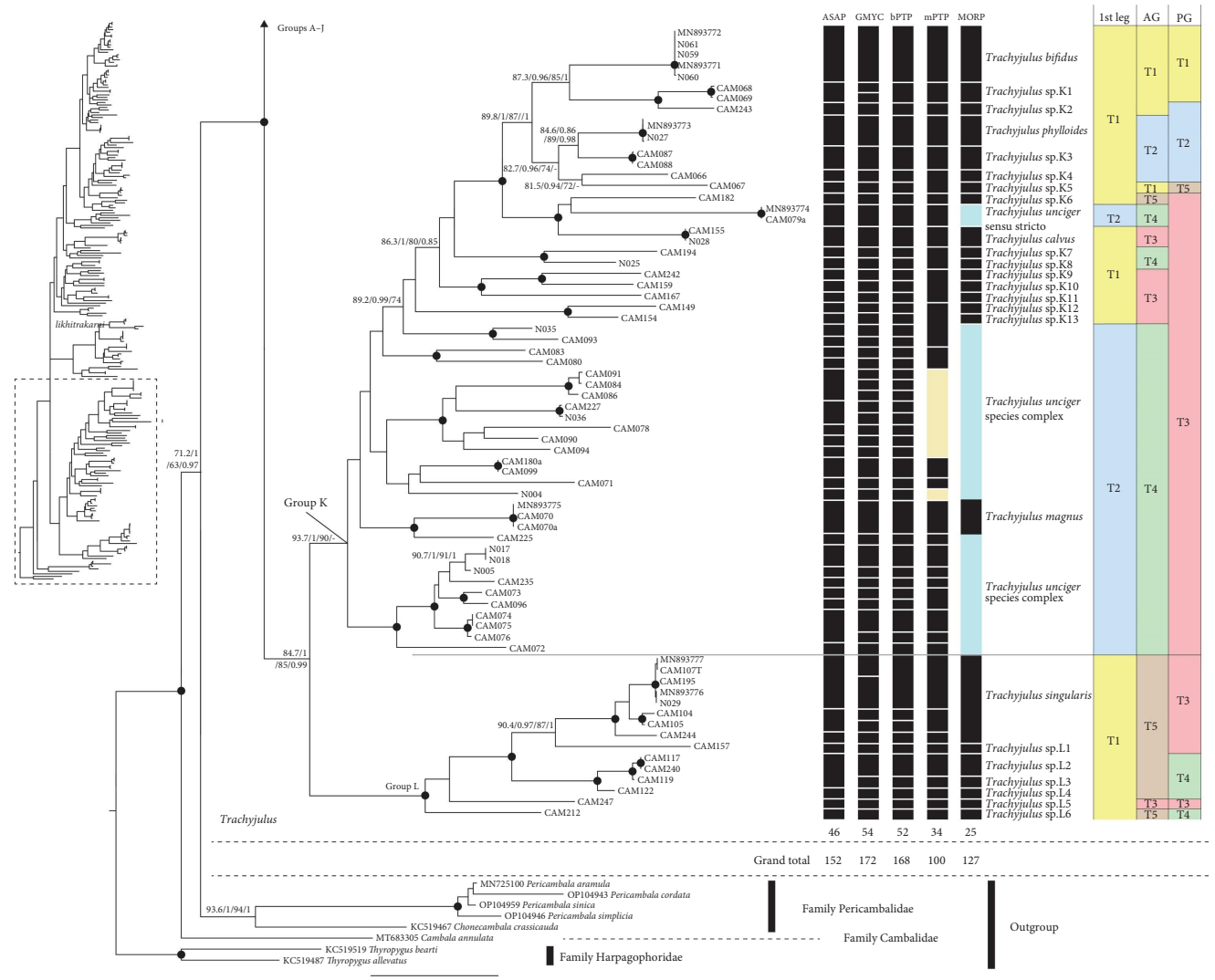

Figure 6: Maximum likelihood tree of the family Cambalopsidae indicating clade support level, species delimitation clustering results, and character states of male first legs, anterior (AG), and posterior gonopods (PG), featuring the genus *Trachyjulus*. Box colors indicate split (yellow) and lumped (blue) MOTUs recognized by each species delimitation method. For abbreviations used on the tree, see Figure 4. Codes and colors of character states correspond to those in Figure 3 and Table 1.

Table 2: Percentage of uncorrected pairwise intergeneric distances based on partial COI gene fragments among the cambalopsid genera in this study.

Genus	1	2	3	4	5	6
1. *Cambalomorpha*	**16.44**	—	—	—	—	—
2. *Glyphiulus*	21.87	**18.59**	—	—	—	—
3. *Hypocambala*	21.84	20.16	**17.31**	—	—	—
4. *Somsakiulus* gen. nov.	21.93	19.64	18.13	**14.50**	—	—
5. *Plusioglyphiulus*	22.00	20.43	19.76	19.83	**15.61**	—
6. *Trachyjulus*	22.23	21.18	21.41	21.76	21.68	**18.92**

Note: Intrageneric distances for COI are shown on the diagonal (bold).

designated as *Cambalomorpha*, which is resurrected as a valid genus herein (see below). The remaining groups (Groups G–I) were retained in the genus *Glyphiulus*. The recognition of *Cambalomorpha* is further supported by the higher value of the intergeneric distance between *Cambalomorpha* and *Glyphiulus* (21.87%; Table 2) than the intrageneric distances of both *Cambalomorpha* (16.44%) and *Glyphiulus* (18.59%).

Apart from *Hypocambala*, *Trachyjulus* was the only genus that was retrieved as monophyletic with mostly well-supported values and could be separated into two groups (Groups K–L).

Table 3: Percentage range of uncorrected pairwise interspecific and intraspecific distances based on partial COI gene fragments among taxa or OTUs in each cambalopsid genus in this study.

Genus	Interspecific distance		Intraspecific distance	
	% Range	% Average ± SD	% Range	% Average ± SD
1. *Cambalomorpha*	13.17–23.32	18.48 ± 2.71	0.00–7.00	2.43 ± 2.72
2. *Glyphiulus*	3.68–23.57	18.48 ± 2.06	0.00–4.12	1.54 ± 2.12
3. *Hypocambala*		17.31		NA
4. *Somsakiulus* gen. nov.	13.00–15.70	14.36 ± 0.98		NA
5. *Plusioglyphiulus*	0.90–21.82	15.77 ± 2.51	0.00–2.89	0.35 ± 0.85
6. *Trachyjulus* with *T. unciger* species complex	1.35–24.59	19.40 ± 2.75	0.00–16.33	2.34 ± 5.42
7. *Trachyjulus* with separate OTU within *T. unciger* species complex	1.35–25.71	18.86 ± 2.66	0.00–4.36	0.64 ± 1.24

Only group L was retrieved as monophyletic with all well-supported values, whereas group K was supported only by SH-aLRT and aBayes support values of the ML analysis (Figure 6). This genus has the highest intrageneric distance in this study (18.92%; Table 2). When considering separate OTUs within the *Trachyjulus unciger* Golovatch et al., 2012 [24] species complex, *Trachyjulus* exhibits the highest percentage range of interspecific distances (1.35%–25.71%; Table 3). In contrast, the percentage range of intraspecific distances within *Trachyjulus* is the highest (0.00%–16.33%), when lumping different OTUs under the same *T. unciger* species complex.

3.3. Species Delimitation Based on DNA Sequence Data. Species delimitation based on COI sequences revealed that the 213 specimens were assigned to 152 molecular operational taxonomic units (MOTUs) using the ASAP method, 172 using GMYC, 168 using bPTP, and 100 using mPTP (Figures 4–6). Across the four molecular delimitation methods (ASAP, GMYC, bPTP, and mPTP), most genera showed strong congruence with morphology-based delimitation (MORP), although minor discrepancies were detected among a few lineages. Within the genus *Plusioglyphiulus* (groups A–D), species delimitation analyses identified 58 MOTUs using ASAP, 62 with GMYC, 61 with bPTP, and 33 with mPTP, whereas morphological assessment recovered 60 distinct morphospecies (Figure 4). Among all methods, bPTP showed the highest congruence with morphological data, recovering 61 MOTUs that closely matched the 60 morphospecies. The only notable discrepancy involved *Plusioglyphiulus saksit* Golovatch et al., 2011 [39], where all delimitation analyses split the specimen CAM141 from MN893781.1 and N021, despite their shared morphological features. The GMYC and mPTP also differed slightly from ASAP and bPTP by separating the specimen CAM178 of *Plusioglyphiulus erawan* Golovatch et al., 2011 [39] from MN893780.1, N031, and N002, which were grouped in MORP. The GMYC and MORP results were fully congruent in Group A, both recognizing 15 MOTUs. In Group B, ASAP, GMYC, and bPTP yielded 12 MOTUs, whereas MORP identified 11 morphospecies, differing only by the separation of specimen CAM141 as an additional unit. Groups C and D exhibited complete agreement between molecular and morphological analyses, identifying 8 and 26 species, respectively. In the genus *Somsakiulus* gen. nov. (Group E), ASAP, GMYC, and bPTP each recovered five MOTUs, while MORP recognized four species. The discrepancy resulted from the molecular separation of specimens N062 and N063, which were morphologically indistinguishable. For the genus *Hypocambala* (Group F), molecular analyses (ASAP, GMYC, and bPTP) and morphology-based delimitation were in full agreement, each recognizing two species. Within the genus *Glyphiulus* (Groups G–I), ASAP produced eight MOTUs compared to seven morphospecies in Group G, splitting specimens TW400, TW401, and TW412 from TW411, TW413, and TW414. In Group H, ASAP and bPTP identified 15 MOTUs, whereas MORP recognized 14, grouping specimens N030, N041, and CAM209 together. Group I showed complete congruence among all methods, identifying four species. For the genus *Cambalomorpha* (Group J), mPTP identified 12 MOTUs, which closely matched the 11 morphologically defined species. Finally, within the genus *Trachyjulus* (Groups K–L), mPTP recovered 25 and 9 MOTUs, respectively, corresponding to 18 and 7 morphospecies. The significant disparity between molecular and morphological results is due to the *T. unciger* species complex, in which morphologically similar specimens were consistently split into multiple MOTUs by all four species delimitation methods.

3.4. Taxonomy.

Class Diplopoda Blainville in Gervais, 1844
Order Spirostreptida Brandt, 1833
Family Cambalopsidae Cook, 1895
Subfamily Cambalopsinae Cook, 1895

3.4.1. Genus Cambalomorpha Pocock, 1895 stat. resurr. Cambalomorpha Pocock, 1895 [66]: 363 (D, K).

Cambalomorpha–Cook in Cook & Collins, 1896 [67]: 6 (L); Silvestri, 1923 [68]: 188 (K); Attems, 1926 [69]: 207 (K); Attems, 1938 [70]: 265 (M); Verhoeff, 1936 [71]: 50 (K); Carl, 1941 [72]: 288 (M); Jeekel, 1971 [73]: 108 (L).

Glyphiulus (part)–Mauriès, 1970 [65]: 516 (L), synonymy of *Cambalomorpha*; Hoffman, 1980 [74]: 91 (L); Jeekel, 2004 [23]: 51 (L).

3.4.1.1. Diagnosis. Male legs I significantly reduced to small appendages consisting of two or three segments, bearing a pair of medial coxosternal hooked processes in medial contact. Male legs II normal with small penes. Male legs III modified, with a generally slender and extended coxa. A typical carinotaxic

formula of the collum I-III+P+M. Metatergal crest well-developed, with crests segmented into two transverse rows of tubercles, carinotaxic formula 2/2+I/i+3/3+I/i+2/2. Ozoporiferous tubercles exhibiting rounded tips, larger than other tubercles. Anterior gonopods reduced to a plate-like coxosternum, often with elongated mesal processes that are distinctly elevated above the telopodites. Telopodites unsegmented, laterally positioned, curved, and mobile, bearing several distal setae and a field of microsetae at the base. Posterior gonopods significantly compressed, exhibiting a subflagelliform or plumose apical flagellum.

3.4.1.2. Type Species. Cambalomorpha formosa Pocock, 1895, by original designation.

3.4.1.3. Species Included Based on Phylogenetic Analyses and Morphology.

Cambalomorpha calcea (Jiang, Guo, Chen & Xie, 2018) **comb. nov.**

Cambalomorpha conuliformis (Zhao & Liu, 2022) **comb. nov.**

Cambalomorpha foetida (Jiang, Guo, Chen & Xie, 2018) **comb. nov.**

Cambalomorpha formosa Pocock, 1895

Cambalomorpha fortis (Jiang, Chen & Xie, 2022) **comb. nov.**

Cambalomorpha hainanensis (Jiang, Chen & Xie, 2022) **comb. nov.**

Cambalomorpha impleta (Jiang, Guo, Chen & Xie, 2018) **comb. nov.**

Cambalomorpha portaliformis (Zhao & Liu, 2022) **comb. nov.**

Cambalomorpha scutata (Zhao & Liu, 2022) **comb. nov.**

Cambalomorpha sinuatoprocessa (Zhao & Liu, 2022) **comb. nov.**

Cambalomorpha xiniudong (Zhao & Liu, 2022) **comb. nov.**

3.4.1.4. Additional Species Included Based on Morphology.

Cambalomorpha echinoides (Golovatch, Geoffroy, Mauriès & van den Spiegel, 2011) **comb. nov.**

Cambalomorpha pulcher (Loksa, 1960) **comb. nov.**

Cambalomorpha recticulla (Zhang & Li, 1982) **comb. nov.**

3.4.1.5. Remarks. The genus *Cambalomorpha* was established by Pocock [66] to accommodate a new species, *Cambalomorpha formosa* from Hong Kong, which he designated as the type species. In his original description, Pocock stated that the only difference from *Glyphiulus* was the structure of the tergal crests, with segments possessing only nine crests: three between the ozoporiferous tubercle rows and two on each side below. Unfortunately, this description was based solely on a female specimen, which limited its diagnostic utility. In the same work, Pocock also included *Cambala feae* Pocock, 1893 and *Cambala doriae* Pocock, 1893, both from Myanmar, in his new genus, although both species were subsequently transferred to *Podoglyphiulus* by Mauriès [65]. Silvestri [68] opined that *Cambalomorpha* could be considered a subgenus of *Glyphiulus* and placed one of his new species in this subgenus. Subsequently, based on the limited information available, Mauriès [65] formally synonymized *Cambalomorpha* with *Glyphiulus*.

More recently, comprehensive studies on the Chinese members of *Glyphiulus* have provided new insights, and Chinese species previously assigned to the *G. javanicus* species group were re-assessed [35, 36]. These analyses, integrating both morphological and DNA sequence data, revealed that these species could be reliably divided into two distinct lineages: the newly circumscribed *G. formosus* and *G. sinensis* species groups. The *G. formosus* species group, corresponding to the monophyletic Group J in our phylogenetic analysis, which is separated from the remaining *Glyphiulus* species, is distinguished by a unique combination of characters, including a specific carinotaxy formulae of the collum (I–III+P+M) and metaterga (2/2+I/i+3/3+I/i+2/2) and a particular structure of the male first legs. These diagnostic features are identical to those defined here for *Cambalomorpha*. This strong congruence between recent phylogenetic findings and the original (though incomplete) concept of Pocock [66] provides robust justification for the resurrection of *Cambalomorpha* as a valid genus. We further note that *Cambalomorpha* in this sense is only restricted to the former *G. formosus* species group, different from the suggestion by Golovatch et al. [15] to apply *Cambalomorpha* to the whole *G. javanicus* species group. This is because other *Glyphiulus* species in the *G. javanicus* species group (Group G) are not phylogenetically related to the *Cambalomorpha* clade (Figure 5).

3.4.2. Genus Somsakiulus Seesamut & Likhitrakarn, gen. nov.

3.4.2.1. Diagnosis. Male legs 1 strongly reduced; coxosternum with a short, medial, hook-shaped process; telopodites 2- or 3-segmented, each terminating in a small, sharp claw. Male legs 2 typically enlarged (modestly to strongly), with high coxae; penes broad, oblong-subtrapeziform or subtriangular, fused basally. Male legs 3 modified, with coxae elongated and telopodites shortened and compact.

Collum and body ring 2 often strongly enlarged, subequal in width to posterior body third, resulting in a conspicuously narrow postcollar constriction. Carinotaxy of collum somewhat variable. Crests never obliterated or reduced, often subdivided into 2–3 parts, with 1–3 intercalary tubercles or short crests; typically 15 or 17 crests reaching anterior margin. Metatergal crests well-developed, divided into two transverse rows of tubercles; carinotaxic formula 2/2+I/i+3/3+I/i+2/2. Ozoporiferous tubercles with rounded tips, larger than other tubercles.

Anterior gonopods reduced to a plate-like coxosternum, similar to *Glyphiulus*, with a concave notch separating a pair of high, apicomesal, terminally rounded processes from lower, basolateral, terminally rounded processes. Telopodite 1-segmented, movable, stout, typically curved, and setose.

Posterior gonopods smaller than anterior ones, complex. Coxites well-separated from sternum, densely setose paramedially. Each anterior coxal process elongate, distally represented by an apical flagellum or fovea. Telopodite 1-segmented, clearly separated, rather erect.

3.4.2.2. Type Species. Plusioglyphiulus panhai Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2011, by present designation.

3.4.2.3. Species Included.

Somsakiulus panhai (Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2011) **comb. nov.**

Somsakiulus antiquior (Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2011) **comb. nov.**

Somsakiulus digitiformis (Likhitrakarn, Golovatch, Srisonchai, Brehier, Lin, Sutcharit & Panha, 2018) **comb. nov.**

Somsakiulus sp. E1.

3.4.2.4. Etymology. The new genus is named in honor of Professor Somsak Panha, a pioneering and distinguished Thai malacologist, in recognition of his immense contributions to the study of invertebrate biodiversity, including millipedes in Southeast Asia. The suffix '-iulus' is a conventional ending for juliform millipedes. The gender is masculine.

3.4.2.5. Remarks. The establishment of the new genus *Somsakiulus* is strongly supported by our molecular phylogenetic analysis, which demonstrates that the species included herein form a distinct and well-supported monophyletic clade (Group E). In our phylogenetic tree, this clade is not the sister group to the remaining species of *Plusioglyphiulus* (Groups A–D). Instead, *Somsakiulus* gen. nov. is recovered as a sister lineage to a clade of two *Hypocambala* species (Figure 4). This phylogenetic placement renders the previous, broader concept of *Plusioglyphiulus* paraphyletic, thus necessitating the erection of a new genus to maintain monophyly.

This molecular divergence is corroborated by a unique combination of morphological characters as outlined in the diagnosis. Keys among these (Table 4) are the strongly reduced first pair of male legs featuring a short coxosternal hook and 2- or 3-segmented telopodites, the conspicuously enlarged collum and second body segment, which create a narrow and distinct postcollar constriction, and the specific conformation of both anterior and posterior gonopods (both types P1; Figure 3). The unique combination of morphological character states corroborates the molecular divergence. For example, some character states are shared with members of *Glyphiulus* [21, 32, 35], such as the reduced metatergal carinotaxy (i.e., the presence of only two, not the usual three, transverse rows of crests), a small central outgrowth on the first male legs, and simple, plate-like anterior gonopods. However, when viewed together, these shared and other unique derived character states clearly define the monophyly of *Somsakiulus* gen. nov. and distinguish it from both *Plusioglyphiulus* sensu stricto and *Glyphiulus*.

The new genus is geographically restricted to Myanmar and western Thailand. At present, *Somsakiulus* gen. nov. comprises three described species, all transferred from *Plusioglyphiulus*, and at least one undescribed species identified in our analysis.

4. Discussion

4.1. Phylogenetic Relationship and Classification of the Cambalopsidae. This study is the first to construct the molecular phylogeny of the cave millipede family Cambalopsidae. It is also the most comprehensive in terms of genera and species diversity and the distribution range of specimens from East and mainland Southeast Asia. Although the use of only one mitochondrial DNA barcode (COI) marker yielded limited support for deeper nodes, the current phylogeny could imply the phylogenetic relationship of the cambalopsid genera to some extent. Our results showed that representative species of *Hypocambala* were retrieved as a sister clade to *Somsakiulus* gen. nov., the relationship of which challenges the current morphology-based systematics. *Hypocambala* was deemed to be morphologically closely related to *Glyphiulus*, due to the similarity in the male first legs to the *G. javanicus* species group [18], and the sharing of anterior gonopod type G1 and posterior type G3 (Figure 3 and Supporting Information: Table S1). In contrast, species of *Somsakiulus* gen. nov. were formerly classified in *Plusioglyphiulus*, due to a strongly carinate collum with its crests often subdivided into 2–4 parts, a prominent feature of *Plusioglyphiulus*, coupled with complex, usually elongate and non-compressed posterior gonopods retaining evident telopodites, a conformation more aligned to that in *Plusioglyphiulus*. However, these *Somsakiulus* gen. nov. species also show a distinct appearance similar to some *Glyphiulus* species in their reduced metatergal carinotaxy (i.e., the presence of only two, not the usual three, transverse rows of crests), a small central outgrowth on male leg 1, and simple, plate-like anterior gonopods that closely resemble those found in the majority of *Glyphiulus* species [21, 39]. Consequently, Golovatch et al. [39] suggested that these species of *Somsakiulus* gen. nov. (recognized as *Plusioglyphiulus*) demonstrate a transition between the *G. javanicus* species group and *Plusioglyphiulus* sensu stricto. The discrepancy between morphology-based and molecular systematics among *Glyphiulus*, *Hypocambala*, *Plusioglyphiulus*, and *Somsakiulus* gen. nov. was therefore evident in this study, and there are still no synapomorphies that unite the phylogenetically related *Hypocambala* and *Somsakiulus* gen. nov.

With the introduction of *Somsakiulus* gen. nov., the remaining *Plusioglyphiulus* species were retrieved together as monophyletic (Figure 4). Based on the current phylogeny, the synapomorphies of the speciose genus *Plusioglyphiulus* could be defined as given in Table 4. A number of species groups within *Plusioglyphiulus* were also proposed by Golovatch et al. [16], but the system was not further adopted in later studies [12, 21, 39]. The present phylogenetic analysis fails to support the validity of the *P. deharvengi* species group, a species assemblage previously proposed by Golovatch et al. [16]. In our phylogenetic reconstruction (Figure 4), two constituent members of this group, *P. deharvengi* Golovatch et al., 2009 [16] and *P. steineri* Golovatch et al., 2009 [16], are not retrieved together as a monophyletic lineage. This phylogenetic placement strongly suggests that the morphological characters used to define the *P. deharvengi* species group, such as the long and well-developed coxal processes of the anterior gonopods and the presence of distinct arms on the posterior gonopods, are homoplasious and represent instances of convergent evolution rather than shared ancestry.

As the genus *Glyphiulus* was not retrieved as monophyletic, synapomorphies of *Glyphiulus* are still not available from this study. Only one group (Group I) was retrieved as a supported clade (Figure 5). The remaining groups, although still not supported as a clade, aligned with different species groups recognized in previous studies. Group G belongs to the *G. javanicus*

Table 4: Comparison of diagnostic characters, autapomorphies and geographical distribution for genera of the Cambalopsidae in this study.

Diagnostic characters and geographical distribution	***Trachyjulus* Peters, 1864**	***Cambalomorpha* Pocock, 1895, stat. resurr.**	***Glyphiulus* Gervais, 1847**	***Somsakiulus* gen. nov.**	***Plusioglyphiulus* Silvestri, 1923**
Male legs 1 (1st leg)	Strongly reduced to a broad transverse coxosternum with a pair of central, often completely fused, hook-shaped coxal processes, flanked by 1-segmented, rudimentary telopodites	Strongly reduced; with 2- or 3-segmented telopodites; coxosternal processes paired, hooked, in medial contact	Highly variable by species group: *G. granulatus* species group: strongly reduced, 1- or 2-segmented telopodites, sternal prongs widely separated; *G. javanicus* species group: subnormal, 4- or 5-segmented telopodites, coxal processes medially contiguous but not fused	Strongly reduced; 2- or 3-segmented telopodites with a small claw; coxosternum with a short, medial hook	Highly variable; strongly reduced, with a single, high, strong, median unciform sternal process directed frontally; rudimentary, 1- or 2-segmented or completely reduced telopodites
Male legs 2	Nearly normal; only coxae evidently elongated	Normal or nearly normal	Normal or nearly normal	Typically enlarged; coxae high and large; penes broad, fused basally	Typically strongly enlarged and longitudinally flattened
Male legs 3	Slightly reduced; coxae very evidently elongated (at least 2x as long as broad)	Modified; coxae slender and extended	Modified; coxae slender and extended	Modified; coxae elongated; telopodites short and compact	Usually with elongated coxae and shortened, compact telopodites
Collum and collum carinotaxy	Collum smooth (acarinate) or with faint traces of impression crests on the posterior edge	Carinotaxic formula fixed: 1–3+P+M	Carinotaxy variable by species-group: *G. granulatus* species group: typically 1–6+7a+pc+ma; *G. javanicus* species group sensu stricto: typically 1–3(4, 5)+P+M; *G. sinensis* subgroup: typically 1–4+5c+6a+pc+ma	Collum and second body ring conspicuously enlarged, creating a narrow and distinct postcollar constriction. Carinotaxy variable; crests never reduced, often subdivided; typically 15 or 17 crests on anterior margin	Highly variable, always strongly carinate; crests often subdivided into 2–4 parts, often with 1–3 intercalary tubercles or short crests; usually 10 crests reaching anterior margin
Mid-body (metatergal) carinotaxy	Well-developed and strongly carinate; crests often nearly complete, almost undivided; typical formula: 10–3/10–3+I/i+5/5+I/i+10–3/10–3	Well-developed; crests segmented into two transverse rows of tubercles; typical formula: 2/2+I/i+3/3+I/i+2/2	Prominently crested, varying by species group: *G. granulatus* species group typically with anteriorly bifurcated median crest (3(2) +I+4+I+3(2)); *G. javanicus* species group with a simple median crest (2(1)/2(1)+I/i+3/3+I/i+2(1)/2(1))	Well-developed; crests segmented into two rows of tubercles; formula: 2/2+I/i+3/3+I/i+2/2	Well-developed; crests typically arranged in three transverse rows, but sometimes only two; formula variable
Anterior gonopod (AG)	Coxosternum supporting two, only basally contiguous, diverging, subtriangular halves; each with a large, 1-segmented telopodite subtended by 1 or 2 coxal processes (medial and lateral)	Reduced to plate-like coxosternum, often with elongated mesal processes distinctly elevated above telopodites; telopodite 1-segmented, lateral, movable	Reduced to plate-like coxosternum; telopodite 1-segmented, lateral, movable	Plate-like coxosternum with notch separating high apicomesal and lower basolateral processes; telopodite 1-segmented, stout, movable	Highly variable; can be deeply divided into coxosternal processes or simple and shield-like (resembling *Glyphiulus*). Telopodite is 1-segmented and movable

Table 4: Continued.

Diagnostic characters and geographical distribution	***Trachyjulus* Peters, 1864**	***Cambalomorpha* Pocock, 1895, stat. resurr.**	***Glyphiulus* Gervais, 1847**	***Somsakiulus* gen. nov.**	***Plusioglyphiulus* Silvestri, 1923**
Posterior gonopod (PG)	Contiguous medially; usually crowned with a lateral setose field and a higher, medial, complex flagellum (rarely absent)	Strongly compressed; with subflagelliform or plumose apical flagellum	Strongly compressed; with subflagelliform or plumose distal process	Smaller than anterior, complex; coxal process elongate, ending in flagellum or fovea; telopodite 1-segmented, erect	Complex, usually elongate, not compressed, retaining evident telopodites, and more elaborate than in *Glyphiulus*; often with an apical fovea but lacking the plumose flagella characteristic of *Glyphiulus*
Geographical distribution	Nepal, India, and Sri Lanka in the west, through Bangladesh and Myanmar, to Vietnam, Thailand, Peninsular Malaysia, Singapore, and Indonesia (Sumatra and Java) in the east; one species (*T. calvus*) pantropical	China	Southeast Asia (esp. Thailand, Laos) and Southern China; one species (*G. granulatus*) pantropical	Myanmar and Western Thailand	Southeast Asia (Myanmar, Thailand, Laos, Cambodia) to Borneo

Note: Hypocambala was excluded due to a limited number of taxa in the analysis. Autapomorphies for these genera are given in bold.

species group (*sinensis*-subgroup), and Group H (except for *G. longus*) along with Group I belongs to the *G. granulatus* species group (Supporting Information: Table S1). Furthermore, all species of *Cambalomorpha* included in this study, formerly belonging to the *G. formosus* species group (see Remarks of *Cambalomorpha*), are also retrieved as a monophyletic lineage (Figure 5). The synapomorphies defining *Cambalomorpha* are summarized in Table 4. Future multi-locus phylogeny constructed from more mitochondrial and nuclear gene fragments are required to resolve deeper relationships among *Cambalomorpha* and different *Glyphiulus* groups, and clarify whether the current species groups of *Glyphiulus* are phylogenetically supported as in previous works [35, 36].

All species of *Trachyjulus* were also retrieved together as monophyletic (Figure 6), with synapomorphies defined as in Table 4. This genus is the sole member of the subfamily Cambalopsinae, whereas the remaining genera in this study (*Cambalomorpha*, *Glyphiulus*, *Hypocambala*, *Somsakiulus* gen. nov., and *Plusioglyphiulus*) belong to the subfamily Glyphiulinae ([23]; this study). The primary morphological differences used to distinguish between these two subfamilies are the configurations of (1) the gnathochilarium and (2) the telopodite of the anterior gonopod. Members of the Cambalopsinae are characterized by a gnathochilarium with an undivided or indistinctly divided mentum, and a telopodite of the anterior gonopod generally long and slender, sometimes bifid, longer or as long as the paramedian processes which extend the coxosternite. In contrast, members of the Glyphiulinae are characterized by a gnathochilarium with a divided mentum, in which a prementum is separated from a eumentum by a distinct suture, and a telopodite of the anterior gonopod generally small, articulating laterally on the side of the much larger coxosternal plate [75]. However, the specific gnathochilarium configuration is not exclusive to all members of that respective subfamily. For example, two species of *Trachyjulus* (*T. singularis* (Attems, 1938) and *T. beroni* Golovatch et al., 2012 [24]) possess a divided gnathochilarium [24, 28], whereas one *Glyphiulus* species (*G. deharvengi* Golovatch et al., 2007 [15]) and one *Plusioglyphiulus* species (*P. jaydee* Golovatch et al., 2011 [17]) possess an undivided gnathochilarium [38, 39]. Likewise, some unidentified *Glyphiulus* and *Trachyjulus* species in this study have a telopodite of the anterior gonopod not conforming with that of their respective subfamily (anterior gonopod types G2 and G3 in *Glyphiulus*; type T6 in *Trachyjulus*; Figure 3). Therefore, the different configurations of the gnathochilarium and the telopodite of the anterior gonopod could not be assuredly regarded as subfamilial synapomorphies. The validation of the subfamilial classification of the Cambalopsidae also requires the resolved phylogeny along with the discovery of new shared derived morphological characters of each subfamily.

4.2. Species Delimitation and Cryptic Diversity in the Cambalopsidae. Our comparative analysis implemented four single-locus delimitation methods (ASAP, GMYC, bPTP, and mPTP) on COI data from 213 specimens of six cambalopsid cave millipede genera from mainland Southeast Asia. The results reveal both congruence and divergence between molecular-based hypotheses and traditional morphology-based taxonomy. The high variability in number of MOTUs among different methods, ranging from 100 (mPTP) to 172 (GMYC), highlights the sensitivity of species delimitation outcomes to the choice of algorithm, as noted in previous studies [57, 76, 77]. For instance, the bPTP method showed the greatest concordance with morphology in *Plusioglyphiulus*, differing by only one MOTU. In contrast, GMYC often resulted in over-splitting, and mPTP over-lumping, likely due to differences in their assumptions about lineage branching patterns and rate heterogeneity [58, 59]. The results in this study echo findings in other invertebrate taxa, both with high dispersal capacity such as earthworms [77, 78] and freshwater prawns [79], and with low dispersal capacity such as land snails [80] and centipedes [81], where single-locus methods detected cryptic lineages not evident from morphology.

In the genus *Trachyjulus*, large discrepancies between morphological and molecular results, particularly the extreme MOTU inflation in the *T. unciger* species complex, underscore how morphological conservatism can mask genetic divergence [82, 83]. On the other hand, the high congruence between morphological and molecular results in genera like *Plusioglyphiulus* and *Somsakiulus* gen. nov. suggests more stable species boundaries, possibly due to deep species divergence or divergent selection [84, 85]. Yet, even in these taxa, minor discrepancies (e.g., between the specimens N063 and N062 in *Somsakiulus digitiformis*) reveal the subtlety with which molecular approaches can detect hidden species diversity. Alternatively, different levels of congruence may be partially attributed to the relatively small sample sizes analyzed for some genera (e.g., *Hypocambala* and *Somsakiulus* gen. nov.) compared to others in this study, which could affect the species delimitation results and the resolution to detect cryptic species [86, 87].

The *T. unciger* species complex stood out as a notable example of cryptic diversification among the various taxa examined in this study. While populations from several localities show highly similar gonopod morphology, leading to their previous assignment to a single species, our molecular data reveal deep interspecific genetic divergences. This indicates the presence of cryptic species, a phenomenon frequently observed in cavernicolous animal taxa where morphological evolution can be conservative or subject to convergence [82, 88, 89]. Similar cases of cryptic diversity have been documented in other millipedes, where significant genetic structuring and deep evolutionary lineages undetected by morphological analysis alone, especially that of the gonopod, reinforce the need for integrative approaches [90, 91]. Likewise, the detection of divergent lineages could lead to the description of new species based on integrated evidence of genetic data and a revised morphological circumscription [92]. The deep genetic divergence observed within the *T. unciger* species complex, in accordance with other millipede studies, highlights the challenges of defining species boundaries in lineages that seem conserved in form. Together, the observation that the *T. unciger* species complex includes multiple cryptic lineages emphasizes the need for molecular delimitation methods along with further morphological approaches, either using previously overlooked somatic characters or applying morphometric analysis [93–95],

in order to accurately determine species boundaries in millipedes.

4.3. Significance of Gonopod and Peripheral Characters in Systematics of the Cambalopsidae. The structure of the gonopods (both anterior and posterior) remains the fundamental standard for species delimitation and classification of the Cambalopsidae (e.g., [13, 35]). The high diversity and complexity of their constituent parts—such as processes, flagella, and setose fields—are often highly distinctly species-specific, possibly indicative of sexual selection mechanisms and reproductive isolation [96, 97]. In the present study, numerous morphospecies and some genera could be recognized based on unique gonopodal conformations, which, despite showing variation in fine details, were largely congruent with the molecular data. However, this study also highlights the significant limitations of gonopods, particularly in cases of cryptic diversification, as exemplified by the *T. unciger* species complex and other cases as mentioned above. These cases serve as a significant warning that even the most reliable sexual characters, such as gonopods, may be insufficient to reveal the true extent of biodiversity without supporting molecular evidence. This issue of morphological conservatism, or "gonopod monotony," has been documented in numerous other genera, such as *Orthomorpha* Bollman, 1893 (Polydesmida: Paradoxosomatidae) [98] and *Nepalmatoiulus* Mauriès, 1983 (Julida: Julidae) [99].

Our phylogenetic results also elevate the importance of non-gonopodal or peripheral characters [100], especially the conformation of the male first legs and carinotaxy, as effective tools for diagnosing at both specific and supra-specific levels. The male leg 1 has demonstrated its significance as a reliable indicator of some cambalopsid genera. The establishment of the new genus *Somsakiulus* and the resurrection of *Cambalomorpha* are both founded on the presence of the unique male leg 1 structures within each genus. Although not retrieved as monophyletic in this study, the internal subdivision of *Glyphiulus* into the *G. granulatus* and *G. javanicus* (sensu lato) species groups is predominantly based on this character [15, 17, 18, 35, 38]. On the other hand, the cryptic and non-monophyletic *T. unciger* species complex shares the same conformation of the male first legs, rendering this character homoplasious or plesiomorphic for this group. This suggests that the evolution of male leg 1 occurred early in the diversification of these lineages and has remained more conserved than the often rapidly evolving, species-specific gonopod structures.

Carinotaxy of the collum and metaterga has shown significant potential for diagnosis in the millipede family Cambalopsidae. The patterns on the collum, in particular, can be highly effective for species-level identification within diverse genera like *Plusioglyphiulus* [12, 16, 39]. Even in *Glyphiulus*, where crests can be less prominent, interspecific differences are frequently evident (e.g., [13, 36]). In contrast, the genus *Cambalomorpha* is defined by a remarkably stable collum formula (I–III+P+M) (Supporting Information: Table S1), which serves as a synapomorphy for the lineage. Therefore, the use of carinotaxy requires caution, as these structures are susceptible to reduction or even complete obliteration as a result of troglomorphism—a distinct example of convergent evolution that can obscure true phylogenetic signals [101].

Data Availability Statement

The data that supports the findings of this study are available in the supporting information of this article.

Conflicts of Interest

The authors declare no conflicts of interest.

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Supporting Information

Table S1: List of specimens used in this study in relation to their voucher code, locality, morphological characters, GenBank accession number, and BOLDSYSTEMS identification. (*Supporting Information*)

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