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On a taxonomic feature that has been overestimated in classification practice: an integrative taxonomic revision of *Stephoblemmus* Saussure, 1877 based on morphology and molecular phylogeny (Orthoptera: Grylloidea; Gryllidae; Gryllinae)

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Abstract

The hemispherical head is prevalent in Gryllinae crickets, so the rare crickets that have a unique form of head will be extremely unusual. In previous studies, this special feature can be one of the important features to distinguish and identify these crickets. But does this particular head shape truly reflect a clear-cut taxonomic relationship? The species of the genus *Loxoblemmus* have a typical truncate head; species of the genus *Stephoblemmus* have a more exaggerated truncate head, with the frontal end even extending into a lamellar. The genus *Mitius* is relatively unusual in that species of this genus have both globose or truncate heads. How are these species related? Does the cephalic shape perfectly reflect the natural classification of these species? Based on these questions, the study applied species definition and morphological classification to explore the intergeneric and intrageneric species relationships of the genera *Mitius*, *Stephoblemmus*, and *Loxoblemmus*, and derived the following main conclusions: (1) *Mitius* and *Stephoblemmus* are related and distinct from *Loxoblemmus*; (2) *Mitius* species bear two types of frons (truncated and rounded), but this feature disallows them to be classified as natural groups; (3) one genus synonym and three species synonyms are raised (*Mitius* Gorochov, 1985 **syn. n.**, *Mitius splendens* (Shiraki, 1930) **syn. n.**, *Mitius eryuanensis* Yuan, Xie & Liu, 2021 **syn. n.** and *Mitius brevipennis* Yuan, Ma & Gu, 2022 **syn. n.**), and seven new status combinations are proposed (*Stephoblemmus blennus* (Saussure, 1877) **comb. n.**, *Stephoblemmus castaneus* (Chopard, 1937) **comb. n.**, *Stephoblemmus enatus* Gorochov, 1994 **comb. n.**, *Stephoblemmus flavipes* (Chopard, 1928) **comb. n.**, *Stephoblemmus minor* (Shiraki, 1911) **comb. n.**, *Stephoblemmus minutulus* (Yang & Yang, 1995) **comb. n.** and *Stephoblemmus vaturu* (Otte & Cowper, 2007) **comb. n.**). The studies indicated that frons shapes that appear to be significantly different might not always reflect the correct Gryllinae species relationships and a combination of more taxonomic features and taxonomic techniques is needed often to reveal the true taxonomic relationships.

Keywords

1.   Introduction

Taxonomy involves delimitating closely related species and grouping similar species into higher taxonomic units (Bailey, 1994; Nickerson et al., 2013). Taxonomists have to carefully choose appropriate characteristics of the species (usually morphological traits) and different selections of characteristics often result in distinct classification systems (Mayr, 1969). When a small group of species presents one or two very unique features (e.g., filiform hairs on foretibia, ectoparamere enormously enlarged, without tegmina), some taxonomy practice tends to establish a new higher-ranked taxon (e.g., *Fodigryllus* He, 2022, *Flospes* Ma & He, 2022 and *Goniogryllus* Chopard, 1936) for these species (Chopard, 1936a; He et al., 2022; Liu & He, 2022). Alpha taxonomy that creates new units of classification by one or two unique features merely distinguishes between species, but does not make the classification consistent with the true species

relationships and might be problematic from a phylogenetic perspective. However, the established taxon might be polyphyletic if the feature has undergone convergent evolution, or it might render another taxon (i.e., the remaining collection of species without the feature) paraphyletic (Fig 1a).

The head shape of field crickets is one example. Most field cricket (Orthoptera: Gryllidae; Gryllinae) species have round, smooth heads that look cute and cuddly (Fig. 1b-c). Still, there are a few species with unusual head morphology—with slanted facial truncations or crown ornaments (Fig. 1d-e). These "uncommon" traits were the key features based on which taxonomists erected new genera; *Stephoblemmus* Saussure, 1877 is one of them—the species *Stephoblemmus humbertiellus* Saussure, 1877 has an obliquely truncated frons and membranous crown ornaments (Fig. 1f). However, as the field collections revealed more and more species diversity and within-species variation, the definition of this monotypic genus must be amended. First, researchers have noted the within-species
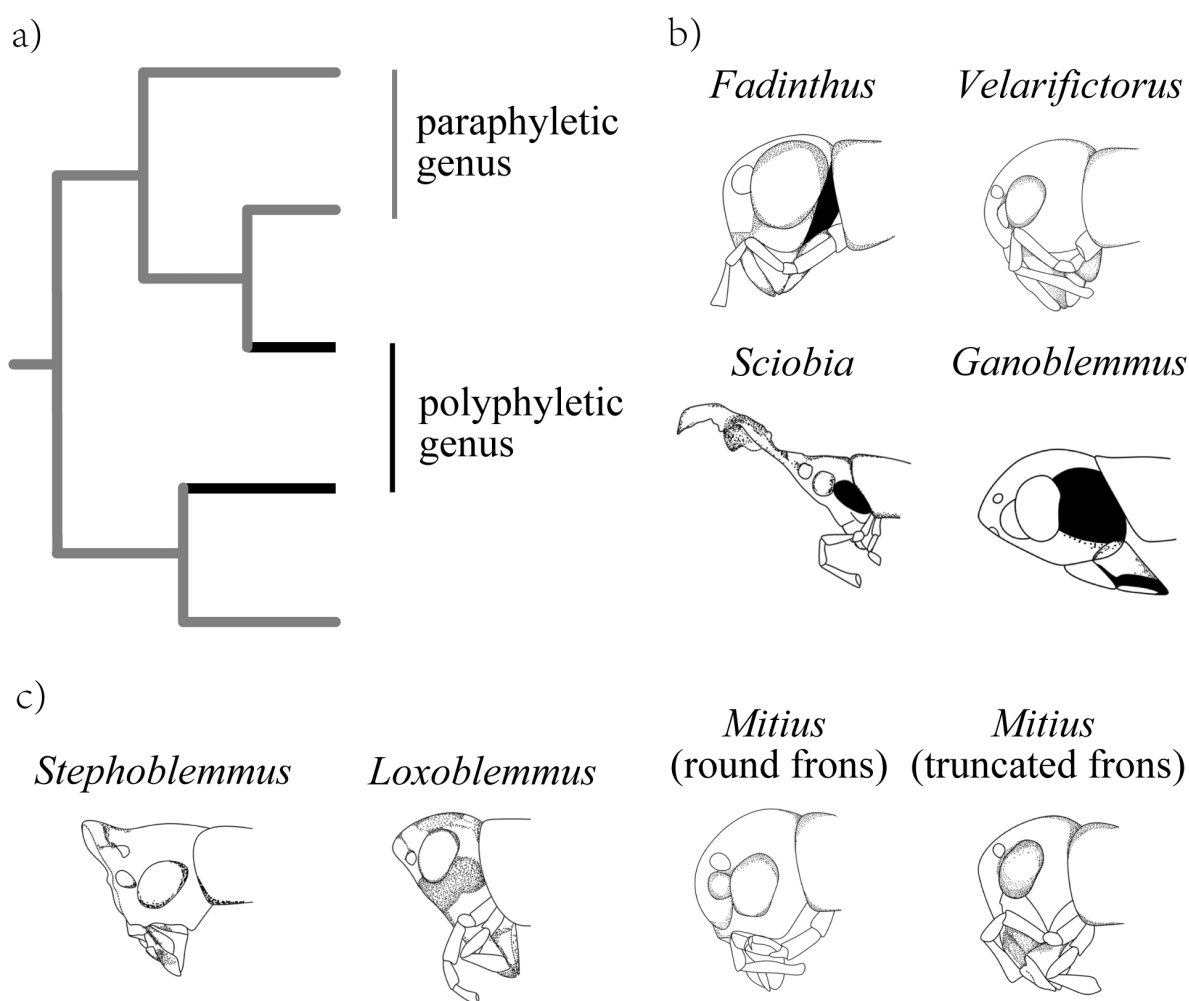

Figure 1. a Paraphyletic or polyphyletic genera resulted from establishing a new genus with uncommon morphological features. Lineages with (without) the features are black (grey); **b–c** examples of typical head shapes of field crickets; **d–e** examples of genera with unusual head morphology; **f** head morphology of *S. humbertiellus*; **g** head of *Loxoblemmus*; **h** examples of species with round frons in *Mitius*; **i** examples of species with truncated frons in *Mitius* (Species notes in the figure: b – *Fadinthus tehtari* Tan, Wahab & Robillard, 2021; c – *Velarifictorus zhengi* Zheng & Ma, 2022; d – *Sciobia barbara* (Saussure, 1877); e – *Ganoblemmus rasilis* Karsch, 1893; f – *S. humbertiellus*; g – *Loxoblemmus rectilineus* Ma & Qiao, 2020; h – *Stephoblemmus minor* (Shiraki, 1911); i – *S. brevipennis* **syn. n.** (= *S. humbertiellus*)).

Table 1. The head shape of *Stephoblemmus* (= *Mitius*).

Species	Male's head shape
S. blennus	round
S. castaneus	truncated
S. enatus	round
S. flavipes	round
S. humbertiellus	truncated
S. minor	round
S. minutulus	round
S. vaturu	truncated

variation in the head shape of *S. humbertiellus* (Qiao et al., 2020). While typical males have well-developed membranous crown ornament (Fig. 1f), a few individuals seem to have "undeveloped" heads (Fig. 1i) and some even have female-like bulbous heads (Fig. 1h). These observations suggest that head shape is intraspecifically variable. Second, when examining the specimen of *S. humbertiellus* collected from southeast Tibet and western Yunnan Province in China, Qiao et al. (2020) found that except for the head shape, they highly resemble *Loxoblemmus nigriceps* Chopard, 1933, an Indian species described by Chopard (1933). *Loxoblemmus* Saussure, 1877 is a field cricket genus with a bevel-like face (frons of the head) as if being cut off flush with a knife (Fig. 1g). Given the geographic proximity, *S. humbertiellus* may be closely related to species of *Loxoblemmus*. Third, the genus *Mitius* Gorochov, 1985 contains species with unusual head morphology of China. Although most members in this genus have typical hemispherical heads, *Mitius castaneus* (Chopard, 1937) described initially under *Loxoblemmus* has been moved into *Mitius* according to male genitalia features by Gorochov (1996). Similarly, the truncate head species *Mitius vaturu* (Otte & Cowper, 2007), originally under *Loxoblemmus*, also have been moved into *Mitius* (Ma et al., 2021). Yuan et al. (2022) reported a new species (*Mitius brevipennis* Yuan, Ma & Gu, 2022) with slanted facial truncations. Hence, among the ten *Mitius* species worldwide, there are three species with *Loxoblemmus*-like truncated frons (Table 1). Moreover, the genitalia feature of *S. humbertiellus* resembles that of *Mitius*; *S. humbertiellus* could be closely related to some *Mitius* species.

In this study, we first assembled a molecular dataset to study the phylogenetic relationships among the genera *Loxoblemmus*, *Mitius*, and *Stephoblemmus*. The estimated phylogeny confirmed that *Stephoblemmus* is nested within *Mitius*, while only distantly related to the *Loxoblemmus*. That is, *Mitius* Gorochov, 1985 should be a synonym for *Stephoblemmus* Saussure, 1877 according to nomenclature rules. Then, to further investigate the species limits and evolutionary history in the combined genus, we broadly sampled *Mitius* specimens across China and applied both single- and multi-locus species delimitation approaches. Based on the phylogenetic analyses and species delimitation results, we synthesized a species checklist and identification key for the genus, along with detailed descriptions of within-species morphological variations for species in China.

2. Materials and methods

2.1. Specimen collection and morphological measurements

For the monotypic genus *Stephoblemmus*, *S. humbertiellus* is only recorded in the Yunnan Province in China. We collected eleven individuals of *S. humbertiellus* from two sites (Table S1). For the genus *Mitius*, four species had been recorded in mainland China: *M. brevipennis*, *Mitius eryuanensis* Yuan, Xie & Liu, 2021, *Mitius flavipes* (Chopard, 1928), *Mitius minor* (Shiraki, 1911). We managed to collect *Mitius* specimens from ten provinces in mainland China—a broad geographic range covering most of Southern China (Fig. S1). We also obtain a few samples from surrounding regions (e.g., *Mitius enatus* Gorochov, 1994 from Thailand and *M. minor* from Japan; see Table S1 for the list of specimens in this study).

The specimens were first preserved in 100% ethanol during fieldwork. In the laboratory, specimens have one leg stored at –4°C for molecular sampling, with the rest pinned and dry-preserved. All specimens studied in the article were deposited in the Museum of Flora and Fauna of Shaanxi Normal University, Xi'an, China (SNNU).

Genitalia was prepared by placing dissected genitalia into a solution of alkaline protease (0.2 g/ml, AOBOX, Beijing, China) with a water temperature of 40–50°C for 48 hours. Whole-body and head specimen photographs were obtained using a VHX-6000 Super-high magnification lens zoom 3D microscope (Keyence, Japan). The details of the ovipositor were obtained using JEC-6500 Ion sputtering instrument (Hitachi, Japan) and TM3030Plus tabletop electron microscopy (Jeol, Japan). Photos of genitalia and quantitative measurements were obtained using the ToupCam digital camera and bundled software (ToupTek, Hangzhou, China). All measurements are in millimeters (mm). We use the following abbreviations of measurements: BL body length (from head to tip of abdomen); HL head length; HW head width; PL pronotum length; PW pronotum width (maximum width of pronotum); FWL tegmen (forewing) length; HFL hind femur length; OL ovipositor length.

2.2. DNA sequencing

Total genomic DNA was extracted from the leg muscle preserved in ethanol using the TIANamp Genomic DNA kit (Tiangen Biotech, Beijing, China), as directed by the manufacturer. One mitochondrial marker (cytochrome c oxidase subunit 1 [COX1]) and two nuclear markers (18S rRNA [18S], 28S rRNA [28S]) were amplified and sequenced. We used the primers in Hillis and Dixon (1991), and the primer sequences are provided in Table S2. PCR amplifications started with pre-denaturation at 94°C for 2min, followed by 40 cycles of denaturation at 94°C for 30s, annealing at 42/56/57°C (for COX1, 18S, and 28S, respectively) for 30s, elongation at 72°C for 1 kb/min, and ended with a final elongation step at 65°C for 10 min.

The sequence data was then manually edited in GENE-IOUS PRIME 2021.1.1 (https://www.geneious.com).

2.3. Phylogenetic analyses

To investigate relationships between the *Mitius*, *Stephoblemmus*, and *Loxoblemmus*, we compiled a dataset of COX1, 18S, and 28S with nine species. For the genera *Mitius* and *Stephoblemmus*, we selected a total of eight morphologically distinct species, and for *Loxoblemmus*, we selected one representative species. Moreover, we selected representative species from 34 genera in the subfamily Gryllinae (Table S1). One individual per species was randomly selected from *Mitius* and *Stephoblemmus*. For *Loxoblemmus*, we downloaded the sequences of the three genes (COX1, 18S, and 28S) of *L. campestris* from GenBank (see Table S1 for accession number). For other genera in the subfamily Gryllinae, searching the GenBank database with the keywords "Gryllinae and COX1/18S/28S" identified 49, 45, and 36 Gryllinae species (including those labeled as "unknown" species) with COX1, 18S and 28S records, respectively (as of 9/11/2022). We picked one representative species for each genus. Since mitochondrial genes usually have higher mutation rates and more informative sites, priority was given to species with COX1 records. If a genus has multiple species with COX1 records, we randomly selected one species with the 18S and 28S sequences. For outgroups, only the families Mogoplistidae, Oecanthidae, Phalangopsidae, and Trigonidiidae had sequence records for the three genes. We selected one species from each subfamily in these families. In total, there are 43 species from 37 genera in Gryllidae and eight from four other families in Grylloidea as outgroups (Table S1).

We performed the maximum-likelihood (ML) phylogenetic analysis using the concatenated mitochondrial and nuclear genes in IQ-TREE v1.6.12 (Nguyen et al., 2015) with the best-fitting substitution model for each gene selected by ModelFinder (Kalyaanamoorthy et al., 2017). The nodal supports were estimated using ultrafast bootstrapping with 1,000 replicates (Hoang et al., 2018). We also conducted the Bayesian inference with the same dataset in MRBAYES 3.2.1 (Ronquist et al., 2012) and estimated the majority-rule consensus tree by Markov chain Monte Carlo (MCMC) sampling. The concatenated sequences were first partitioned into genes, and three codon positions in COXI (i.e., five partitions in total), and PARTITIONFINDER v2.1.1 (Lanfear et al., 2017) identified the best substitution models were selected according to the Bayesian information criterion (BIC). Samples were drawn every 1,000 steps over 10 million steps, with the initial 25% discarded as burn-in. We used FIGTREE v1.4.4 (Rambaut, 2021) to visualize and manipulate the phylogenies.

2.4. Divergence dating analyses

BEAST v1.10.4 (Suchard et al., 2018) was used for molecular clock dating with an uncorrelated log-normal relaxed clock model and a Yule tree prior. Three fossils were used for age constraints. The fossil of *Protogryllus grandis* Zeuner, 1937, considered the oldest fossil of Grylloidea (Sharovm, 1971; Zeuner, 1937), was used to assign an exponential prior for the stem Grylloidea with a minimum bound of 199.00 million years ago (Ma; BEAUti setting: Mean = 16, Offset = 200.15). The fossil of *Pseudarachnocephalus dominicanus* Gorochov, 2010, the oldest fossil of Mogoplistinae (Gorochov, 2010), was used to specify an exponential prior for the stem Mogoplistinae with a minimum bound of 98.17 Ma (BEAUti setting: Mean = 26.8, Offset = 100). Lastly, an exponential prior for the stem Gryllinae with a minimum bound of 56.00 Ma (BEAUti setting: Mean = 11.4, Offset = 55.8) was set according to the age of the fossil *Gryllus vociferans* Cockerell, 1925, the oldest fossil of Gryllinae.

Substitution models were selected under PARTITIONFINDER 2.1.1 (Lanfear et al., 2017) with the 'beast' set of models. For the Markov Chain Monte Carlo (MCMC) run, samples were drawn every 10,000 steps over a total of 50 million steps, with the first 25% of samples discarded as burn-in. The BEAGLE library was used to improve and speed up the likelihood calculation (Ayres et al., 2012). We used TRACER v1.7.1 (Rambaut et al., 2018) to ensure that all ESS values were above the recommended threshold (200). The time-scaled tree was generated using TreeAnnotator in BEAST and visualized in FIGTREE v1.4.4 (Rambaut, 2021).

2.5. Species delimitation

For species delimitation analysis, our dataset includes 38 specimens of *Mitius* and *Stephoblemmus* (33 specimens from our collection, for which we have COXI, 18S, and 28S sequenced, and five COXI sequences from the Genebank (Table S1)). *Acheta domesticus* was included as the outgroup.

We first applied four single-locus species delimitation approaches with the COX1 sequences to discover the putative species boundaries in *Mitius* and *Stephoblemmus*: automatic barcode gap discovery (ABGD; Puillandre et al., 2012), generalized mixed Yule-coalescent (GMYC; Fujisawa & Barraclough, 2013), Bayesian Poisson tree process model (bPTP; Zhang et al., 2013) and Refined Single Linkage (RESL; Ratnasingham & Hebert, 2013). Then, we added the other two nuclear genes and used a multi-locus species delimitation method to validate these putative species delimitation hypotheses: Bayesian Phylogenetics and Phylogeography (BPP; Yang, 2015).

ABGD is a genetic distance-based method that does not require prior species assignment (Puillandre et al., 2012). We performed ABGD analyses online (https://bioinfo.mnhn.fr/abi/public/abgd) based on Kimura's 2-parameter model (K2P; Kimura, 1980), with a minimum intraspecific variability of Pmin = 0.001, maximum intraspecific variability of Pmax = 0.1 and a minimum gap width of X = 1.5. RESL analysis was performed on the BOLD (Barcode of Life Data) platform, which can group COX1 barcode sequences into clusters. We used this platform to assign our COXI sequences to MOTUs (molecular op-

erational taxonomic units). The bPTP analysis (Zhang et al., 2013) was conducted on the bPTP website (https://species.h-its.org/ptp). We estimated an ML tree with the COXI dataset using IQtree and used it as the input after pruning the outgroup. To check for convergence, we ran two independent MCMC analyses. Each run is 1000,000 steps in total and was sampled every 10,000 steps, and the first 10% was discarded as burn-in. For GMYC, another tree-based species delimitation method, we conducted the analysis using the single-threshold model in the "*splits*" package (Ezard et al., 2009) in R v3.6.3 (R Core R et al., 2020). We inferred the ultrametric guide tree using BEAST v1.10.4 (Suchard et al., 2018) with a strict clock model and a birth-death tree prior, a suitable tree prior for data sets with a mixture of intra- and inter-species sampling (Ritchie et al., 2017). For calibration, we used our molecular dating results: a normal prior (mean 11.16, standard deviation 6.40) for the MRCA (most recent common ancestor) of clade *Mitius/Stephoblemmus*; a normal prior (mean 13.47, standard deviation 7.11) for the MRCA of *Mitius/Stephoblemmus* and *A. domesticus*. The posterior distribution was estimated by MCMC sampling, with samples drawn every 1,000 steps over a total of 10 million steps, discarding the first 10% as burn-in. We used TRACER v1.7.1 (Rambaut et al., 2018) to ensure that all ESS values were above the recommended threshold (200). The time-scaled tree was generated using TreeAnnotator in BEAST.

For multi-locus species delimitation, we conducted unguided Bayesian species delimitation in BPP v4.3.8 (Yang, 2015) to explore different species-delimitation models while allowing changes in species-tree topology (A11 analysis; (Yang & Rannala, 2014)). For the priors of population sizes (θ) and divergence times (τ), we used inverse-Gamma priors with α = 3. The β parameter was adjusted according to the mean estimate of nucleotide diversity for θ (β = 0.01) and node height for τ (β = 0.001). We performed the analyses using the reversible-jump MCMC algorithm 0 (ε = 2) and algorithm 1 (α = 2, m = 1), with duplicated runs to check for convergence. Analyses were run for 20,000 MCMC steps, with samples drawn every five steps and the first 20% discarded as burn-in.

3.   Results

3.1.   Phylogeny analysis

We used the concatenated COXI, 18S, and 28S sequences, with a total of 2492 sites. Our ML and BI tree-estimation analyses obtained similar tree topologies (Fig. S2 and S3). Both results showed *Mitius* and *Stephoblemmus* form a monophyletic clade with the highest support (PP of 1 and BS of 100), and the species of *Stephoblemmus* is nested within the genus *Mitius*, suggesting that *Mitius* and *Stephoblemmus* are synonyms. Moreover, although the tree topology inferred using the Bayesian relaxed-clock analysis (Fig. 2) is slightly different from that inferred

using maximum likelihood and Bayesian analyses (Fig. S2; Fig. S3), all analyses supported the monophyly of the genus *Mitius* and *Stephoblemmus*, and have consistent internal species relationships. Our divergence dating result placed the stem age of the genus *Stephoblemmus* (= *Mitius*) in the Tortonian at 9.18 Ma with a 95% credibility interval (95% CI) of 15.21 to 4.08 Ma, the stem age of *S. enatus* at 3.5 Ma with 95% CI of 8.97 to 1.79 Ma, and the stem age of *S. minor* and *S. humbertiellus* at 1.81 Ma with 95% CI of 4.38 to 1.45 Ma.

Different species delimitation methods yielded similar results (Fig. 3). Single-locus methods, ABGD, bPTP, and RESL, identified three MOTUs (molecular operational taxonomic units; Fig. 3). One comprised of all *S.minor* individuals (yellow clade on Fig. 3). One includes both *S. humbertiellus* and *M. brevipennis* individuals (green clade on Fig. 3), suggesting that not only the two genera should be combined, the two species are also synonyms. The last MOTU has individuals of *M. flavipes* and *M. enatus*. The result from GMYC was slightly different— it recognized one lineage of *S. minor* as an additional MOTU. The multi-locus approach BPP supported the three-MOTU hypothesis with a high posterior probability of 0.90 (Fig. 3).

3.2.   Systematics and morphology

3.2.1.   Checklist of *Stephoblemmus* (= *Mitius*) species worldwide

***Stephoblemmus blennus* (Saussure, 1877) comb. n.**
    Distribution. Malesia (type locality), Australia, Indonesia, Myanmar, Solomon Islands.

***Stephoblemmus castaneus* (Chopard, 1937) comb. n.**
    Distribution. Malesia (type locality).

***Stephoblemmus enatus* (Gorochov, 1994) comb. n.**
    Mitius eryuanensis **syn. n.**
    Distribution. China (Tibet, Yunnan, Guangxi, Chongqing, Fujian), Vietnam (type locality), Thailand.

***Stephoblemmus flavipes* (Chopard, 1928) comb. n.**
    Distribution. Indian Subcontinent (type locality).

***Stephoblemmus humbertiellus* Saussure, 1877**
    Mitius brevipennis Yuan, Ma & Gu, 2022 **syn. n.**
    Distribution. China (Yunnan, Tibet), India (type locality).

***Stephoblemmus minor* (Shiraki, 1911) comb. n.**
    Mitius splendens **syn. n.**
    Distribution. China (Taiwan, Henan, Hubei, Shanghai), Japan (type locality).

***Stephoblemmus minutulus* (Yang & Yang, 1995) comb. n.**
    Distribution. China (Taiwan; type locality).

***Stephoblemmus vaturu* (Otte & Cowper, 2007) comb. n.**
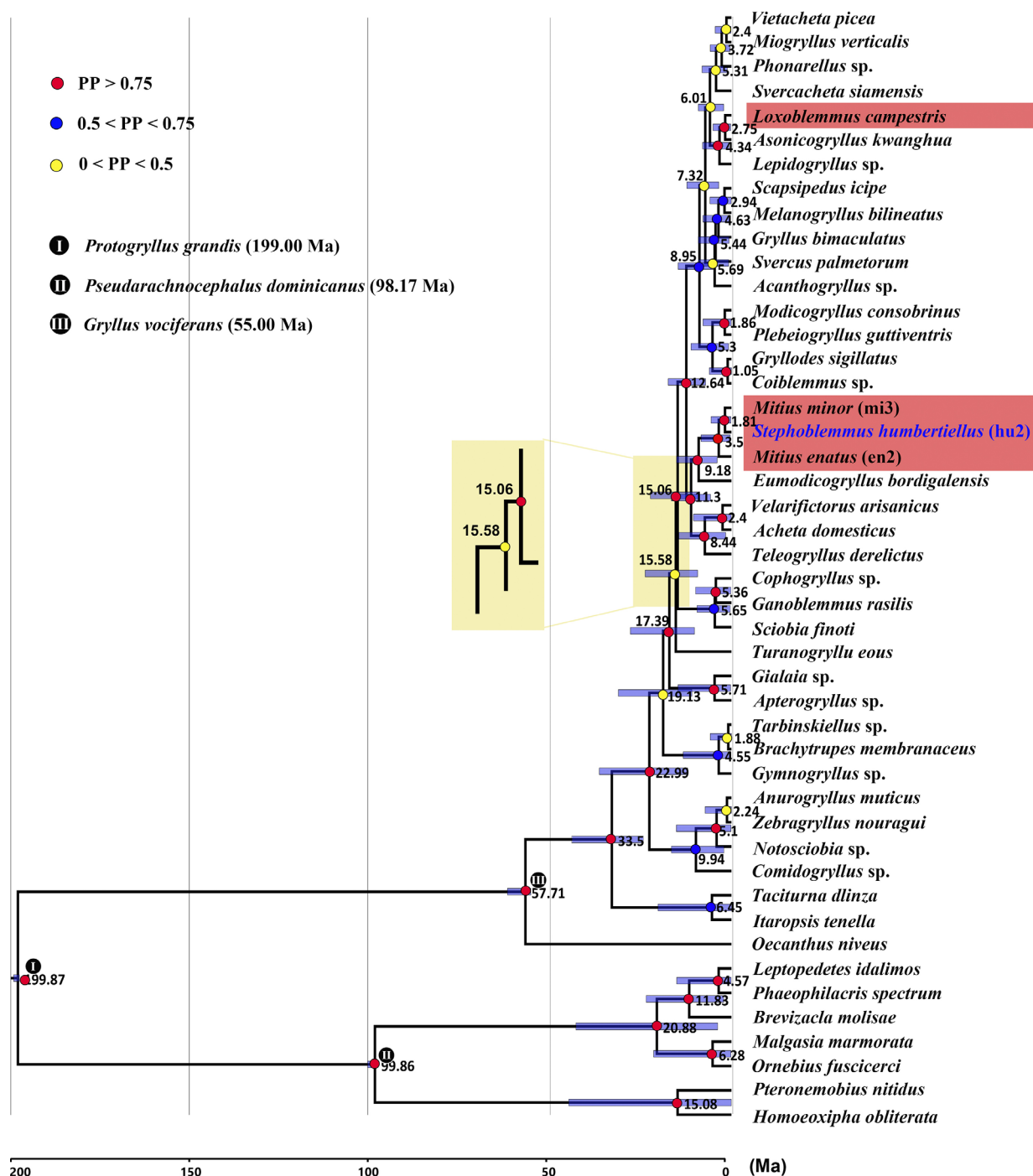   **Distribution.** Fiji (type locality).

Figure 2. Time-calibrated phylogeny inferred using BEAST. Posterior probability (PP) values are indicated by node color. Node numbers next to nodes represent the divergent times. Purple bars indicate 95% credibility intervals of estimated node ages. The left in Roman numbers represents fossil calibration points. The primary species of study for this article are shaded red, including species of *Loxoblemmus*, *Mitius*, and *Stephoblemmus*. The blue letter is the type species of *Stephoblemmus*. The geological timescale is shown at the bottom (Ma = million years ago).

3.2.2. Key to *Stephoblemmus* (= *Mitius*) species in China

1 Frons truncated, which extremely protruding forward, forming an angle in lateral view .... ***S. humbertiellus***

1' Frons slightly protruding forward, arc-like in lateral view **2**

2 Length of ovipositor longer than 9 mm..***S. minor*** **comb. n.**

2' Length of ovipositor about 6 mm...**3**

3 Tegmina not reaching the fifth abdominal tergum and apical margin of middle lobe concave ....

....***S. minutulus*** **comb. n.**

3' Tegmina longer than the fifth abdominal tergum and apical margin of middle lobe convex........***S. enatus*** **comb. n.**
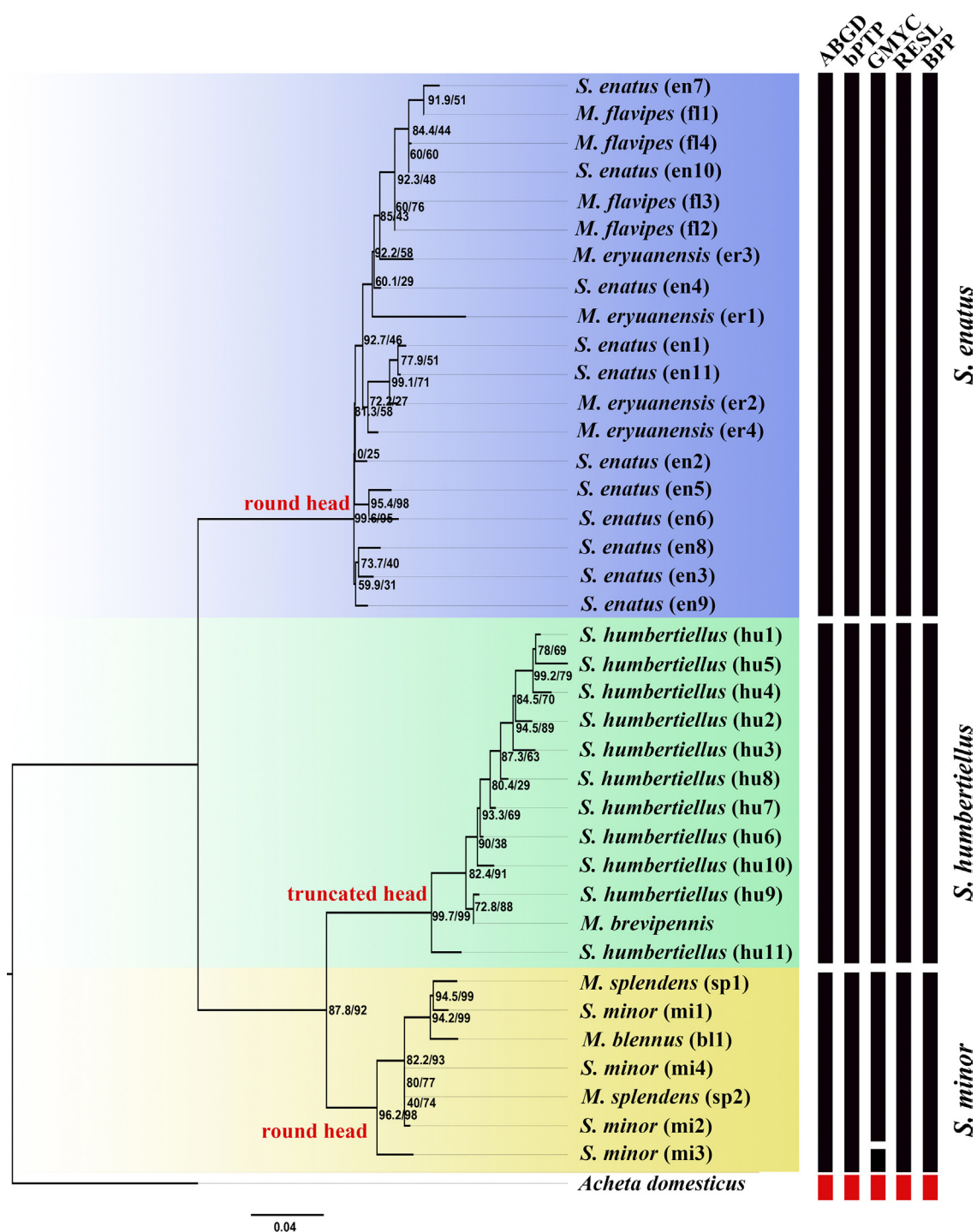
Figure 3. The maximum-likelihood (ML) tree for 30 samples of *Mitius* and *Stephoblemmus* using the concatenated COX1 + 18S + 28S data set, and the species delimitation results. Posterior probabilities from MRBAYS (left) and bootstrap supports from IQTREE (right) are indicated for all nodes. Clade nodes are marked in red to indicate the morphology of the male's head.

3.2.3. Orthoptera: Grylloidea; Gryllidae; Gryllinae; Modicogryllini

Genus *Stephoblemmus* Saussure, 1877

Mitius Gorochov, 1985: 95, **syn. n.**

Type species. *Stephoblemmus humbertiellus* Saussure, 1877.

Chinese name. 素蟋属

Emended diagnosis. Male: Vertex broad and flattened, slightly inclined. Occiput slightly convex. Frons inclined dorsally and ventrally, and nearly two times wider than antennal scape. Antennal scape shield-like. Median ocellus ovoid, lateral ocelli transversely ovoid. Two lateral ocelli located on the upper edge of the antennal scape and distributed in an inverted triangle with the median ocellus. Eyes ovoid. Pronotum broad and flattened. The me-
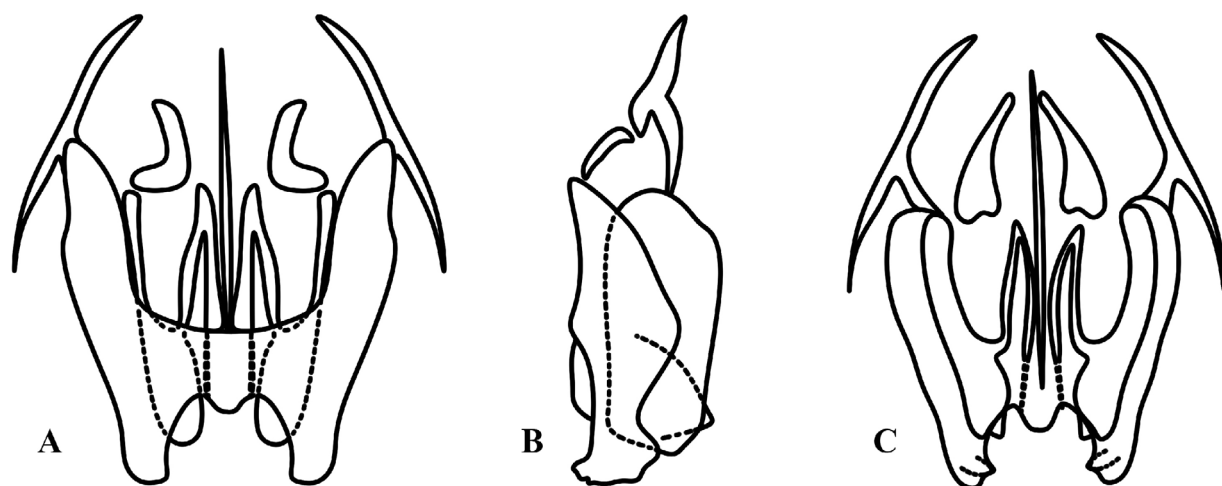
Figure 4. Pattern of male genitalia of *Stephoblemmus*. **A** dorsal view, **B** lateral view, **C** ventral view.

dian groove of the pronotal disc distinct. Posterior margin straight, the middle of the anterior margin concave, and the posterior and anterior margins almost equal in width. In the dorsal field of tegmina, bearing three chord veins, with the apical one connecting to the proximal part of the mirror by two veins; diagonal vein proximally bifurcated, both branches connecting to CuA vein; two oblique veins; mirror shield-like; dividing vein absent. Outer tympanum shaped as an elongate oval, inner tympanum ovoid or absent. Hind tibiae armed with dorsal spurs which almost equal in length. Epiphallus armed with a finger-like median lobe (Fig. 4). **Female:** Similar to male in the head, pronotum, and feet features. Tegmina don't reach the end of the abdomen, with longitudinal veins interspersed with false veins. Ovipositor smooth, arrow-like.

Included species. *Mitius blennus* (Saussure, 1877) *Mitius castaneus* (Chapord, 1937), *Mitius enatus* (Gorochov, 1994), *Mitius flavipes* (Chopard, 1928), *Mitius minor* (Shiraki, 1911), *Mitius minutulus* Yang & Yang, 1995, *Mitius vaturu* (Otte & Cowper, 2007), and *Stephoblemmus humbertiellus* Saussure, 1877.

Remarks. *Stephoblemmus* was established by Saussure (1877) and its dominant feature is the flat frons of males (Fig. S5C–D, G–H). *Mitius* was established by Gorochov (1985) and species of the genus possess two types of frons (truncated and rounded) (Fig. S5A–B, E–F, I–P). The phylogenetic relationship reveals that *Stephoblemmus* (*S. humbertiellus*) and *Mitius* (*M. minor* (= *S. minor* **comb. n.**)) are sister group (Fig. 2) and their male genitalia are also similar. Accordingly, *Mitius* should be a junior synonym of *Stephoblemmus* and we combine them.

Stephoblemmus humbertiellus Saussure, 1877

Figures 2, 3, 5A–D, 6A–F, 9A, C, D, S1–3, S5A, B, E, F

Stephoblemmus humbertiellus Saussure, 1877: 428; Chopard, 1936: 31; Qiao et al., 2020: 482

Loxoblemmus nigriceps Chopard, 1933: 120, synonymized by Qiao et al., 2020: 482
Mitius brevipennis Yuan, Ma & Gu, 2022: 596-600, **syn. n.**

Chinese name. 战素蟋

Examined materials. CHINA–**Tibet Autonomous Region** • 8 ♂, 5 ♀. Motuo County, 29°24.5′N, 95°17.6′W, May 31, 2019, Ma, Libin and Zhang, Tao coll. (SNNU); **Yunnan Prov.** • 5 ♂, 9 ♀. Mengxiu Township, Ruili County, 24°14.9′N, 97°87.6′W, Jun. 13, 2013, Ma, Libin coll. (SNNU); **Yunnan Prov.** • 1 ♂. Banlao Township, Cangyuan City, 24°22.5′N, 99°19.1′W, Jun. 7, 2013, Ma, Libin coll. (SNNU); **Yunnan Prov.** • 1 ♂. Longmen Village, Shangyong Town, Mengla County, 21°40.1′N, 101°64.1′W, May 15, 2013, Ma, Libin coll. (SNNU); **Yunnan Prov.** • 2 ♂. Nanping, Mengman Town, Mengla County, 21°29.6′N, 101°30.3′W, May 18, 2013, Ma, Libin coll. (SNNU).

Measurements (mm). ♂ **(n = 6):** BL 7.84±0.03, HL 1.35±0.32, HW 2.77±0.21, PL 1.96±0.02, PW 2.54±0.65, FWL 4.07±0.78, HTL 4.32; ♀ **(n = 6):** BL 9.00±0.43, HL 1.48±0.21, HW 2.70±0.08, PL 1.99±0.08, PW 2.77±0.23, FWL 3.19±0.98, HTL 4.81±0.76, OL 5.23±0.43.

Emended diagnosis. Male: Vertex broad and flattened, slightly inclined. Frons truncated. Tegmina reaching the middle of the fifth abdominal tergum. The apical margin of the epiphallic middle lobe slightly and medially concaved. Ectoparamere stripe-like, distally enlarged, and with apical margins concaved. **Female:** Similar to male for pronotum and feet features. Frons not produced forwards. Tegmina reaching the middle of the third abdominal tergum. Ovipositor smooth, arrow-like, and as long as the hind femur.

Description. Male: Eyes ovoid, about 1/4 length of head. Postclypeus shaped like a narrow band; the anteclypeus shaped like a broad shield and twice wider than the postclypeus. Labrum shield-like, apical margin slightly round. Last article of the maxillary palpi slightly longer than the third. The last article of labial palpi depressed and widened, almost equal to the total length of the remainder articles. Tegmina reaching the middle of the fifth abdominal tergum. In tegmina dorsal field, presenting three chord
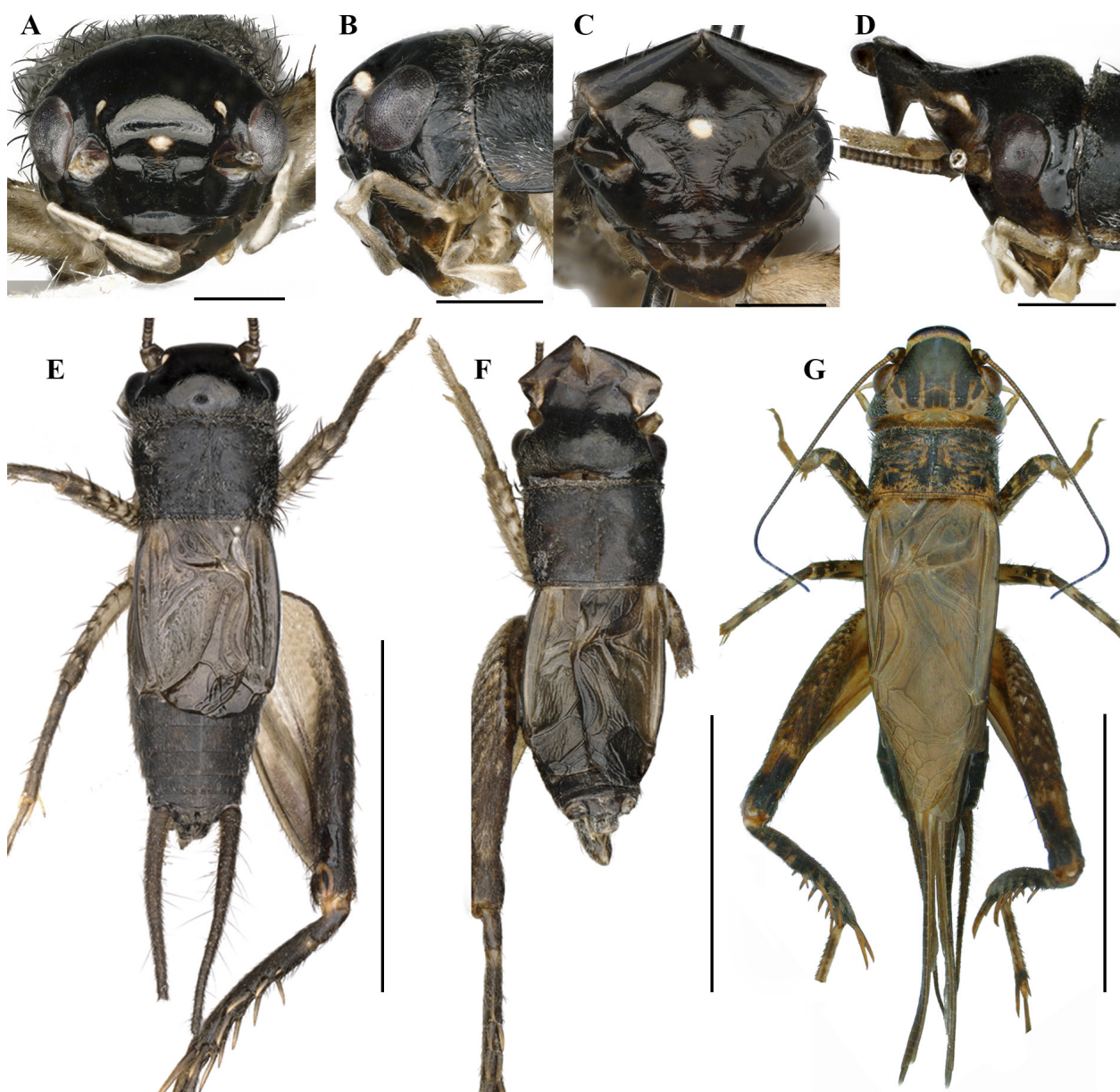
Figure 5. A–D Males' heads of *S. humbertiellus*, scale bar: 1 mm. **A, B** *S. brevipenis* **syn. n.**; **C, D** holotype; **E, F** males' bodies of *S. humbertiellus*, scale bar: 5 mm. **E** *S. brevipenis* **syn. n.**; **F** specimen bearing extremely protruding frons; **G** male body of *Loxoblemmus detectus* (Serville, 1838), scale bar: 5 mm.

veins, connecting to the proximal of the mirror by two veins; diagonal vein proximally bifurcated, both branches connecting to CuA vein; with two oblique veins; mirror shield-like; dividing vein absent; apical field slightly short, about 1/5 length of the basal field and armed with irregular cells. In the lateral dorsal field, five branches of the subcostal vein. Inner tympanum absent. Hind tibiae armed with dorsal spurs, five inner dorsal spurs, and six outer dorsal spurs; outer apical spurs three (this dorsal apical spur about 3/2 length of the dorsal spurs, ventral and middle ones almost equal in length and about half the length of the dorsal spurs) and inner two (equal in length and slightly longer than the dorsal spurs).

Genitalia. Epiphallic middle lobe about 1/4 length of the lateral lobe and its apical margin slightly and medially concaved. Epiphallic lateral lobe sheet-like, distally broad, and armed with an apex dorsally protruding (Fig. 6E). Ectoparamere stripe-like, distally enlarged, and with apical margins concaved.

Female. Similar to males for pronotum and feet features. Frons not produced forwards. Tegmina reaching the middle of the third abdominal tergum (Fig. 9A). Ovipositor smooth, arrow-like (Fig. 9C–D), and as long as the hind femur.

Coloration. Body dark brown. Tegmina, clypeus, and labrum brown. Ocelli, maxillary palpi, and labial palpi yellowish.

Remarks. It is the type species of the genus *Stephoblemmus*. The species is distinguished by its truncated frons of the male (Fig. S5C–D, G–H), and it is very
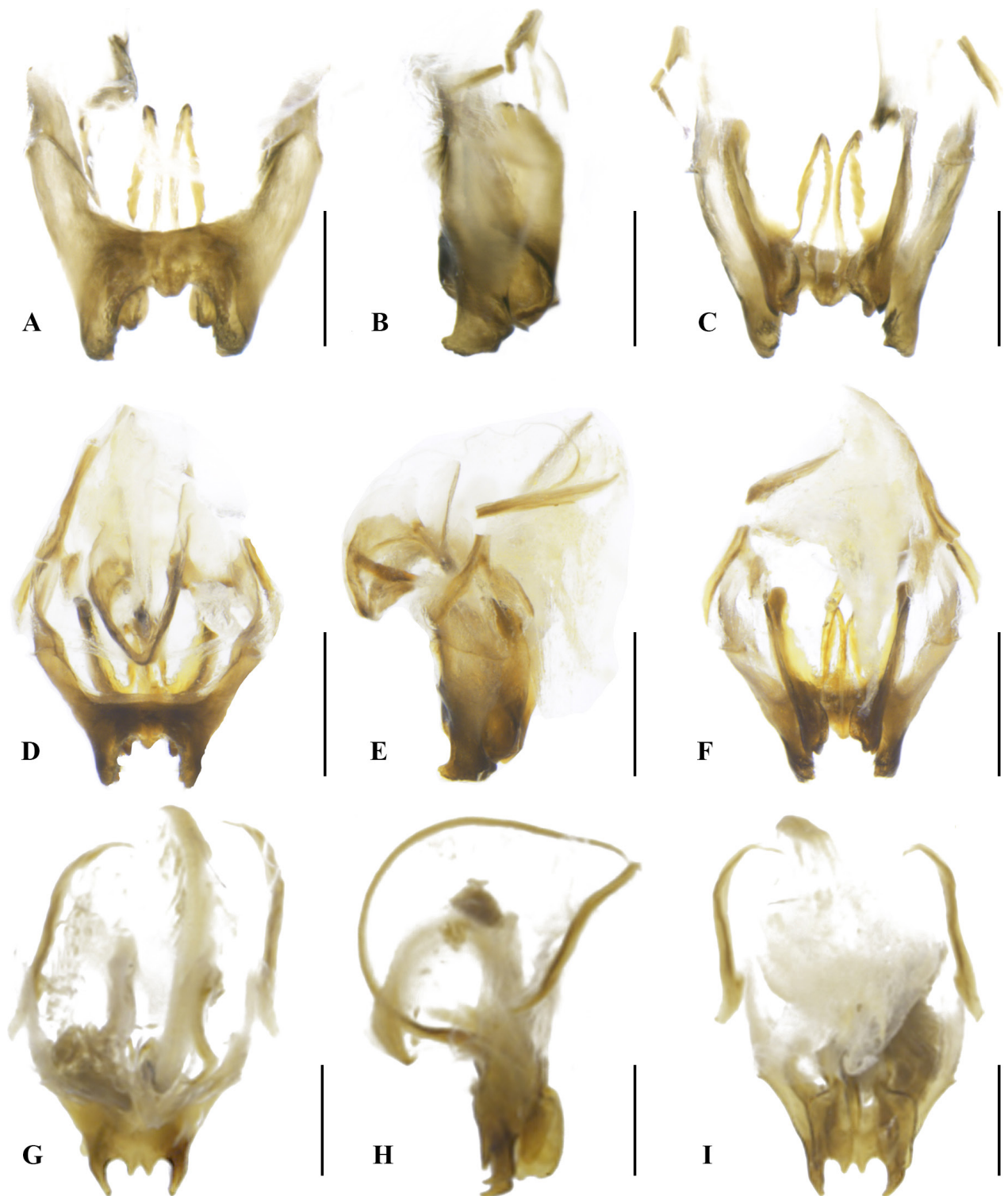
Figure 6. **A–F** Genitalia of *S. humbertiellus*, scale bar: 0.5 mm. **A–C** *S. brevipenis* **syn. n.**, **D–F** holotype, **G–I** Genitalia of *L. detectus*. Notes: These two species are distinguished in epiphallic media lobe.

close to *M. brevipenis*. We examined all the specimens of *S. humbertiellus* in hand and the holotype of *M. brevipenis* and found that its genitalia is very similar to those of *M. brevipenis*, but in the apical margin of the epiphallic middle lobe somewhat different. *M. brevipenis* apical margin of epiphallic middle lobe slightly concave. However, as there was only one specimen of *M. brevipenis*, we analyzed their DNA barcode to determine whether the difference in the apical margin of the epiphallic middle lobe was interspecific or intraspecific. And all methods supported *M. brevipenis* and *S. humbertiellus* was one MOTU. Thus, *M. brevipenis* and *S. humbertiellus* should be one species, and *M. brevipenis* should be a junior synonym of *S. humbertiellus*.

Stephoblemmus enatus (Gorochov, 1994) comb. n.

Figures 2, 3, 7, 9B, E, F, S1–3, S5K, L, O, P

Mitius enatus Gorochov, 1994: 9; Ingrisch, 1998: 341; Kim & Hong, 2014: 61
Mitius eryuanensis Yuan, Xie & Liu, 2021: 499, **syn. n.**

Chinese name. 混沌素蟋

Examined materials. CHINA–**Yunnan Prov.** • 7 ♂, 2 ♀. Zhiwuyuan, Menglun Town, Mengla County, 21°91.7′N, 101°27.4′W, on grass, Aug. 15, 2021, He, Zhixin, Wang, Ning and Yuan, Wei coll. (SNNU); **Yunnan Prov.** • 1 ♂. Wulaoshan, Lincang City, 23°91.7′N, 100°19.0′W, on grass, Aug. 15, 2021, He, Zhixin, Wang, Ning and Yuan, Wei coll. (SNNU); **Yunnan Prov.** • 1 ♂. Nanping Village, Mengman Town, Mengla County, 21°93.5′N, 101°24.9′W, on grass, May 18, 2013, Ma, Libin coll. (SNNU); **Hainan Prov.** • 1 ♂, 2 ♀. Wuzhishan City, 18°77.5′N, 109°51.7′W, on grass, Aug. 17, 2019, He, Zhixin and Zhang, Tao coll. (SNNU); **Hainan Prov.** • 2 ♂, 1 ♀. China: Yinggeling, Baisha County, 19°18.3′N, 109°44.7′W, on grass, Apr. 3–10, 2021, He, Zhixin coll. (SNNU); **Hainan Prov.** • 1 ♂. Jianfengling, 18°72.2′N, 108°90.8′W, on grass, Jul. 20, 2009, Fu, Qiang coll. (NWAFU); **Hainan Prov.** • 7 ♀. Maoyang Town, 18°61.2′N, 109°29.6′W, on grass, Aug. 8, 2009, Ma, Libin coll. (SNNU); **Hong Kong** • 1 ♂, 1 ♀. Dapujiao, 22°43.3′N, 114°19.3′W, on grass, May 12, 2018, Ma, Libin, coll. (SNNU); **Guangxi Prov.** • 10 ♂, 7 ♀. Longbang Town, Jingxi County, 22°96.1′N, 106°28.5′W, on grass, May 1, 2019, Ma, Libin and Zhang, Tao coll. (SNNU); **Chongqing City** • 1 ♂. Jinyunshan, 23°83.2′N, 106°38.5′W, on grass, Rong, Xia coll. (SNNU).

Measurements (mm). ♂ **(n = 20):** BL 10.14±0.21, HL 1.66±0.08, HW 2.77±0.06, PL 1.93±0.19, PW 3.04±0.21, FWL 5.25±0.09, HTL 6.62±0.37; ♀ **(n = 13):** BL 10.41±0.72, HL 1.33±0.13, HW 2.73±0.19, PL 1.89±0.03, PW 2.87±0.26 FWL 4.66±1.02, HTL 5.06±1.72, OL 6.05±0.07.

Emended diagnosis. Male: Frons round. Tegmina reaching the middle of the eighth abdominal tergum. Apical field armed with irregular cells. Apical margin of epiphallic middle lobe arc-like. Epiphallic lateral lobes sheet-like, with apex varied. Dorsally observing some specimens, with apex bifurcating with branches variable in length. Viewed laterally, apical margin of epiphallic lateral lobes with 1–3 protrusions, variable in shape. **Female:** Similar to male in the head, pronotum, and feet features. Tegmina reaching the sixth abdominal tergum. Ovipositor arrow-like and slightly shorter than the hind femur.

Description. Male: Eyes ovoid, nearly 1/3 length of head. Postclypeus shaped as a narrow band; the anteclypeus shaped as a broad shield and about half the length of the postclypeus. Labrum shield-like, apical margin slightly round. Last article of maxillary palpi almost as long as the third; the last article of labial palpi depressed and widened, almost equal to the total length of the remainder articles. Tegmina reaching the middle of the eighth abdominal tergum. In tegmina dorsal field, with three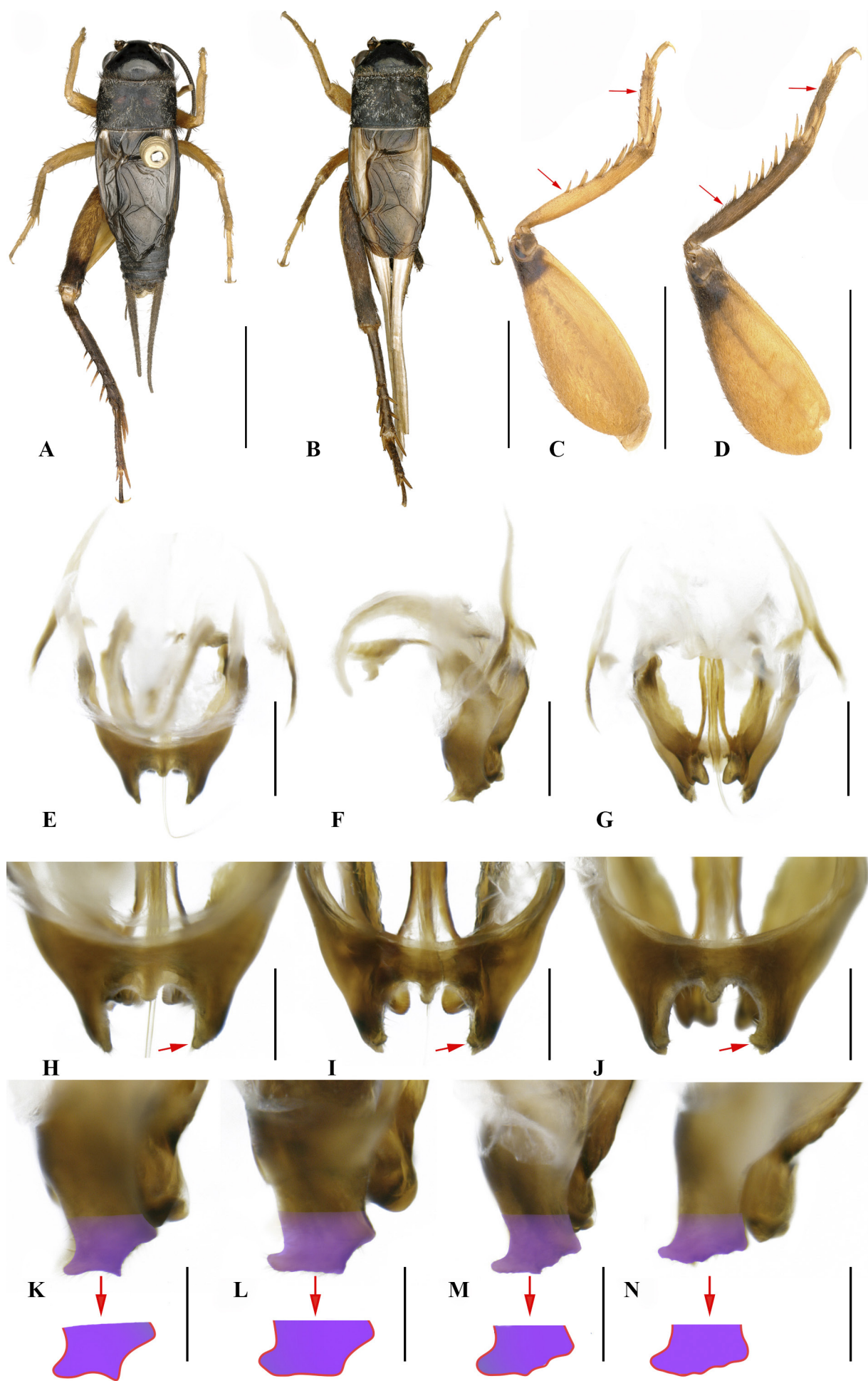 chord veins, connecting to the proximal part of the mirror by two veins; diagonal vein proximally bifurcated, both branches connecting to CuA vein; bearing two oblique veins; mirror shield-like; dividing vein absent; apical field armed with irregular cells. In the lateral dorsal field, five branches of the subcostal vein. Inner tympanum relatively small, outer tympanum shaped as an elongated oval. Hind tibiae armed with dorsal spurs, five inner dorsal spurs, and six outer ones; inner apical spurs three (its dorsal and middle inner apical spurs almost equal in length and about two times longer than the dorsal spurs; ventral one nearly equal in length to the dorsal spurs) and outer two (equal in length and slightly longer than the dorsal spurs).

Genitalia. Epiphallic middle lobe about 1/3 length of the epiphallic lateral lobe and armed with an apical margin arc-like. Epiphallic lateral lobes sheet-like, with apex varied. Dorsally observing some specimens, this apex bifurcating with branches and variable in length (Fig. 7H–J). And viewed laterally, the apical margin of epiphallic lateral lobes possesses 1–3 protrusions and varing in shape (acute or round) (Fig. 7K–N).

Female. Similar to males for head, pronotum, and feet features. Tegmina reaching the sixth abdominal tergum (Fig. 9B). Ovipositor arrow-like (Fig. 9E–F) and slightly shorter than the hind femur.

Coloration. Body dark brown. Ocelli, maxillary palpi, and labial palpi yellowish. Leg yellow-brown and hind femur apically dark brown.

Remarks. Yuan et al. (2021) identified some Yunnan specimens as *M. eryuanensis*, which resemble *S. enatus* **comb. n.** and noted differences in genitalia morphology and the presence or absence of hind wings. As mentioned above, the existence of hind wings should not be used as a feature to identify species in most cases. In Yuan et al. (2021), they show that *M. eryuanensis* possesses male genitalia with epiphallic lateral lobes not bifurcated. In our study, the male genitalia of *S. enatus* **comb. n.** not only with these features diversity (Fig. 7H), but also have morphological diversity (Fig. 7I–J). Accordingly, *M. eryuanensis* should be a junior synonym of *S. enatus* **comb. n.**. Besides, Yin and Liu (1995) identified the species from Yunnan as *M. flavipes* and noted differences with *S. enatus* **comb. n.** in the color of the hind tibiae and the first section of hind tarsus, which we determined morphologically to be intraspecific, and the phylogenetic tree also shows these species very closely related (Fig. 3). Therefore, Chinese *M. flavipes* recorded in Yunnan Province should be a misidentification.

Stephoblemmus minor (Shiraki, 1911) comb. n.

Figures 2, 3, 8, S1–S3, S5M, N

Gryllus minor Shiraki, 1911: 54; 1930: 211; Wu: 1929; 25; Hsu. 1929:37; 1931: 30

Gryllulus minor Chopard, 1936:5; Hisumatsu, 1952: 43; synonymized by Roberts, 1941: 33

Modicogryllus minor Chopard, 1961: 274; Randell, 1964: 1586

Mitius minor Yin & Liu, 1995: 59; Ichikawa, Murai & Honda, 2000: 263; Storozhenko & Paik, 2007, 97; Storozhenko, Kim & Jeon, 2015: 118

Gryllus splendens (= *M. splendens*) Shiraki, 1930: 215; Yang & Yang, 1995: 5, **syn. n.**

Gryllodes blennus (= *M. blennus*) Saussure, 1877: 383; Yang & Yang, 1995: 2, **misidentification**

Chinese name. 小素蟋

Examined materials. CHINA–**Henan Prov.** • 2 ♂. Liankangshan, Xin Country, 31°64.1′N, 114°79.4′W, on grass, Sep. 4–8, 2014, Ma, Libin coll. (SNNU); **Hubei Prov.** • 5 ♂, Wuhan City, 30°62.1′N, 114°13.3′W, on grass, Sep. 1, 2018, Xie, Lingde coll. (SNNU).

Measurements (mm). ♂ **(n = 6):** BL 10.30±1.05, HL 1.96±0.12, HW 2.86±0.76, PL 2.12±0.14, PW 2.96±0.09, FWL 4.37±0.32, HTL 3.57±0.75.

Emended diagnosis. Male: Frons round. Tegmina reaching the middle of the ninth abdominal tergum. Apical field armed with irregular cells. Apical margin of epiphallic middle lobe arc-like. Apical margin of epiphallic lateral lobes truncated or arc-like; ventrally viewed, the distal of epiphallic lateral lobes possessing two small protrusions or a truncate projection. Epiphallic lateral and middle lobes connected in a V-shaped.

Description. Male: Postclypeus shaped like a narrow band; the anteclypeus shaped like a broad shield and slightly wider than the postclypeus. Labrum shield-like, apical margin slightly round. Tegmina reaching the middle of the ninth abdominal tergum. In tegmina dorsal field, bearing three chord veins, connecting to the proximal part of the mirror by two veins; diagonal vein proximally bifurcated, both branches connected to CuA vein; with two oblique veins; mirror shield-like; dividing vein absent; apical field armed with irregular cells. In the lateral dorsal field, five branches of the subcostal vein. Outer tympanum about three times more than the inner. Hind tibiae armed with dorsal spurs which almost equal in length, five inner dorsal spurs and six outer ones; outer apical spurs three (this dorsal apical spur about 3/2 length of the dorsal spurs, middle one slightly shorter than the dorsal and ventral one almost equal in length of the dorsal spurs) and inner two (equal in length and slightly longer than the dorsal spurs).

Genitalia. Epiphallic middle lobe about 1/3 length of the epiphallic lateral lobe and armed with an apical margin arc-like. Epiphallic lateral lobes sheet-like, in dorsal view, apical margin of epiphallic lateral lobes truncated (Fig. 9G) or arc-like (Fig. 9H); ventrally viewed, distal of epiphallic lateral lobes possessing two small protrusions (Fig. 9K–M) or a truncate projection (Fig. 9N). Epiphallic lateral and middle lobes connected in V-shaped (Fig. 9D). Ectoparamere stripe-like, distally enlarged.

Female. Unknown.

Coloration. Body dark brown. Maxillary palpi and labial palpi yellowish. Legs yellow-brown.

Remarks. This species was first reported in Japan and subsequently recorded in China (Taiwan, Shanghai, Zhejiang, Jiangsu, etc.) (Shiraki, 1930; Yin & Liu, 1995). There is an intraspecific variation of male genitalia in this species, and both the original and the later literature provide less and almost useless information on the feature of genitalia. This situation may end up making some taxonomic problems, such as the Chinese species of *M. blennus* and *M. splendens*. Yang & Yang (1995) reported them in Taiwan Province and only pointed out that they slightly differ in *S. minor* **comb. n.** in body size and some detailed features of male genitalia. In our study, *S. minor* **comb. n.**, an intraspecific varied species possesses all characteristics of *M. blennus* (Fig. 8F and I) and *M. splendens* (Fig. 8E, H and L) as described and illustrated by Yang & Yang (1995). The details of these features of *S. minor* **comb. n.** as (1) body size is varied from 9.48–11.12 mm; (2) apical margin of epiphallic lateral lobes are truncated (Fig. 8E) or arc-like (Fig. 8F) in dorsal view; (3) distal of epiphallic lateral lobes possesses two small protrusions (Fig. 8I–K) or a truncate projection (Fig. 8L) in ventral view. Fur-

Figure 7. *S. enatus* **comb. n.** A–B male body, scale bar: 5 mm (A – without hindwings; B – with hindwings). **C–D** Hind Legs, scale bar: 2 mm (C – color of posterior tibiae and the first section of posterior tarsus yellowish-brown; D – color of posterior tibiae and the first section of posterior tarsus dark brown). **E–N** Genitalia, scale bar of chart E–G: 0.5 mm; scale bar of chart H–M: 0.25 mm (E – dorsal view; F – lateral view; G – ventral view; H–J – dorsal enlarged view). K–N – Apex of lateral enlarged view. Notes: E – apex of epiphallic lateral lobes not bifurcate; I–J – the apex of epiphallic lateral lobes bifurcate, and length of branches varied in different materials; K – apex of epiphallic lateral lobes possessing an acute protrusion; L – apex of epiphallic lateral lobes possessing an obtuse protrusion; M – apex of epiphallic lateral lobes possessing two obtuse protrusions; N – apex of epiphallic lateral lobes possessing three obtuse protrusions. Of these, D–G and K are the same as that of *M. flavipes* in Yunnan (Yin & Liu, 1995); A, H, and L are the same as that of *M. eryuanensis* (Yuan et al., 2021)).
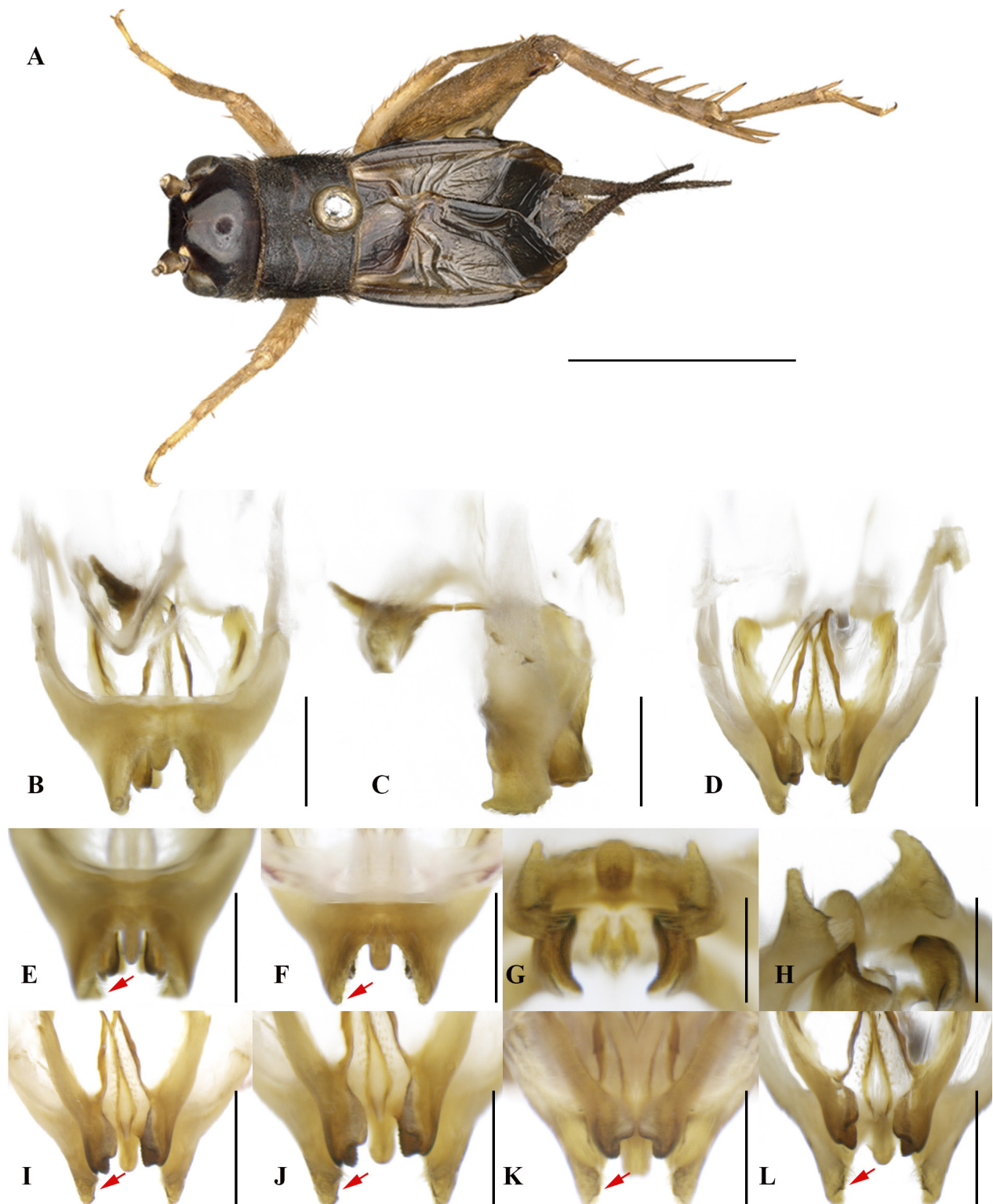
Figure 8. A body of *S. minor* **comb. n.**, scale bar: 5 mm; **B–L** Genitalia of *S. minor* **comb. n.**, scale bar of chart B–F, I–L: 0.5 mm, scale bar of chart G–H: 0.25 mm (B – dorsal view; C – lateral view; D – ventral view; E–F – dorsal enlarged view; G – caudal view; H – anterodosolateral view; I–L – apex of a lateral enlarged view). Notes: E – epiphallic lateral lobes apical margin truncated; F – epiphallic lateral lobes apical margin arc-like; I–J – distal of epiphallic lateral lobes possessing two small protrusions; L – distal of epiphallic lateral lobes possessing a truncate projection. Of these, C, G, and I are the same as that of *M. blennus* in Taiwan; E, H, and J are the same as that of *M. splendens* (Yang & Yang, 1995)).

thermore, based on the phylogenetic relationship (Fig. 3), all samples from China (including the sample of *M. splendens* collected in Taiwan), Thailand and Japan are closely related and clustered into a single lineage. There-fore, Chinese *M. blennus* should be a misidentification of *S. minor* **comb. n.** and *M. splendens* should be a synonym of *S. minor* **comb. n.**
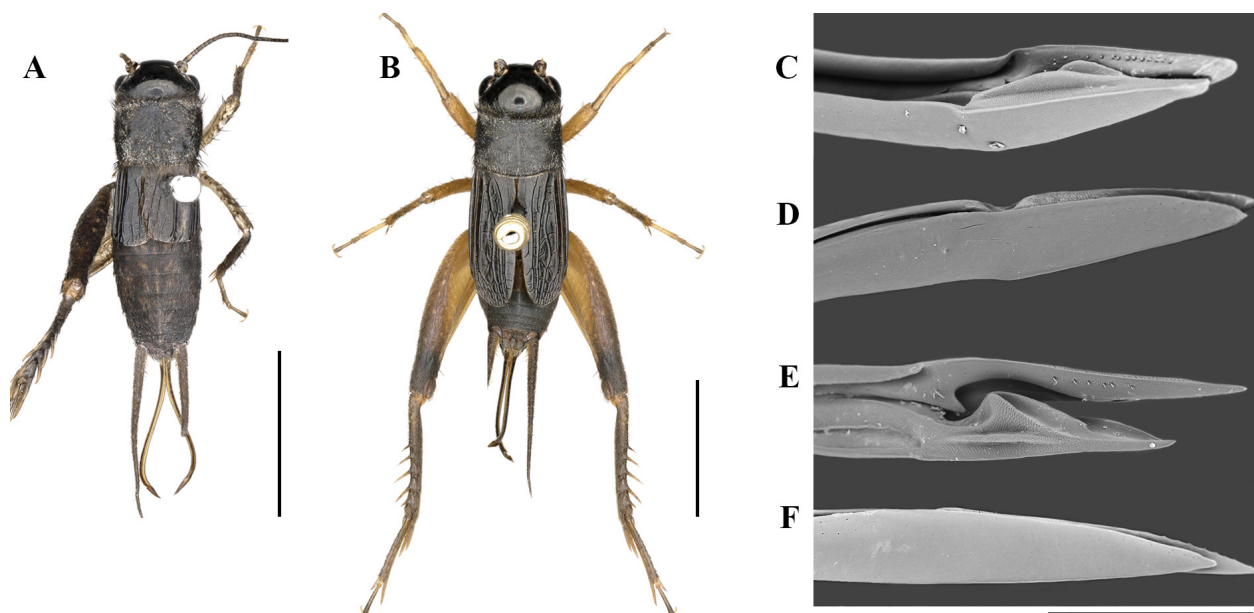
Figure 9. A–B Female body, scale bar: 5 mm; A – *S. humbertiellus*; B – *S. enatus* **comb. n.**; C–F ovipositor, scale bar: 0.5 mm, C – inside of ovipositor of *S. humbertiellus*; D – outside of ovipositor of *S. humbertiellus*; E – inside of ovipositor of *S. enatus* **comb. n.**; F – outside of ovipositor of *S. enatus* **comb. n.**

Stephoblemmus minutulus (Yang & Yang, 1995) comb. n.

Mitius minutulus Yang & Yang, 1995:7

Chinese name. 晋王素蟋

Materials not examined.

Remarks. According to Yang and Yang (1995), this species was reported in Taiwan. Its frons is rounded as *S. minor* **comb. n.** and *S. enatus* **comb. n.**. But it is distinct with them in features of tegmen and male genitalia. Its tegmina are rather short, only reaching the third abdominal tergum, and it does not have a mirror. Especially, its genitalia is different from all the species of *Stephoblemmus* (= *Mitius*) (its epiphallic middle lobe is bifurcated, not the typical unique lobe of the genus). Thus, we doubt if this species should be put in *Stephoblemmus*.

4.   Discussion

We conducted a morphological and molecular phylogenetic study of *Stephoblemmus* species distributed in China, Japan, and Thailand, and found that these species can be roughly divided into northern taxa represented by *M. minor* (= *S. minor*), southern taxa represented by *M. enatus* (= *S. enatus*), and southwestern taxa represented by *M. humbertiellus* (= *S. humbertiellus*). Among these three taxa, the southern taxon is the oldest, and they separated from the remaining two taxa around the Piacenzian (ca. 3.5 Ma), while the northern and southwestern taxa separated from each other around the Calabrian (ca.

1.81 Ma) (Fig. 2). Among them, the southwestern taxa are the very species of coronary crickets with special crowns. At first glance, it resembles the *Loxoblemmus*, the horn-headed crickets known for their exaggerated head shapes. However, our analyses firmly showed that its only species, *S. humbertiellus*, was nested within the clade of the genus *Mitius*, supporting the synonymy between these two genera.

4.1.   Relationship between the genera of *Stephoblemmus* and *Mitius*

Mitius was established by Gorochov in 1985 and diagnostic features were their smaller body and genitalia shape. The type species of *Mitius* was *Gryllus flavipes* (= *Mitius flavipes*) Chopard, 1928 which possess rounded frons. Later, based on genitalia features, some species with special head shapes were also moved into the genus. *Loxoblemmus castaneus* Chopard, 1937 (= *S. castaneus*) is very similar to *M. blennus* (= *S. blennus*), except for the truncated frons in males, and was moved into the *Mitius* (= *Stephoblemmus*) by Gorochov (1996) for the genitalia features. For the same reason, *Loxoblemmus vaturu* Otte & Cowper, 2007 (= *S. vaturu*) and *Mitius brevipennis* Yuan et al., 2022 (= *S. brevipennis*) were also separately assigned to the genus (Qiao et al., 2020; Yuan et al., 2022). *Stephoblemmus* was established by Saussure (1877) and their difference is more exaggeratedly truncated frons and forms a lamellar extension at the ends. Because of the peculiar head shape and the very small number of species (only the monotypy has been found since its discovery), no one has ever associated *Stephoblemmus* with *Mitius*. At most, their relationship with *Loxoblemmus* has been considered (Chopard, 1933; Qiao et al., 2020).

In this study, we found that the male external genitalia of genera *Stephoblemmus* and *Mitius* belong to a similar type while being distinct from *Loxoblemmus*. *Stephoblemmus* and *Mitius* both possess a unique and distinct epiphallic median lobe (Fig. 6) but for *Loxoblemmus*, its epiphallus with a pair of median lobes. In addition, their forewing patterns reflect similar species associations. We found that the apical fields of tegmina of species of both genera are shorter than half of the basal field, and that of *Loxoblemmus* is longer than half of the basal field (Fig. 5E–G). In the above, based on morphological characters, we argue that the genus *Stephoblemmus* and *Mitius* are extremely closely related.

4.2.   Relationship in species of *Stephoblemmus*

To date, there are ten species worldwide (Cigliano et al., 2023) According to the shape of the frons, all the species could be divided into two groups. However, there are still many problems with the classification of these species. For example, there may be intraspecific species morphological variation (e.g., coloration, frons, hind wings, body size, and male genitalia, etc.) in species *M. brevipennis* (= *S. brevipennis*), *M. enatus* (= *S. enatus*), *M. minor* (= *S. minor*), etc.; and there may be problems with the species relationship in species of *M. enatus* (= *S. enatus*), *M. eryuanensis*, *M. minor* (= *S. minor*), *M. blennus* (= *S. blennus*), and *M. splendens*, etc.

Here, we used five methods to delimit *Mitius* (= *Stephoblemmus*) species and found that those species with truncated frons (*S. humbertiellus*) are mixed up with those species with spherical frons. Thus, although the type of frons can identify *Mitius* (= *Stephoblemmus*) species, it cannot naturally classify them. In this study, we collected *Mitius* (= *Stephoblemmus*) specimens from ten provinces, a broad geographic range covering most of Southern China (Fig. S1). We also obtain a few samples from surrounding regions (e.g., *M. enatus* from Thailand and *M. minor* from Japan; see Table S1 for the list of specimens in this study). Although the methods used to distinguish species differed, the results of all methods except GMYC were the same and identified three different MOTUs. The GMYC methods define species based on an ultrametric guide tree (Reid & Carstens, 2012). Thus, GMYC shows *S. minor* from Hainan is different from *S. minor* elsewhere on MOTU, this may be due to the large gap in divergence times. Accordingly, *Stephoblemmus* includes eight species, and four of them can be found in China.

All models consider *M. enatus* (= *S. enatus* **comb. n.**), *M. eryuanensis*, and *M. flavipes* in China as MOTU, and morphological identification also supports this result. Yin & Liu (1995) identified the species from Yunnan as *M. flavipes* and noted differences with *S. enatus* **comb. n.** in the color of posterior tibiae and the first section of posterior tarsus. However, we observed about twenty specimens of *M. enatus* (= *S. enatus*) collected from Yunnan, Guangxi, Hainan, and Hong Kong, and found the color-

ation of the hind leg is varied, and the hind tibiae and tarsus might color yellow (Fig. 7C) or dark brown (Fig. 7D). Therefore, Chinese *M. flavipes* recorded in Yunnan Province should be a misidentification. Yuan et al. (2021) distinguished *M. eryuanensis* and *S. enatus* **comb. n.** through the presence or absence of bifurcation of epiphallic lateral lobes and hind wings. We found hind wings are present in some specimens or absent in others (indeed, hind wings always fall off in cricket adults) (Fig. 7A–B), and the bifurcate situation of the epiphallic lateral lobe is dependent, and the angle between the apex of lobe and its dorsal side would determine whether we observe the branches. When this angle is right or acute, we could find the epiphallic lateral lobe bifurcated; if it is obtuse, we could not observe it (Fig. 7H–N). *M. eryuanensis* should be a junior synonym of *S. enatus* **comb. n.**

Besides, the results of all methods except GMYC consider *S. minor* **comb. n.**, *M. splendens* and *M. blennus* as a MOTU. In terms of morphology, Yang and Yang (1995) recorded *M. blennus* and *M. splendens* in Taiwan and specified that they were slightly different in body size and male genitalia. But the diversity of *S. minor* **comb. n.** has been observed and it includes the situations of body size (the minimum body length is 9.25 mm, the maximum is 11.35 mm, and the average is 10.52 mm) and male genitalia (in dorsal view, epiphallic lateral lobe has two types of apical margin: truncated or arc-like margin (Fig. 8H–J); in ventral view, epiphallic lateral lobe also possesses two types of protrusion: only one truncate projection or two small protrusions (Fig. 8K–N)) in *M. splendens* (body length: 10.64–12.37 mm; Fig. 8C, G and I) and *M. blennus* (body length: 9.46–9.78 mm; Fig. 8E, H and J). Accordingly, we conclude that *S. minor* **comb. n.** and *M. splendens* should be one species, and *M. blennus* in Taiwan should be a misidentification.

In addition, *M. brevipennis* and *S. humbertiellus* both with truncated frons. We compared the holotype of *M. brevipennis* with *S. humbertiellus* in the same location, the genitalia are very similar (Fig. 6A–F) but the male frons is more prominent in *S. humbertiellus* (Fig. 5A–D). Furthermore, all of the barcoding analysis methods that supported *M. brevipennis* and *S. humbertiellus* were combined into one MOTU. Therefore, we think *M. brevipennis* and *S. humbertiellus* should be one species.

4.3.   Morphological variation of frons and sexual dimorphism in *Stephoblemmus*

The study reveals that the evolution of head shape in field crickets has not only undergone a long and complex historical process but also exhibits a complicated and variable diversity (Fig. S5). The frons of both *Stephoblemmus* and *Loxoblemmus* crickets appear to be specialized, but their basic structure is not similar, and they are not related in morphological changes. *Stephoblemmus* has a predominantly morphological variation on the dorsal side of the frons, with clypeus and labrum normal as in common crickets, and almost no very specific flattening; its com-

pound eyes are normal, with most of the two compound eyes visible in frontal view; the antennal sockets are also normal, and not only are their relative positions similar to those of common crickets, but the size of the antennal sockets is also similar to those of common crickets. In contrast, the entire face of *Loxoblemmus* is flattened, with the frontal, clypeus, and labrum all flattened; meanwhile, the compound eyes are located on the dorsal side of the face, and only a few of them are visible in the frontal view; the antennal sockets are smaller and located on or near the dorsal side of the face. Therefore, the special head shape of *Stephoblemmus* should be the result of independent evolution. In terms of divergence time (Fig. 2), the clade in which these two genera are located diverged in 9.18 Ma, and within both clades, the taxa adjacent to these two genera are also dominated by common hemispherical heads.

The special head shape of *Stephoblemmus* is not only the result of independent evolution but has also undergone several independent evolutions within the genus. Although we do not have the molecular data for the *S. castaneus* **comb. n.** and *S. vaturu* **comb. n.**, but based on geographic distribution (*S. castaneus* **comb. n.** distributed in Malesia and *S. vaturu* **comb. n.** distributed in Fiji), it is likely that truncated frons have evolved independently multiple times within the genus *Stephoblemmus*. In addition, the particular head features of *Stephoblemmus* may not be stable within the species. Not only are there individual differences in head characteristics, but there is also male and female dimorphism. Within the species of *S. humbertiellus*, the males' frons are truncate, and in most individuals, the apex of the frons expand dorsally in a lamellar form; however, in a few individuals the frons are only slightly convex dorsally, as in *Loxoblemmus* species. Sexual dimorphism of frons in *S. humbertiellus* is also observed. The males of this species present with frons specialization as described previously, while the females have a normal hemispherical head with no shape specialization. Therefore guess that the presence of the trait might be related to sexual selection in this species.

Sexual selection is responsible for the evolution of various sexually dimorphic traits such as elaborate weapons, ornaments, and behaviors (Andersson, 1994). In cricket studies on sexual dimorphism, the size, morphology and pigment of a male's head may all be associated with positive selection for more aggressive behavior (Sean et al., 2008). In studies of *Loxoblemmus* species, it has also been speculated that this particular head style is used as a weapon for male competition, but studies have been unable to confirm the involvement of this feature in male competition (Kuriwada, 2016). Although the specific function of the head trait is unknown, this trait also shows polymorphism within species. Compared to dimorphic traits, polymorphic traits may reflect more context of the occurrence of traits, such as the presence of transition states or the presence of diversity. However, there are few discussions on polymorphic traits in field crickets, and this study provides new material and information for related discussions.

5. Competing interests

6. Acknowledgments

7. References

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Supplementary Material 1

Tables S1–S3

Authors: Zheng Y-N, Gu J-J, He Z-Q, Huang H, Ma LB (2023)
Data type: .xlsx
Explanation note: Table S1. Collecting information and GenBank for phylogenetic analysis. — **Table S2.** Primers of COX1, 18S rRNA, and 28S rRNA. — **Table S3.** List of MOTUs.
Link: https://doi.org/10.3897/asp.81.e104772.suppl1

Supplementary Material 2

Figures S1–S4

Authors: Zheng Y-N, Gu J-J, He Z-Q, Huang H, Ma LB (2023)
Data type: .jpeg
Explanation note: Figure S1. The relationship of *Stephoblemmus* (= *Mitius*). — **Figure S2.** The maximum-likelihood (ML) tree. Posterior probabilities are indicated for all nodes. The species of interest for the study were shaded red, including species of *Loxoblemmus*, *Mitius*, and *Stephoblemmus*. The blue species are named the type species of *Stephoblemmus*.— **Figure S3.** Posterior probabilities are indicated for all nodes. The species of interest for the study were shaded red, including species of *Loxoblemmus*, *Mitius*, and *Stephoblemmus*. The blue species are named the type species of *Stephoblemmus*.— **Figure S4.** Heads of *Stephoblemmus* (A–B, E–F) **S. brevipenis syn. n.** (= *S. humbertiellus*), (C–D, G–J) *S. humbertiellus*, (K–L, O–P) *S. enatus* **comb. n.**, (M–N) *S. minor* **comb. n.**, (A–D, G–H, K–N) male, (E–F, I–J, O–P) female..
Link: https://doi.org/10.3897/asp.81.e104772.suppl2