



Molecular data resolving the systematics of the related Blattellidae genera *Symploce*, *Episymploce*, and *Blattella* (Blattodea: Blaberoidea)

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Abstract

Members of the morphologically and ecologically diverse Blattellidae provide a dilemma: their systematic assignment, whether morphologically similar or different, is uncertain. We pay special attention to several taxa: the morphologically similar *Episymploce* Bey-Bienko, 1950 and *Symploce* Hebard, 1916, which were strongly disputed because of their extremely similar generic diagnosis in the past century, and one brachypterous species of *Blattella* Caudell, 1903, which can be easily distinguished from other macropterous members, but is at risk of being misassigned to other genera on the basis of morphological characters. We address the phylogeny of Blattellidae using DNA sequences (mitochondrial *12S rRNA*, *16S rRNA*, *COII*, nuclear *28S rRNA*, histone *H3*) from a broad sample of taxa. A new genus (*Centrocolumna* gen. nov.) and four new species (*Centrocolumna ericea* sp. nov., *Symploce nigra* sp. nov., *Symploce tubercularis* sp. nov., *Blattella foliolata* sp. nov.) are established on the basis of morphological characters combined with the molecular data. The phylogenetic results indicate the relationships ((*Episymploce* + *Blattella*) + *Centrocolumna* gen. nov.) + *Symploce*. Furthermore, we delimited the taxonomic status of 12 new combinations, which involve *Centrocolumna* gen. nov., *Episymploce*, *Symploce*, and *Blattella*.

Keywords

Bayesian Inference, interspecific competition, key, Maximum Likelihood, mimicry, new species

1. Introduction

Blattellidae is an extremely species-diverse family in Blaberoidea, which contains approximately 1070 species from 79 genera (Beccaloni 2014). Blattellidae was recovered as a monophyletic group (Djernæs et al. 2015, 2020; Wang et al. 2017; Evangelista et al. 2021) based on molecular data, while clear morphological apomorphies are not known. Most species of Blattellidae are yellowish-brown to dark brown, and small to medium-sized.

Although the monophyly of most genera has not been verified until now, the accumulated evidence resolves a variety of unclear species assignments in *Episymploce* and *Symploce* owing to the former ambiguity of the generic diagnoses (Asahina 1979a; Roth 1984, 1985a, 1997; Wang 2006). But some species are still problematic.

Bey-Bienko (1950) established *Episymploce* with *Episymploce paradoxura* Bey-Bienko, 1950 as type species and compared it with the morphologically similar genus *Symploce*, which had been proposed by Hebard in 1916 with *Symploce hebardei* Princis, 1969 as type species (Princis 1969). After that, some taxonomists who focused on *Episymploce* and *Symploce* have also compared the two genera in detail, supplemented the generic diagnoses, and transferred many *Symploce* species to *Episymploce*, or vice versa (Asahina 1979a; Roth 1984, 1985a, 1985b, 1997; Wang 2006). Until now, there have been 70 species in *Symploce* and 73 species in *Episymploce* (Beccaloni 2014). Recent studies of *Episymploce* (Li et al. 2020; Zhang et al. 2019) highlighted the diversity of the Chinese cockroach fauna.

Because of the notorious German cockroach, *Blattella germanica*, people have a relatively good understanding of the genus *Blattella*, which is characterized by its generally small size, the tongue-shaped tergite 10 (supra-anal plate) and the tergal glands on abdominal tergites VII and VIII. Developed tegmina and hindwings are very common in *Blattella* males with the exception of *Blattella kevani* Roth, 1985, whose tegmina and hindwings are missing or possibly reduced (Roth 1985b). Up to now, 53 *Blattella* species distributed all over the world are recognized (Beccaloni 2014). It was easier to catch *Blattella* nymphs than adults (Wang ZQ, personal experience), but whether adults or nymphs, they have no specific characteristics that can be used for species identification in the field. It was challenging to confirm the taxonomic status of the brachypterous Blattellidae species, which is morphologically different from the *Blattella* species, only on the basis of morphological characters. Just like the jumping cockroach, *Saltoblattella montistabularis* Bohn, Picker, Klass and Colville, 2010, was discovered owing to its special morphological characters: hind legs modified into long jumping legs, fore wings reduced to small lateral lobes and hind wings absent (Bohn et al. 2010), but its taxonomic status was unclear and it was preliminarily placed in Blattellidae, which emerged as sister species to *Ectobius sylvestris* (Poda, 1761) based on the results of a molecular phylogeny study of cockroaches (Djernæs et al. 2012). But based on the strong phylogenetic evidence, *Saltoblattella* was assigned into Pseudophyllodromiidae (Evangelista et al. 2021).

During the last decade, a number of well-accepted molecular phylogenetic studies obtained excellent results in cockroach systematics, including Inward et al. (2007), who confirmed that termites are eusocial cockroaches; Djernæs et al. (2015) and Wang et al. (2017); Djernæs et al. (2020), who clarified the taxonomic status of *Anaplecta* and *Attaphila*; Evangelista et al. (2019, 2021), who established newly named clades. On this basis, the classification of cockroaches was considerably modified as to match the new phylogenetic findings (Djernæs 2018; Djernæs et al. 2020; Inward et al. 2007). These studies, whether based on selected mitochondrial and nuclear genes or on transcriptome data, have all proved molecular data to be successful in discovering relationships among different cockroach groups. *Episymploce* and *Symploce*

are very similar in morphology with a confused taxonomy, and the same situation also exists in the brachypterous Blattellidae species; therefore, molecular data are needed to infer the relationships of these genera.

Here we used targeted taxon sampling (mainly from Blattellidae) and generated molecular data (mitochondrial *12S rRNA* (*12S*), mitochondrial *16S rRNA* (*16S*), cytochrome *c* oxidase subunit II (*COII*), nuclear *28S rRNA* (*28S*) and histone *H3* (*H3*)), in order to infer the relationships of the species of the morphologically similar genera *Episymploce* and *Symploce*, and the morphologically different brachypterous Blattellidae species, and clarify the taxonomic status of these problematic groups. Finally, we present one new genus *Centrocolumna* **gen. nov.**, four new species of *Symploce*, *Blattella* and *Centrocolumna* **gen. nov.**, and 12 new combinations based on morphological characters and molecular data.

2. Materials and methods

2.1. Taxon sampling

Samples of Blattellidae were collected from southeast and southwest localities in China, mainly in Yunnan, Hainan, and Guangdong (supplementary material Table S1). Specimens were preserved in analytical pure ethanol and stored at -80°C until processing. All voucher specimens (more information in Table S1) are kept at the Institute of Entomology, College of Plant Protection, Southwest University, Chongqing, China.

2.2. Morphological study

Morphological terminology used mainly follows McKittrick (1964), Roth (2003), and Li et al. (2018). Terminology abbreviations in this article are as follows: **L3** – sclerites of the left phallomere; **L2vm** – median phallomere; **R2**, **R3** – sclerites of the right phallomere; **T** – tergite; **ScP** – subcosta posterior; **R** – radius; **RA** – radius anterior; **RP** – radius posterior; **M** – media; **CuA** – cubitus anterior; **CuP** – cubitus posterior; **V** – vannal veins; **Pcu** – postcubitus.

Measurements are based on specimens examined by vernier caliper as follows: the body length: from the anterior to the posterior; the body length including tegmina: from the anterior to the tip of tegmina; and pronotum length \times width: the length at the longest and the width at the widest part. Genital segments of examined specimens were placed in centrifuge tubes and soaked with 10% NaOH, then the centrifuge tube was immersed in hot water for 15–20 minutes and rinsed with distilled water, and then observed in glycerin under a SZ780 Continuous Zoom Stereo Microscope. Specimen and genital photographs were taken by a Leica M205A stereomicroscope with a Leica DFC Camera. All photos provided here were edited and assembled into plates in Adobe Photoshop

CS6. Male postabdominal structures are shown at greater detail in supplementary material Fig. S2 than in the figures included in the main article. Type material of new taxa is deposited in the Institute of Entomology, Southwest University, Chongqing, China.

2.3. DNA extraction, amplification and sequencing

We sequenced five genes in 48 samples across 26 species (Table S1) of Blattellidae: three mitochondrial genes: *12S*, *16S*, *COII*, and two nuclear genes: *28S*, *H3*. Total genomic DNA was extracted with the HiPure Tissue DNA Mini Kit (Magen, Guangzhou) from the hindleg tissue of the specimens according to the manufacturer's protocol. The legs were retained afterwards and stored in 100% ethanol.

All gene fragments were amplified by PCR. The primers used for amplification are given in supplementary material Table S2. For PCR amplification, the 25 μ L reaction system included 22 μ L of 1.1 \times T3 Super PCR Mix (Tsingke Biological Technology, Beijing), 2 μ L of each primer and 1 μ L of DNA template. Amplification conditions were as follows: initial denaturation at 98°C for 2 min, followed by 35 cycles of 10 s at 98°C, 10 s at annealing temperature (depending on the amplified gene fragment; see Table S2 for more details), and 10 s at 72°C, and with a final extension of 2 min at 72°C.

PCR products were checked by agarose gel electrophoresis and then sent to Tsingke Biological Technology for purification and sequencing. We used an unrestricted BLAST search to check for contamination in all new sequences. All sequences were deposited in GenBank (accession numbers given in Table S1).

2.4. Sequence alignment and phylogenetic analysis

In our study, the lengths of five genes excluding the primer were 422 nt (*12S*), 464 nt (*16S*), 681 nt (*COII*), 726 nt (*28S*), and 330 nt (*H3*). Sequences were aligned by MAFFT online version 7 (<https://mafft.cbrc.jp/alignment/server>). For the alignment of the ribosomal sequences (*12S*, *16S* and *28S*), an adjusted direction according to the first sequence was selected to check if there was the reverse sequence. The Q-INS-i algorithm was selected for the ribosomal sequences, the G-INS-i algorithm for protein-coding genes *COII* and *H3*, while other parameters were set to default values. Alignments of *12S*, *16S* and *28S* were checked visually in MEGA 7 (Kumar et al. 2016) and some poorly aligned characters within the intergenic region were removed. Alignments of protein-coding genes (*COII* and *H3*) were manually corrected after translating into amino acids, usually with few gaps deleted, resulting in a total length of the concatenated fragments of 2623 nt.

We assembled a data set with 93 samples from 42 Blattellidae species combined with some samples sequenced

in previous studies, and 17 outgroup species (ten from other families of Blaberoidea Blattodea except Blaberidae, three from Mantodea, and one each from Phasmatoidea, Mantophasmatodea, Grylloblattodea and Orthoptera) downloaded from GenBank (<https://www.ncbi.nlm.nih.gov>) to infer the position of the root in our phylogenetic analysis (supplementary material Table S1). Phylogenetic analysis was performed based on the combined data set, using maximum likelihood (ML) and Bayesian inference (BI). We performed ML using RAxML version 7.7.1 (Stamatakis et al. 2008) with model GTRGAMMA, and 1000 bootstrap replicates to estimate node support. PartitionFinder 2.0 (Lanfear et al. 2016) was used to select optimal partitioning scheme and substitution models for the data subsets for BI: GTR+I+G for *12S*, *16S* and *COII* codon position 1 and 2; HKY+I+G for *COII* codon position 3; GTR+G for *28S*; SYM+I for *H3* codon position 1 and 2; and TVM+G for *H3* codon position 3. Posterior distribution was estimated by Markov chain Monte Carlo (MCMC) sampling with four chains (three hot and one cold). Samples were drawn every 1000 steps over a total of MCMC 6×10^6 . Convergence was inferred when the standard deviation of split frequencies was < 0.01 . The first 25% of samples were discarded as burn-in and contype was set to allcompat.

3. Results

3.1. Phylogenetic inference

Our ML and BI phylogenetic analyses yielded almost identical topologies with generally high support values (Fig. 1, supplementary material Fig. S1). In both analyses, there were four main lineages of Blaberoidea recovered with high support values; they showed the relationships Blattellidae + (Ectobiidae + (Nyctiboridae + Pseudophyllodromiidae)); the clade Pseudophyllodromiidae + Nyctiboridae + Ectobiidae was highly supported, as was the Blattellidae clade. In this it should be noted that no member of Blaberidae was included in the analyses.

In Blattellidae, the topology derived from both analyses showed that *Symptloce ligulata* (Bey-Bienko, 1957), the brachypterous Blattellidae species, and *Blattella* samples formed a clade with high support values (ML bootstrap support (bs) 100%, posterior probability (pp) 1.0). Then this clade was placed as sister to the monophyletic *Episymploce* (bs 100%, pp 1.0), followed by the clade *Symptloce evidens* Wang and Che, 2013 + one unknown species (bs 100%, pp 1.0). Other species of the genus *Symptloce* were grouped together to form a clade in the ML analysis, which was recovered to be the sister of clade comprised of the three groupings listed above (bs 100%) (Fig. 1). But in BI, *Symptloce* was obtained as paraphyletic (supplementary material Fig. S1) with respect to the groups listed above.

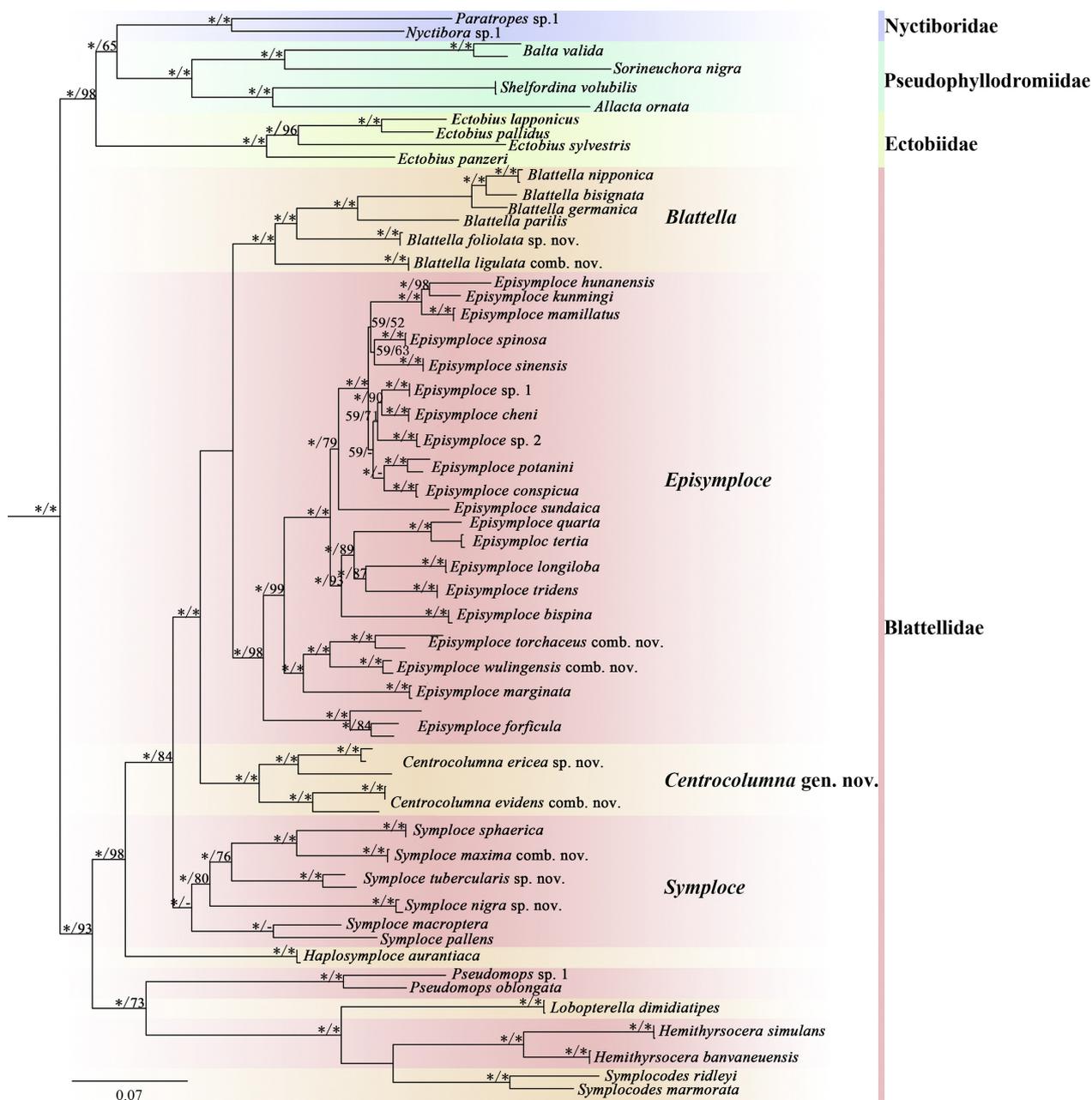


Figure 1. Maximum likelihood (ML) tree based on three mitochondrial genes *12S rRNA*, *16S rRNA*, *COII* and two nuclear genes *28S rRNA*, histone *H3*. The topologies yielded by Bayesian inference (BI) are almost identical with ML tree (see supplementary material Fig. S1). Branch labels provide bootstrap support (bs) of nodes in ML and posterior probability (pp) (%) of nodes in BI; (*) indicates the branch label of the corresponding analysis is 100 or 1.0, respectively; (-) means the node is absent for the given analysis.

3.2. Establishment of new genus, new species and new combinations

Our phylogenetic inference and subsequent critical examination of morphology led us to propose one new genus, four new species and 12 new combinations as follows.

3.2.1. *Centrocolumna* Jin and Che gen. nov.

<http://zoobank.org/B6744ADB-FE0C-4ACE-90FA-0582683-FB0FF>

Note. Both the ML analyses and BI highly support that the clade *Symploce evidens* Wang and Che, 2013 plus one unknown species is the sister to the clade of *Blattella* + *Episymploce* (bs 100%, pp 1.0). Hind margin of subgenital plate with an obvious protrusion and with the right stylus located on it make them obviously distinguishable from other related genera. Therefore, we establish for them and some other taxonomic units the new genus *Centrocolumna* Jin and Che gen. nov. and also propose one new species and eight new combinations.

Type species. *Symploce evidens* Wang and Che, 2013, by present designation.

Diagnosis. Male. Tegmina and hindwings fully developed or slightly reduced. Hindwings with RP branched near the middle, M simple and unbranched, CuA curved with 1–4 complete and 0–5 incomplete branches; apical triangle small or absent. Anteroventral margin of front femur usually Type A. Tergal specialization and medial setal tuft always present on T1, T7 and T10. Subgenital plate asymmetrical, hind margin with a prominent protrusion in the middle, and the right stylus arising upon the protrusion. Bases of two styli obtuse, apices tapering.

Etymology. *Centrocolumna*, the combination of the Latin words *centr-* and *columna*, refers to the right stylus arising upon the protrusion. The gender of *Centrocolumna* is feminine.

Remarks. This genus is similar to *Symploce* Hebard, 1916, but it can be distinguished from *Symploce* by the following characters: 1) T10 usually specialized with setal tuft at disk (absent in *Symploce*); 2) hind margin of subgenital plate with a prominent protrusion (absent in *Symploce*).

Note. According to the generic diagnosis of *Centrocolumna* **gen. nov.**, we transferred the following species of *Symploce* to this genus after our critical examination of the original literature, especially the grouping of species of *Symploce* collected from Taiwan and Japan in Asahina (1979b) and Roth (1987).

3.2.2. Checklist of *Centrocolumna* gen. nov. worldwide

- (1) *Centrocolumna evidens* (Wang and Che, 2013) **comb. nov.**
Symploce evidens Wang and Che, 2013: 13.
- (2a) *Centrocolumna striata striata* (Shiraki, 1906) **comb. nov.**
Periplaneta striata Shiraki, 1906: 27.

- Ischnoptera striata*: Shiraki, 1931: 194.
- Symploce striata striata*: Asahina, 1979b: 223; Roth, 1987: 158.
- (2b) *Centrocolumna striata wulaii* (Asahina, 1979b) **comb. nov.**
Symploce striata wulaii Asahina, 1979b: 225; Roth, 1987: 159.
- (3) *Centrocolumna yayeyamana* (Asahina, 1979b) **comb. nov.**
Symploce yayeyamana Asahina, 1979b: 225–226; Roth, 1987: 159.
- (4a) *Centrocolumna gigas gigas* (Asahina, 1979b) **comb. nov.**
Symploce gigas gigas Asahina, 1979b: 226; Roth, 1987: 160.
- (4b) *Centrocolumna gigas okinawana* (Asahina, 1979b) **comb. nov.**
Symploce gigas okinawana Asahina, 1979b: 228; Roth, 1987: 160.
- (5) *Centrocolumna japonica* (Shelford, 1907) **comb. nov.**
Phyllodromia (?) *japonica* Shelford, 1907: 33–34.
Symploce japonica: Asahina, 1979b: 229; Roth, 1987: 157.
- (6) *Centrocolumna okinoerabuensis* (Asahina, 1974) **comb. nov.**
Symploce okinoerabuensis Asahina, 1974: 151, 1979b: 230; Roth, 1987: 158.
- (7) *Centrocolumna furcata* (Shiraki, 1931) **comb. nov.**
Ischnoptera furcata Shiraki, 1931: 190–191.
Symploce furcata: Asahina, 1979b: 230; Roth, 1987: 160.
- (8) *Centrocolumna acuminata* (Shiraki, 1931) **comb. nov.**
Ischnoptera acuminata Shiraki, 1931: 195.
Symploce acuminata: Asahina, 1979b: 231; Roth, 1987: 157.
- (9) *Centrocolumna ericea* Jin and Che **sp. nov.**

3.2.3. Key to species of *Centrocolumna* gen. nov. (males)

- 1 Tegmina and hindwings reduced, length about 0.5 times body length *C. acuminata* **comb. nov.**
- 1' Tegmina and hindwings fully developed, length about 1.2 times body length.....2
- 2 T1 without a medial setal tuft3
- 2' T1 with a medial setal tuft.....4
- 3 T10 without a setal tuft*C. striata striata* **comb. nov.**
- 3' T10 with an obvious setal tuft..... *C. striata wulai* **comb. nov.**
- 4 Styli elongate, slender and straight, apically acute *C. yayeyamana* **comb. nov.**
- 4' Styli relatively short and slightly curved5
- 5 CuA branches of hindwings all reaching the wing margin6
- 5' CuA branches of hindwings partly not reaching the wing margin.....7
- 6 T10 with a setal tuft in the middle *C. japonica* **comb. nov.**
- 6' T10 apparently without setal tuft in the middle*C. furcata* **comb. nov.**
- 7 Right paraproct with a cockscomb-like process8
- 7' Right paraproct without such a process9
- 8 T7 with a setal tuft*Centrocolumna ericea* **sp. nov.**
- 8' T7 without a setal tuft *C. evidens* **comb. nov.**

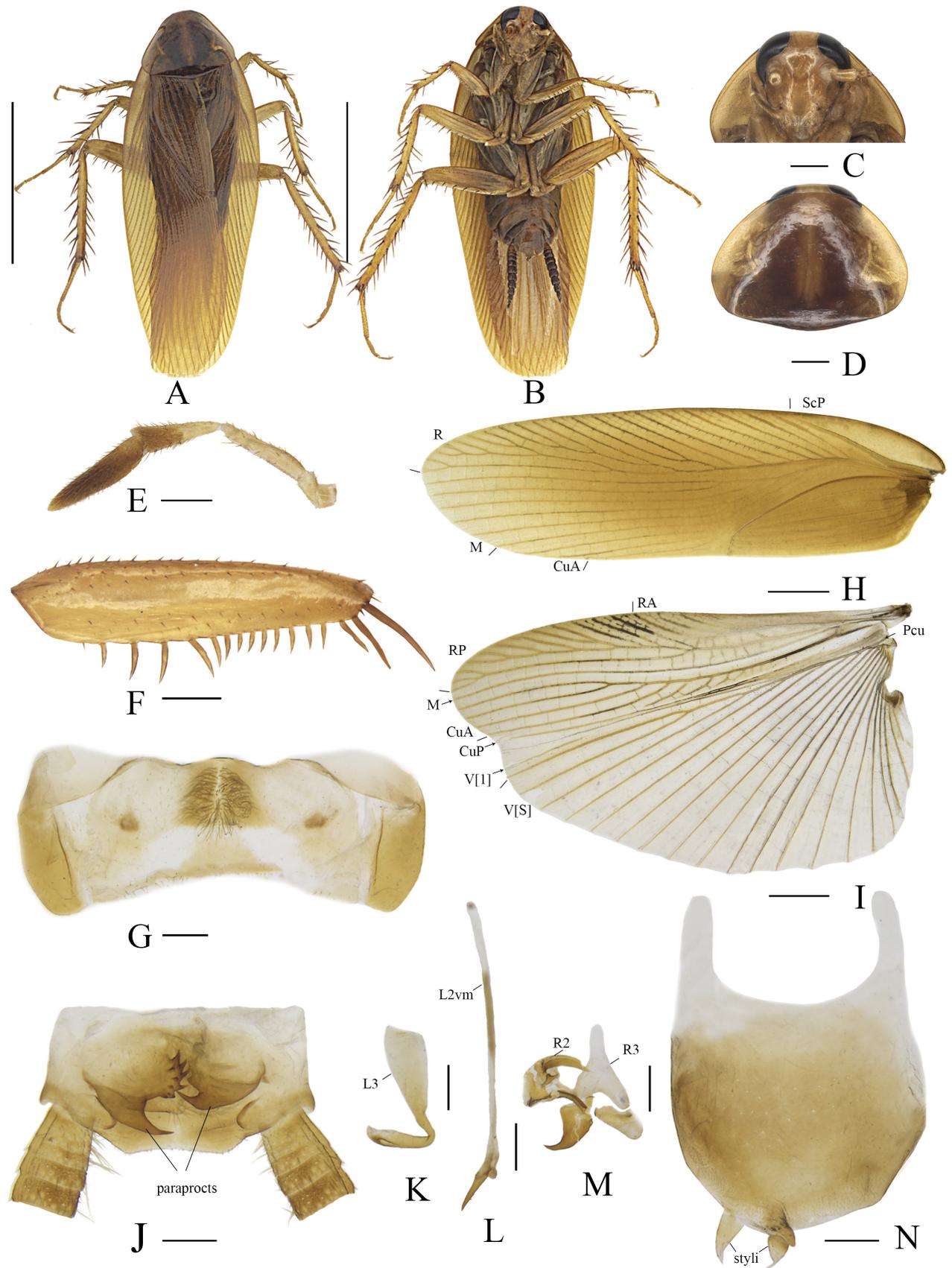


Figure 2. *Centrocolumna ericea* gen. et sp. nov., male: **A** holotype, dorsal view; **B** holotype, ventral view; **C** head, ventral view; **D** pronotum; **E** maxillary palp; **F** front femur, ventral view; **G** seventh abdominal tergite; **H** tegmen; **I** wing; **J** supra-anal plate, ventral view; **K** left phallomere; **L** median phallomere; **M** right phallomere; **N** subgenital plate, dorsal view. Scale bars: 10 mm (A, B), 1 mm (C, D), 2 mm (H, I), 0.5 mm (E–G, J–N).

- 9 Left phallomere with one hook-like structure and an additional irregular sclerite..... *C. okinoerabuensis* **comb. nov.**
- 9' Left phallomere with only one hook-like structure..... **10**
- 10 CuA of hindwings with 3 complete and 4–5 small incomplete branches..... *C. gigas gigas* **comb. nov.**
- 10' CuA of hindwings with 2 complete and 1 long incomplete branches..... *C. gigas okinawana* **comb. nov.**

3.2.4. *Centrocolumna ericea* Jin and Che **sp. nov.**

<http://zoobank.org/6074B78F-034E-4775-B5F4-CA5E919-CD773>

Fig. 2

Type material. Holotype: CHINA • ♂; Chongqing, Qianjiang County, Zhuoshui Town; 19–26 June 2013; Shunhua Gui, Yan Shi leg. **Paratypes:** CHINA • 1 ♂, Fujian Prov., Mt. Wuyi, Tongmu Village; 8 July 2013; Shunhua Gui, Yan Shi leg. • 1 ♂, 1 ♀; Guangxi Prov., Jinxiu County, Mt. Shengtang; 4–5 June 2014; Shunhua Gui, Xinran Li leg. • 2 ♂♂; Hunan Prov., Changde City, Taoyuan County, Wuyunjie, Tujindong; 19 June 2019; Rong Chen, Hao Xu leg.

Measurements (mm). Overall length: ♂ 20.6, ♀ 19.6; pronotum length × width: ♂ 4.3 × 4.9, ♀ 4.2 × 5.1; tegmina: ♂ 17.5, ♀ 16.4.

Description. Male. Coloration: Body yellowish brown or brown (Fig. 2A, B). Ocelli pale yellow. Antennae yellowish brown with base pale yellow. Maxillary palps with fourth and fifth palpomeres yellow brown, others pale yellow (Fig. 2E). Pronotum yellowish brown, with a light-colored vertical stripe at disk (Fig. 2C, D). **Head:** Interocular space slightly less than ocelli width and distinctly narrower than width of antennal sockets. Third and fifth maxillary palpomeres about same length, and slightly longer than the fourth (Fig. 2E). Posterior margin of pronotum slightly convex in the middle (Fig. 2D). **Tegmina and hindwings:** Both fully developed, extending beyond end of abdomen (Fig. 2H, I). RP of hindwings with branches near the middle, CuA curved as “S” with 4 complete and 3 incomplete branches (Fig. 2I); apical triangle small. **Legs:** Anteroventral margin of front femur Type A₃ (Fig. 2F), pretarsal claws symmetrical and unspecialized. **Abdominal tergites:** T1 specialized with a setal tuft in the middle; T7 specialized with a pair of shallow fossae and a setal tuft in the middle, two dark brown spots on each side of the tuft (Fig. 2G). T10 with a median ridge, where a bunch of bristles is born, hind margin broadly and weakly concave. **Paraprocts:** Dissimilar, right one with a long spine and a cockscomb-like process, and left one with a shorter spine-like process distad (Fig. 2J). **Subgenital plate:** Asymmetrical, styli cone-shaped, the right one located on the apex of a protrusion arising from middle of hind margin, and left one slightly larger and near base of right one (Fig. 2N). **Male genitalia:** L3 on the left side with a subapical incision (Fig. 2K); proximal end of L2vm with an inconspicuous bifurcation, and the apex sharp (Fig. 2L); R2, R3 complex with a Y-shaped sclerite (Fig. 2M). — **Female.** Like male (except for postabdomen).

Etymology. The specific epithet is derived from the Latin word *ericeus*, referring to the right paraproct scattered with spines.

Remarks. *Centrocolumna ericea* Jin and Che **sp. nov.** resembles *Centrocolumna striata striata* **comb. nov.**, but differs from it as follows: 1) the former with a setal tuft on T1, but the latter without; 2) the former with the left stylus larger than right one, but the latter with the right stylus larger than left one. Furthermore, the general color differs greatly among specimens of the new species collected in different provinces: specimens from Chongqing and Fujian are generally yellowish brown, specimens from Hunan are brown, and specimens from Guangxi are dark brown. In terms of paraprocts, there are some minor differences exhibited in the cockscomb-like process of right paraproct, the teeth usually ranging from 2 to 8.

Distribution. China (Chongqing, Fujian, Guizhou, Jiangxi, Guangxi, Guangdong, Yunnan, Hunan).

3.2.5. *Symploce* Hebard, 1916

Note. In this genus, with the type species *S. hebardii* Princis, 1969 (not included in our analyses), we establish two new species mainly according to the morphological characters. In addition, inferred from our phylogenetic analyses (Fig. 1), *Episymploce maxima* Li, Liu, Qiu and Yue is grouped together with other *Symploce* species; thus, we propose one new combination.

3.2.6. *Symploce maxima* (Li, Liu, Qiu and Yue, 2020) **comb. nov.**

Fig. 3

Episymploce maxima Li, Liu, Qiu et Yue, 2020: 40.

Material examined. CHINA • 1 ♂, 1 ♀; Guangxi Prov, Guiping City, Longtan National Forest Park; 386 m; 2 June 2014; Shunhua Gui, Xinran Li leg. • 1 ♂, Guizhou Prov., Qiannan Dushan County, Mawei Town; 9 June 2019; Lu Qiu, Wenbo Deng leg. • 1 ♂, Guizhou, Prov., Leishan County, Changbei Village; 8 June 2013; Guiqiang Huang, Xi-angxiang Zhang leg.

Remarks. Li et al. (2020) established *Episymploce maxima*, but we transfer this species (Fig. 3) to *Symploce* based on the following reasons: 1) in morphology, body size large (Fig. 3A–D), T9 unspecialized, and no incrasate or crimping on the posterior margin of the subgenital plate (Fig. 3N); 2) in phylogenetic analysis, *Episymploce*

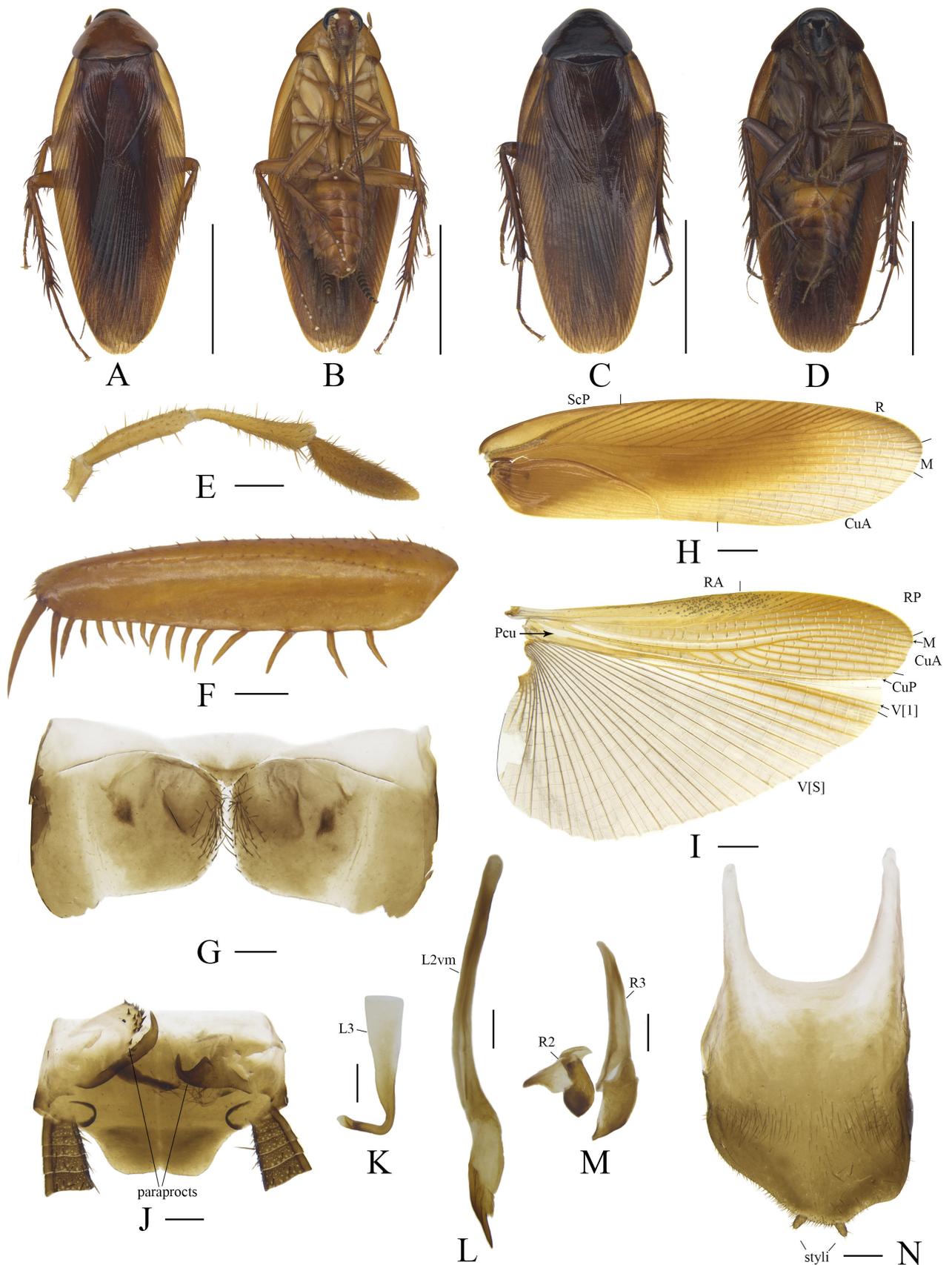


Figure 3. *Symploce maxima* (Li et al, 2020) **comb. nov.**, male: **A, B** Duwei County, Guizhou: **A** dorsal view; **B** ventral view; **C, D** Leishan County, Guizhou: **C** dorsal view; **D** ventral view; **E** maxillary palp; **F** front femur, ventral view; **G** seventh abdominal tergite; **H** tegmen; **I** wing; **J** supra-anal plate, ventral view; **K** left phallomere; **L** median phallomere; **M** right phallomere; **N** subgenital plate, dorsal view. Scale bars: 10 mm (A–D), 2 mm (H, I), 0.5 mm (E–G, J–N).

maxima Li, Liu, Qiu and Yue was placed as the sister of *Symploce sphaerica* with a high support value (Fig. 1, supplementary material Fig. S1), forming a clade together with other *Symploce* species. In addition, different individuals of this species exhibit some variations in body color, especially on the pronotum: the sample from Duwei County are black brown (Fig. 3A, B), others from Leishan County are yellowish brown (Fig. 3C, D).

Distribution. China (Guangxi, Guizhou).

3.2.7. *Symploce nigra* Jin and Che sp. nov.

<http://zoobank.org/F2EAAF44-796C-41D3-ADB3-BC4318-8317A6>

Fig. 4

Type material. Holotype: CHINA • ♂; Hainan Prov., Ledong County, Mt. Jianfengling; 26–28 June 2014; Bing Liu leg.; light traps. **Paratypes:** CHINA • 2 ♂♂, same data as for holotype.

Measurements (mm). Overall length: ♂ 21.5; pronotum length × width: ♂ 4.6 × 6.0; tegmina: ♂ 18.5.

Description. Male. Coloration: Body chestnut brown (Fig. 4A, B). Vertex black, lower half of face chestnut brown. Ocelli milky. Base of antenna yellowish brown, the rest dark brown (Fig. 4C). Maxillary palps brown (Fig. 4E). Pronotum chestnut brown, posterior and narrow lateral borders shiny black (Fig. 4D). Tegmina anterior edge black, the rest blackish brown (Fig. 4H). Legs with tibiae and tarsi dark brown, remainder chestnut brown (Fig. 4B). **Head:** Interocular space shorter than the distance between ocelli and slightly less than the width of an antennal socket. Third maxillary palpomere as long as the fourth, slightly longer than the fifth (Fig. 4E). Posterior margin of pronotum slightly convex (Fig. 4D). **Tegmina and hindwings:** Both fully developed, extending beyond the end of abdomen (Fig. 4H, I). Hind wings with RP branched after the midpoint, the apical region of M with a bifurcation, CuA slightly curved with 5 complete and 3 incomplete branches (Fig. 4I). **Legs:** Front femur Type A₃ (Fig. 4F), pretarsal claws symmetrical and unspecialized, pulvillus present. **Abdominal tergites:** T1 specialized as a ridge scattered with a cluster of setae. T7 also specialized with a pair of unobvious fossae in the middle (Fig. 4G). T10 symmetrical, posterior margin rounded. **Paraprocts:** Dissimilar, the right one bifurcate with one apex enlarged, left one with a curved finger-like process (Fig. 4J). **Subgenital plate:** Slightly asymmetrical, middle part of posterior margin distinctly convex with tiny bristles, two styli similar and cylindrical with tiny bristles; right middle area with a large spine-like protrusion pointed to supra-anal plate (Fig. 4N). **Male genitalia:** L3 on the left side and the apex with an incision (Fig. 4K); L2vm rod-like, the apex acute (Fig. 4L); R3 complex, a part of the sclerites rake-shaped (Fig. 4M). — **Female.** Unknown.

Etymology. The Latin word *niger*, meaning black, refers to the posterior and lateral border areas of pronotum being black.

Remarks. *Symploce nigra* Jin and Che sp. nov. is similar to *Centrocolumna evidens* comb. nov. in general morphology, however, they can be distinguished by the following characteristics: 1) pronotum of the former chestnut brown, posterior and narrow lateral borders shiny black, but lateral region of the pronotum of the latter species yellowish brown with dark U-shaped maculae at disc; 2) supra-anal plate of the former specialized with setal tuft near the posterior margin, but the latter without; 3) two styli similar and cylindrical, both situated at the posterior margin of subgenital plate, while the right stylus of the latter, arising at the protrusion of subgenital plate.

Distribution. China (Hainan).

3.2.8. *Symploce tubercularis* Jin and Che sp. nov.

<http://zoobank.org/67527858-52DA-4295-86AD-ED-C519763921>

Fig. 5

Type material. Holotype: CHINA • ♂, Guangxi Prov., Jinxiu County, Mt. Shengtang; 4–5 June 2014; Shunhua Gui, Xinran Li leg. **Paratypes:** CHINA • 2 ♂♂, Guangxi Prov., Wuming County, Mt. Daming; 3 July 2015, Lu Qiu and Qikun Bai leg. • 1 ♀, Guangxi Prov., Jinxiu County, Yinshan Park; 16–17 July 2015; Lu Qiu, Qikun Bai leg.

Measurements (mm). Overall length: ♂ 25.0, ♀ 23.0; pronotum length × width: ♂ 5.4 × 6.2, ♀ 5.5 × 6.4; tegmina: ♂ 22.5, ♀ 18.7.

Description. Male. Coloration: Large body, yellowish-brown to dark brown (Fig. 5A, B), face brown, ocelli milky (Fig. 5C). Maxillary palps brown (Fig. 5E). The base of antenna yellowish brown, the rest dark brown. Pronotum yellowish-brown with posterior border black brown (Fig. 5D). **Head:** Interocular distance obviously less than the distance between antennal sockets. Third segment of maxillary palps as long as the fifth segment, slightly longer than the fourth (Fig. 5E). Posterior margin of pronotum obviously convex (Fig. 5D). **Tegmina and hindwings:** Both fully developed, extending beyond the end of abdomen (Fig. 5H, I). Hind wings with RP bifurcated near the midpoint; the apex of M branched; CuA curved with 5–6 complete branches and 3 incomplete branches (Fig. 5I). **Legs:** Front femur Type A₃ (Fig. 5F), pretarsal claws with pulvillus symmetrical and unspecialized. **Abdominal tergites:** Center of T1 ridged with a cluster of setae, T7 with a pair of obvious depressions and a tubercular process, where some bristles are present in the middle (Fig. 5G). T10 symmetrical, posterior margin slightly concave, and anterior margin with a cluster of setae. **Paraprocts:** Dissimilar, the right one with a curved

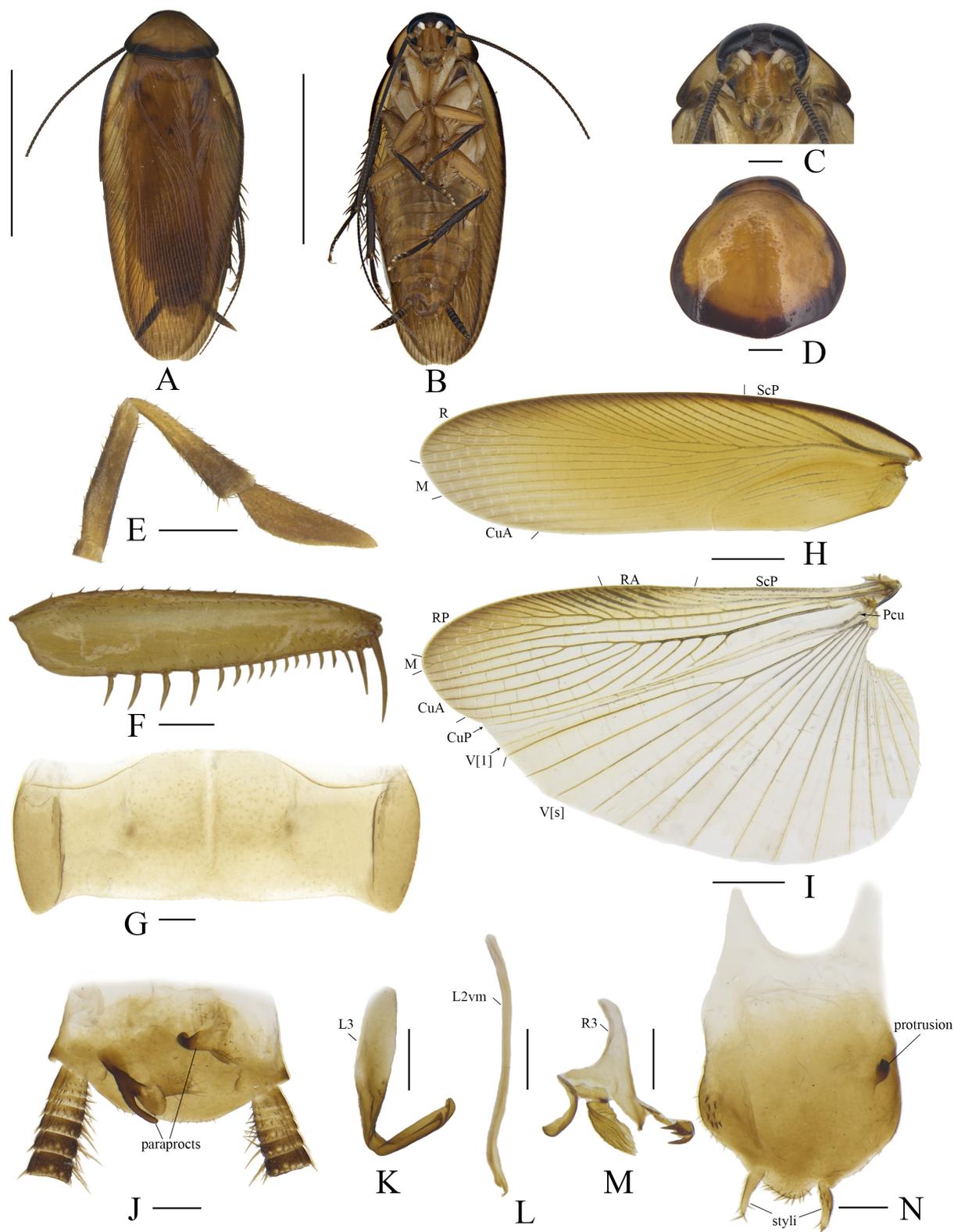


Figure 4. *Symploce nigra* sp. nov., male: **A** holotype, dorsal view; **B** holotype, ventral view; **C** head, ventral view; **D** pronotum; **E** maxillary palp; **F** front femur, ventral view; **G** seventh abdominal tergite; **H** tegmen; **I** wing; **J** supra-anal plate, ventral view; **K** left phallomere; **L** median phallomere; **M** right phallomere; **N** subgenital plate, dorsal view. Scale bars: 10 mm (A, B), 1 mm (C, D), 2 mm (H, I), 0.5 mm (E–G, J–N).

and spine-like process at base, left one with 3 spine-like processes of variable size (Fig. 5J). **Subgenital plate:** Hind margin asymmetrical, left stylus arising at posterior margin with some spinules; right stylus crooked and ir-

regular (Fig. 5N). **Male genitalia:** L3 on the left side, of which the apex has an incision (Fig. 5K); L2vm rod-like and with branches at apex (Fig. 5L); R2, R3 made up of several sclerites (Fig. 5M).

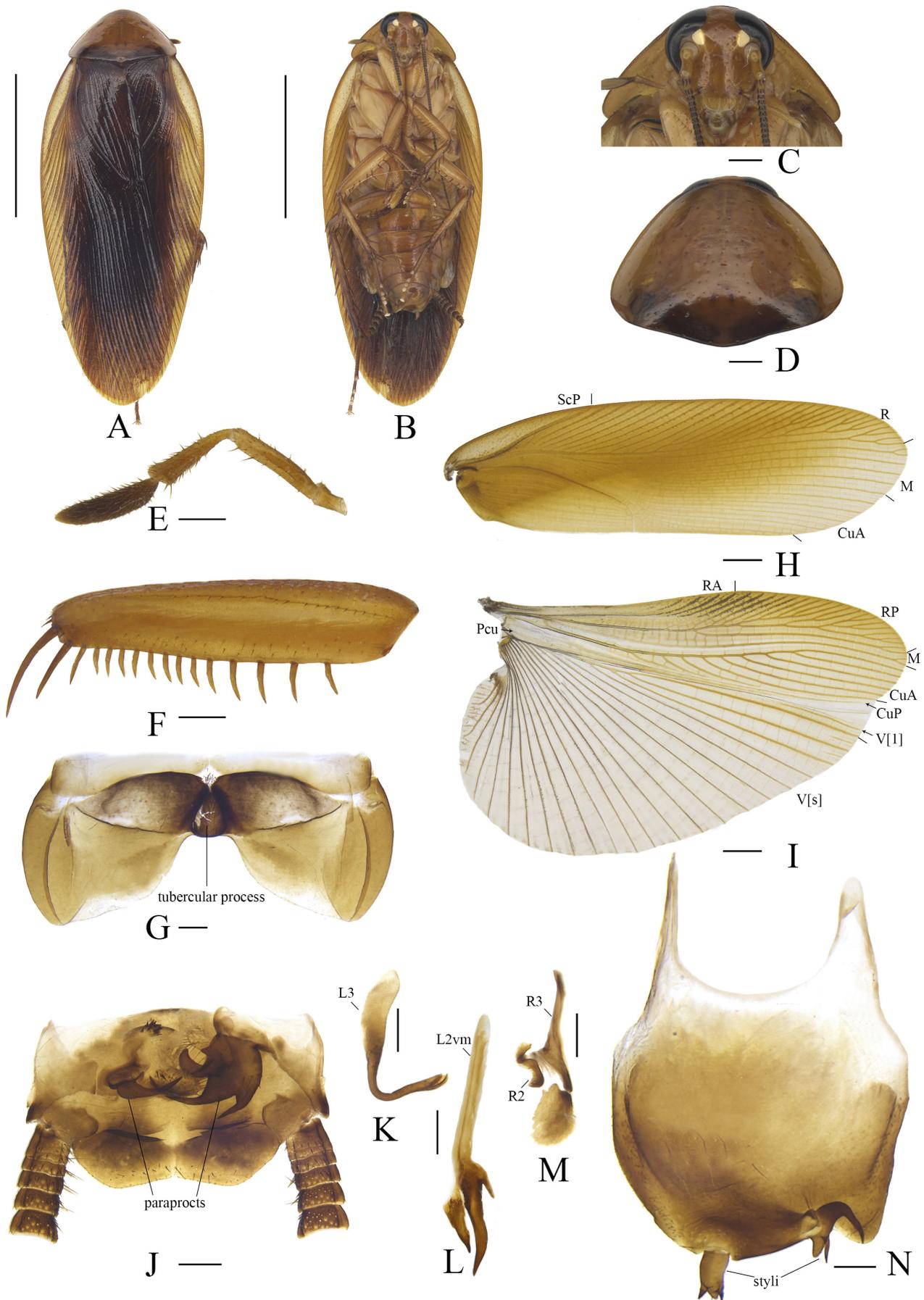


Figure 5. *Symploce tubercularis* sp. nov., male: **A** holotype, dorsal view; **B** holotype, ventral view; **C** head, ventral view; **D** pronotum; **E** maxillary palp; **F** front femur, ventral view; **G** seventh abdominal tergite; **H** tegmen; **I** wing; **J** supra-anal plate, ventral view; **K** left phallomere; **L** median phallomere; **M** right phallomere; **N** subgenital plate, dorsal view. Scale bars: 10 mm (A, B), 1 mm (C, D), 2 mm (H, I), 0.5 mm (E–G, J–N).

Etymology. The Latin word *tubercularis* indicates T7 with a tubercular process in the middle.

Remarks. *Symploce tubercularis* Jin and Che **sp. nov.** is closely related to *Symploce maxima* (Li et al. 2020) **comb. nov.**, however, they can be distinguished by the following characteristics: 1) the former with a tubercular process in the middle of T7 that is absent in the latter; 2) the former with the right stylus crooked and irregular, while the latter has two small and simple styli; 3) the former with a setal tuft on supra-anal plate, but the latter without.

Distribution. China (Guangxi).

3.2.9. *Episymploce* Bey-Bienko, 1950

Note. In our phylogenetic analysis (the type species *Episymploce paradoxura* Bey-Bienko, 1950 not included), *Symploce torchaceus* Feng and Woo, 1999 and *Symploce wulingensis* Feng and Woo, 1993 were recovered as sister taxa and deeply embedded within the clade of *Episymploce*. 2 new combinations were set up accordingly, and 1 synonymy was proposed as follows.

3.2.10. *Episymploce torchaceus* (Feng and Woo, 1999) **comb. nov.**

Symploce torchaceus Feng and Woo, 1999: 51 (Type locality: Fujian, China); Wang and Che, 2013: 4.

Material examined. CHINA • 1 ♂ (holotype of *S. torchaceus*); Fujian Prov., Mt. Wuyi; 10 July 1982; Feng Xia leg. • 1 ♂ (paratype of *S. torchaceus*); Hainan Prov., Mt. Jianfengling; 21 March 1983; Shaoying Liang leg. • 2 ♂♂; Hainan Prov., Linshui County, Mt. Diaoluo; 3 May 2013; Shunhua Gui leg.

Remarks. *Symploce torchaceus* Feng and Woo, 1999 was established based on the samples from Mt. Wuyi and Mt. Jianfengling, which was redescribed by Wang and Che (2013) where the detailed information on genitalia was provided for the first time. Herein, we transfer this species to genus *Episymploce* on basis of characteristics as follows: body medium-sized; posterior margin of subgenital plate slightly thickened and setaceous. And in our ML and BI inferences *Symploce torchaceus* Feng and Woo, 1999 was grouped together with other *Episymploce* members forming a monophyletic group (Fig. 1, supplementary material Fig. S1).

3.2.11. *Episymploce wulingensis* (Feng and Woo, 1993) **comb. nov.**

Fig. 6

Symploce wulingensis Feng and Woo, 1993: 40 (Type locality: Sichuan, China).

Symploce stellatus Feng and Woo, 1999: 52 (Type locality: Fujian, China). Liu et al. 2017: 127, synonymized with *S. wulingensis* **syn. nov.**

Material examined. CHINA • 1 ♂ (holotype of *S. stellatus*); Fujian Prov., Mt. Wuyi; 10–18 June 1980; Shiyang Xia leg. • 1 ♂ (paratype of *S. stellatus*); Fujian Prov., Sangang; 15 June 1981; Jingying Liu leg. • 1 ♂, 1 ♀; Hainan Prov., Lingshi, Mt. Diaoluo; 3 May 2013; Yan Shi leg. • 1 ♂; Guangxi Prov., Jinxiu County, Mt. Shengtang; 900–1200 m; 28 June 2000; Jian Yao leg.

Measurements (mm). Overall length: ♂ 17.7–18.0; pronotum length × width: ♂ 3.8 × 4.2; tegmina: ♂ 15.0–15.2.

Redescription. Male. Coloration: Medium body, yellowish brown (Fig. 6A, B). Ocelli pale yellow; base of antenna brown, the rest dark brown (Fig. 6C). The fourth and fifth maxillary palps dark brown, the rest yellow brown (Fig. 6E). Pronotum yellowish with a pair of reddish-brown V-shaped stripes, and lateral border yellowish brown (Fig. 6D). **Head:** Interocular space less than the distance between ocelli and narrower than width of antennal sockets (Fig. 6C). First three segments of maxillary palps almost the same length (Fig. 6E). Pronotum subelliptical, hind margin slightly convex in the middle (Fig. 6D). **Tegmina and hindwings:** Both fully developed, extending beyond the end of abdomen (Fig. 6H, I). RP of hindwings with branches near the middle; M simple and unbranched; CuA with 3 complete branches and many small incomplete branches, apical triangle small but visible (Fig. 6I). **Legs:** Front femur Type A₃ (Fig. 6F), pretarsal claws symmetrical and unspecialized, pulvillus present. **Abdominal tergites:** T1 unspecialized, T7 specialized with a pair of shallow fossae (Fig. 6G), lateral plates of T9 similar. T10 symmetrical and trapezoidal. **Paraprocts:** Dissimilar, base of right one with a curved and long spine-like process; left one with a curved finger-like process on which three small thorns are situated (Fig. 6J). **Subgenital plate:** Asymmetrical, both margins curly and covered with thin thorns. Left stylus bifurcated and obtuse angle present; right stylus near the left one, with 2 or 3 branches near the apex (Fig. 6N). **Male genitalia:** L3 on left side, and apex with a deep incision (Fig. 6K); L2vm rod-shaped and apex branched (Fig. 6L); R2, R3 consisting of several irregular sclerites (Fig. 6M). — **Female.** Unknown.

Remarks. Wang and Che (2013) suggested that *Symploce wulingensis* Feng and Woo, 1993 should be transferred to *Episymploce* according to the morphological characters. In this paper, we also consider it more appropriate to move this species to *Episymploce* on basis of the morphological information: body size medium, T7 specialized with a pair of shallow fossae without setae, subgenital plates lightly incrassate and setaceous. Our phylogenetic analysis also supports this view (Fig. 1, supplementary material Fig. S1): *Symploce wulingensis* Feng and Woo was placed as the sister of *Episymploce torchaceus*, which together were deeply embedded within the clade of *Episymploce*.

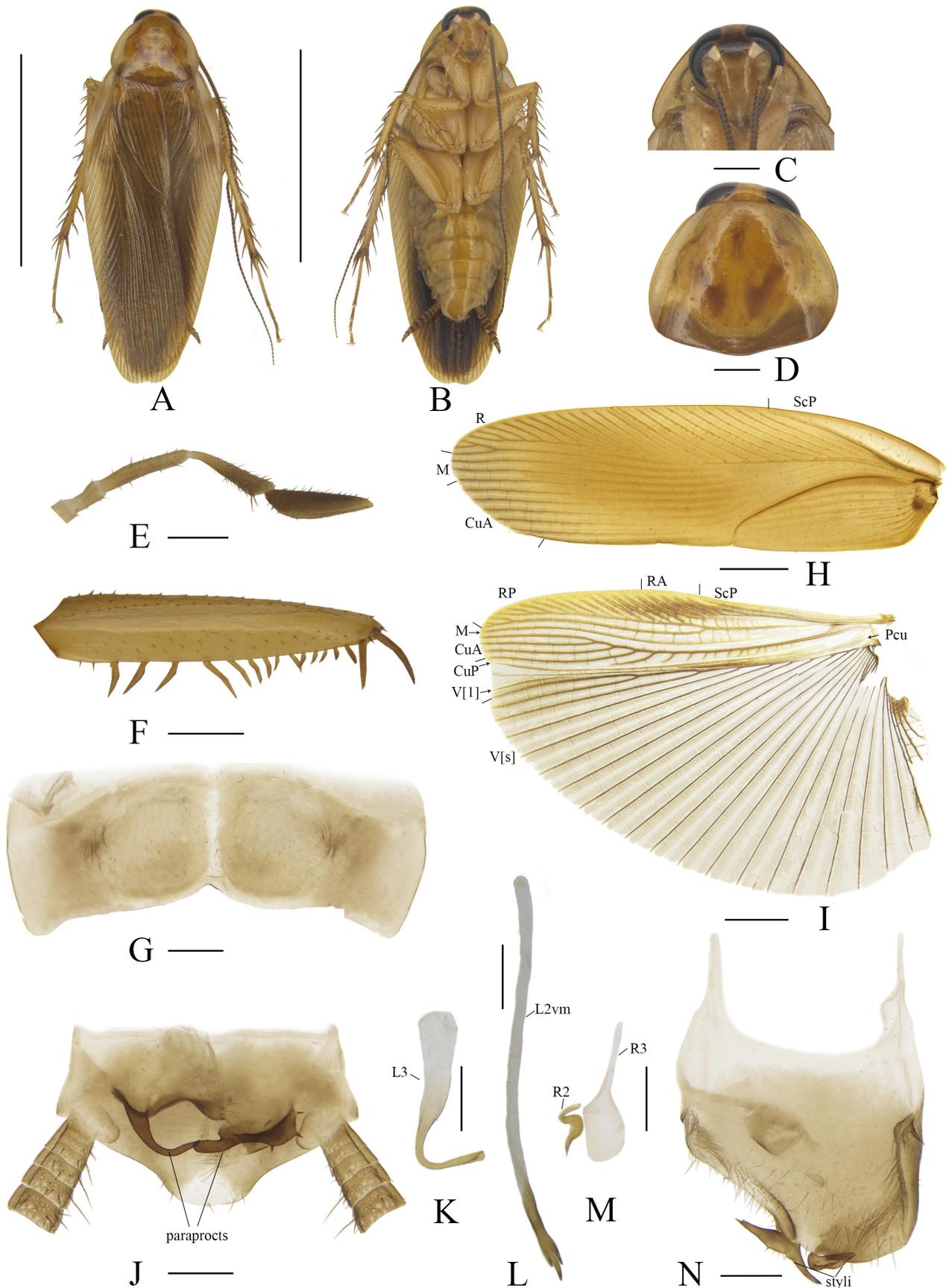


Figure 6. *Episymphloe wulingensis* (Feng et Woo, 1993) comb. nov., male: **A** dorsal view; **B** ventral view; **C** head, ventral view; **D** pronotum; **E** maxillary palp; **F** front femur, ventral view; **G** seventh abdominal tergite; **H** tegmen; **I** wing; **J** supra-anal plate, ventral view; **K** left phallomere; **L** median phallomere; **M** right phallomere; **N** subgenital plate, dorsal view. Scale bars: 10 mm (A, B), 1 mm (C, D), 2 mm (H, I), 0.5 mm (E–G, J–N).

Distribution. China (Fujian, Guangdong, Hainan, Guangxi, Sichuan, Guizhou, Chongqing).

3.2.12. *Episymploce kunmingi* (Bey-Bienko, 1969)

Symploce kunmingi Bey-Bienko, 1969: 855 (Type locality: Yunnan, China).

Episymploce kunmingi: Roth, 1985b: 215.

Symploce quadrispinis Woo and Feng, 1992: 54 (Type locality: Yunnan, China) **syn. nov.**

Material examined. CHINA • 1 ♂ (holotype of *S. quadrispinis*); Yunnan Prov., Lushui City, Liuku Town, 12 June 1981, Jianmin Zhao leg. • 1 ♂, 1 ♀; Yunnan Prov., Kunming City; 13 June 1986; Pingzhang Feng leg. • 1 ♂, 1 ♀; Sichuan Prov., Leshan City, Jinhekou County; 26–27 May 2011, Keliang Wu leg.

Remarks. *Episymploce kunmingi* was published by Bey-Bienko in *Symploce* and was transferred to *Episymploce* by Roth (1985b) based on the asymmetric T10. After examination of *Episymploce kunmingi* (Bey-Bienko, 1969) and comparison with the holotype of *Symploce quadrispinis* Woo and Feng, 1992, we found that there was no difference in their external morphology and male genitalia. So we regard *Symploce quadrispinis* as a synonym of *Episymploce kunmingi* (Bey-Bienko, 1969).

3.2.13. *Blattella Caudell*, 1903

Note. In our molecular analyses, *Symploce ligulata* (Bey-Bienko, 1957) and the brachypterous Blattellidae species are clustered together with *Blattella* samples to form a monophyly with high support values. Therefore, we proposed one new combination and assign the brachypterous species into the genus *Blattella*.

3.2.14. *Blattella ligulata* (Bey-Bienko, 1957) **comb. nov.**

Fig. 7

Episymploce ligulata Bey-Bienko, 1957: 911 (Type locality: Yunnan, China); Princis, 1969: 877; Roth, 1997: 107.

Symploce ligulata: Roth, 1985c: 391.

Material examined. CHINA • 1 ♂, 3 ♀; Yunnan Prov., Xishuangbanna, Dadugang; 3 May 2013; Zongqing Wang leg. • 2 ♂♂; Yunnan Prov., Xishuangbanna, Naban River Reserve; 4 July 2020; Yishu Wang leg. • 3 ♂♂; Yunnan Prov., Xishuangbanna, Mengban Town; 8 July 2020; Duting Jin leg.

Remarks. *Blattella ligulata* (Bey-Bienko, 1957) **comb. nov.** (Fig. 7), originally in the genus *Episymploce*, was transferred to *Symploce* by (Roth 1985c) because of the symmetrical T10. However, both morphological and molecular data analysis support that this species should be in

the genus *Blattella*. *Blattella ligulata* (Bey-Bienko, 1957) **comb. nov.** shares some characteristics with *Blattella*: male T10 tongue-shaped (Fig. 7J) and T7 specialized with a pair of large pouch-like depressions with a setal tuft between them (Fig. 7G). In our phylogenetic analysis, *Blattella ligulata* (Bey-Bienko, 1957) forms the basal clade of *Blattella*, being the sister of all other *Blattella* samples (Fig. 1, supplementary material Fig. S1).

Distribution. China (Yunnan).

3.2.15. *Blattella foliolata* Jin and Che sp. nov.

<http://zoobank.org/8BECE4E4-8948-4AAA-9CC7-5836B92-1CE53>

Figs 8, 9

Type material. Holotype. CHINA • ♂; Sichuan Prov., Panzhihua City, Wuben Town; 8 June 2014; Xinran Li leg. **Paratypes:** CHINA • 2 ♂, 2 ♀, same data as for holotype.

Measurements (mm). Overall length: ♂ 7.7–7.8, ♀ 7.7–10.2; pronotum length × width: ♂ 1.9–2.1 × 2.9–3.2, ♀ 2.0–2.5 × 3.4–3.7; tegmina: ♂ 1.6–1.7, ♀ 1.7–1.9.

Description. Male. Coloration: Body blackish brown with yellowish brown lateral border (Fig. 8A, B, E, F). Pronotum blackish brown with a pair of large black stripes, which are separated or contiguous near the anterior margin, lateral borders and disc yellowish brown (Fig. 8L); mesonotum and metanotum blackish brown with disc yellowish brown (Fig. 8A, E). Head yellowish brown with a black patch at vertex, antenna brown with a black spot near outer margin of antennal sockets respectively or forming a T-shaped stripe on the face (Fig. 8M). Legs yellowish brown with some irregular blackish brown stripes (Fig. 8A, E). **Head:** Interocular space slightly less than ocelli width and distinctly narrower than width of antennal sockets (Fig. 8M). The third and fifth of maxillary palps about the same length, and slightly longer than the fourth (Fig. 8I). Pronotum trapezoidal (Fig. 8L). **Tegmina and hindwings:** Both scaly and strongly reduced, only extending to about the end of mesonotum and metanotum, respectively (Fig. 8N, O). **Legs:** Anteroventral margin of front femur Type B₃ (Fig. 8J), pretarsal claws symmetrical and unspecialized. **Abdominal tergites:** Middle of T7 slightly raised with setal tuft, and a pair of inconspicuous fossae on either side (Fig. 8K). T10 flat with anterior border concave and hind margin also slightly concave in the middle. **Paraprocts:** Dissimilar, the right one with a strongly curved and slender process, the left one bifurcated with apices rounded (Fig. 8P). **Subgenital plate:** Distinctly asymmetrical, the left posterior margin broadly and concavely excavated; styli nearly conical and arising from the right posterior angle, the right one slightly larger than the left one (Fig. 8T). **Male genitalia:** L3 on the left side (Fig. 8Q); L2vm rod-shaped (Fig. 8R); R2, R3 consisting of several sclerites (Fig. 8S).

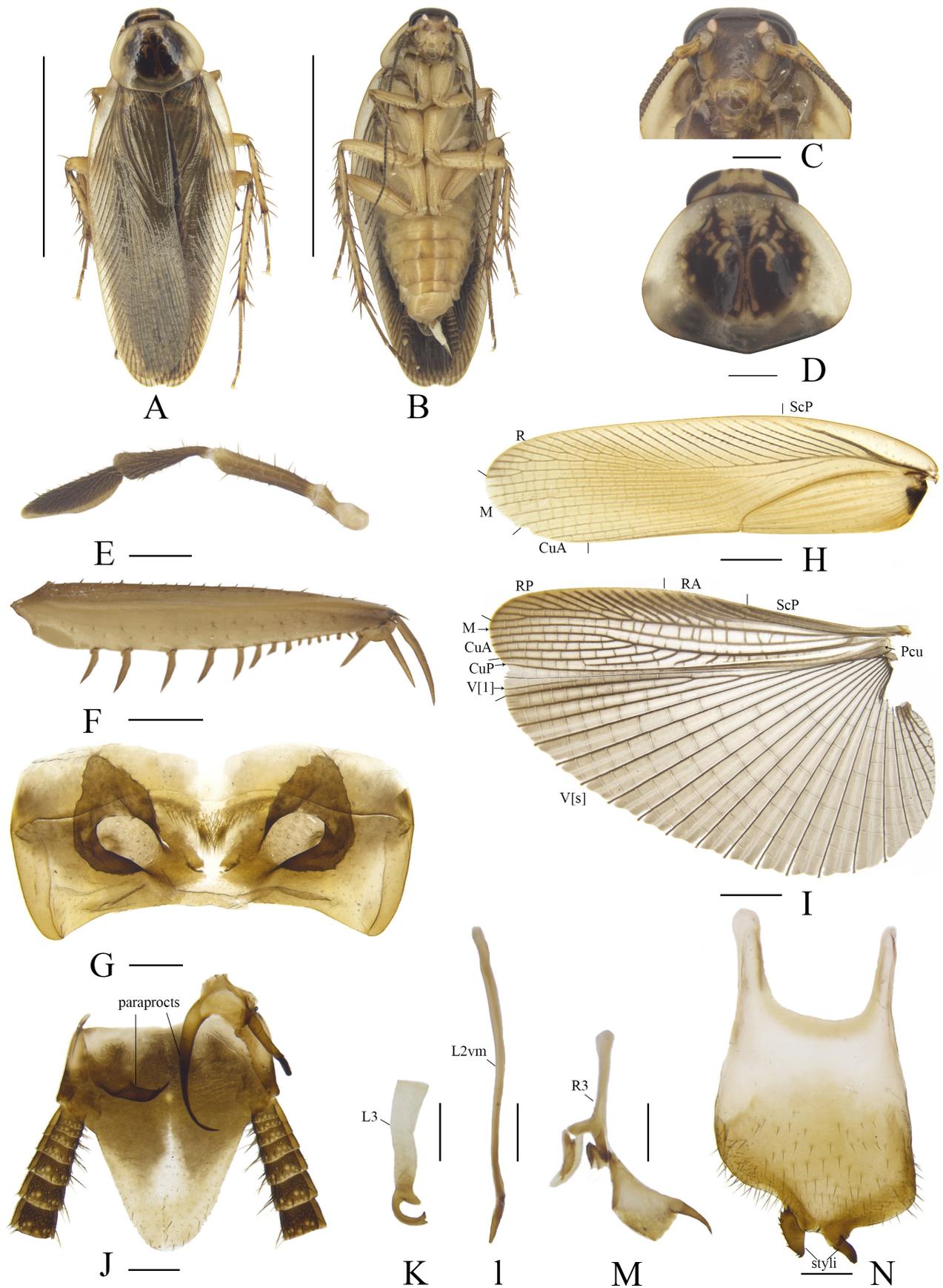


Figure 7. *Blattella ligulata* (Bey-Bienko, 1957) comb. nov., male: **A** dorsal view; **B** ventral view; **C** head, ventral view; **D** pronotum; **E** maxillary palp; **F** front femur, ventral view; **G** seventh abdominal tergite; **H** tegmen; **I** wing; **J** supra-anal plate, ventral view; **K** left phallomere **L** median phallomere; **M** right phallomere; **N** subgenital plate, dorsal view. Scale bars: 10 mm (A, B), 1 mm (C, D), 2 mm (H, I), 0.5 mm (E–G, J–N).

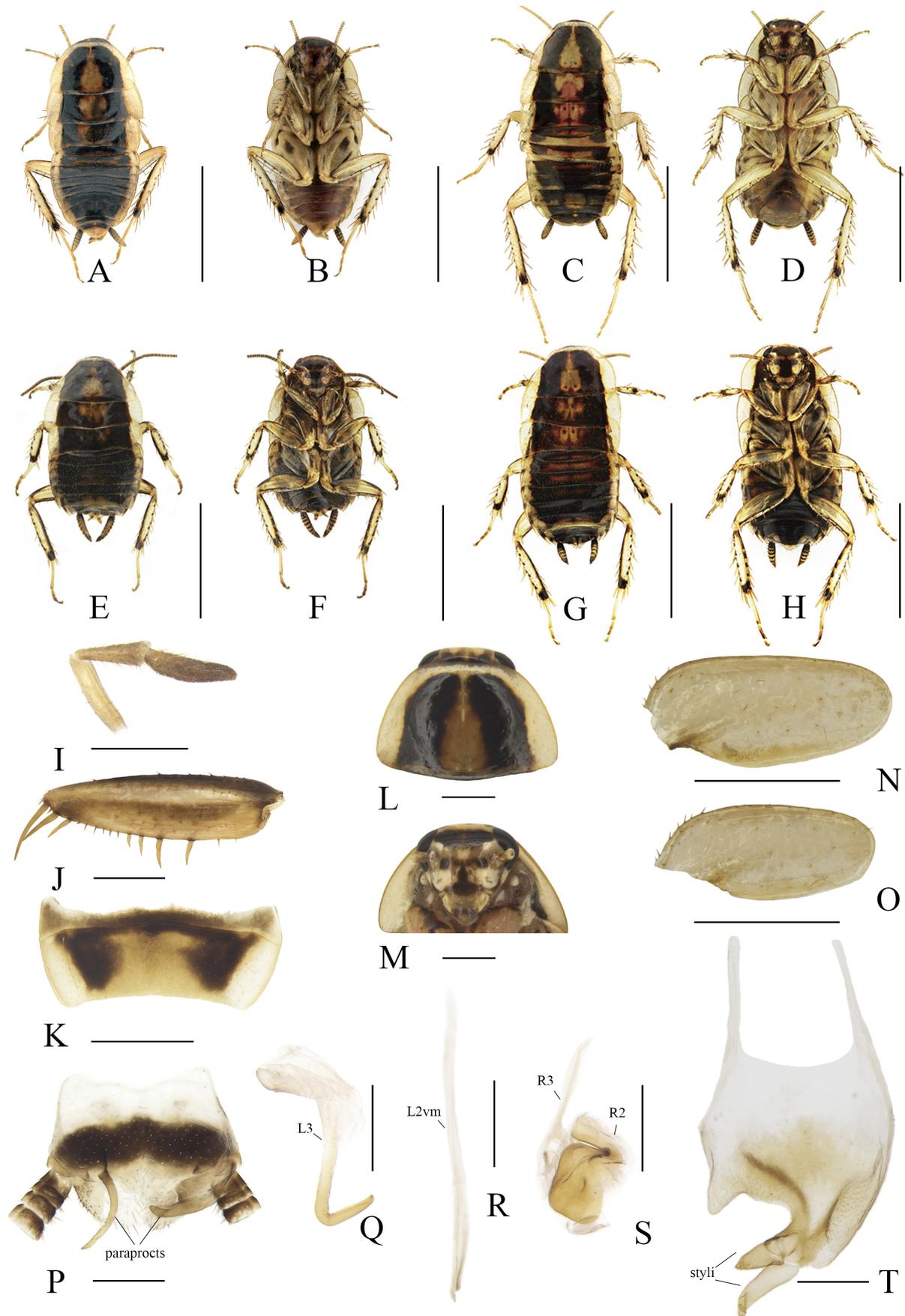


Figure 8. *Blattella foliolata* sp. nov., **A, B** male, adult: **A** holotype, dorsal view; **B** holotype, ventral view; **C, D** female, adult: **C** paratype, dorsal view; **D** paratype, ventral view; **E, F** male, nymph: **E** dorsal view; **F** ventral view; **G, H** female, nymph: **G** dorsal view; **H** ventral view; **I** maxillary palp; **J** front femur, ventral view; **K** seventh abdominal tergite; **L** pronotum; **M** head, ventral view; **N** tegmen; **O** wing; **P** supra-anal plate, ventral view; **Q** left phallomere; **R** median phallomere; **S** right phallomere; **T** subgenital plate, dorsal view. Scale bars: 5 mm (A–H), 1 mm (K–O), 0.5 mm (I, J, P–T).



Figure 9. **A** Habitat of *Blattella foliolata* sp. nov.; **B** Collecting habitat of Wuben Town, Panzhihua City, Sichuan; **C** Photographed in the field, **D** Collected specimens were observed on the tweezer and in a container under laboratory feeding conditions. Photos: A, B, D by Keliang Wu, C by Lu Qiu.

— **Female.** Similar to the male but body larger (Fig. 8C, D, G, H).

Remarks. *Blattella foliolata* Jin and Che **sp. nov.** is similar to *Ignaboliaria bilobata* Chopard, 1929 because of nearly identical scale-shaped tegmina and wings. However, they can be distinguished by the following: 1) the former with black markings on the face, but the latter entirely dark brown; 2) abdominal T7 longer than the previous tergites in the former, but shorter than most of previous tergites in the latter; 3) styli close to each other in the former, but separated by a distance of about the length of one stylus in the latter. Meanwhile, this species is easily recognized and distinguished from other macropterous *Blattella* species owing to the strongly reduced wings, but it is very challenging to distinguish them from the nymphs of *Blattella bisignata* (Brunner von Wattenwyl, 1893) in the wild. Like most species of *Blattella*, the brachypterous *Blattella foliolata* Jin and Che **sp. nov.** has a small body, pronotum blackish brown with a pair of large black stripes, a symmetrical T10, and an asymmetrical subgenital plate with a concave excavation on the left posterior margin. Moreover, *Blattella foliolata* Jin and Che **sp. nov.** was deeply embedded within the clade of *Blattella* in our phylogenetic analysis, and is retrieved as the sister group of *B. bisignata* + *B. nipponica* + *B. germanica* + *B. parilis* **comb. nov.**

Etymology. The Latin word *foliolatus* refers to the tegmina and hindwings strongly reduced as a lobule.

Distribution. China (Sichuan).

4. Discussion

4.1. Molecular analysis solves problems caused by the high similarity in morphology

For the similar genera *Episymphloe*, *Symphloe* and *Centrocolumna* Jin and Che **gen. nov.**, a morphology-based placement and delimitation is currently difficult because of the absence of obvious discontinuities in diagnostic features and the large structural diversity in Blattodea and in Blaberoidea, with considerable homoplasy (see e.g. Bohn et al. 2021).

Episymphloe and *Symphloe* are morphologically similar, but they were proposed to be distinguishable by a few diagnostic features: the specialized shape of T7 and T9, the symmetry or asymmetry of T10, and the posterior margin of the subgenital plate being incrassate and setaceous or not (Roth, 1984; 1985a; 1985b; 1997). Previous

research about *Episymploce* and *Symploce* based only on a non-phylogenetic evaluation of morphological characters revealed that the taxonomic status of some species was controversial, such as Roth (1984, 1985b) (at least 39 taxa listed by Princis under *Symploce* were transferred to *Episymploce*), and Roth (1985a) (believed that only two of six *Episymploce* species listed by Princis 1969, 1971 belonged to this genus, whereas others should be in *Symploce*). The main reason for this confusion is that some species show a mixture of the diagnostic features of the two genera. In this study, two species (*E. torchaceus* **comb. nov.** and *E. wulingensis* **comb. nov.**) originally assigned to *Symploce*, are typically equipped with characters of both *Symploce* (the symmetrical T10) and *Episymploce* (the lightly incrassate and setaceous subgenital plate). Therefore, it is very challenging to assign them to any genus only according to the morphological characters regarded as diagnostic. Our phylogenetic analysis showed that these two species were embedded in the clade of *Episymploce* with high support (ML bootstrap 100%, posterior probability 1.0), which supports our transferring them to *Episymploce*. These two species share the same characteristics (Fig. 6): body size medium, T7 specialized with a pair of shallow fossae without setal tuft or sparsely, and posterior margin of subgenital plate thickened and covered with setae. In spite of their high morphological similarity, our study suggests a distant phylogenetic relationship between *Symploce* and *Episymploce*. *Episymploce* was obtained as the sister group of *Blattella*, whereas *Symploce* is the putative sister to *Centrocolumna* **gen. nov.** + *Episymploce* + *Blattella* (Fig. 1, supplementary material Fig. S1). These relationships are consistent with Wang et al. (2017).

In our study, the new genus *Centrocolumna* Jin and Che **gen. nov.** is established, with *Symploce evidens* Wang and Che, 2013 as type species. At present, there are nine species included in *Centrocolumna* Jin and Che **gen. nov.**, of which eight are transferred from *Symploce* except for the new species, *Centrocolumna ericea* **sp. nov.** Herein, all of them consistently share generic diagnostic features: their T1, T7, T10 always specialized with medial setal tufts, subgenital plate asymmetrical with a prominent protrusion in the middle of hind margin, and the right stylus arising on it; and their grouping is also supported by our ML and BI analyses with high support values (bs 100%, pp 1.0). A tuft on tergite X (T10) was present at the base of clade *Centrocolumna* Jin and Che **gen. nov.**, but absent at the base of clade *Symploce* + (*Centrocolumna* **gen. nov.** + (*Episymploce* + *Blattella*)), which means the unspecialized T10 was their common ancestral state. *Symploce* was once thought to be an unnatural unit containing several natural groups (Roth 1984). Our study confirms this based on both morphological and molecular evidence. In our Bayesian inference, *Symploce* was recovered to be paraphyletic (Fig. 1), but the type species of *Symploce* was not included in our study, and the paraphyly of *Symploce* was not sufficiently strong to convincingly resolve this issue. Herein we also take the opportunity to make corrections to a previous study where the new species *Centrocolumna ericea* **sp. nov.**

described in this paper was identified as *Symploce striata* *striata* in Wang et al. (2017).

Another point worth noting is that the different geographical populations of the new species *Centrocolumna ericea* **sp. nov.** exhibit some differences in coloration: they are overall dark brown from Guangxi, light-yellow brown from Chongqing and Fujian, while those from Hunan range between dark brown and light-yellow brown. After checking the male genitalia of different geographical samples combined with the molecular clustering, we confirmed these color differences as intraspecific variation.

4.2. Molecular analysis solving problems caused by a high divergence in morphology

As in the case of the jumping cockroach, the morphology-based placement of brachypterous species with a high divergence in external morphology can also be difficult.

The small brachypterous species in our study has a blackish brown pronotum with a pair of large black stripes, a symmetrical supra-anal plate, the subgenital plate distinctly asymmetrical with a concave excavation on the left posterior margin, and the ootheca rotates prior to desposition, like most species of *Blattella*. But all known species of *Blattella* usually have fully developed tegmina and hindwings, or the hind wings are micropterous: female of *Blatta lamotteana* (Princis, 1963), *Blatta rossi* Roth, 1985, male and female of *Blatta portalensis* (Giglio-Tos, 1907), except for *Blatta kevani* Roth, 1985, whose tegmina are missing (possibly reduced) and hindwings reduced (Roth 1985b). The factors mentioned above cause confusion on the placement of the brachypterous species. But according to molecular analysis, *B. foliolata* **sp. nov.** together with other *Blattella* samples form a monophyletic group with high support values (ML bootstrap 100%, posterior probability 1.0) which supports placing *B. foliolata* **sp. nov.** into the genus *Blattella* from the molecular perspective.

4.3. The brachypterous species of *Blattella* and its biology habit

In Blattodea, the reduction of wings usually manifests itself in forewings being larger than the hindwings, or in micropterous forewings and completely absent or extremely reduced hindwings (Bey-Bienko 1950). But in the case of the new brachypterous species *Blattella foliolata* **sp. nov.**, the wing reduction reflects a special synchronization. Roff (1990) believed that cockroaches living in a relatively stable environment increasingly lose their ability to fly. Bell et al. (2007) also agreed that the reduction of wings is usually associated with specific habitats.

Samples of *Blattella foliolata* **sp. nov.** (Fig. 9) were collected from shrubs, rubble, and small streams whe-

re they were discovered to live in the same habitat with *Blattella bisignata*. Thus *B. foliolata* is readily confused with the nymphs of *B. bisignata* (Wu KL, personal observation). *B. bisignata* is widely distributed in the world, and in China it is a dominant species in the wild. Tsai and Lee (2001) reported that there was interspecific competition between the related cockroach species that possessed similar external morphology. Therefore, we speculate that the reduced wings are a manifestation of insect mimicry, where they mimic the nymphs of *B. bisignata* and thus coexist peacefully with *B. bisignata*. This might be a survival strategy to reduce the pressure of interspecific competition with *B. bisignata*, although more field observation and experimental evidence are necessary to test this idea.

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Supplementary material 1

Table S1

Authors: Jin et al. (2022)

Data type: .xlsx

Explanation note: The species and details used in the study.

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Supplementary material 2

Table S2

Authors: Jin et al. (2022)

Data type: .docx

Explanation note: Primers used in the study.

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Supplementary material 3

Figure S1

Authors: Jin et al. (2022)

Data type: .pdf

Explanation note: Bayesian inference (BI) tree.

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Supplementary material 4

Figure S2

Authors: Jin et al. (2022)

Data type: .pdf

Explanation note: Paraprocts, subgenital plate, and male genitalia shown in greater detail.

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