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Female-biased froghoppers (Hemiptera, Cercopoidea) from the Mesozoic of China and phylogenetic reconstruction of early Cercopoidea

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Cercopoidea is a diverse insect group, but its early evolution, disparity and ecology remain unclear. *Juroala daohugouensis* Chen & Wang gen. et sp. nov., from the Middle–Upper Jurassic of north-eastern China, is established herein and described on the basis of 42 whole-bodied fossils, representing a new subfamily, Juroalinae subfam. nov. of the primitive family Sinoalidae. *Chengdecercopis* Hong, 1983 is transferred from Procercopidae to this new subfamily and *Stictocercopis* Fu & Huang, 2018 is also attributed to the new subfamily. Fangyuanini Chen & Wang trib. nov. is erected for *Fangyuania* Chen, Szwedo & Wang, 2018 from mid-Cretaceous Burmese amber. Our cladistic analyses recover the relationships within the Cercopoidea as follows: (Juroalinae + (Sinoalini + Fangyuanini)) + (Procercopidae + (Cercopionidae + five modern families)). The evolutionary history and morphological diversification in the Mesozoic is discussed based on our phylogenetic reconstruction. In addition, the abundant material in the present study not only indicates high intra-specific or even intra-individual variation caused by biological and/or taphonomic factors, but also reveals an extremely female-biased propensity, suggesting that the new taxon probably had adaptations to special palaeoenvironments in physiology, ecology and ethology (e.g. parthenogenesis and sociability).

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Keywords: Cercopoidea; Mesozoic; taxonomy; phylogeny; female bias

Introduction

Froghoppers, the common name for the insect superfamily Cercopoidea, are so-called from their frog-like appearance and good leaping ability (Hamilton & Morales 1992; Burrows 2003). To avoid predation, parasitism and desiccation, some juvenile forms of froghoppers live in spittle deposited on plants caused by tiny air bubbles being trapped in processed plant fluids (Cercopidae, Aphrophoridae and Clastopteridae), and are therefore called spittlebugs; other froghopper nymphs live in sap-filled tubes (Machaerotidae) (Hamilton 2001; Rakitov 2002; Cryan & Svenson 2010). Modern froghoppers are commonly small phytophagous insects, feeding on xylem sap of a wide variety of plants, including grasses, herbs and trees (Hamilton & Morales 1992; Cryan & Svenson 2010; Chen *et al.* 2015a).

With nearly 3000 described species, the Cercopoidea is a large and worldwide insect group occurring in most terrestrial habitats (Cryan & Svenson 2010; Chen *et al.* 2015a, b, 2018; Soulier-Perkins 2012). This morphologically and ecologically diverse superfamily, however, has not been well studied to date: most of the world's fauna still needs to be described (Kosztarab *et al.* 1990; Carvalho & Webb 2005), the higher classification is a subject of debate (Chen *et al.* 2018; Paladini *et al.* 2018), and little is known about the group's origin and diversification as well as palaeoecology and palaeogeography (Wang *et al.* 2012).

Molecular and fossil data are considered to be sufficiently robust to infer evolutionary history, but different results have been recovered for the early evolution of Cercopoidea: divergence date estimates calculated on the basis of molecular phylogeny suggest that modern cercopoid families were derived from the stem group from the latest Triassic to Early Cretaceous (Cryan & Svenson 2010); fossils give a contradictory picture, with the common ancestor of modern groups separating from the

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extinct family Procercopidae by the mid-Cretaceous and subsequently undergoing diversification (Shcherbakov & Popov 2002; Wang *et al.* 2012; Chen *et al.* 2017). According to a recent molecular analysis, Paladini *et al.* (2018) presented an alternative chronogram of Cercopoidea and indicated that the modern cercopoid group are rooted in the Cretaceous and their major line-ages diverged mainly in the early Cenozoic, largely clos-ing the gap between molecular and fossil data. However, due to an extremely fragmentary fossil record and most fossils being in poor preservation, just represented by solitary tegmina or hind wings (Wang *et al.* 2012; Chen *et al.* 2018), the evolution, diversification and ecology of early Cercopoidea is still not clear.

A new froghopper, *Juroala daohugouensis* Chen & Wang gen. et sp. nov., from the Middle–Upper Jurassic Daohugou beds of north-eastern China, is described herein, representing a new subfamily, Juroalinae subfam. nov., attributed to the extinct family Sinoalidae. The new genus and species is erected on the basis of 42 fos-sil specimens with well-preserved body structures, teg-men and hind wing venations, providing some new insights into the morphological diversity as well as the evolutionary history of Mesozoic Cercopoidea. Furthermore, the abundant material reveals a strong female-biased propensity in the new taxon, probably requiring its special physiological, ecological and etho-logical adaptation (e.g. sociability and parthenogenesis).

In addition to reconstructing the evolutionary relation-ships within Cercopoidea, phylogenetic analyses based on 26 morphological characters were performed using maximum parsimony (MP).

Material and methods

The new fossil material was collected from the Daohugou beds (Middle–Upper Jurassic of Inner Mongolia, China) (Fig. 1), and is housed in the Shandong Tianyu Museum of Nature in Pingyi, China (STMN) and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences in Nanjing, China (NIGP). The geological age of the Daohugou beds is somewhat controversial (Chen & Wang 2016); we here consider it to be latest Middle–earliest Late Jurassic (Callovian–Oxfordian) (Wang H. *et al.* 2015). The insect fossils from the Daohugou beds are taxonomically diverse and provide some significant insights into the taxonomy, evolution and ecology of insects (e.g. Ren *et al.* 2009; Huang *et al.* 2012; Chen *et al.* 2014; Liu *et al.* 2018).

The fossil material described herein was examined and photographed dry or under alcohol, using stereomi-croscopes ZeissSteREO Discovery V8 for fossils housed
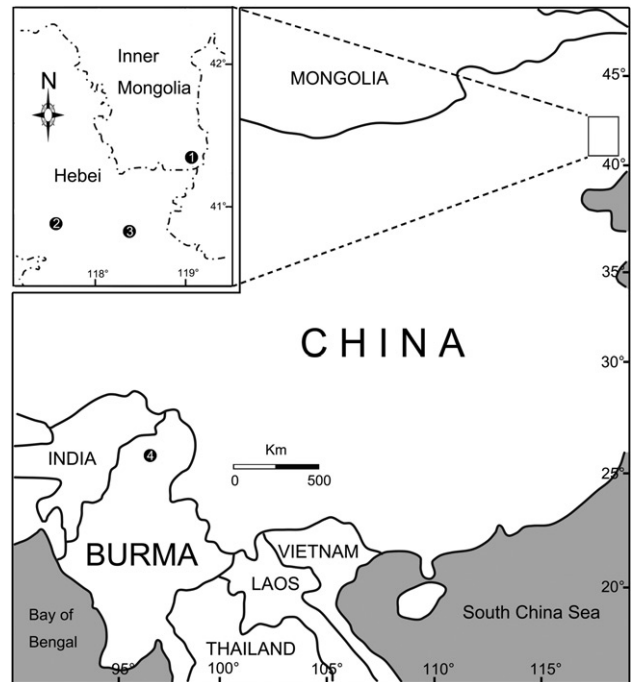

Figure 1. Map showing localities of Sinoalidae. 1, Middle–Upper Jurassic Daohugou, Ningcheng, Inner Mongolia, China; 2, Middle Jurassic Zhouyingzi, Luangping, Heibei, China; 3, Middle Jurassic Xiaofanzhangzi, Chengde, Hebei, China; 4, mid-Cretaceous Hukawng Valley, Myitkyina District, Kachin, Myanmar.

in STMN and Nikon SMZ1000 for fossils housed in NIGP. Illustrations and line drawings were prepared with software programs CorelDraw 12.0 and Adobe Photoshop CS3. In the line drawings, faintly seen and extrapolated details are indicated by dotted lines. All measurements were made in the software ImageJ 1.42q (Wayne Rasband; National Institutes of Health, Bethesda, MD, USA).

The venational terminology used herein follows Chen *et al.* (2018), which is slightly modified from Nel *et al.* (2012). In the latter study, a new interpretation of the wing venation pattern for all Paraneoptera was pro-posed, assuming that CuA becomes fused with the $MP + R$ stem at the wing base and is connected with CuP by a specialized crossvein *cua-cup*, which is remarkably different from the traditional interpretation.

Tribe- and subfamily-level relationships within Sinoalidae and family-level relationships within Cercopoidea are reconstructed on the basis of phylogen-etic analyses. Hylicelloidea is chosen as the ultimate out-group because this Mesozoic superfamily is considered to be the ancestral group to all modern Cicadomorpha (Wang *et al.* 2012). We also selected Cicadoidea as the outgroup, due to its sisterhood with Cercopoidea based on molecular data (Cryan 2005).

Twenty-six morphological characters are employed in our cladistic analyses: characters 1–5, 6–11, 12, 13–22 and 23–26 are from the head, thorax, abdomen, tegmen and hind wing respectively (see character list in the Supplemental material). Nineteen characters are coded as binary and seven as multistate, and multistate characters are treated as non-additive. All the characters are unordered and of equal weight, and missing and inapplicable data are coded with question marks and dash respectively. The data matrix and Nexus file used for the analyses are presented in the Supplemental material.

Maximum parsimony in PAUP* (Swofford 2003) was performed. Heuristic searches were executed for 1000 replicates to conduct MP analysis with TBR branch swapping. The only most parsimonious tree (MPT) was used in character mapping, executed in the morphological analysis software program WinClada v. 1.00.08 (Nixon 2002).

Systematic palaeontology

Order **Hemiptera** Linnaeus, 1758
Suborder **Cicadomorpha** Evans, 1946
Superfamily **Cercopoidea** Leach, 1815
Family **Sinoalidae** Wang & Szwedo, 2012

Revised diagnosis. Antenna with flagellum of a few elongate segments; postclypeus flat and wide; three ocelli on crown; disc of crown and pronotum wrinkled or with granules; ovipositor extending beyond tip of wings; hind tibia with two rows of lateral spines (four at most in each row); tegmen usually with costal cell and/or clavus more sclerotized and remainder membranous, appendix very narrow, vein MP with 2, 4 or 5 terminals and crossvein *imp* present; hind wings commonly without submarginal vein and appendix, or just with very narrow appendix at wing tip.

Subfamily **Sinoalinae** Wang & Szwedo, 2012 stat. nov.
Tribe **Fangyuanini** Chen & Wang trib. nov.

Type genus. *Fangyuania* Chen, Szwedo & Wang, 2018.

Occurrence. Mid-Cretaceous Burmese amber of Kachin Province, Myanmar.

Diagnosis. Head with anterior margin with angularapex, crown broad, extending into distinct carinate supraantennal ledges, ocelli on vertex disc arranged in isosceles triangle with wide base; pronotum reduced and distinctly shorter than mesonotum; single lateral anteroventral spine and two lateral anterodorsal spines in row on hind tibia; tegmen with Pc + CP long, relatively distant from CA, basal cell long and broad with a short common portion of MP + CuA closing it apically; hind wing with peripheral membrane just at wing apex.

Remarks. The genus *Fangyuania* was recently described from mid-Cretaceous Burmese amber. We erected a new tribe, attributing it to the subfamily Sinoalinae stat. nov., for this genus, considering that the genus differs markedly from its con-familial Jurassic relatives (i.e. Sinoalini stat. nov.) in having some special body and wing features, namely: crown broad with anterior margin with angular apex, pronotum distinctly reduced, number of lateral spines in hind tibia reduced, tegmen with Pc + CP long, relatively distant from CA, hindwing with peripheral membrane present.

Subfamily **Juroalinae** Chen & Wang subfam. nov.

Type genus. *Juroala* Chen & Wang gen. nov.

Other genera. *Chengdecercopis* Hong, 1983; *Stictocercopis* Fu & Huang, 2018.

Occurrence. Middle–Upper Jurassic of northern China.

Diagnosis. Postclypeus somewhat flat, wide and slightly exceeding to crown (tylus present), discs of both crown and pronotum wrinkled or partly punctate; forefemur distinctly thickened; ovipositor slightly extending beyond tegmen tips; tegmen with RA multi-branched (2 to 4), MP with at least four branches; hind wing with MP two-branched.

Remarks. The Juroalinae subfam. nov. can be placed into the Sinoalidae (Cercopoidea) by a combination of characters: antenna with a flagellum of a few elongate segments; three ocelli on crown; two rows of lateral spines on hind tibia; tegmen with costal area and/or clavus more sclerotized; appendix very narrow; hind wing with ambient vein and appendix absent. It is different from Sinoalinae stat. nov. in the following characters: head wider; discs of both crown and pronotum wrinkled; forefemur thickened; ovipositor shorter; tegmen with Pc + CP short and ending far away from wing tip, RA multi-branched and vein MP with at least four terminal branches; hind wing with vein MP with two terminal branches.

Genus **Juroala** Chen & Wang gen. nov.

Type species. *Juroala daohugouensis* Chen & Wang sp. nov.

Locality and horizon. Daohugou Village, Ningcheng County, Inner Mongolia, China; the Middle–Upper Jurassic (Callovian–Oxfordian) Daohugou beds.

Etymology. The generic name is formed by the combination of the prefix 'Juro' from Jura Mountains, which gave their name to the Jurassic and the Latin word '*ala*' (wing).

Diagnosis. Total body length with genitals about 12 mm to 18 mm; head semicircular in dorsal view, with lateral ocelli large, and flagellum with 10 segments; pronotum with anterior margin straight; tegmen with apex truncate, basal cell about 0.3 times as long as tegmen length, closed with anastomosis, apical cells at most 11 in number, Pc + CP short, ending at costal margin not beyond tip of basal cell, stem CuA strongly curved at base, forking near or after claval apex and connecting to crossvein *mp-cua* just at its bifurcation.

Remarks. *Juroala* gen. nov. differs from the con-subfamilial genus *Chengdecercopis* Hong, 1983 in having a larger body and possessing a tegmen with basal cell distinctly longer, Pc + CP ending at costal margin not beyond tip of basal cell, stem CuA curved at base, and crossveins *r-mp* and *mp-cua* singular; from *Stictocercopis* Fu & Huang, 2018 in having head semicircular in dorsal view, lateral ocelli large, pronotum with anterior margin straight, tegmen with only costal area and/or clavus obviously punctate, without small elliptical spots on longitudinal veins, R single-branched, M four-branched and crossvein *mp-cua* connecting to CuA just at its bifurcation.

*Juroala daohugouensi*s Chen & Wang sp. nov.
(Figs 2–5, Supplemental Figs S1–S6)

Material. Holotype: STMN48-1555a, b, female adult in dorsoventral aspect with wings on both sides of the body. Paratypes: STMN48-1811a, b, NIGP169641a, b, NIGP169648a, b, NIGP169663, all female adults in dorsoventral aspect; NIGP169660, female adult in laterodorsal aspect; NIGP169650, male adult in dorsoventral aspect. Additional material: STMN48-1213, STMN48-1231a, b, STMN48-1812, STMN48-1813a, b, STMN48-1814a, b, STMN48-1815, STMN48-1816a, b, STMN48-1817a, b, STMN48-1818a, b, STMN48-1819, STMN48-1820, STMN48-1821a, b, STMN48-1822, STMN48-1823, STMN48-1824, STMN48-1825, NIGP169638, NIGP169639a, b, NIGP169640a, b, NIGP169662a, b, NIGP169659, NIGP169643, NIGP169644, NIGP169645a, b, NIGP169646a, b, NIGP169647a, b, NIGP169649, NIGP169651, NIGP169652, NIGP169653, NIGP169656, NIGP169657, NIGP169658, all female adults in dorsoventral aspect; NIGP169661, female adult in laterodorsal aspect; NIGP169642, male adult in dorsoventral aspect.

Etymology. The specific name is after Daohugou, the type locality.

Diagnosis. As for genus, as it is the only included species.

Description. Total body length 11.6–18.1 mm, average 15 mm (Supplemental Table S1).

Head. Head width with compound eyes *c.* two-thirds of pronotal width and length in midline 0.4 times greater than width. Postclypeus flat and wide, slightly extending to crown (tylus). Rostrum long, extending to middle coxae. Antenna with segmented flagellum of 10 segments. Compound eyes somewhat large. Lateral ocelli large, median ocellus small. Coronal suture weak; disc of crown wrinkled.

Thorax. Pronotum *c.* twice as wide as long in midline, nearly twice as long as head; anterior margin straight, posterior margin shallowly concaved; lateral margins converging anteriad; anterior angles widely angulate, posterior angles rounded; disc of pronotum wrinkled. Mesonotum in midline slightly shorter than pronotum, wider at base than long; scutellum separated; disc of mesonotum wrinkled. Forefemur thickened, foretibia longer than forefemur; basi- and midtarsomere of similar length, apical tarsomere slightly longer, tarsal claws distinct. Hind leg with femur of similar length as fore and mid femora; hind tibia *c.* 1.4 times as long as mid tibia, with two rows of 4 (anterodorsal) and 3/4 (anteroventral) lateral spines respectively, somewhat widened in apical portion and with two rows of apical teeth with thick subapical setae; basi- and midtarsomere with distinct apical teeth. Arolium present.

Abdomen. Abdomen flat. Genital valve short and wide, fused with lateral portions of pygofer, with indistinct sutures visible. Genital styles elongated, sclerotized apically, slightly extending beyond apex of pygofer. Female pygofer long, with ovipositor slightly extending beyond tips of forewings.

Tegmen. Tegmen about 2.74 to 4.10 times as long as wide (probably strongly impacted by taphonomic deformation), with costal margin thickened and distinct with hypocostal carina. Costal cell and claval area punctate; apex of clavus reaching 0.7 of tegmen length. Basal cell reaching nearly 0.3 of tegmen length. Longitudinal veins thick. Pc + CP ending at costal margin not beyond tip of basal cell. ScP fused with R + MP + CuA at about 1/3rd of basal cell length. ScP + R, MP and CuA separating from ScP + R+MP + CuA almost at same point. Crossvein *cua-cup* long, connected to CuA almost at branching point of ScP + R+MP + CuA. Stem ScP + R shorter than basal cell, forked distinctly basad of stem MP, at basal 0.42 to 0.47 of wing length; ScP dividing from RA at basal 0.69 to 0.76 of wing length; number of
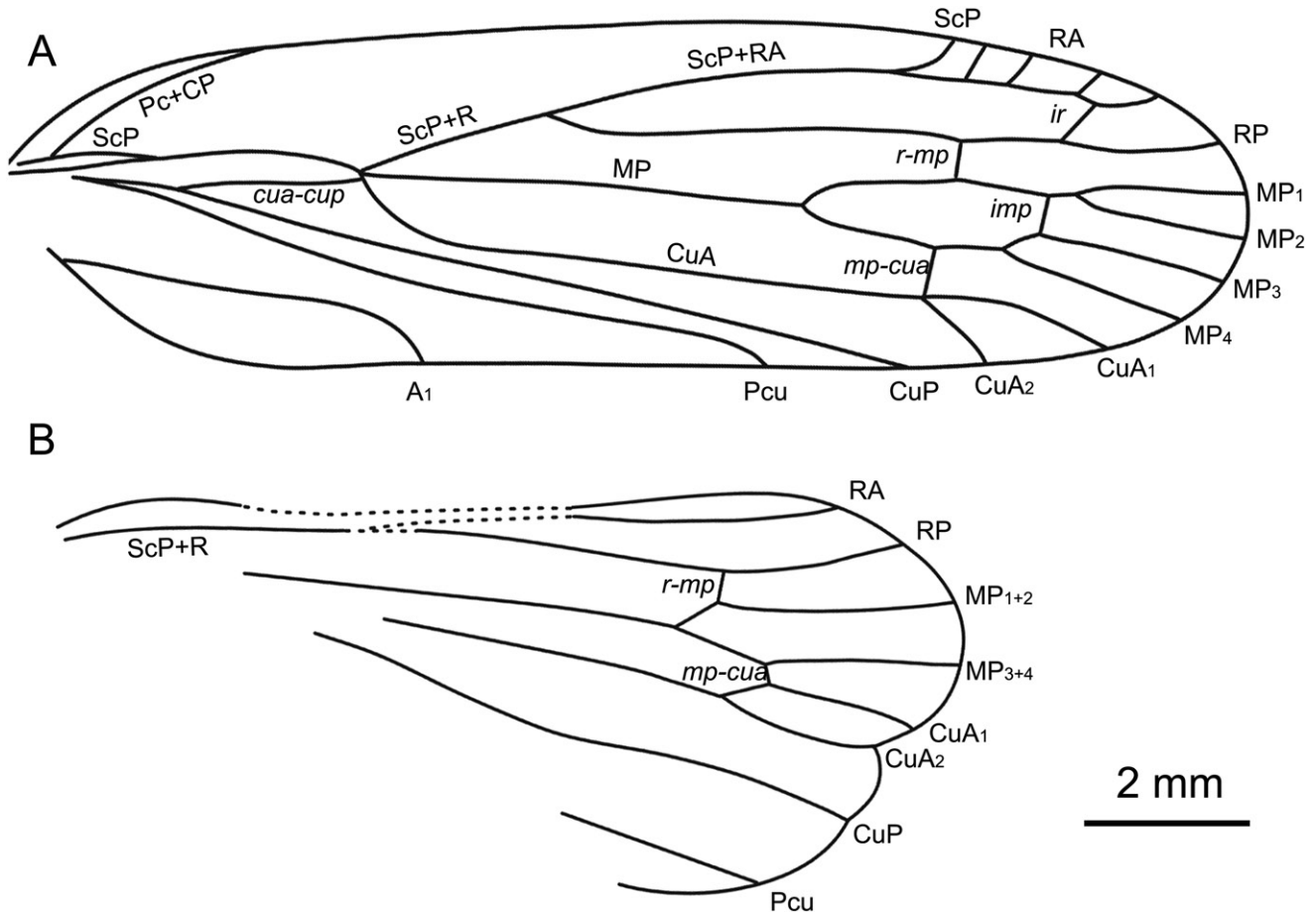
Figure 2. Line drawings of *Juroala daohugouensis* Chen & Wang gen. et sp. nov. **A,** right tegmen of holotype STMN48-1555. **B,** right hind wing of paratype STMN48-1811. All to same scale bar.

independent terminal branches of RA variable (2 to 4); RP single, connected to RA by crossvein *ir* and connected to MP_{1+2} by crossvein *r-mp*. Stem MP forking at basal 0.62 to 0.70 of wing length; MP_{1+2} forking at basal 0.78 to 0.90 of wing length; MP_{3+4} forking at basal 0.80 to 0.89 of wing length; relative branching position of MP_{1+2} and MP_{3+4} variable; crossvein *imp* present, with position variable, connecting to MP_{1+2} or MP_2, MP_{3+4} or MP_3. Stem CuA curved at base then subparallel to stem MP, forking at basal 0.73 to 0.79 of wing length, apicad of bifurcation of stem MP, nearly at same level as apex of clavus, connecting to crossvein *mp-cua* just at its bifurcation; branch CuA_1 curved smoothly, about twice as long as CuA_2; CuA_2 oblique and nearly straight.

Hind wing. Hind wing shorter than tegmen, without peripheral membrane; wing apex rounded; outer margin distinctly incised at level of terminal CuA_2. RA and RP unbranched. MP with two terminal branches, ending near wing apex; position of MP fork variable: basad, at same level, or even apicad of bifurcation of CuA. CuA

with two terminal branches; CuA_1 slightly longer than CuA_2. Crossveins *r-mp* and *mp-cua* present, with their relative positions variable.

Remarks. *Juroala daohugouensis* gen. et sp. nov. described herein is based on 42 whole-bodied fossil specimens. The abundant material provides some novel insights into the taxonomy and biology of early froghoppers. Wing venation provides most of the available information for extinct froghoppers, especially for compression materials. Venation patterns, however, show a considerable intra-specific or even intra-individual variation (e.g. relative position of bifurcation of MP_{1+2} and MP_{3+4}, position of crossvein *imp* on tegmen, and relative branching position of MP and CuA, and relative position of crossveins *r-mp* and *mp-cua* on hind wing (Supplemental Table S1; Figs 3, 4, 6; Supplemental Figs S1–S6). In spite of the high variation, these traits show a continuity when abundant individuals are included (42 specimens in this study; Fig. 6), and so it is reasonable to assign these specimens to the same species, suggesting that recognition of fossil cercopoids
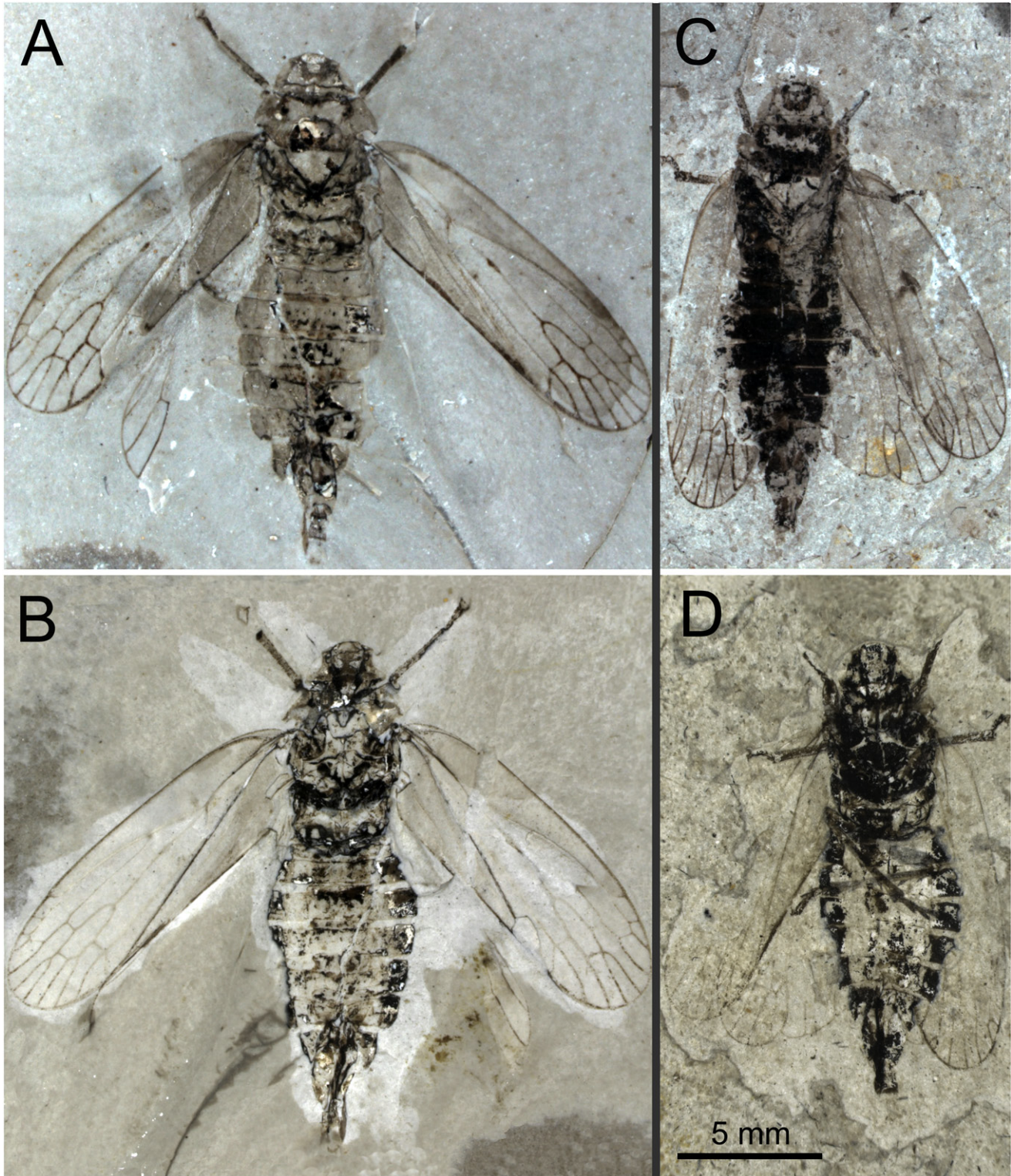
Figure 3. *Juroala daohugouensis* Chen & Wang gen. et sp. nov. **A,** part of holotype STMN48-1555. **B,** counterpart of holotype STMN48-1555, under alcohol. **C,** part of paratype STMN48-1811. **D,** counterpart of paratype STMN48-1811, under alcohol. All to same scale bar.
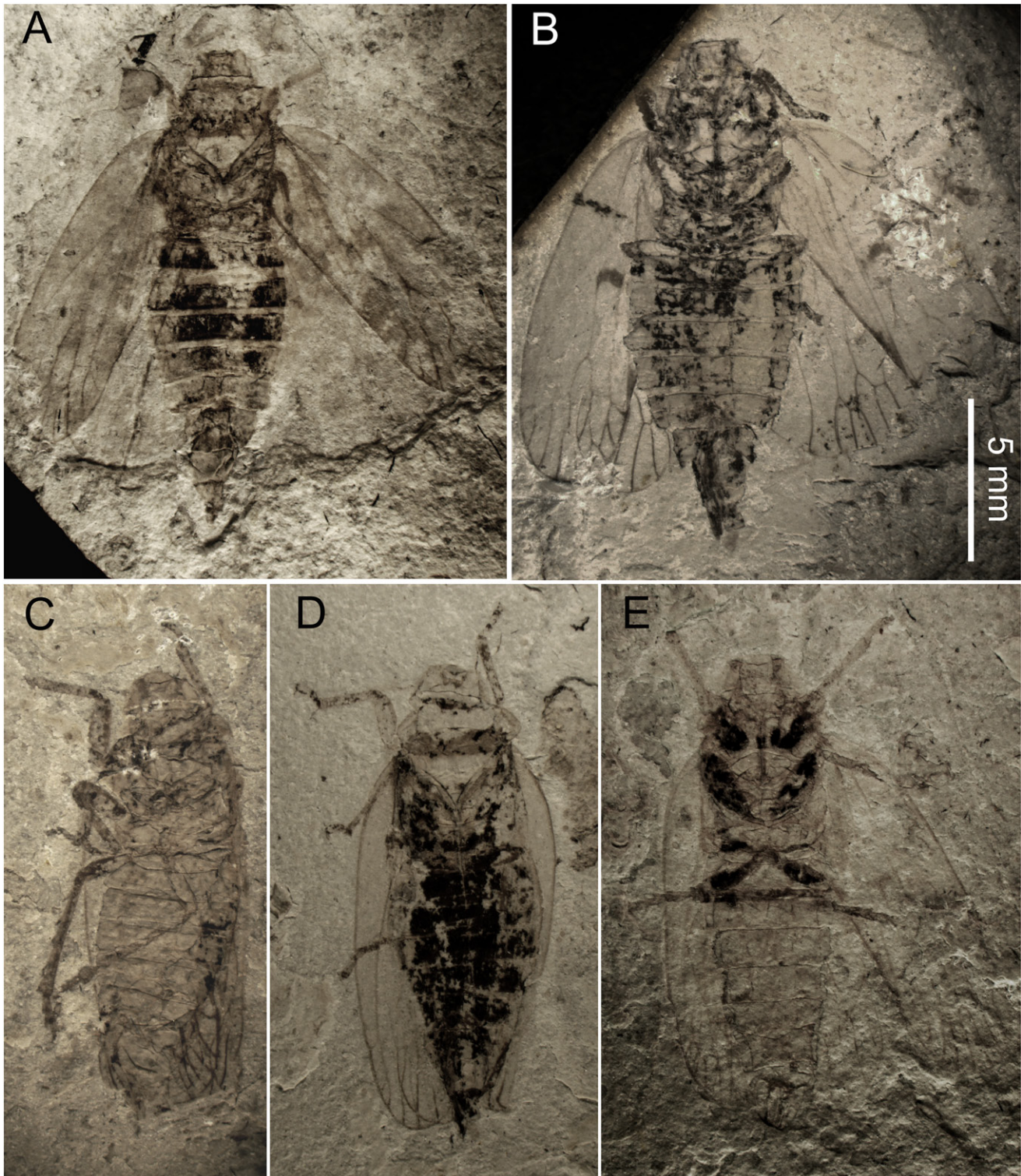
Figure 4. *Juroala daohugouensis* Chen & Wang gen. et sp. nov. **A,** part of paratype NIGP169641. **B,** paratype NIGP169663. **C,** paratype NIGP169660. **D,** part of paratype NIGP169648. **E,** paratype NIGP169650. All to same scale bar.

based solely on slight morphological discrepancies of a few isolated wings should be regarded with caution. Another intriguing feature revealed by our fossil

material is that *Juroala daohugouensis* gen. et sp. nov. shows an extremely female-biased propensity: of 42 fossil specimens we collected, 40 individuals are female

Figure 5. Details of *Juroala daohugouensi*s Chen & Wang gen. et sp. nov. **A,** head of paratype NIGP169641. **B,** right antenna of paratype NIGP169648. **C,** right antenna of paratype NIGP169663. **D,** mouthpart of paratype NIGP169663. **E,** right foreleg of paratype NIGP169648. **F,** right middle leg of paratype NIGP169648. **G,** right hind tibia of paratype NIGP169660. **H,** left hind tibia of paratype NIGP169660. **I,** male pygofer of paratype NIGP169650. **J,** female pygofer of paratype NIGP169663. **B–J** under alcohol. Probable joints between segments of antennae are indicated by arrows. Lateral spines on tibia are indicated by triangles. **Abbreviations: tyl.,** tylus; **cro.,** crown; **oce.,** ocellus; **sca.,** scape; **ped.,** pedicel; **fla.,** flagellum; **pos.,** postclypeus; **ros.,** rostrum; **fem.,** femur; **tib.,** tibia; **tar.,** tarsus; **VII**, sternite VII; **VIII**, sternite VIII; **pyg.,** pygofer; **gv.,** genital valve; **gs.,** genital style; **ovi.,** ovipositor. Scale bars = 1 mm.
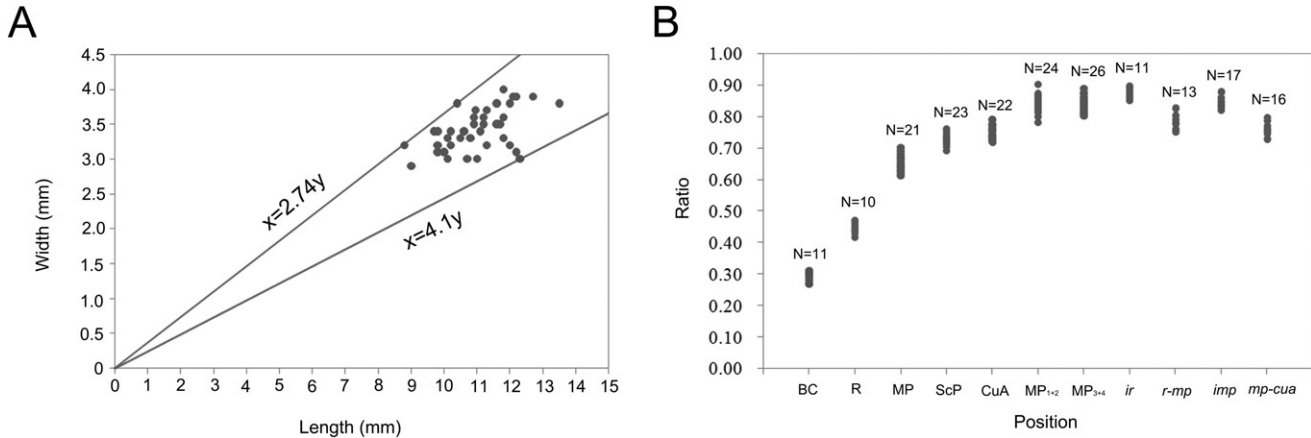
Figure 6. Scatter plots showing morphometric statistics of tegmina of *Juroala daohugouensi*s Chen & Wang gen. et sp. nov. **A,** bivariate plots of wing length and width. **B,** ratios of branching position of longitudinal veins and mid-point position of crossveins to tegmen length. BC, ScP, R, MP, CuA, MP_{1+2}, MP_{3+4}: branching position of vein MP + CuA (basal cell length), RA + ScP, R + ScP, MP, CuA, MP_{1+2}, MP_{3+4}/tegmen length; *ir, r-mp, imp, mp-cua*: mid-point positon of crossvein *ir, r-mp, imp, mp-cua*/ tegmen length. 'N' represents the sample size.
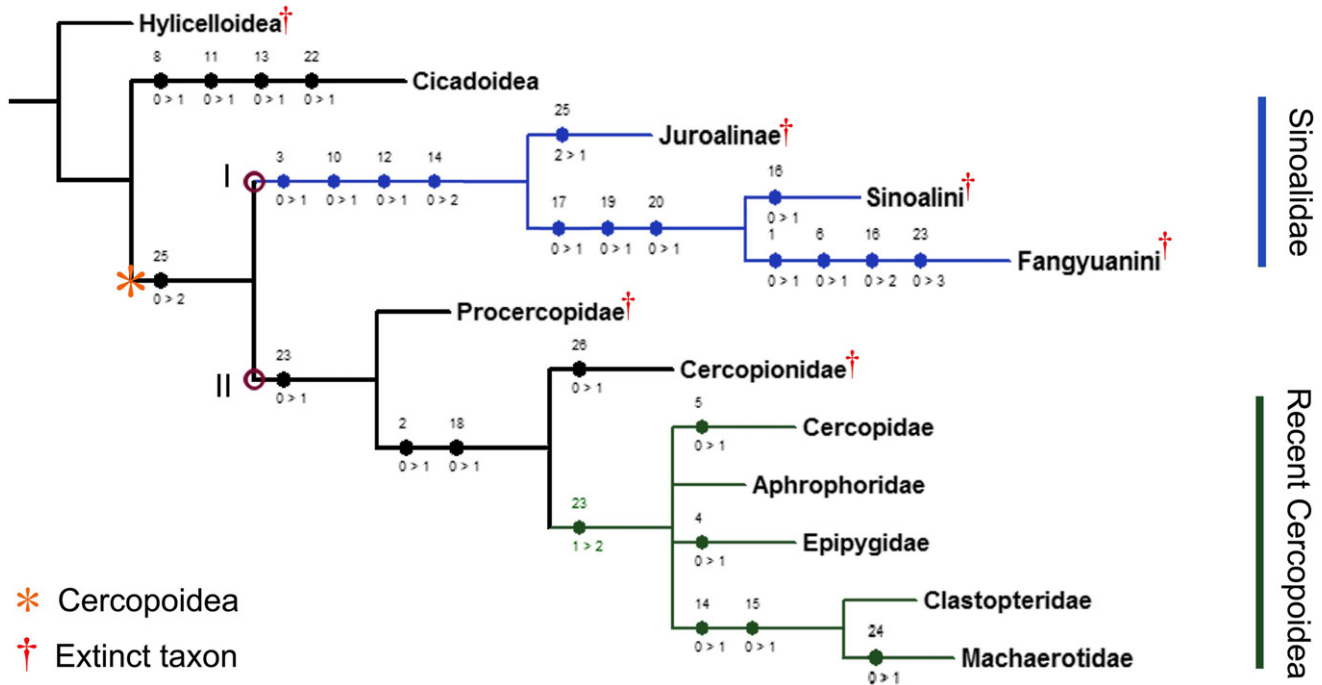

Figure 7. The most parsimonious tree inferred from maximum parsimony analysis with character mapping. White circles indicate homoplasious characters and black circles indicate non-homoplasious characters. Numbers above branches are character numbers, and below branches are character state changes. Labelled nodes (hollow circles) refer to specific clades discussed in the text.

adults and only two are male (see Discussion for details).

Phylogenetic inference

Maximum parsimony yielded only one MPT tree (Fig. 7), with the following characteristics: tree length = 35 steps,

consistency index (CI) = 0.963 and retention index (RI) = 0.971. The monophyly of the superfamily Cercopoidea was recovered in this MPT tree, but not well supported (character: 25: 0 > 2). Two major clades (Clades I and II) were recovered. The family Sinoalidae occupied the basal position with Cercopoidea and constituted a monophyletic clade (Clade I) with high support (3: 0 > 1, 10: 0 > 1, 12:

0 > 1, 14: 0 > 2). The subfamilies Juroalinae subfam. nov. and Sinoalinae stat. nov. were revealed as two independent clades, and the latter, constituted by two tribes Sinoalini stat. nov. and Fangyuanini trib. nov., was recovered as a monophyletic lineage with significant support (17:　0 > 1,　19:　0 > 1,　20:　0 > 1). The family Procercopidae was resolved as the basal group to Cercopionidae plus the five modern cercopoid families (Clade II), and the latter two constituted a well-supported monophyletic group (2: 0 > 1; 18: 0 > 1). The monophyly of modern cercopoid lineages was recovered (23: 1 < 2). The modern families Clastopteridae and Machaerotidae constituted a monophyletic clade with high support (14: 0 > 1, 15: 0 > 1).

Discussion

As one of the three extant groups of Clypeata, Cercopoidea, with numerous primitive characters, is closer to its stem group (i.e. Hylicelloidea) than the other two superfamilies, Cicadoidea and Membracoidea (Shcherbakov 1992). Along with new fossils discovered, the boundary between Cercopoidea and Hylicelloidea becomes increasingly ambiguous: punctate tegmen with ScP independent from R + MP + CuA at wing base were treated as discriminatory features for Cercopoidea (Wang *et al.* 2012), but in fact the characters are shared by Hylicelloidea (e.g. Conjucellinae; Shcherbakov 2012) and thus likely derived from the latter, or even from the more basal Cicadomorpha. According to our phylogenetic analyses, the validity of Cicadoidea is well supported by a series of synapomorphies, but the monophyly of Cercopoidea is poorly supported. A single-branched MP on the hind wing (25: 2) was mapped as the synapomorphy, and this character is likely not an ancestral state, since basal groups of the two lineages (Juroalinae subfam. nov. for Clade I and Jurassic Procercopidae for Clade II) have hind wings with MP two-branched. Decrease in branches of MP in the hind wings (from three to two, and then to one) is likely a common character for Cercopoidea; however, this trait is also present in Membracoidea, probably due to parallel evolution.

Up till now, three extinct families (Procercopidae Handlirsch, 1906; Cercopionidae Hamilton, 1990; Sinoalidae Wang & Szwedo, 2012) have been attributed to the superfamily Cercopoidea, representing ancestral froghoppers in the Mesozoic. The Procercopidae, an extinct family from the Early Jurassic to Early Cretaceous in Eurasia, is believed to gradually transform morphologically into modern cercopoid forms (Shcherbakov 1992; Chen *et al.* 2018). The view is confirmed in our phylogenetic analyses: this family is recovered as the basal group to Cercopionidae plus the five modern cercopoid families.

The systematic position of Cercopionidae from the Lower Cretaceous Crato Formation of Brazil is now controversial (Hamilton 1990; Wang *et al.* 2012). This family is resolved as the descendant of Procercopidae and the sibling group to modern cercopoid families in our phylogenetic trees. Cercopionid and modern cercopoids share a remarkable character (18: 1; tegemen with independent basal part of ScP extremely long, extending beyond basal cell and fused with R) which is unique within Clypeata. Cercopionid and modern cercopoids also share some other common traits, that were very probably derived from the late Procercopidae, e.g. MP of both tegmen and hind wing being single-branched (Hamilton 1990), suggesting that Cercopionidae is probably a primitive representative of modern cercopoid forms.

Sinoalidae, having a mixture of ancestral features (shared with Hylicelloidea and the Jurassic Procercopidae) and some derived traits, is recorded in Middle Jurassic deposits in north-eastern China and mid-Cretaceous Burmese amber (Wang *et al.* 2012; Chen *et al.* 2017, 2018; Fu et al. 2017; Fu & Huang 2018). This family is well supported as a monophyletic group with a series of synapomorphies: postclypeus flat and wide at base (3: 1), lateral spines arranged in two rows on hind tibiae (10: 1), abdomen with ovipositor extending beyond tip of forewings (12: 1), and tegmen with costal area and clavus more sclerotized (14: 2). Juroalinae subfam. nov. retains some ancestral features of Cercopoidea or even Clypeata, e.g. tegmen with Pc + CP short (17: 0), RA and MP with branches not decreasing in number (19: 0; 20: 0), and hind wing with MP two-branched (25: 1), suggesting that this new subfamily likely represents the ancestral linage of Sinoalidae. The Cretaceous genus *Fangyuania* shows a series of remarkably derived traits: crown broad and extended with distinct carinate supraantennal ledges (1: 1), pronotum reduced and distinctly shorter than mesonotum (6: 1), tegmen with cell between Pc + CP and CA long and broad (16: 2), and hind wing with peripheral membrane at wing apex (23: 3). Considering that the genus differs remarkably from its con-subfamilial Jurassic relatives (i.e. Sinoalini stat. nov.), a new tribe Fangyuanini trib. nov. is erected herein.

The relative branching positions of longitudinal veins were commonly chosen as one of the significant diagnostic characters at species-, genus- or even family-level for Cicadomorpha (e.g. Wang *et al.* 2012; Kaulfuss & Moulds 2015; Chen *et al*. 2016). However, the branching positions of longitudinal veins have been revealed to possess a high intra-specific or even intra-individual variability in fossil cercopoids (Chen *et al.* 2015b, 2017;

this study), and so it is not desirable to delimit and/or erect new extinct cercopoid taxa based on a few slight venational discrepancies of isolated wings. The hind wing venation of known sinoaline froghoppers is less variable, probably due to the simplified topology and reduced branches (Chen *et al.* 2017); however, the hind wing of Juroalinae subfam. nov. shows a considerable intra-specific variation, with the relative branching positions of both MP and CuA and the relative position of crossveins *r-mp* and *mp-cua* being highly variable, suggesting that the evolutionary rate of hindwing venational change is likely vary in different sinoalid lineages.

The tegminal length/width ratio of *Juroala daohugouensis* gen et sp. nov. displays an extremely high variation from 2.74 to 4.10. The high variation might reflect the biological characteristics to some degree, but on the other hand, it is also strongly influenced by taphonomic factors: some fossil specimens included in the present study are obviously distorted by deformation of sedimentary rocks (e.g. STMN48-1231; Supplemental Fig. S1D). Body structure characters have also obviously been influenced by similar factors: the shape of the head in dorsal view, for example, is semicircular (e.g. STMN48-1555; Fig. 3A) to nearly isosceles-trapezoid-like (e.g. STMN48-1818; Supplemental Fig. S2D), and the latter situation likely results from poor preservation of the tylus and compound eyes. A new taxon, therefore, should be established in consideration of tectonic factors and taphonomic conditions (Wang *et al.* 2008).

It is intriguing that among the 42 fossil specimens of *Juroala daohugouensis* gen. et sp. nov. we collected, 40 individuals are female adults and only two are male, showing an extremely strong asymmetric sex ratio. So far, however, only a few palaeontological studies have focused on the sex ratio of sexually dimorphic organisms in fossil assemblages and they are mostly in Cenozoic palaeovertebrate fauna, e.g. rhinoceroses (Mihlbachler 2003), moas (Allentoft *et al.* 2010) and woolly mammoths (Pečnerová *et al.* 2017). To our knowledge, the present study is the first detailed report on remarkably unbalanced sex ratios in fossil insects.

Distortion of the sex ratio towards females is common in extant insect populations (Hoy 1994), stimulated by various factors such as seasonal fluctuation (Sequeira & MacKauer 1993), feminization (Kageyama *et al.* 1998), haplodiploid determination (Reuter & Keller 2001), thelytoky (Hagimori *et al.* 2006), or low survival rate to adulthood for males (Hayashi *et al.* 2016). Extremely high female bias, as shown in *Juroala daohugouensis* gen. et sp. nov., is commonly accompanied by unique physiology, ecology and ethology, i.e. parthenogenesis, sociability and parental care (Stouthamer *et al.* 1990; Tang *et al.* 2014). For fossil insects, taphonomical bias might be another factor leading to differential preservation states of male and female remains, including dimorphic male individuals with body small in size and more easily degraded, poor flying and leaping capabilities, inactivity, short life-circle and so on. If the new taxon represents a social insect group, then the nymphs might not live in spittle masses or sap-filled tubes as do modern cercopids, or be subterranean such as Cicadoidea or ancient Hylicelloidea (Shcherbakov & Popov 2002), because if so, juveniles would be protected and also separated by the overlays, reducing the necessity and accessibility for parental care.

Distinctly female-biased sex ratios among extant cicadomorph groups are not common, but have been reported from some membracoids and indeed explained as a result of sub-sociability/parental care (Wood & Dowell 1984; Masters *et al.* 1994) and seasonal variation (Narhardiyati & Bailey 2005). Although disproportionate sex ratios have been recorded in froghoppers, the data are mixed (Nilakhe *et al.* 1987) or strongly male-biased (Peck 1999). Our results indicate that the early Cercopoidea in the Mesozoic not only had a great morphological disparity, but also likely evolved some unique features in their ecology and ethology, caused by special anatomical structures, biochemical features, or even symbiotic microorganisms.

Acknowledgements

Supplemental material

Supplemental material for this article can be accessed at: https://doi.org/10.1080/14772019.2019.1587526

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Associate Editor: Vladimir Blagoderov