



Short communication

A new sinoalid froghopper in mid-Cretaceous Burmese amber, with inference of its phylogenetic position (Hemiptera, Cicadomorpha)

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ABSTRACT

The froghopper family Sinoalidae was previously recognized from the uppermost Middle–lowermost Upper Jurassic Daohugou Biota and coeval strata of northeastern China. Very recently, a froghopper bearing some unique morphological characters from mid-Cretaceous Burmese amber was described and placed in this family. Here, a second sinoalid taxon *Jiaotouia minuta* Chen and Wang, gen. et sp. nov., is described and illustrated from Burmese amber, and a cladistic analysis is also performed to establish its phylogenetic position. The new taxon can be discriminated from all known sinoalids by displaying some unique tegminal characters as follows: Pc+CP extremely long, extending to apical margin and slightly concave at end of longitudinal veins at apical margin, and MP connected to CuA₁ by fusing into a common stalk instead of crossvein *mp-cua*. Our find further explores the taxonomic diversity and morphological disparity of Sinoalidae.

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1. Introduction

The clade Clypeata Qadri, 1967, uniting all modern Cicadomorpha superfamilies, comprises Cicadoidea (singing and hairy cicadas), Cercopoidea (froghoppers) and Membracoidea s.l. (leafhoppers and treehoppers) and their common ancestral group Hylicelloidea. It is typified by some morphological characters such as postclypeus hypertrophied (presumably for xylem feeding), antennae segmented, and Y-vein (Pcu + A₁) on tegminal clavus obscured (Wang et al., 2012). As one of the most speciose insect lineages, Clypeata arose in the late Permian and its subsequent radiations resulted in a diverse and successful group in the Mesozoic, represented by some primitive groups, such as Hylicelloidea, Membracoidea s.l.: Archijassidae, Cicadoidea: Tettigarctidae, and

Cercopoidea: Procercopidae, Cercopionidae and Sinoalidae (Shcherbakov and Popov, 2002; Wang et al., 2012; Szwed, 2018).

Sinoalidae, the most recently described extinct froghopper family, was erected from the well-known uppermost Middle–lowermost Upper Jurassic Daohugou beds and coeval strata of northeastern China (Wang et al., 2012). This family likely represents an ancestral form of Cercopoidea, possessing a mixture of ancestral features shared with Hylicelloidea and Procercopidae (Wang et al., 2012; Chen et al., 2018). In Wang et al. (2012), 6 species in 5 genera were assigned to Sinoalidae, with some easily recognized characters: hind tibia with two rows of lateral spines, tegmen with the costal area and clavus commonly more sclerotized and punctate than the remaining part and terminal branches reduced, and hindwing with MP un-branched (Fig. 2B). Subsequently, one additional genus and two species with a similar venational topology from the Daohugou locality were added to this family (Chen et al., 2017; Fu et al., 2017). Fu and Huang (2018) reported a remarkable monotypic genus *Stictocercopsis* from Daohugou with a relatively complex wing venation: tegmen with RA possessing three or four independent terminal branches, and RP two-

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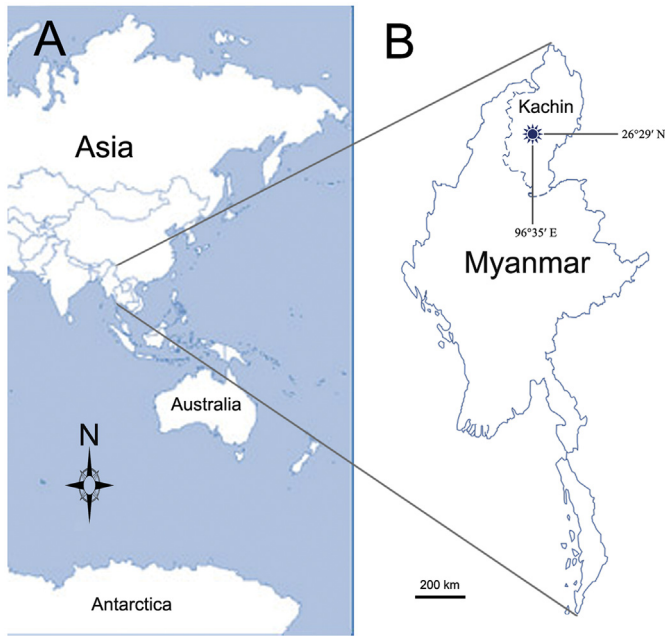


Fig. 1. Maps showing the location of the Cretaceous amber fossils from Kachin, Myanmar. (A), part of the world map; (B), Myanmar map with fossil locality indicated by a solar symbol.

branched, MP with five terminal branches, and hindwing with MP two-branched (Fig. 2A). The monobasic genus *Chengdecercopsis* from the Jiulongshan Formation, originally ascribed to Procercopidae (Hong, 1983), is venationally similar to the genus *Stictocercopsis*, and so should be transferred to Sinoalidae. All taxa mentioned above are preserved as imprint fossils from the Middle–Upper Jurassic of northeastern China. Very recently, Chen et al. (2018) described and illustrated a new taxon from mid-Cretaceous Burmese amber with some unique morphological characters, adding some valuable information to our knowledge of the taxonomic diversity and morphological disparity within the family Sinoalidae.

We herein describe another sinoalid, *Jiaotouia minuta* gen. et sp. nov., from Burmese amber. A cladistic analysis based on morphological characters of body structures as well as wings is also performed to determine its phylogenetic position.

2. Material and methods

The transparent yellowish amber piece containing the holotype of the new taxon is from the Hukawng Valley, Kachin State, Myanmar (Fig. 1). All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:8A1B2132-738E-42EF-8AB9-2C86ED079812.

The age of the rock yielding the amber was determined to be 98.79 ± 0.62 Ma (earliest Cenomanian) based on U–Pb dating of zircon crystals (Shi et al., 2012). The amber displays traces of redeposition, such as presence of pholadid bivalve borings; the centres of the resin pieces, however, were still soft when bored, so

Table 1
Definition of morphological characters and states.

No. Morphological characters and states	
Body structure	
1	Crown: 0, short, not extended; 1, anteriorly slightly extended; 2, distinctly extended.
2	Anterior margin of crown: 0, rounded; 1, slightly angled in the middle; 2, obviously angled in the middle.
3	Area of crown before compound eyes: 0, not expanded; 1, expanded.
4	Postclypeus: 0, narrow and distinctly inflated; 1, broad and relatively flat.
5	Antenna: 0, short, with flagellum aristiform; 1, long, with flagellum somewhat filiform.
6	Pronotum: 0, well-developed, largely concealing mesonotum; 1, reduced, as long as or even shorter than mesonotum.
7	Position of lateral spine on hind tibiae: 0, one row; 1, two rows.
8	Ovipositor: 0, not exceeding tips of tegmen; 1, slightly exceeding tips of tegmen; 2, distinctly exceeding tips of tegmen.
Tegmen	
9	Level of scleriosis: 0, strongly all over; 1, wing tip more sclerotized than other parts; 2, costal area and clavus commonly more sclerotized than other parts.
10	Elliptical spots on veins: 0, absent; 1, present and numerous.
11	Pc+CP: 0, ending far away from wing tip; 1, almost ending at wing tip; 2, extending to apical margin.
12	Pc+CP: 0, smooth at ending of longitudinal veins; 1, slightly concave at ending of longitudinal veins.
13	Common stalk of ScP+R+MP: 0, absent; 1, present, but very short; 2, relatively long.
14	Length of stem ScP+RA: 0, at most 3 times as long as ScP+R; 1, much longer than ScP+R, at least 4.5 times as long as the latter
15	RA: 0, multi-branched (with at least two independent terminal branches); 1, just with one independent terminal branch.
16	RA2 connecting crossvein <i>ir</i> when RA with one independent terminal branch: 0, far away from bifurcation of ScP+RA; 1, very close to bifurcation of ScP+RA.
17	Common stalk of MP+CuA: 0, long; 1, present, but extremely short; 2, absent.
18	MP: 0, multi-branched (at least four in number); 1, reduced, two-branched.
19	Bifurcation of CuA: 0, basad or almost at same level as costal area; 1, apparently distad of costal area.
20	Crossvein <i>cua-cup</i> connecting to: 0, MP+CuA at its bifurcation; 1, stem ScP+R+MP+CuA at its forking.
21	Crossvein <i>imp</i> : 0, present; 1, absent.
22	Crossvein <i>mp-cua</i> : 0, present; 1, absent; 2, replaced by a short anastomosis.
23	MP connected to CuA: 0, at stem MP; 1, at MP3+4.
24	CuA connected to MP: 0, at CuA ₁ ; 1, at or extremely near to bifurcation of CuA; 2, at CuA.
25	Apex of costal area: 0, basad of apex of clavus; 1, almost at same level as apex of clavus; 2, distinctly distad of apex of clavus.
26	Cell between Pc+CP and CA: 0, short, not beyond middle of wing length; 1, long, near to wing tip but extremely narrow; 2, long, extending to wing tip and relatively broad.
27	Length of the first apical cell: 0, apparently shorter than radial cell (C1); 1, almost as long as C1.
28	Apical cell between branches of CuA: 0, elongate; 1, shortened and nearly triangular.
Hindwing	
29	Peripheral membrane: 0, absent or extremely narrow; 2, present at wing apex.
30	Stem ScP+R: 0, apparently shorter than stem ScP+RA; 1, as long as, or even longer than stem ScP+RA.
31	MP: 0, multi-branched (at least three in number); 1, two-branched; 2, single-branched.
32	Crossvein <i>mp-cua</i> when MP not single-branched: 0, connecting to MP3+4; 1, connecting to stem MP.

longitudinal veins; MP_{3+4} connected to CuA_1 by fusing into a common portion instead of crossvein *mp-cua*. Hindwing without outer membrane; stem R long.

Jiaotouia minuta Chen and Wang, gen. et sp. nov.
(urn:lsid:zoobank.org:act:C4B465F9-7DF4-488B-8AF5-8D6BF2CFAC65)

Figs. 2D, 3–5

Etymology. The specific epithet refers to its small size.

Holotype. NIGP163576, an adult insect with overlapped wings on the top of the body, abdomen not preserved and gender unknown.

Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; lowermost Cenomanian, Upper Cretaceous (Shi et al., 2012).

Diagnosis. Size small, about 5 mm long; tegmen with ScP fused with R+M+CuA at basal 1/3rd of length of basal cell, ScP+R+MP+CuA branching into ScP+R and MP+CuA at about basal 0.28 of tegminal

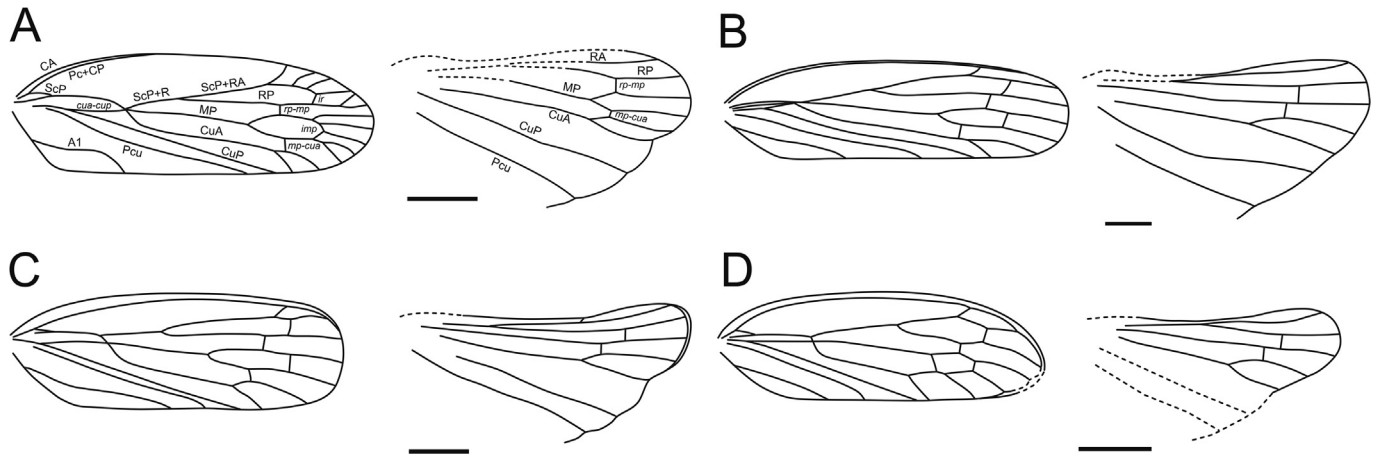


Fig. 2. Representative tegmina and hindwings of Sinoalidae. (A), *Stictocercopis wuhuaensis*; (B), *Jiania crebra*; (C), *Fangyuania xiai*; (D), *Jiaotouia minuta* gen. et sp. nov. Scale bars = 2 mm (A, B), 1 mm (C, D).

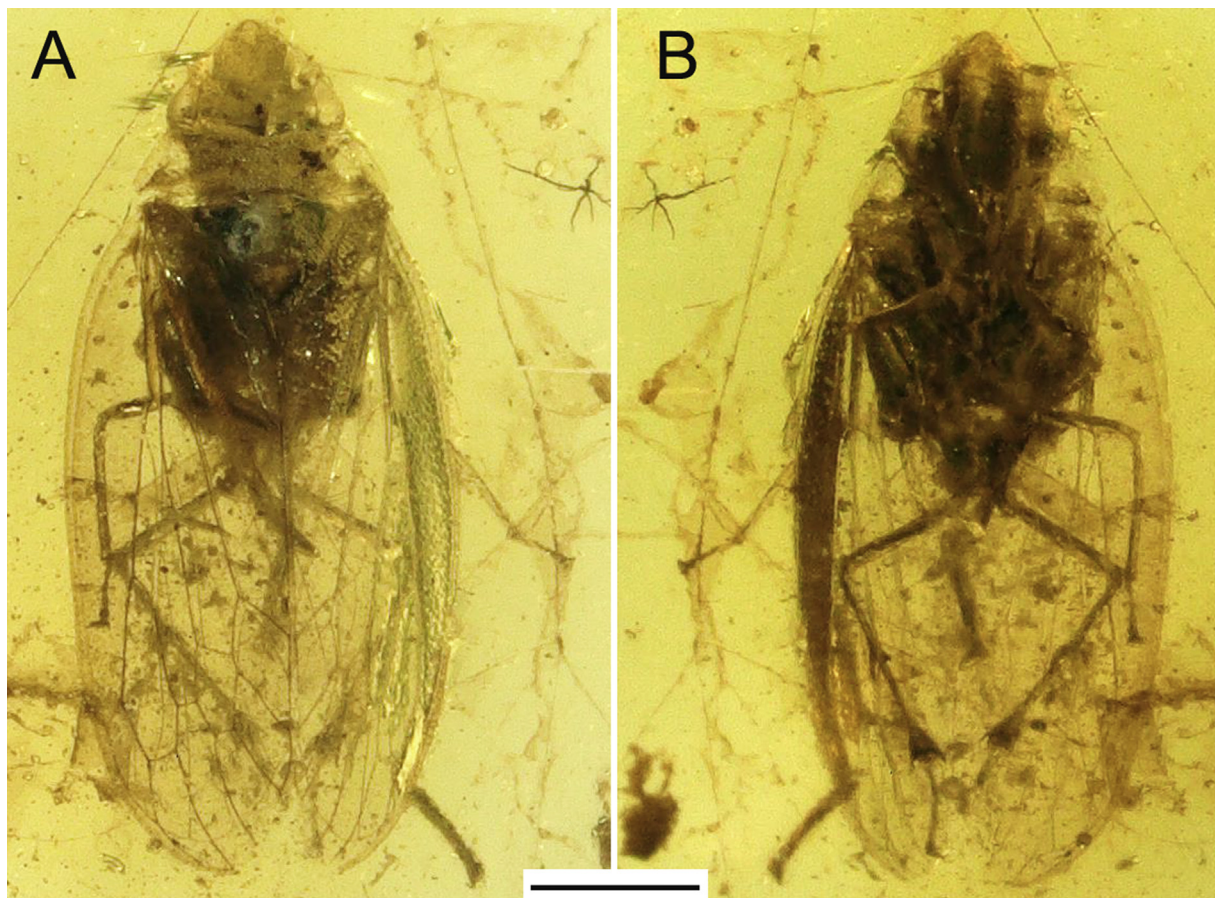


Fig. 3. Photographs of the holotype of *Jiaotouia minuta* gen. et sp. nov. (A), dorsal view; (B), ventral view. Scale bar = 1 mm.

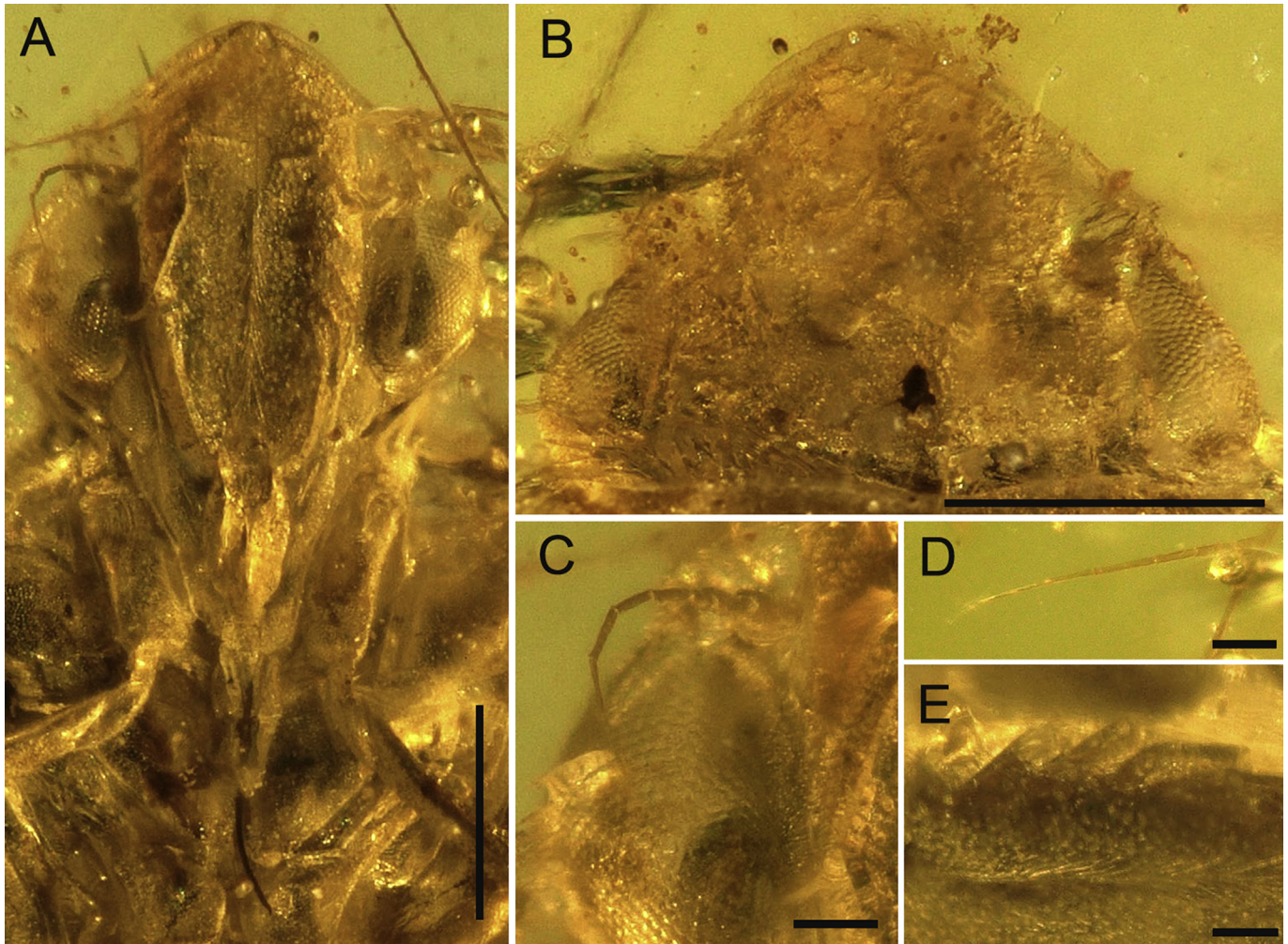


Fig. 4. Head of holotype of *Jiaotouia minuta* gen. et sp. nov. (A), overview of head in ventral view; (B), overview of head in dorsal view; (C), right antenna; (D), part of postclypeus. Scale bars = 0.5 mm (A, B), 0.1 mm (C, D, E).

length, ScP+R apparently longer than ScP+RA, MP+CuA short, bifurcating into MP and CuA just beyond its separation from ScP+R+MP+CuA, MP branching into MP₁₊₂ and MP₃₊₄ distad of claval apex, CuA branching into CuA₁ and CuA₂ basad of claval apex. **Description.** Measurements (in mm). Body including tegmen in repose length 5.42; head length 0.68, width 1.14; compound eye in dorsal view length 0.33, width 0.16; postclypeus length 1.08, width 0.52; anteclypeus length 0.37, width 0.24; rostrum length 0.80; pronotum length 0.37, width 1.64; mesonotum with scutellum included length 0.99, width 1.18; fore coxa length 0.53, trochanter length 0.27, femur length 0.62, tibia length 0.66, tarsus length 0.34; middle coxa length 0.24, trochanter length 0.21, femur length 0.66, tibia length 0.85, tarsus length 0.34; hind coxa length 0.35, trochanter length 0.21, femur length 0.75, tibia length 1.27, tarsus length 0.57.

Head. (Figs. 3–4). Head apparently narrower than pronotum. Crown produced anteriorly, disc with tiny granules; anterior margin angled medially. Coronal margin not expanded before compound eyes. Three ocelli on crown, with distance between lateral ocelli shorter than distance between ocellus and compound eye; median ocellus slightly smaller. Compound eyes large, somewhat drop-shaped in dorsal view with anterior margin very sharp. Postclypeus broad, widest at middle, somewhat depressed, with distinct transverse grooves and a medial carina. Anteclypeus oval.

Rostrum extending to middle coxae. Antennal pit shallow, emarginate, not sunken in antennal ridge; antenna long; scape apparently thicker and longer than pedicel; flagellum long, likely with at least seven segments.

Thorax. (Figs. 3,5). Pronotum short, shorter in midline than at lateral margins, widest at lateral angle; disc granulate; anterior margin concave medially; anterolateral margins straight, posterolateral margins slightly shorter, almost transverse; posterior margin smoothly concave. Mesonotum broad, with disc granulate. Fore legs with coxae thick and cylindrical; trochanters long; femora with distinct ridges; tibiae nearly as long as femora; tarsi with apical tarsomere enlarged apically; tarsal claws well-developed, arolia lamelliform. Middle legs with coxae apparently shorter than fore coxae; femora slender; tibia setose and ridged, apparently longer than femora, with basitarsomere much longer than mid- and apical tarsomeres; two large tarsal claws, arolia lamelliform. Hind legs with coxae and trochanters thick; femora with distinct ridges; tibiae extremely slender, inflated at apex, with two rows of lateral spines (one and two in number for each row), and two rows of apical teeth (teeth of apical row with long setae at apex and teeth of basal row without setae); tarsi densely covered with setae, with basitarsomere much longer than mid- and apical tarsomeres; two tarsal claws well-developed, arolia lamelliform.

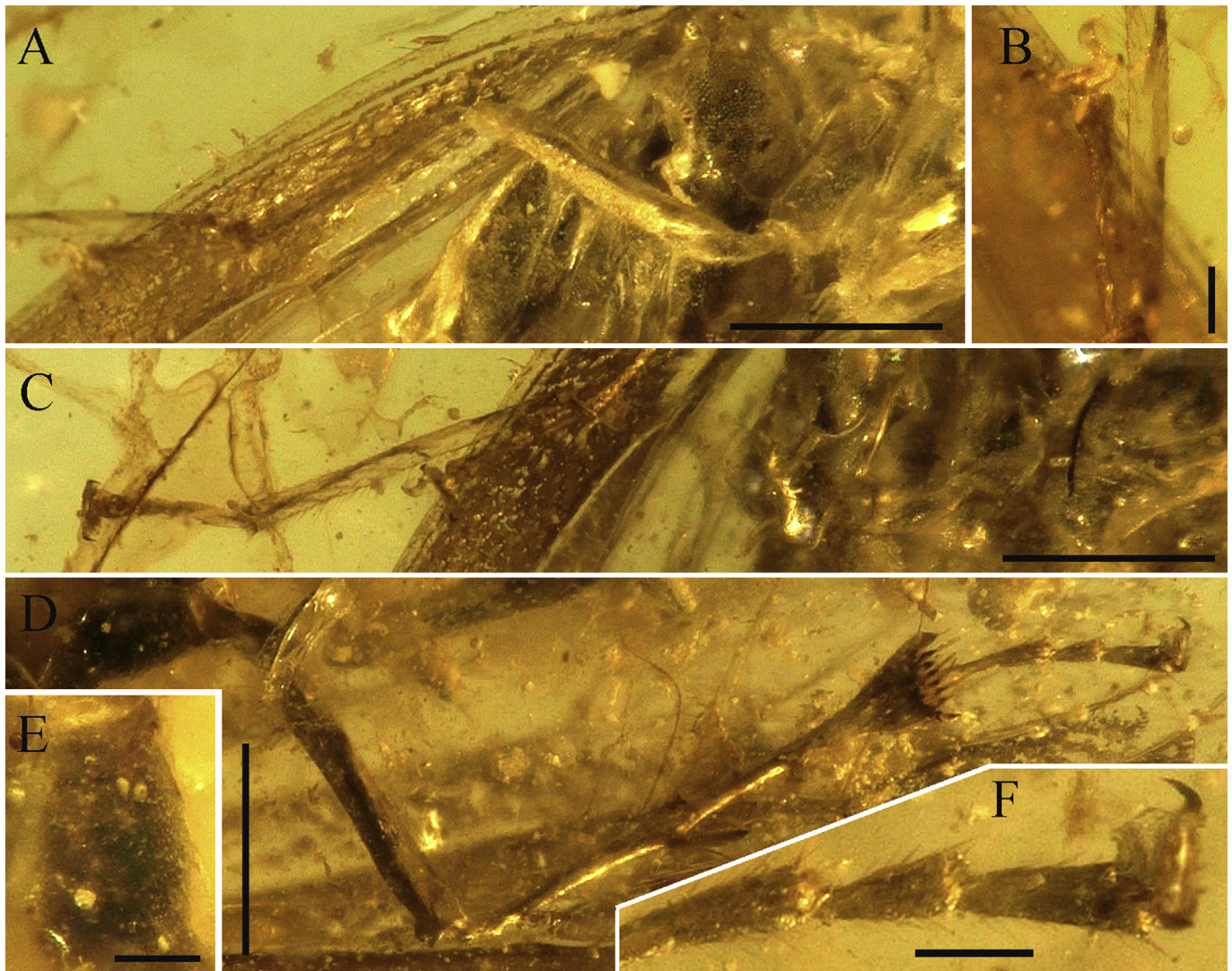


Fig. 5. Legs of holotype of *Jiaotouia minuta* gen. et sp. nov. (A), right fore leg; (B), right fore tarsus; (C), right middle leg; (D), right hind leg; (E), right hind coxa; (F), right hind tarsus. Scale bars = 0.5 mm (A, C, D), 0.1 mm (B, E, F).

Tegmen. (Figs. 2D, 3). Tegmen with clavus and costal area more punctate and sclerotized than other parts. Tegminal apex sharp. Appendix narrow. Costal margin smoothly arched. Postclaval margin almost straight. Claval margin strongly arched. Costal area long and narrow, much longer than clavus. Basal cell long and narrow. Cell between CA and Pc+CP extremely long, extending to apical margin. Pc+CP extremely long, extending to apical margin as ambient vein, slightly concave at termination of longitudinal veins. ScP with independent part short, running to and then fusing with R+M+CuA at basal 1/3rd length of basal cell. ScP+R+MP+CuA almost straight, branching into ScP+R and MP+CuA at about basal 0.28 of tegminal length. Stem ScP+R apparently longer than ScP+RA. RA₂ curved at connection with crossvein *ir*, much longer than ScP+RA₁. RP long, slightly sinuous. Crossvein *cua-cup* long, straight and parallel to ScP+R+MP+CuA, connecting to MP+CuA at its bifurcation. Stem MP+CuA short, bifurcating into MP and CuA just beyond its separation from ScP+R+MP+CuA. Stem MP long, branching into MP₁₊₂ and MP₃₊₄ distad of claval apex; MP₁₊₂ and MP₃₊₄ curved at connection with crossveins *rp-mp* and *imp*; MP₃₊₄ connected to CuA₁ by fusing into a stalk instead of crossvein *mp-cua*. Stem CuA strongly curved at base, then nearly straight, branching into CuA₁ and CuA₂ basad of

claval apex. CuA₁ much longer than CuA₂. CuP straight. Pcu straight, sub-parallel to CuP, and strongly curved apically. A₁ nearly straight and oblique.

Hindwing. (Figs. 2D, 3). Hindwing with outer membrane extremely narrow. Stem R extremely long, longer than RA and RP. MP unbranched, connected to RP and CuA₁ by crossveins *rp-mp* and *mp-cua*. CuA two-branched, with CuA₁ longer than CuA₂.

4. Results of phylogenetic analyses

For the Bayesian analysis, the standard deviation of split frequencies was below 0.01 after 10 million generations, and the potential scale reduction factor was close to 1.0 for all parameters in summaries of the samples of the substitution model parameters by typing sump burnin = 250. The 50% majority-rule consensus tree from Bayesian analysis is shown in Fig. 6. The monophyly of the Sinoalidae was recovered and significantly supported (Clade I; PP: 0.96; character number and state: 17: 2, 20: 1), with *Stictocercopis wuhuaensis* and *Chengdecercopis xiaofanzhangziensis* from the Middle to Upper Jurassic of northeastern China occupying a basal position. The remaining sinoalids constituted a monophyletic clade with high PP value and a series of synapomorphies (Clade II: 0.99;

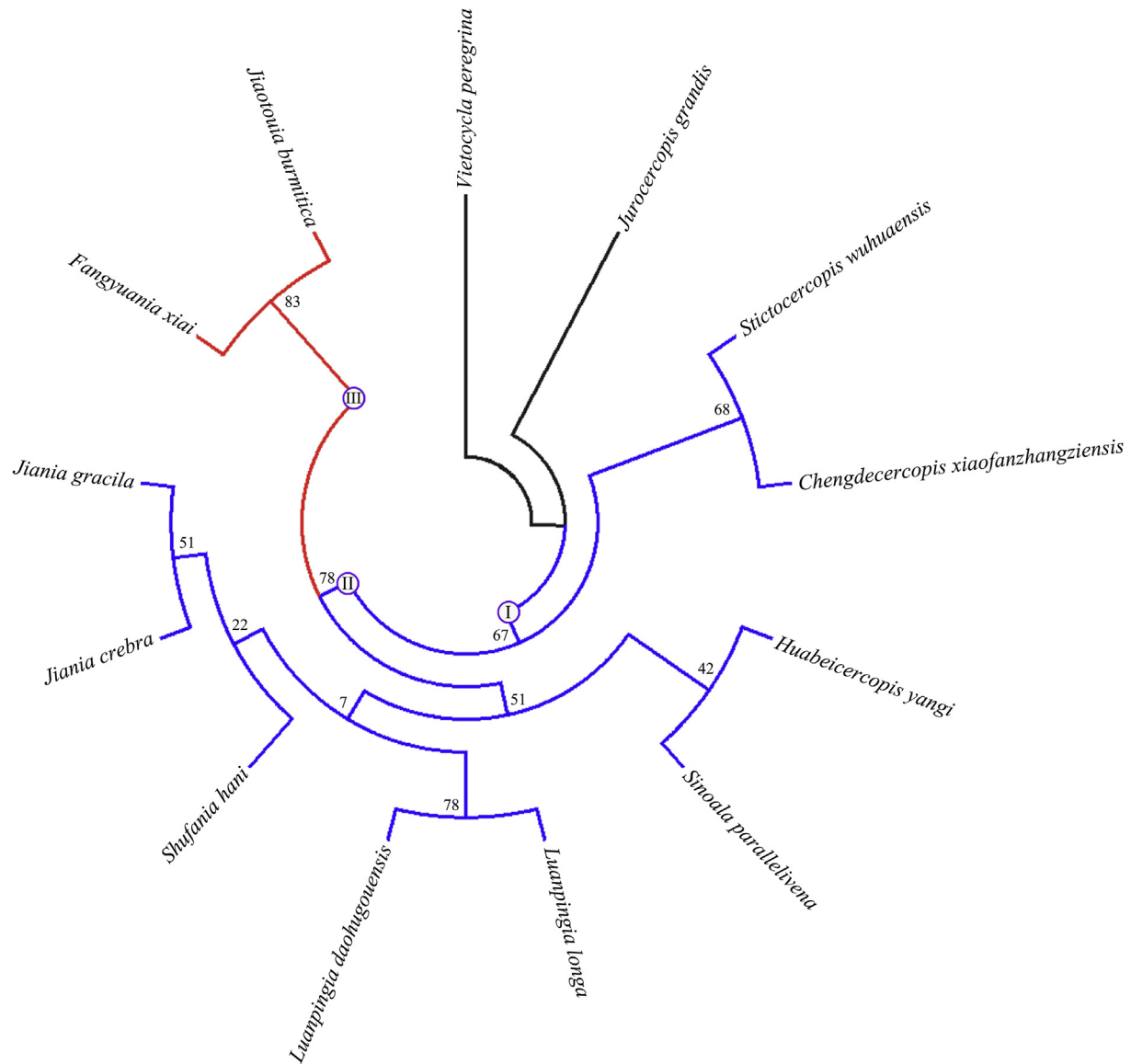


Fig. 7. 50% majority-rule consensus tree of Sinoalidae inferred from maximum parsimony analysis, with the numbers near the nodes are bootstrap support values. I, II and III indicate three clades of Sinoalidae discussed in the text.

remaining taxa from the Middle to Upper Jurassic of northeastern China (*Huabeicercopis*, *Luanpingia*, *Sinoala*, *Juania*, and *Shufania*), share some unique apomorphic traits with the sinoalids from mid-Cretaceous Burmite, likely representing transitional forms from the primitive Jurassic group to their Cretaceous descendants. The two mid-Cretaceous genera *Fangyuania* and *Jiaotouia* gen. nov., share a series of derived apomorphies and probably constitute a monophyletic lineage.

Wing venation provides us majority of the available information from fossil insects, especially from adpression material (e.g., Carpenter, 1992; Béthoux et al., 2011; Ross, 2012; Chen et al., 2015b). Not surprisingly, the α -taxonomy and high-level classification of fossil Hemiptera including Cicadomorpha, are mainly based on isolated wings (see Carpenter, 1992). Nevertheless, our find indicates it is imprudence to infer the taxonomic position and/or evolutionary relationship of fossil hemipterans just based on a few venational features: the sinoalids in Burmese amber nested well in Sinoalidae in our cladistic tree with a series of autapomorphies on both body structures and wings, but they display some

common venational characters in Clypeata. *Fangyuania* and *Jiaotouia* gen. nov. have a tegminal basal cell with a short common portion of $MP+CuA$ closing it apically; the character is distinctly discriminating from their Jurassic relatives, but is shared with early Cercopoidea: Procercopidae, as well as with other stem Clypeata Hylicellidae: Vietocyclinae and early Tettigarctidae (e.g., Becker-Migdisova, 1962; Shcherbakov, 1988; Wang and Zhang, 2009; Chen et al., 2015a, b; 2016b; Chen and Wang, 2016; see Chen et al., 2018). MP_{3+4} and CuA_1 on the tegmen of Sinoalidae are commonly connected by a short crossvein *mp-cua*; conversely, *Jiaotouia* gen. nov. possesses a tegmen with MP_{3+4} and CuA_1 fused into a short anastomosis, shared with the ancient Clypeata-Hylicellidae (Evans, 1956; Carpenter, 1992; Wang et al., 2012) and some stem leafhopper Archijassidae: Karajassinae (Shcherbakov, 2012). These characters seem to be homoplastic, appearing independently among various lineages of Clypeata. Considering that the sinoalids in Burmese amber, as the latest representatives of this insect group, likely represent one derived lineage, the characters mentioned above are likely derived independently (homoplastic),

and so are noisy signals in taxonomic assignments and phylogenetic inferences.

6. Conclusions

Representatives of the froghopper family Sinoalidae were exclusively known from Middle to Upper Jurassic deposits in northeastern China (Hong, 1983; Wang et al., 2012; Chen et al., 2017; Fu et al., 2017; Fu and Huang, 2018). Discovery of the monotypic genus *Fangyuania* from mid-Cretaceous Burmese amber, however, greatly extended the duration of Sinoalidae for more than 60 million years and also its geographic distribution (Chen et al., 2018). *Jiaotouia* gen. nov., the second sinoalid taxon erected from Burmese amber, bears some morphological characters markedly distinguishing it from *Fangyuania* and so suggests that Sinoalidae were likely highly diversified in the Burmese amber biota. Although the Cretaceous sinoalids were recovered as a derived lineage in our phylogenetic analysis, they bear some common characters shared with stem Cercopoidea, Cicadoidea, Membracoidea and even ancient Hylcellidae. Our find further confirms the view that early Cercopoidea diversified rapidly in the Mesozoic (Chen et al., 2018).

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