

Short communication

The first Mesozoic froghopper in amber from northern Myanmar (Hemiptera, Cercopoidea, Sinoalidae)



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ABSTRACT

Representatives of the froghopper family Sinoalidae were exclusively known from Jurassic deposits in northeastern China. A new taxon, *Fangyuania xiai* Chen, Szwedo and Wang, gen. et sp. nov., is erected from mid-Cretaceous Burmese amber and assigned to this family. The remarkable new sinoalid distinctly differs from its con-familial Jurassic relatives in having a tegmen with cell between costal margin and Pc + CP broad, stem MP + CuA relatively long and connecting crossvein *cua-cup* just at its bifurcation, and having a hind wing with posterior margin strongly ripple-like and wing tip with narrow peripheric membrane wrinkled. This finding greatly expands the duration and geographic distribution of the family Sinoalidae. The new taxon, as the first Cercopoidea reported in Mesozoic amber, provides some insights on morphological diversification and evolutionary history of early Cercopoidea and Clypeata as well.

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1. Introduction

The hemipteran superfamily Cercopoidea Leach, 1815, collectively named froghoppers, spittlebugs or cuckoo-spit insects, is a large and worldwide distributed insect group comprising over 2600 recent species and occurring in most terrestrial habitats (Cryan and Svenson, 2010; Hamilton, 2012; Wang et al., 2012; Chen et al., 2015a, b). The higher classification of Cercopoidea is subject of debate (Hamilton, 2001, 2012, 2013, 2014, 2015, 2016; Carvalho & Webb, 2005; Cryan and Svenson, 2010). Traditionally this superfamily includes extant families, i.e. Aphrophoridae Amyot et Serville, 1843, Cercopidae Leach, 1815, Clastopteridae Dohrn, 1859, Epipygidae Hamilton, 2001 and Machaerotidae Stål, 1866, and three extinct ones, i.e. Cercopionidae Hamilton, 1990, Procercopidae Handlirsch, 1906 and Sinoalidae Wang et Szwedo, 2012 (Wang et al., 2012).

There are controversies over the number, content and subdivisions of families within Cercopoidea (Hamilton, 2001, 2012, 2013, 2014, 2015, 2016; Dietrich, 2002, 2005; Cryan and Svenson, 2010; Cryan and Urba, 2012), inferred from various interpretations of morphological and molecular data, and these results do not resolve family-level relationships among modern cercopoids. So far, about one hundred fossil taxa are known to be placed in Cercopoidea (EDNA, 2015), but with a few exceptions they are in need of urgent revision, with number of fossils named in 19th and in beginning of 20th centuries (Metcalf and Wade, 1966) and never analyzed since then.

Cercopoidea, similarly as other Clypeata, are descendants of extinct Hylicelloidea. The family Procercopidae, reported from the Early Jurassic to Early Cretaceous in Eurasia, gradually transforms morphologically into modern cercopoid forms (Shcherbakov and Popov, 2002), with a quite rich fossil record from the Palaeogene and Neogene (Metcalf and Wade, 1966; Carpenter, 1992). The little known family Cercopionidae comes from the Lower Cretaceous Crato Formation, Brazil (Hamilton, 1990). The placement of *Mesojassula* Evans, 1956 (represented by a hindwing from the Carnian of Mt. Crosby, Queensland, Australia) in Cercopoidea *incertae sedis*

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(Becker-Migdisova, 1962) or Cercopionidae (Hamilton, 1992) is unresolved yet, but this fossil more probably represents Hylcellidae or earliest Membracoidea. The family Sinoalidae was established based on fossils from the uppermost latest Middle Jurassic of Daohugou, Ningcheng County, Inner Mongolia of northeastern China (Wang et al., 2012).

The Sinoalidae distinctly differs from the widely distributed Procercopidae mainly in the following characteristics: tegmen with costal area and clavus more sclerotized and punctate (vs. whole tegmen punctate in the latter), hind wing without submarginal vein and appendix (vs. ambient vein and narrow appendix in the latter), and hind tibia with two rows of lateral spines (vs. one small single lateral spine in the latter) (Wang et al., 2012). Up to now, six genera (*Luanpingia* Hong, 1983, ?*Hebeicercopis* Hong, 1983, *Huabeicercopis* Hong, 1983, *Sinoala* Wang and Szwed, 2012, *Jiania* Wang and Szwed, 2012, and *Shufania* Chen et al., 2017) exclusively recorded from Jurassic deposits of northeastern China have been attributed to this distinct frog hopper family (Wang et al., 2012; Chen et al., 2017).

The Cercopoidea has been widely recorded in Mesozoic deposits of Germany, Russia, Central Asia, China and Brazil (Hamilton, 1990; Chen et al., 2015a, b). However, all reported Mesozoic cercopoids are imprint fossils and most of them are incomplete, even just with sole tegmen or hind wing preserved. Amber affords exceptional three-dimensional preservation of insects, often providing more details than imprint fossils (Chen et al., 2016a). We here report a complete male adult frog hopper, referable to Sinoalidae, in mid-Cretaceous Burmese amber.

2. Geological context

The amber specimen comes from the Hukawng Valley of Kachin Province in northern Myanmar (Burma) (locality in Kania et al., 2015: fig. 1). The age of Burmese amber had been obscure for a long time, even considered as young as Miocene (Grimaldi et al., 2005). In this century, some studies based on different biological inclusions widely considered Burmese amber to be Albian-Cenomanian (mid-Cretaceous) (e.g., Cruickshank and Ko, 2003; Grimaldi et al., 2005; Ross et al., 2010). Recent U–Pb zircon dating of the volcanoclastic matrix indicates the Burmese amber at an earliest Cenomanian age (98.79 ± 0.62 Ma) (Shi et al., 2012).

Burmese amber contains probably the most diverse Mesozoic palaeobiota (Shi et al., 2012), and its inclusions have been studied for about a century (Cruickshank and Ko, 2003; Kania et al., 2015; Zheng et al., 2016). Insects known from Burmese amber are abundant and highly diverse, providing some great insights into their ecology, ethology and evolutionary history (e.g., Delclòs et al., 2016; Wang et al., 2016). Some hemipterans have been reported in Burmese amber to date, with most being true bugs (the suborder Heteroptera) (e.g., Grimaldi and Engel, 2008; Poinar and Brown, 2016). The new frog hopper is the first representative of the suborder Cicadomorpha.

3. Material and methods

The fossil frog hopper (specimen no. BA16003), in yellow and transparent amber, is deposited in the Lingpoge Amber Museum in Shanghai, China. 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:D6AD6905-DAC8-4A14-B016-AFAD78010D3D.

The specimen was examined, photographed and measured using the VHX 5000 digital microscope platform, with incident and transmitted light used simultaneously. The line drawings of tegmen

and hind wing were prepared with two image-editing softwares (CorelDraw 12.0 and Adobe Photoshop CS3).

There is no consensus on Cicadomorpha venation pattern and vein homology; various authors (e.g., Emeljanov, 1987; Pulz and Carvalho, 1998; Hamilton, 2012) used various names and interpretations. Nel et al. (2012) proposed a new interpretation of wing venation pattern for all Paraneoptera, assuming that CuA gets fused with M + R stem at wing base and connected with CuP by a specialized crossvein *cua-cup*, which is remarkably different from the traditional interpretations. The venational terminologies used herein are slightly modified from Nel et al. (2012). The first longitudinal vein on the clavus is treated as open problem in Nel et al. (2012). We herein tentatively treat this longitudinal vein as Pcu rather than A₁. One more point is the complete fusion of MA with R in Paraneoptera, so only MP is present. Besides, the nomenclature of body structures proposed in Evans (1966) is mainly followed.

4. Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Cicadomorpha Evans, 1946

Superfamily Cercopoidea Leach, 1815

Family Sinoalidae Wang and Szwed, 2012

Genus *Fangyuania* Chen, Szwed and Wang, gen. nov.

(urn:lsid:zoobank.org:act:BBCBDD3-9B72-47BB-BA41-F89F8AF9A375)

Type species: *Fangyuania xiai* Chen, Szwed and Wang, gen. et sp. nov.; by present designation and monotypy.

Etymology. The generic name is dedicated to Mr. Fangyuan Xia, Director of the Lingpoge Amber Museum in Shanghai, for his contribution to the study of this amber specimen.

Diagnosis. Head about 1.5 times longer than pronotum in mid line. Anterior margin of head with angulate apex. Ocelli on head disc arranged in isosceles triangle with wide base. Tegmen with length/width ratio about 2.8; hypocostal carina distinct, reaching anteroapical angle; costal area and stigmal cell punctate; stem ScP + R about 0.6 of basal cell length; stem CuA forked basad of calval apex. Single lateral anteroventral spine and two lateral anterodorsal spines in row on metatibia.

Fangyuania xiai Chen, Szwed and Wang, gen. et sp. nov.

(urn:lsid:zoobank.org:act:9AD387FA-9987-4BA3-9F59-2E495F249841)

Figs. 1–3

Etymology. The specific name is in honor of Mr. Fangyuan Xia.

Holotype. BA16003, male adult with wings attached to body, right wings at top of body and left tegmen and hind wing slightly outspread, deposited in the Lingpoge Amber Museum in Shanghai, China.

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

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

Description. Measurements (in mm). Body including tegmen in repose length 7.23; head with compound eyes length 1.24, width 1.60; antenna length 0.85; pronotum length 0.63, width 2.22; scutellum length 1.07, width 1.40; fore femur length 0.69, tibia length 0.65, tarsus length 0.35; middle femur length 0.81, tibia length 0.74, tarsus length 0.32; hind femur length 0.81, tibia length 1.52, tarsus length 0.52; apical process of aedeagus length 0.38; tegmen length 5.61, width 2.02.

Head. (Figs. 1, 3A–C). Head with compound eyes narrower than pronotum, anterior margin obtuse angled, with arcuate arms diverging at angle about 140°. Crown extended, depressed in the

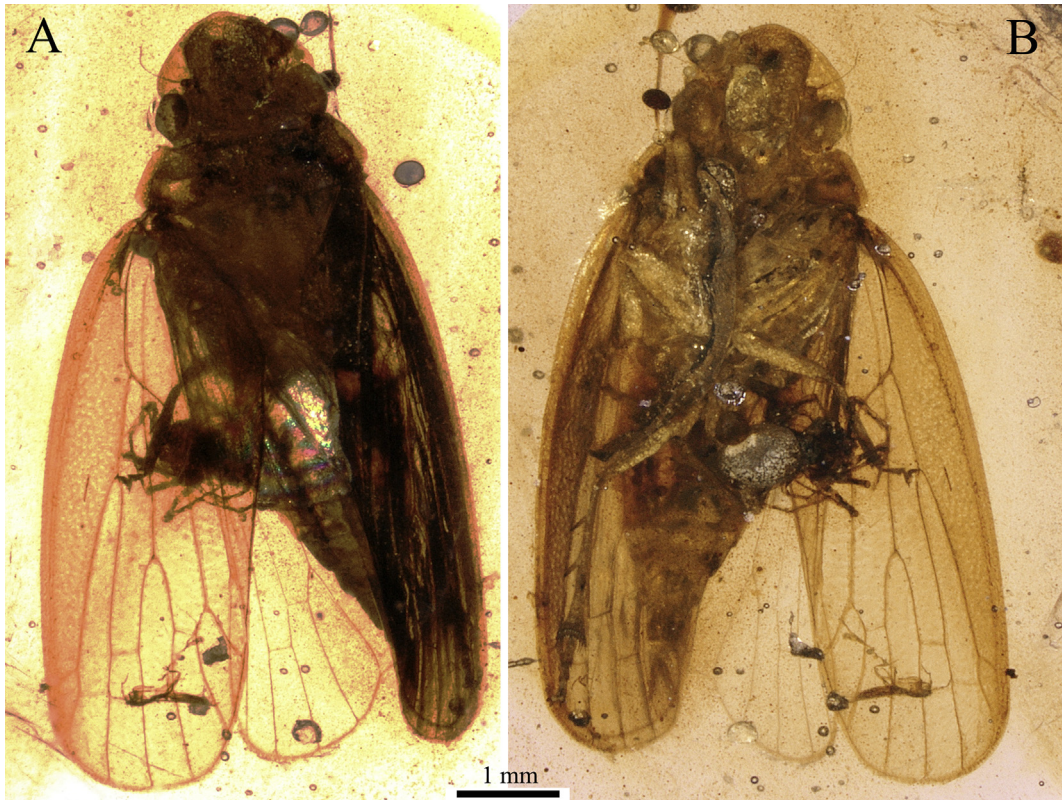


Fig. 1. Photographs of *Fangyuania xiai* Chen, Szwedo and Wang, gen. et sp. nov., holotype. (A), dorsal view; (B), ventral view.

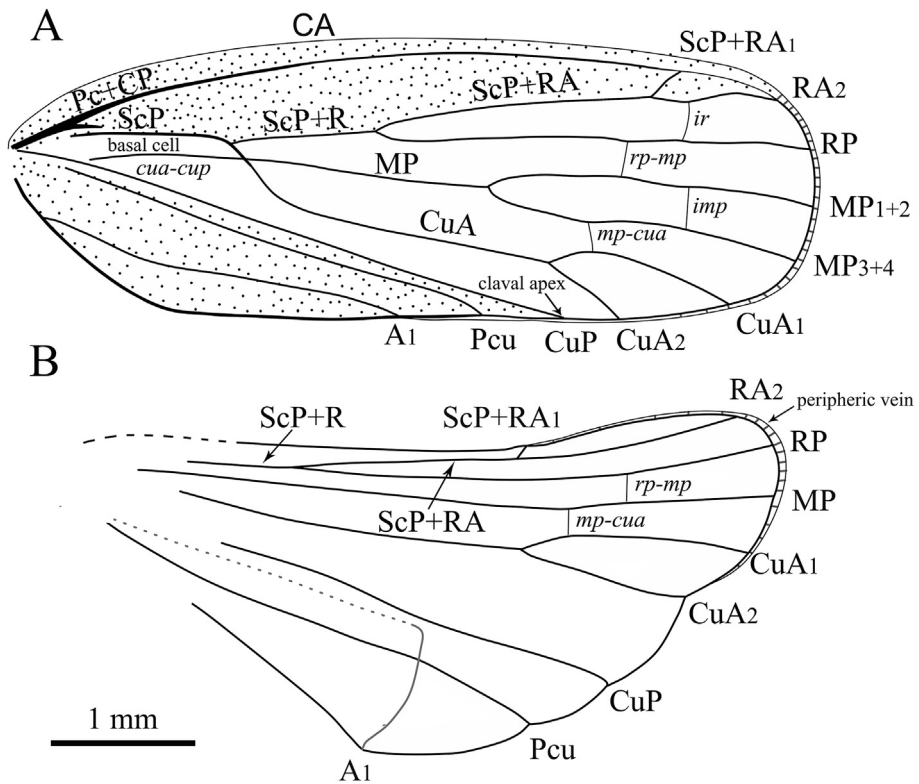


Fig. 2. Line drawings of wings of *Fangyuania xiai* Chen, Szwedo and Wang, gen. et sp. nov., holotype. (A), tegmen; (B), hind wing.

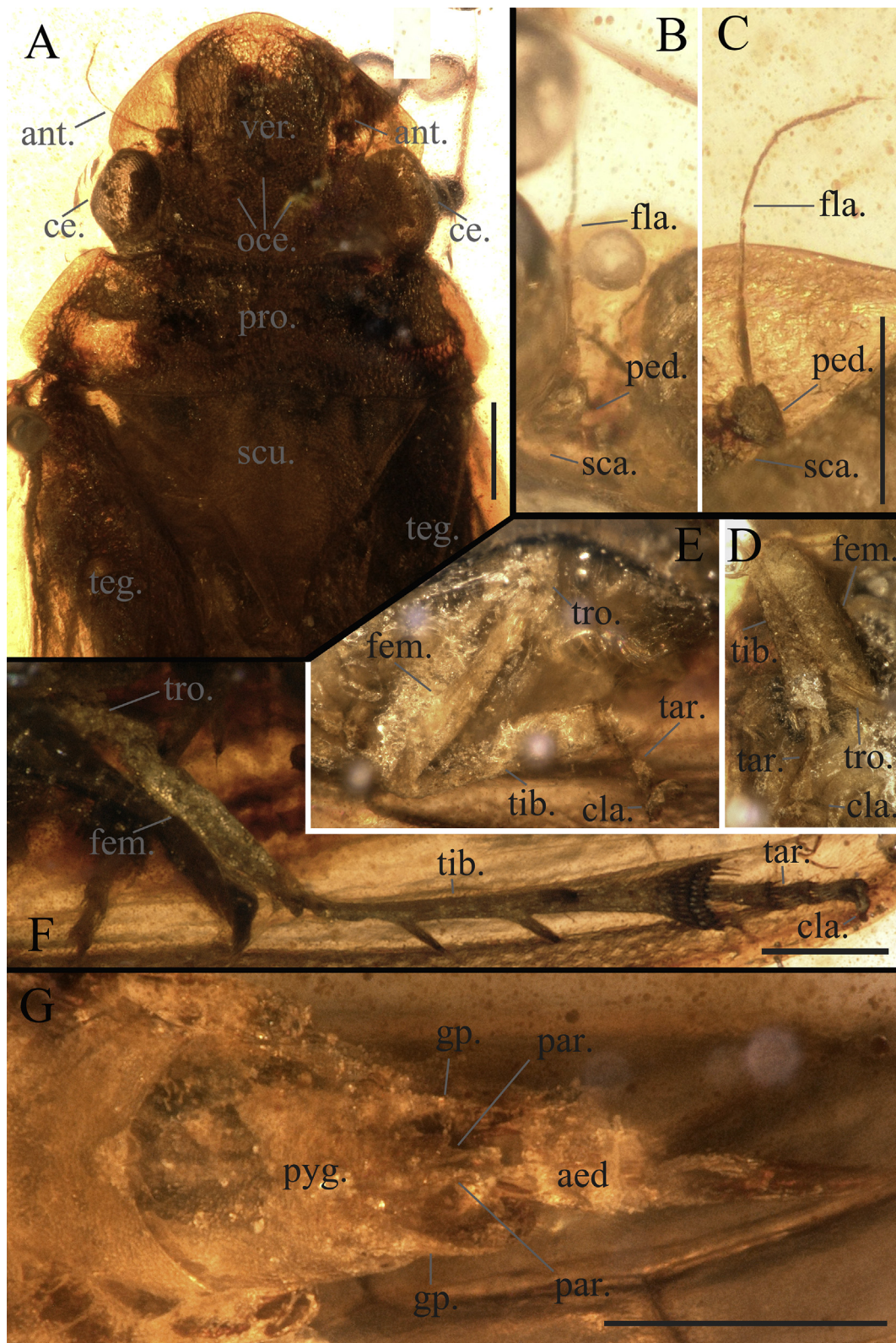


Fig. 3. Details of *Fangyuania xiai* Chen, Szwedo and Wang, gen. et sp. nov., holotype. (A), head and thorax in dorsal view; (B), left antenna; (C), right antenna; (D), right fore leg; (E), right middle leg; (F), right hind leg; (G), pygofer and male genitalia. Symbols: ver., vertex; ant., antenna; ce., compound eyes; oce., ocellus; pro., pronotum; scu., scutellum; teg., tegmen; sca., scape; ped., pedicel; fla., flagellum; tro., trochanter; fem., femur; tib., tibia; tar., tarsus; cla., claw; pyg., pygofer; gp., genital plate; par., paramere; aed., aedeagus. Scale bars = 0.5 mm.

midline, coronal suture absent; tylus delimited by two arcuate lines at level of anterior margins of compound eyes converging anteromedially; disc of crown granulate; compound eyes oval, not distinctly bulging, their line not extending prolongation of margins of head. Ocelli on crown, between compound eyes, distance between lateral ocelli about as distance between ocellus and compound eye, median ocellus slightly smaller.

Thorax. (Figs. 1, 3A, D–F). Pronotum about 3.5 times as wide as long, apparently shorter in mid line than crown, and slightly wider than head with compound eyes, distinctly punctate, with a shallow median groove; anterior margin thickened, nearly straight sinuately concave medially with two lateral concavities; anterolateral angles obtuse; anterolateral margins nearly straight, carinate; lateral angles acute; posterolateral margins slightly sinuous, shorter than anterolateral margins; posterolateral angles extremely obtuse; posterior margin thickened and concave near midline. Mesonotum about 1.9 times as long in midline as pronotum, almost as wide as head with compound eyes, with posterior 1/2 half area of disc with some very shallow transverse grooves and posterior 1/3 area slightly sunkened; a median groove broad. Fore legs with femora strong, with a row of spines on outer margin; tibiae nearly as long as femora, with some setae on surface; tarsi about half as long as femora, basi- and midtarsomere of similar length, apical tarsomere obviously longer; two tarsal claws distinct. Middle legs with femora long and slender; tibiae slightly shorter than femora, with some setae on surface; tarsi about 1/3 as long as femora, with some very long setae, mid- and apical tarsomere of similar length, obviously longer than basitarsomere; two tarsal claws distinct. Hind legs with metafemora long and slender; metatibiae extremely long, about twice as long as femora, with some setae on surface, anteroventral lateral spine at apical 2/3 of metatibia length, anterodorsal row of lateral spines with first spine basad of 1/3 of metatibia length, second basad of 2/3 of metatibia length; apex of metatibia with two rows of a dozen apical teeth with subapical long setae; basimetatarsomere about as long as cumulative length of mid- and apical metatarsomeres; basimetatarsomere and mid-metatarsomere with apical row of five apical teeth with long subapical setae; apical metatarsomere with distinct tarsal claws and wide arolium.

Abdomen. (Figs. 1, 3G). Abdomen flat. Male terminalia with genital plates shorter than lateral lobes of pygofer, triangular, with distinctly acute apex, dark, thickened, with some tiny cilia on outer margin; median incision deeply, triangularly concave. Genital styles elongate, with dark, strong and sharp apical spine (sclerotized?). Aedeagus exposed, with at least two darker and extremely long apical processes.

Tegmina. (Figs. 1, 2). Tegmina exceeding length of body, with length/width ratio about 2.8, slightly curved at base, then almost straight at costal margin; anterioapical angle angulate and posteroapical angle widely angulate; apical margin with narrow and wrinkled peripheric membrane, costal cell and claval area punctate; apex of clavus reaching 0.7 of tegmen length; basal cell about 10 times as long as wide, reaching nearly to 0.3 of tegmen length; cell between costal margin and Pc + CP broad; stem ScP + R leaving basal cell slightly basad of stem MP + CuA, stem ScP + R shorter than basal cell, forked distinctly basad of stem MP forking, at level of vein A1 junction to the claval margin, branch ScP + RA1 shifted distinctly apicad, apicad of apex of clavus level; stem MP forked at level of Pcu junction with claval margin, reaching margin with two terminals; stem CuA curved at base then subparallel to stem MP, forked apicad of stem MP forking, slightly basad of apex of clavus, branch CuA1 curved medially at base, reaching postclaval margin basad of posteroapical angle, branch CuA2 obliquely straight, reaching postclaval margin slightly apicad of claval apex; veinlet ir at level of veinlet imp; veinlet rp–mp slightly apicad of veinlet mp–

cua; all veinlets on membrane apicad of level of claval apex; stigmal cell short, shorter than apical radial cell; cell C1 about 1.64 times as long as cell C3; cell C2 about twice as long as adjoining apical cell; cell C3 lanceolate, slightly longer than cell C5, about 1.4 times as long as adjoining apical cell; cell C5 rhomboid, about 0.55 as long as cell C1.

Hind wing. (Figs. 1, 2) Hind wing membranous, with peripheric vein reaching to terminal CuA1, appendix narrow, wrinkled; apex of hind wing strongly arcuate, posterior margins lobate; anal portion strongly rippled; stem ScP + R forked at very base, terminal ScP + RA1 short, reaching margin at level of wing coupling apparatus; branch RA2 reaching margin slightly basad of wing apex, branch RP reaching margin slightly apicad of wing apex; stem MP single reaching margin slightly basad of wing apex; stem CuA forked at level of ScP + RA1 forking; terminal CuA1 longer than terminal CuA2; margin incised at level of terminal CuA2; branch CuP single, almost straight, with shallow incision at its end, stem Pcu slightly sinusoid, with incision at its terminus; stem A1 straight, anal lobe wide; veinlet rp–mp distinctly apicad of veinlet mp–cua, veinlet mp–cua slightly apicad of stem CuA forking.

5. Discussion

The family Sinoalidae, erected from the latest Middle Jurassic Daohugou Biota, Inner Mongolia of China, is closely related to early Proceropidae and also shares some plesiomorphic characters with ancient Hylacelloidea, likely representing one of distinct diversifications of ancestral Cercopoidea (Wang et al., 2012; Chen et al., 2017). The remarkable new taxon in Cretaceous amber undoubtedly belongs to this family on the following characteristics: ocelli three (one median ocellus and two lateral ocelli); hind tibiae with two rows of strong lateral spines; tegmen with costal area and clavus punctate, apical cell six, Pc + CP long and thicken, almost parallel to costal margin; RA₁ and RA₂ terminally forked; M with two terminal branches.

The new taxon, however, distinctly differs from all known Jurassic sinoalid genera in: Pc + CP far away from costal margin, wide costal cell (much broader than in its Jurassic con-familials); fewer lateral spines in anteroventral and anterodorsal rows, more apical teeth forming double row at metatibia apex; less lobate posterior margin of mesonotum. Some additional apomorphies of *Fangyuania* gen. nov. needing to be pointed are: triangular, broad and thin, carinate suprantennal ledges, concealing bases of antennae, which is the situation different from the Jurassic Sinoalidae as well as in other Mesozoic and modern Cercopoidea (Hamilton, 1990; Wang et al., 2012). Another apomorphy of the new taxon is shortening of pronotum – contrary to Hylacellidae, Proceropidae and modern Cercopoidea, which have a rather enlarged pronotum (Carvalho and Webb, 2005; Hamilton, 2012; Wang et al., 2012; Chen et al., 2015a). The Jurassic Sinoalidae possesses a pronotum with length/width ratio about 2.0 (Wang et al., 2012), but for the mid-Cretaceous genus *Fangyuania* gen. nov., pronotum is extremely short, with length/width ratio up to 3.5.

A striking feature of the new genus is the very long basal cell, with a short common portion of MP + CuA closing it apically. This character, making *Fangyuania* gen. nov. different from other Sinoalidae, is shared with Proceropidae, as well as with other Clypeata–Hylacellidae: 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). This character seems to be a plesiomorphic condition of the new genus. Another feature strictly related to the former is a basally strongly curved CuA – such a situation is present as well among Hylacellidae: Vietocyclinae and Proceropidae. The hind wing of

Fangyuania gen. nov. is very similar to that of the Jurassic Hylicellidae, Procercopidae and Sinoalidae regarding venation pattern, but clearly differs from the latter in having a reduced peripheral membrane at the wing tip. Another interesting feature presented by *Fangyuania* gen. nov. is free portion of ScP at the very base of basal cell. This structure is present in a much more distal position in modern Cercopoidea (e.g. noted as Sc in Anufriev & Emeljanov 1988, “ventral flange” of Hamilton, 2012). This feature seems also to be a plesiomorphic condition, shared by the above described taxon with representatives of Procercopidae.

The Sinoalidae were recorded exclusively from the Jurassic in northeastern China before the present study. The contemporaneous Procercopidae was distributed very widely in Eurasia. This family is recorded from Early Jurassic to Early Cretaceous strata, replaced with modern Aphrophoridae, and, however, is virtually unknown from late Cretaceous to early Paleogene deposits (Shcherbakov & Popov, 2002). This find extends the duration of Sinoalidae for more than 60 million years from the middle Jurassic to the earliest Late Cretaceous. It also marks the first record of Sinoalidae from southern Asia, adding a significant distribution to the family Sinoalidae.

Some novel and unique body characteristics, and a mixture of plesiomorphic and apomorphic features present in *Fangyuania* gen. nov. indicate that early Cercopoidea diversified rapidly and multidimensionally in the Mesozoic. There are several open questions regarding this radiation, as host plant associations of these early froghoppers, nymphal stages and nymphal development of these insects, and reasons for their extinction. It could be hypothesized that sinoalids fed on some gymnosperms, being xylem-feeders as other early Clypeata. Competition with other xylem feeding groups in the Jurassic and Cretaceous shaped their evolutionary ways and lack of available host plants and a high degree of feeding specialization (and maybe also endosymbiotic associations) might have led to their failure in competition with modern froghopper lineages. Most recent species of Cercopoidea feed on sap from herbaceous plants, but some feeding on trees; their nymphs often feed on roots of plants, mostly angiosperms. Shifting to angiosperms which have rapidly evolved since the mid-Cretaceous could be the source of success for modern froghopper lineages, but at the same time expansion of newly emerging angiosperms and extinction of ancient gymnosperms might have resulted extinction of Mesozoic Clypeata groups as Procercopidae, Sinoalidae, Cercopionidae and Hylicellidae.

6. Conclusions

Burmese amber, beautiful and versatile, has a unique capacity to preserve fragile life, opening a special window into the past. Burmese amber comes from the time of great biotic reorganization of the biosphere in the mid-Cretaceous, giving the last glimpse of various Mesozoic insects and other animals. The find presented above is an important contribution to our knowledge of evolutionary and morphological traits of Cercopoidea and Clypeata as well. *Fangyuania xiai* gen. et sp. nov., provides some features whose combination has never previously been observed in the Sinoalidae, adding valuable information to our knowledge of taxonomic diversity and morphological disparity of Mesozoic Sinoalidae. Additionally, this find greatly extends the duration of Sinoalidae for more than 60 million years and its geographic distribution.

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