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Short communication

A remarkable new sinoalid froghopper with probable disruptive colouration in mid-Cretaceous Burmese amber (Hemiptera, Cicadomorpha)

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ABSTRACT

The Mesozoic froghopper family Sinoalidae was reported from the uppermost Middle–lowermost Upper Jurassic Daohugou Biota and coeval strata of northeastern China, and mid-Cretaceous Kachin amber of northern Myanmar. Herein, a remarkably new sinoalid froghopper, *Ornatiala amoena* Chen, Wang and Zhang, gen. et sp. nov., is reported from Kachin amber. The new taxon is distinctly different from all known sinoalids in possessing the following characters: the head strongly produced anteriorly, slightly longer than wide; the pronotum relatively long, with length/width ratio about 0.6; the tegmen with post-claval margin beyond termination of CuP strongly convex, making tegmen widest near termination of CuA_2, and a long stalk ScP+R+MP present. Additionally, this new remarkable sinoalid bears a novel prominent colouration pattern (probable disruptive colouration) on tegmina, further confirming that this froghopper group was likely to be undergoing high morphological and ecological diversification in the mid-Cretaceous.

1. Introduction

The froghopper Sinoalidae is an extinct family recently erected from the well-known uppermost Middle-lowermost Upper Jurassic Daohugou Beds and coeval strata of northeastern China (Wang et al., 2012). This froghopper group is with a mixture of ancestral features shared with Hylicelloidea and Procercopidae and some unique autapomorphies (Wang et al., 2012; Chen et al., 2018, 2019b). Sinoalidae is distinctly different from the other two consuperfamilial Mesozoic families Procercopidae (widely distributed in the Lower Jurassic to Lower Cretaceous of Eurasia; Handlirsch, 1906–1908, 1939; Hong, 1982, 1983; Shcherbakov and Popov, 2002; Wang and Zhang, 2009a; Chen et al., 2015a, b) and Cercopionidae (exclusively recorded in the Lower Cretaceous Crato Formation of Brazil; Hamilton, 1990) in a series of morphological features: tegmina with costal area and clavus more sclerotized and punctate, hindwings without complete submarginal vein, and metatibiae with two rows of lateral spines.

In Wang et al. (2012), Sinoalidae originally comprised 6 species within 5 genera (*Luanpingia* Hong, 1983,?*Hebeicercopis* Hong, 1983, *Huabeicercopis* Hong, 1983, *Sinoala* Wang and Szwedo, 2012, and *Jiania* Wang and Szwedo, 2012), exclusively from Jurassic deposits of northeastern China (Table 1). Subsequently, one new species attributed to *Luanpingia* Hong, 1983 and two additional genera (*Shufania* Chen, Zheng, Wei and Wang, 2017 and *Stictocercopis* Fu and Huang, 2018) were erected from the Daohugou beds (Chen et al., 2017; Fu et al., 2017; Fu and Huang, 2018). Very recently, two new monospecific genera (*Fangyuania* Chen, Szwedo and Wang, 2018 and *Jiaotouia* Chen and Wang, 2019a, 2019b) assigned

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Table 1
Geographical and stratigraphic distribution of the Mesozoic family Sinolidae. J2-3: Middle to Upper Jurassic; K2: Upper Cretaceous.

Horizon	Locality	Taxon and Reference
Cenomanian (K2)	Hukawng Valley, Kachin, Myanmar	*Fangyuania xiai* Chen, Szwedo and Wang, 2018; in Chen et al., 2018 *Jiaotouia minuta* Chen and Wang, 2019, in Chen et al., 2019b *Ornatiala amoena* gen. et sp. nov.; this paper
Jiulongshan Formation, Callovian-Oxfordian (J2-3)	Xiaofanzhangzi, Chengde, China	*Chengdecercopis xiaofanzhangziensis* Hong, 1983; in Hong, 1983
	Zhouyingzi, Luangping, China	*Huabeicercopis yangi* Hong, 1983; in Hong, 1983 *?Hebeicercopis triangulata* Hong, 1983; in Hong, 1983 *Luanpingia longa* Hong, 1983; in Hong, 1983
	Daohugou, Ningcheng, China	*L. daohugouensis* Fu, Cai and Huang, 2017; in Fu et al., 2017 *Sinoala parallelivena* Wang and Szwedo, 2012; in Wang et al., 2012 *Jiania crebra* Wang and Szwedo, 2012; in Wang et al., 2012 *J. gracila* Wang and Szwedo, 2012; in Wang et al., 2012 *Shufania hani* Chen, Zheng, Wei and Wang, 2017; in Chen et al., 2017 *Stictocercopis wuhuaensis* Fu and Huang, 2018; in Fu and Huang, 2018

to Sinoalidae were reported from mid-Cretaceous Kachin amber in northern Myanmar, greatly extending the duration and geographical distribution of this froghopper lineage and also providing new information for its morphological diversification (Chen et al., 2018, 2019b).

We herein describe and illustrate the third sinoalid froghopper, *Ornatiala amoena* gen. et sp. nov., in Burmese amber. The new genus, with prominent colour pattern on the tegminal surface (probable disruptive colouration) as well as some other unique morphological traits, further confirms that this extinct insect group was likely highly diversified in morphology and ecology in the mid-Cretaceous.

2. Material and methods

The new fossil sinoalid froghopper, trapped in the a yellow and transparent amber piece, was from the Hukawng Valley of Kachin Province in northern Myanmar (Kania et al., 2015: fig. 1). Amber affords exceptional three-dimensional preservation of insects as well as other tiny organisms (Chen et al., 2016a), and the Kachin amber biota is now recognized as a significant window to the Cretaceous world (Cruickshank and Ko, 2003; Poinar et al., 2008; Kania et al., 2015; Chen et al., 2019a). The age of Burmese amber is bio-stratigraphically considered to be mid-Cretaceous (e.g., Cruickshank and Ko, 2003; Grimaldi et al., 2005; Ross et al., 2010) and from earliest Cenomanian (98.79 ± 0.62 Ma) based on a recent U–Pb zircon dating study (Shi et al., 2012).

The fossil specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP169680), and was examined, photomicrographed and measured using the VHX 5000 digital microscope platform, with incident and transmitted light used simultaneously. Image-editing software CorelDraw X7 and Adobe Photoshop CS6 were used to prepare line drawings. The venational terminology used herein follows Bourgoin et al. (2015) as in Chen et al. (2018), which was slighted modified from Nel et al. (2012).

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:9772FBA5-9C6A-447A-BDC4-6DB504AD783B.

To infer the phylogenetic position of the new taxon, a cladistic analysis of species within the family Sinoalidae was executed using maximum parsimony analysis (MP) in PAUP* (Swofford, 2003). The morphological matrix was modified from Chen et al. (2019b), with some characters and states added: 1), new state 3 (extremely extended, longer than wide) in character 1 (shape of crown); 2), new state 2 (expanded, almost as long as wide) in character 6 (shape of pronotum); 3), new state 3 (very long) in character 13 (length of common stalk of ScP+R+RA); 4), new character 33 and two states(post-claval margin beyond termination of CuP: 0, smooth; 1, strongly convex); 5), new character 34 and two states (bifurcation of MP: 0, basad of claval apex; 1, slight distad of claval apex). In the matrix, missing data are coded with question marks and inapplicable data are coded with dashes (Table 2). For MP analysis, heuristic searches were executed for 1000 replicates with TBR branch swapping. Non-parametric bootstrap analysis (BS) with 1000 replicates was performed to assess nodal reliabilities. Character mapping based on the 50% majority-rule consensus tree was performed in WinClada ver. 1.00.08 (Nixon, 2002).

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758.
Suborder Cicadomorpha Evans, 1946.
Superfamily Cercopoidea Leach, 1815.
Family Sinoalidae Wang and Szwedo, 2012 in Wang et al., 2012.

Genus ***Ornatiala*** Chen, Wang and Zhang, gen. nov.
(urn:lsid:zoobank.org:act:037F977C-D73A-4373-BB46-9AD4497ABF96).
Type species: *Ornatiala amoena* Chen, Wang and Zhang, gen. et sp. nov.; by present designation and monotypy.

Etymology. The generic name is from Latin words '*ornate*' (elegant) and '*ala*' (wing), referring to the attractive colour pattern on the tegmina.

Diagnosis. Head relatively long, with length/width ratio about 1.1: 1; crown strongly produced anteriorly, with anterior margin sharply angled medially; coronal margin not expanded and obviously concave before eyes; compound eyes distinctly produced. Thorax with pronotum relatively long, widest at its lateral angles, with length/width ratio about 0.6; mesonotum relatively small. Tegmen with surface darkly pigmented in about basal 1/3rd, light-coloured for middle 1/3rd area, and darkly pigmented for in apical 1/3rd with apical cell between two terminal branches of RA much darker; clavus and costal area with basal parts regularly covered with some distinct granules; tegminal apex somewhat truncate; postclaval margin beyond termination of CuP strongly convex, making tegmen widest near termination of CuA_2; costal area with apex near tegminal apex; basal cell somewhat lance-shaped; cell between CA and Pc+CP long, reaching termination of RA_1; cross-vein *cua-cup* connecting R+MP+CuA just at bifurcation of the latter; a relatively long stalk ScP+R+MP present; MP branching basad of bifurcation of CuA.

Table 2
Morphological character state matrix of 34 characters included in the phylogenetic study. The“?” and “–”denote that the state is unknown or inapplicable, respectively.

Taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Vietocylca peregrina	?	?	?	?	?	?	?	?	0	0	0	–	0	0	0	–	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Jurocercopis grandis	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	–	0	0	0	0	1	0	0	0	0	0	0	0	?	?	1	1	0	0
Stictocercopis wuhuaensis	0	0	0	1	1	1	1	?	1	1	0	–	0	0	0	–	2	0	0	1	0	0	0	0	1	0	0	1	0	?	1	0	0	0
Chengdecercopis xiaofanzhangziensis	0	0	0	?	?	1	?	?	?	0	0	–	0	?	?	?	2	0	?	1	0	0	0	{01}	?	0	?	1	?	?	?	?	0	0
Huabeicercopis yangi	1	0	0	?	1	1	?	?	?	0	1	0	0	1	1	0	2	1	0	1	0	0	0	2	1	1	0	0	?	?	?	?	0	0
Luanpingia longa	?	?	?	?	?	?	?	?	?	0	1	0	0	0	1	0	2	1	1	1	0	1	–	–	1	1	1	1	?	?	?	?	0	0
Luanpingia daohugouensis	1	0	0	1	1	1	1	1	2	0	1	0	0	0	1	0	2	1	0	1	0	0	0	2	1	1	1	1	?	?	?	?	0	0
Sinoala parallelivena	1	0	0	1	1	1	1	1	2	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	2	–	0	0
Jiania crebra	1	0	0	1	1	1	1	2	2	0	1	0	2	0	1	0	2	1	0	1	0	0	0	2	1	1	0	0	?	?	?	?	0	0
Jiania gracila	1	0	0	1	1	1	1	1	2	0	1	0	2	0	1	0	2	1	0	1	0	0	0	2	1	1	0	0	0	1	2	–	0	0
Shufania hani	?	?	?	?	?	?	?	?	2	0	1	0	1	0	1	0	2	1	0	1	1	0	1	1	1	1	0	0	?	?	?	?	0	1
Fangyuania xiai	2	1	1	1	1	1	1	?	2	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	2	2	0	0	1	1	2	–	0	0
Jiaotouia burmitica	2	2	0	1	1	1	1	?	2	0	2	1	0	0	1	0	0	1	0	0	0	2	0	0	2	2	0	0	0	1	2	–	0	1
Ornatiala amoena	3	2	0	1	1	2	1	?	2	0	1	0	3	0	1	0	2	1	0	1	0	0	0	0	2	2	0	0	0	?	2	–	1	0

Ornatiala amoena Chen, Wang and Zhang, gen. et sp. nov. (urn:lsid:zoobank.org:act:58223D4B-0E92-47AF-B154-B134497673CE).
Figs. 1-3, 4A, 5

Etymology. The specific epithet derives from the Latin '*amoena*' (lovely), referring to the attractive nature of the taxon.
Holotype. NIGP169680, 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. As for genus as it is the only so far included species.
Description. Body including wings in repose 6.95 mm long.
Head. (Figs. 1-2). Length about 1.01 mm, width with compound eyes about 0.89 mm, length/width ratio about 1.1. Crown strongly produced anteriorly; anterior margin sharply angled medially; disc with granules. Coronal margin not expanded and obviously concave before eyes. Ocelli obscure. Compound eyes large, distinctly produced. Postclypeus long and broad, somewhat depressed; transverse grooves not distinct. Anteclypeus oval, with a median carina. Rostrum with labium stout, extending just beyond procoxae, but stylet fascicle much longer, reaching to mesocoxae. Antenna with antennal pit shallow; scape shorter but thicker than pedicel; flagellum long, with basal three segments long, others not well preserved with joints between segments obscure.
Thorax. (Figs. 1, 2A, B, 3). Pronotum relatively long, about 0.92 mm long, about 1.57 mm wide, widest at its lateral angles, with length/width ratio about 0.6; disc granulate; anterior margin almost straight; slightly shorter than head; anterolateral margins long and straight; lateral angles sharp; posterolateral margins straight, about 2/3rds of anterolateral margin length; posterior margin slightly shorter than anterior margin, smoothly concave. Mesonotum small, about 0.89 mm long, and 0.91 mm wide. Prothoracic legs with coxae and trochanters thick; femora slender, with distinct ridges; tibiae much more slender than femora, almost as long as the latter, densely covered with tiny setae; tarsi with apical tarsomere enlarged apically and longer than basi- and midtarsomere, tarsal claws large. Mesothoracic legs with coxae apparently longer than trochanters; femora slender, with ridges; tibiae slightly longer than femora, very slender, densely covered with tiny setae; tarsi with apical tarsomere much longer than basi- and midtarsomere, tarsal claws extremely large. Metathoracic legs with coxae thick and cylindrical; trochanters thick apically; femora extremely slender basally, then becoming thicker; tibiae much longer than femora, slender, but inflated apically, densely covered with setae; lateral spines arranged in two rows (one and two in number for each row); just one row of apical teeth (or two rows with basal one obscured?), totally ten in number; tarsi with basitarsomere much longer than mid- and apical tarsomeres.
Tegmen. (Figs. 1, 4A). Length about 5.41 mm, width about 1.89 mm, with length/width ratio 2.9. Surface with distinct colour pattern; approximately basal 1/3rd darkly pigmented, middle 1/3rd area light-colored, and apical 1/3rd area darkly pigmented with apical cell between two terminal branches of RA much darker. Clavus and costal area more punctate and sclerotized than other parts, with basal parts (darkly pigmented areas) with some regular distinct granules. Tegminal apex somewhat truncate; costal margin smoothly arched at base, then almost straight; claval margin strongly arched; post-claval margin beyond termination of CuP strongly convex, making tegmen widest near termination of CuA_2. Costal area narrow and extremely long, with apex near tegminal apex; clavus obviously wider than costal area, with apex apparently basad of that of costal area. Basal cell long and narrow with apex sharp, somewhat lance-shaped, about 0.3 of tegminal length. Cell

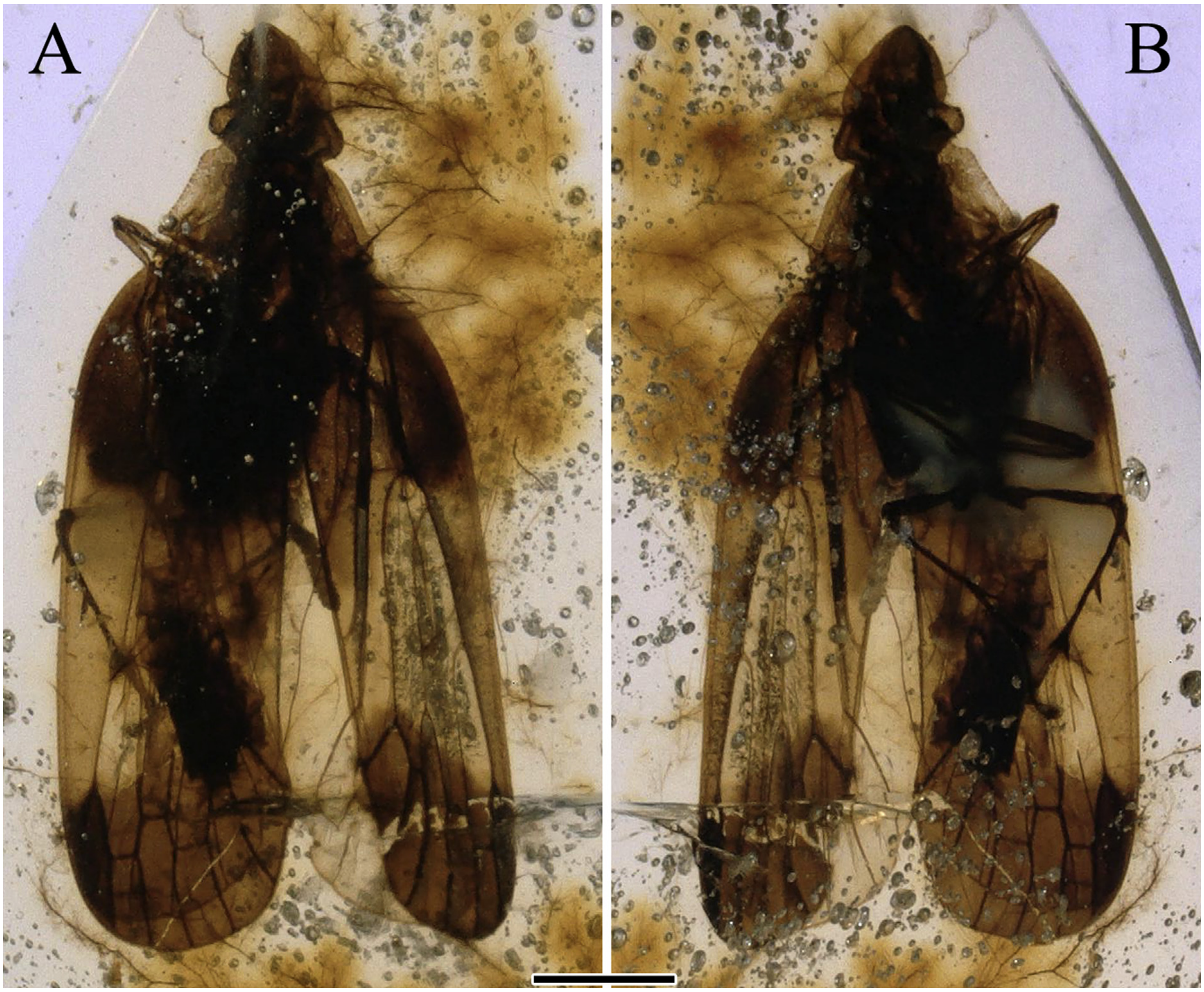

Fig. 1. Photographs of the holotype of *Ornatiala amoena* Chen, Wang and Zhang, gen. et sp. nov. (A), dorsal view; (B), ventral view. Scale bar = 1 mm.

between CA and Pc+CP long, reaching termination of RA_1. ScP with independent part almost as long as stem ScP+Pc+CP, running to and then fusing with R+M+CuA in basal 1/3rd of basal cell. R+MP+CuA curved, branching into ScP+R+MP and CuA at about basal 0.3 of tegminal length. Crossvein *cua-cup* connecting R+MP+CuA just at bifurcation of latter. A relatively long stalk ScP+R+MP present, forking into ScP+R and MP at about basal 0.35 of tegminal length. ScP+R branching into ScP+RA and RP at about basal 0.55 of tegminal length and almost as long as ScP+RA. RA with two terminal branches; RA_2 connected to RP by crossvein *ir*. RP slightly sinuous, connected to MP_{1+2} by crossvein *rp-mp*. Stem MP smoothly curved at base, then nearly straight, branching into MP_{1+2} and MP_{3+4} at about basal 0.64 of tegminal length. Crossveins *imp* and *mp-cua* present. Stem CuA strongly curved at base, then nearly straight, branching into CuA_1 and CuA_2 basad of claval apex; CuA_1 much longer than CuA_2, somewhat geniculate at connection with crossvein *mp-cua*. CuP slightly sinuous, then nearly straight. Pcu obviously curved apcially. A_1 relatively short, strongly curved apically.

Hindwing. (Figs. 1, 4A). Distinct outer membrane absent. Stem R long, much longer than RA and RP, and the latter two almost of equal length. MP with a single terminal branch, connected to RP by crossvein *rp-mp*. CuA bifurcating into CuA_1 and CuA_2 apicad of bifurcation of R; CuA_1 much longer than CuA_2, and connected to MP by crossvein *mp-cua*.

4. Results of phylogenetic analyses

The maximum parsimony analysis yieled 48 most parsimonious trees, with the following characteristics: tree length = 55, consistency index (CI) = 0.891 and retention index (RI) = 0.842. The 50% majority consensus tree is shown in Fig. 6, with characters mapped on and bootstrap support values labelled. This tree is generally same as the MP tree in Chen et al. (2019b). The monophyly of the Sinoalidae was recovered and significantly supported (BS: 86; 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 (Clade I; 66; 28: 1). The remaining sinoalids constituted a monophyletic lineage with high BS value (86) and a series of synapomorphies (11: 1, 15: 1, 18: 1, 31: 2). The remaining taxa from the Middle to Upper Jurassic of northeastern China formed the independent Clade II, but with poor support. The Cretaceous *Fangyuania xiai*, *Jiaotouia minuta* and *Ornatiala amoena* gen. et sp. nov. were recovered as a well-supported monophyletic group (Clade III: 73; 2: 2, 25: 2), with the new taxon occupying a

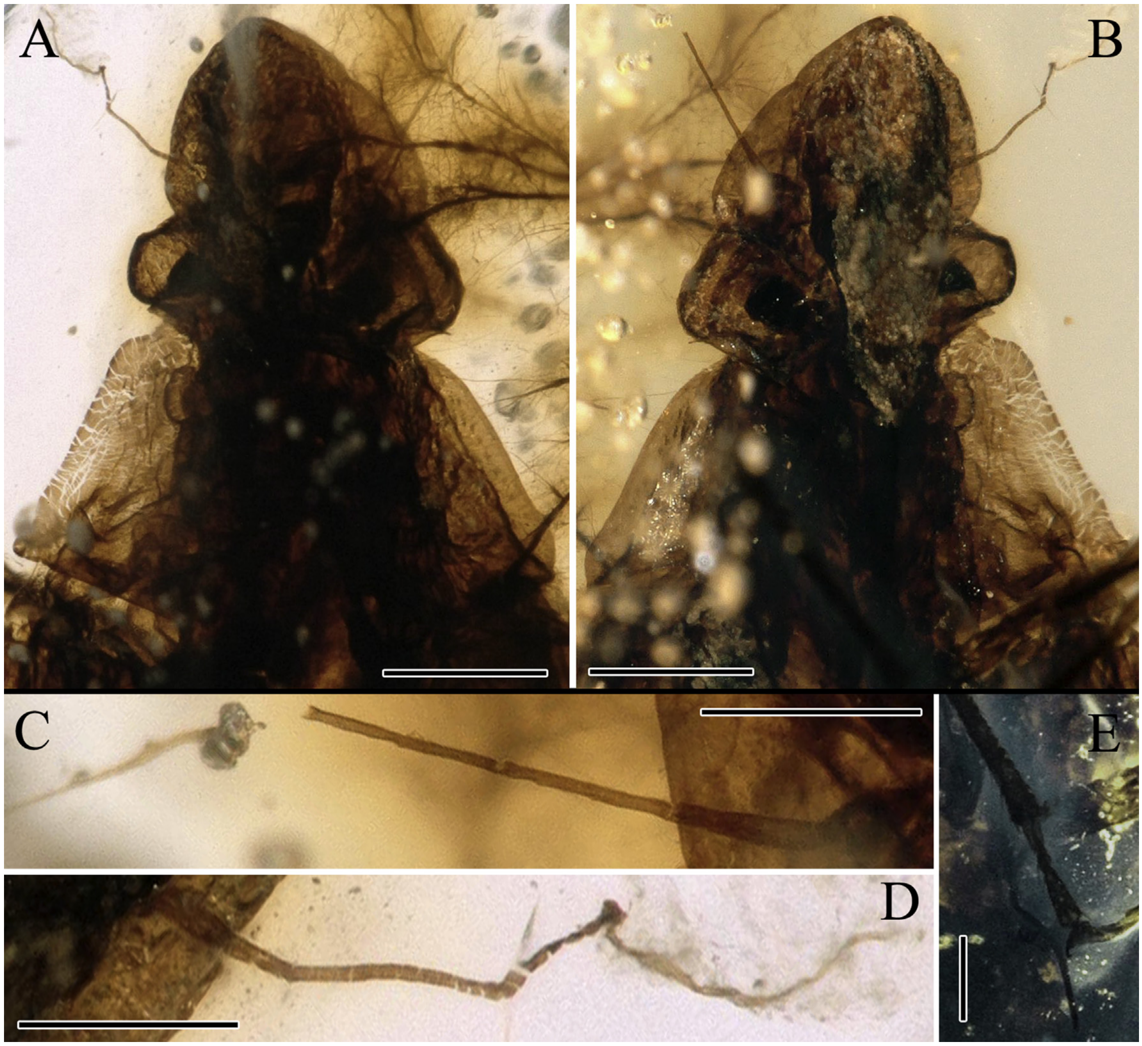

Fig. 2. Head and pronotum of *Ornatiala amoena* Chen, Wang and Zhang, gen. et sp. nov. (A), dorsal view; (B), ventral view; (C), enlarged right antenna; (D), enlarged left antenna; (E), rostrum. Scale bars = 0.5 mm (A, B) and 0.2 mm (C–E).

basal position and displaying three synapomorphic traits (6: 2, 13: 3, 33: 1).

5. Discussion

Sinoalidae, as one of the early families within Cercopoidea, shares some plesiomorphic traits similar to ancient Clypeata and con-superfamilial Procercopidae, and also possesses some unique morphological features (Wang et al., 2012; Fu et al., 2017; Chen et al., 2017, 2018, 2019b; Fu and Huang, 2018). *Ornatiala* gen. nov. erected herein from the mid-Cretaceous Kachin amber undoubtedly belongs to Sinoalidae on the following characters: postclypeus wide; hind tibia with two rows of lateral spines; tegmina with costal area and clavus more sclerotized and remaining parts membranous, MP with two terminal branches and crossvein *imp* present; hindwing with stem ScP+R long and MP un-branched (Wang et al., 2012).

With 13 species attributed to 11 genera (Hong, 1983; Wang et al., 2012; Chen et al., 2017, 2018, 2019b; Fu et al., 2017; Fu and Huang, 2018; this study), Sinoalidae is now the most taxonomically diverse family at the genus level among the three Mesozoic froghopper families (Procercopidae, Cercopionidae and Sinoaldiae). Besides, the known morphological diversity of this extinct insect group is also very high: according to the phylogenetic reconstruction based on 34 characters of body structures, tegmina and hindwings presented herein (Fig. 6), three groups with distinct morphological features were revealed within this family. Taxa from the Middle to Upper Jurassic of northeastern China can be divided to two groups: the two genera *Stictocercopis* and *Chengdecercopis*, possessing tegmina with Pc+CP short, RA and MP multi-branched, and hindwings with MP two-branched, lack derived traits and thus are likely representatives of earlier separated sinoalid lineage; the remaining ones (*Huabeicercopis*, *Luanpingia*, *Sinoala*, *Jiania*, and *Shufania*) were revealed as a sister group of Cretaceous sinoalids from Burmese amber (*Fangyuania* and *Jiaotouia*). The three Cretaceous sinoalid genera constituted a monophyletic lineage with a series of apomorphies. *Ornatiala* gen. nov. described herein remarkably differs from primitive *Stictocercopis* and *Chengdecercopis* in bearing tegmina and hindwings with terminal longitudinal veins reduced in number (R and MP two-branched on tegmina and MP un-branched on hindwings). Besides, the new genus shares a series of common characters with sinoalids in other Burmese amber (e.g., crown extended anteriorly and angled in the middleand tegmina with apex of costal area distad of claval apex), which are distinguishable from the remaining taxa from the Middle to Upper Jurassic of northeastern China.

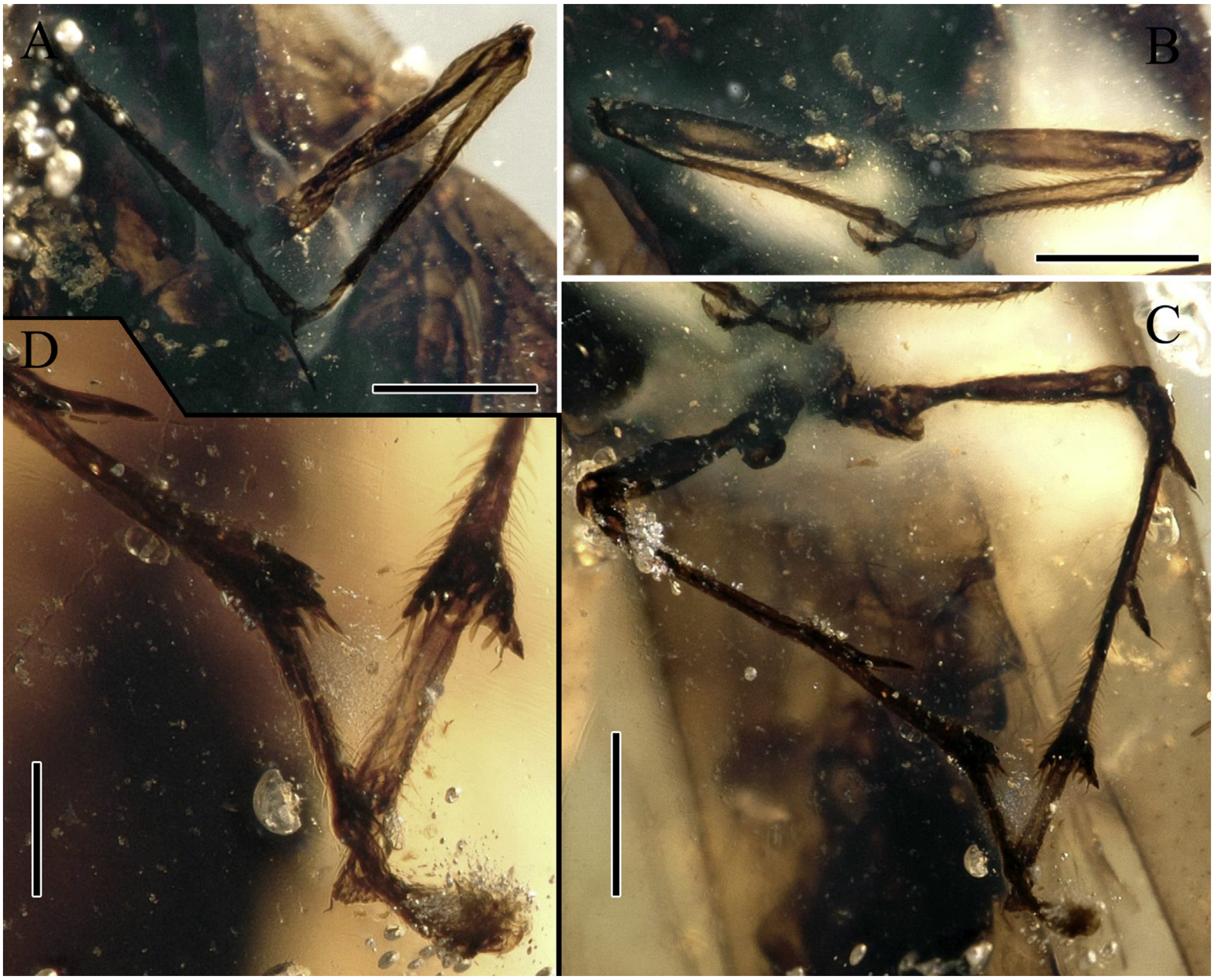

Fig. 3. Legs of *Ornatiala amoena* Chen, Wang and Zhang, gen. et sp. nov. (A), prothoracic legs; (B), mesothoracic legs; (C), metathoracic legs; (D), enlarged metatarsi and apical metatibiae. Scale bars = 0.5 mm (A–C) and 0.2 mm (D).

Up to now, only two monospecific genera (*Fangyuania* and *Jiaotouia*) assigned to Sinoalidae have been recorded in mid-Cretaceous Burmese amber (Chen et al., 2018, 2019b), *Ornatiala* gen. nov., as the third genus, reveals some new unique morphological traits within Sinoalidae. According to our phylogenetic analysis, *Fangyuania* and *Jiaotouia* constituted a monophyletic clade with moderate support (77; 17: 0; 20: 0), and the new genus was recovered as is sister lineage (Fig. 6). The new genus shares some common derived characteristics with the other two genera in Burmese amber as mentioned above, but some novel features confirm its validity at the genus level: head long (slightly longer than wide vs. head with length/width ratio well below 1: 1 for *Fangyuania* and *Jiaotouia*); pronotum relatively long (length/width ratio about 0.6: 1 vs. pronotum extremely shortened for the two known Burmese genera); tegmina with distinct colour pattern (vs. almost colourless for the two above genera), postclaval margin beyond termination of CuP strongly convex, making tegmen widest near termination of CuA_2 (vs. postclaval margin straight for the two above genera), and a relatively long stalk ScP+R+MP present (vs. a relatively long stalk MP+CuA present for the two above genera). The new genus shows another striking feature in the tegmen having the basal cell narrow, somewhat lance-shaped, without MP+CuA (or just CuA) closing it apically, which is similar to that of its con-familial Jurassic relatives, but quite different from that of *Fangyuania* and *Jiaotouia*. The latter bear tegmina with basal cell relatively broad, with a short common portion of MP+CuA closing it apically, similar to Procercopidae, other Clypeata-Hylicellidae: Vietocyclinae as well as early Tettigarctidae (e.g., Becker-Migdisova, 1962; Shcherbakov, 1988; Wang and Zhang, 2009b; Chen et al., 2015a, b; 2016b; Chen and Wang, 2016; see Chen et al., 2018).

Ornatiala gen. nov. bears a shortened rostrum with labium stout, extending just beyond the procoxae, but the stylet fascicle is longer, reaching to the mesocoxae (Figs. 2E, 5B), similar to that of *Jiaotouia* (Fig. 4A in Chen et al., 2019b). In contrast, their Jurassic relatives possess a much longer rostrum, extending to the metacoxae, e.g., *Sinoala parallelivena* Wang and Szwedo, 2012, *Jiania crebra* Wang and Szwedo, 2012, *Jiania Gracila* Wang and Szwedo, 2012, *Sticto-cercopis wuhuaensis* Fu and Huang, 2018, and *Luanpingia daohu-gouensis* Fu, Cai and Huang, 2017 (Wang et al., 2012; Fu et al., 2017; Fu and Huang, 2018). The clade Clypeata (Cercopoidea, Cicadoidea and Membracoidea *s.l.*, and their extinct ancestral group Hylicelliodea) is commonly xylem-feeding, with a greatly inflated frontoclypeus and a long rostrum (Shcherbakov and Popov, 2002; Wang and Zhang, 2009a; Chen et al., 2016b). The known Cretaceous sinoalids, with a relatively short rostrum and depressed postclypeus similar to some modern cicadellid groups, probably fed on thinner twigs and branches. It is striking that the rostrum of the Cretaceous sinoalids bears a stout labium with stylet fascicle distinctly exceeding it, remarkably different to all extinct and living

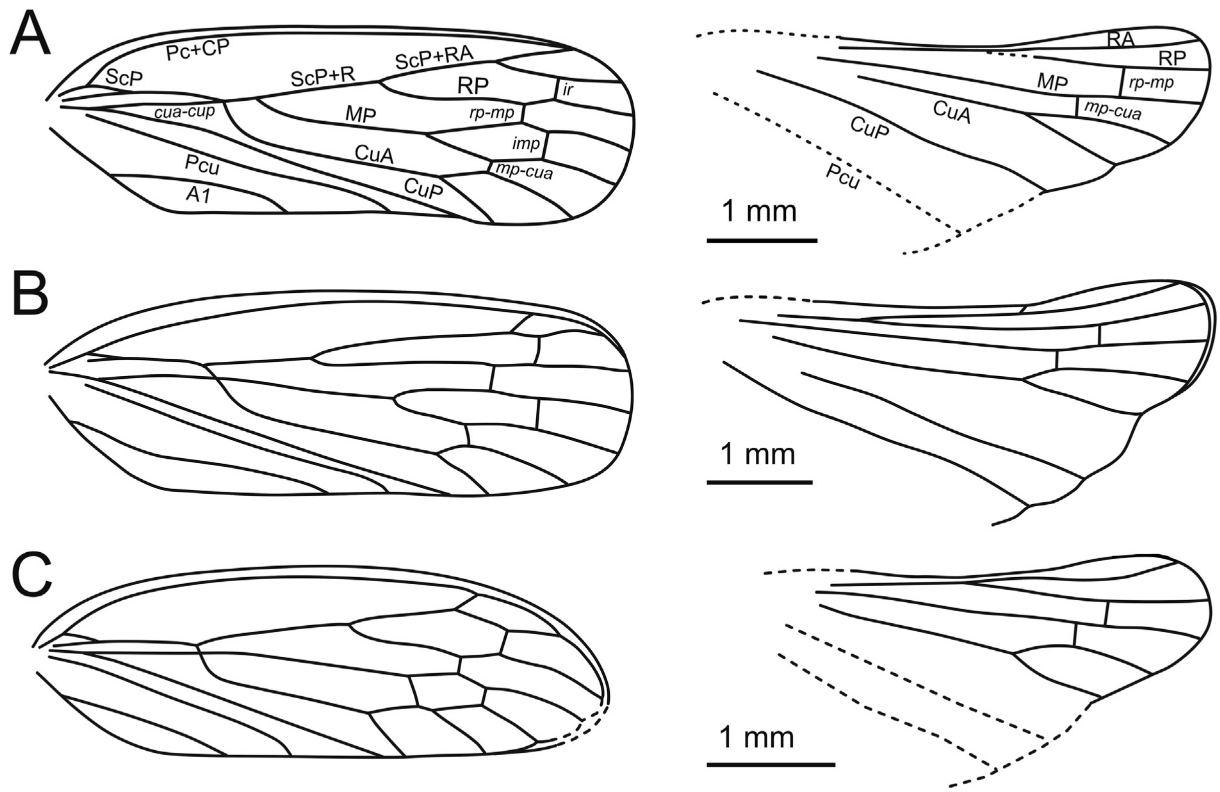

Fig. 4. Line drawings of wings of Sinoalidae in Burmese amber. (A), *Ornatiala amoena* Chen, Wang and Zhang, gen. et sp. nov., with colour pattern of tegmen shown; (B), *Fangyuania xiai*; (C), *Jiaotouia minuta*. All to scale bars.

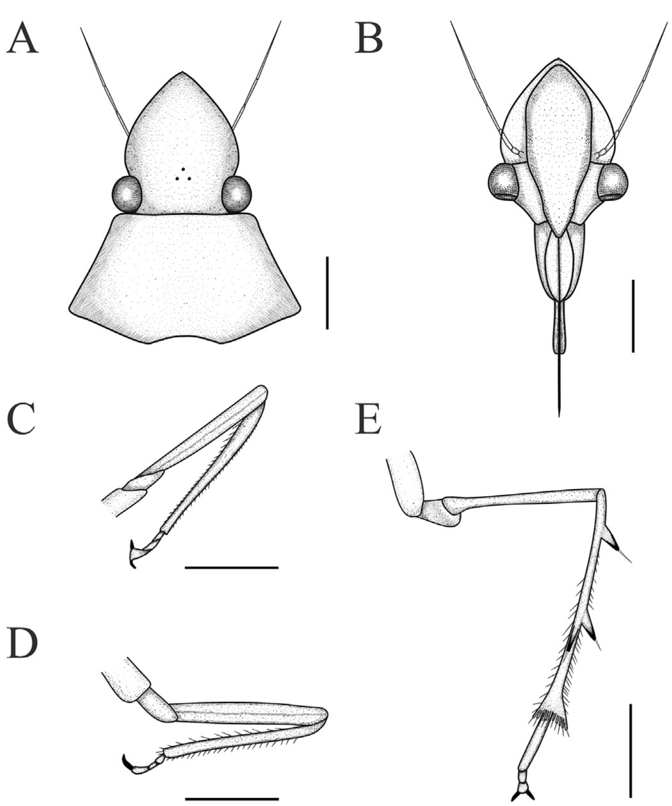

Fig. 5. Reconstruction of body structures of *Ornatiala amoena* Chen, Wang and Zhang, gen. et sp. nov. (A), head and pronotum in dorsal view; (B), head in ventral view; (C), prothoracic leg; (D), mesothoracic leg; (E), metathoracic leg. Scale bars = 0.5 mm.

Clypeata to our knowledge, including their Jurassic relatives. The transformation from a conventional long rostrum to a specialized short one suggests that as compared to Jurassic sinoalids, their descendants in mid-Cretaceous Burmese amber likely evolved quite different feeding strategies and correspondingly occupied different ecological niches.

A noticeable feature of the new genus is its prominent colour pattern on the tegminal surface: the basal 1/3rd (approx.) darkly pigmented, middle 1/3rd area light-coloured, and apical 1/3rd area darkly pigmented with apical cell between two terminal branches of RA much darker. Prominent colour patterns on wings, of different functions in insects (e.g., sexual attraction, mimicry and camouflage), have been widely recorded in fossil Cicadomorpha (e.g., Wang and Zhang, 2009b; Wang et al., 2010; Li et al., 2012; Chen et al., 2015a, 2016b; Zheng et al., 2016). Colour pattern is usually one of the main diagnostic characters in Recent Cercopoidea (Fennah, 1968; Carvalho and Webb, 2005); this character, however, is easily weakened or even erased by diagenetic processes and so usually hard to recognize in fossil specimens (Chen et al., 2017). The distal portion is obviously darkly pigmented on the hindwings of fossil *Jiania*, but is likely completely absent from other Jurassic sinoalids (Chen et al., 2017). Most sinoalid tegmina are likely to be almost monochromatic, except for *Luanpingia daohugouensis* bearing tegmina with transverse alternating dark and light stripes (Figs. 2A-C, 4A in Fu et al., 2017). The two known Cretaceous sinoalid genera (*Fangyuania* and *Jiaotouia*) in Burmese amber likely possess colourless and transparent tegmina and hindwings. The new genus, nevertheless, has tegmina with a prominent colour pattern, which is highly contrasting and extending to the edges of the tegmina. The colour pattern can effectively break up the body outline (Cuthill et al., 2005; Schaefer and Stobbe, 2006), and thus is presumably disruptive camouflage for the sinoalid to hide itself on

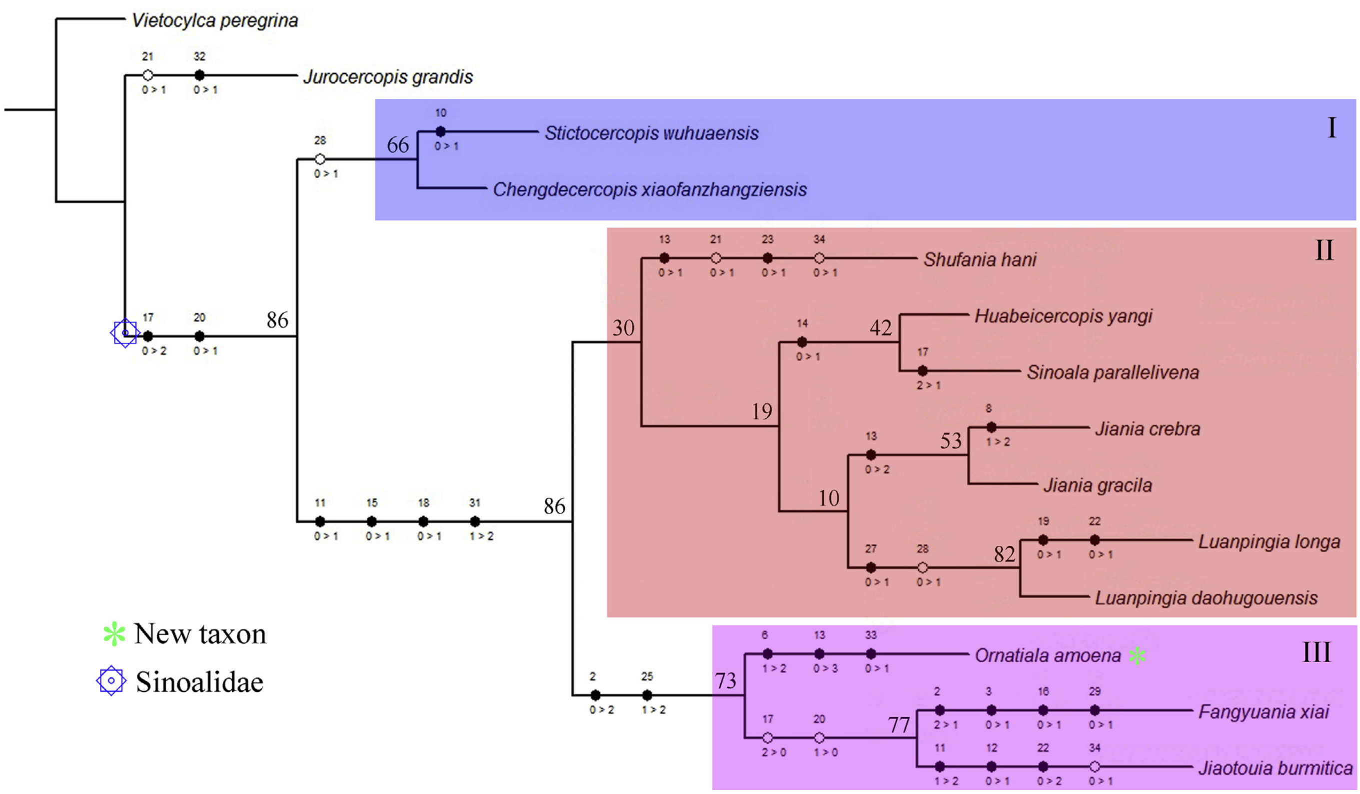

Fig. 6. 50% majority-rule consensus tree of Sinoalidae inferred from maximum parsimony analysis based on 34 morphological characters, with the numbers near the nodes are bootstrap support values. Numbers above branches indicate character numbers, and below branches indicate state changes. White circles indicate homoplasious characters, and black circles indicate non-homoplasious characters. I, II and III indicate three clades of Sinoalidae discussed in the text.

host plants to avoid detection by potential predators, such as early birds, animals, and carnivorous insects.

6. Conclusions

As the third sinoalid reported in mid-Cretaceous Kachin amber, *Ornatiala* gen. nov. shares some common derived characteristics with the other two monospecific genera (*Fangyuania* and *Jiaotouia*) (Chen et al., 2018, 2019b), suggesting that all these known sinoalids constituted a monophyletic group. The new genus bears a shortened and specialized rostrum with labium stout, extending just beyond the procoxae, but the stylet fascicle is longer, reaching to the mesocoxae, similar to that of *Jiaotouia*, indicating that these Cretaceous sinoalids likely evolved a quite different feeding mechanism versus common other Clypeata including their Jurassic ancestors. *Ornatiala* gen. nov. has a prominent colour pattern on tegminal surface and also possesses some other unique autapomorphies, which are quite different from those in the all known sinoalids. Our findings further confirm that sinoalid froghoppers showed high morphological and ecological diversification in the mid-Cretaceous Kachin amber biota.

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