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Short communication

New discovery of Minlagerrontidae in mid-Cretaceous Burmese amber (Hemiptera, Cicadomorpha, Clypeata)

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ABSTRACT

The recently erected family Minlagerrontidae, with a series of extremely unusual or even grotesque morphological features, is a bizarre Clypeata group known from the mid-Cretaceous Kachin amber in northern Myanmar. The hitherto known minlagerrontids are ascribed to two species within one genus (*Minlagerron*). We here report a new genus and species of the family, *Megagerron zhuoi* gen. et sp. nov., from the same amber biota. The new genus differs from the type genus, *Minlagerron*, in having a relatively large body size, somewhat compressed compound eyes and a series of tegminal traits. Noteworthily, the following two tegminal features possessed by the new genus are common in Clypeata, but different from these in *Minlagerron*: the prenodal veinlets on stem R + MP absent (vs. one veinlet present in *Minlagerron*) and the apical cell C5 open (vs. almost closed by the two terminal branches of CuA in *Minlagerron*). Our finding adds some novel information to the knowledge of the morphological and taxonomic paleo-diversity of this enigmatic Mesozoic hemipteran lineage.

1. Introduction

The hemipteran clade Clypeata Qadri, 1967 is one of the most diverse insect lineages, constituting all living cicadomorphs (Cercopoidea, Cicadoidea, Myerslopioidea, Cicadelloidea and Membracoidea) with a unique trait: the greatly enlarged postclypeus with transverse grooves to accommodate the muscles of the cibarial pump needed to ingest xylem fluids that are under negative pressure (Chen et al., 2014; Bartlett et al., 2018; Szwedo, 2018). This insect group firstly appeared in the terminal Paleozoic, being representatives of the extinct superfamily Hylicelloidea, and in the Late Triassic, its modern superfamilies arose in succession and began to diversify (Shcherbakov and Popov, 2002; Chen et al., 2016b, 2019a; Szwedo, 2018). In the Cretaceous, the components of the clade Clypeata changed intensely probably due to rapid floristic shifting from gymnosperms to angiosperms: ancient groups (Hylicellidae, Procercopidae, Sinoalidae, Archijassidae) went extinct; modern families (Aphrophoridae, Cercopidae, Cicadidae, Cicadellidae, Myerslopiidae) explosively appeared and then continued to flourish; some unusual offshoots (Cercopionidae, Minlagerrontidae) were also recorded in this period (Shcherbakov and Popov, 2002; Wang et al., 2012; Szwedo, 2018; Chen et al., 2019a).

The extinct family Minlagerrontidae was recently erected based on some fossils from the mid-Cretaceous Kachin amber, northern Myanmar. This bizarre family, tentatively attributed to Hylicelloidea, derived a series of extremely unusual or even grotesque morphological characters, with some even never recorded in all known fossil and living insects: the family possesses a greatly specialized head, a 'neck' and 'shoulder'-like pronotum, 'grasping' prolegs, and other remarkable body structures as well as specialized tegmina (Chen et al., 2019a). Meanwhile, the family also shares

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a series of plesiomorphies with Hylicelloidea and other Clypeata lineages, such as the enlarged and swollen postclypeus as in Cicadoidea and most Cercopoidea (Dmitriev, 2010; Wang et al., 2012; Chen et al., 2015), primitive antennae as in Cicadoidea and Myerslopioidea (Myers, 1928; Evans, 1941; Anufriev and Emeljanov, 1988), three ocelli as in Cicadoidea, ancient groups of Cercopoidea (Procercopidae and Sinoalidae) and stem Cicadelloidea (Dietrich, 2005; Wang et al., 2012; Chen et al., 2017, 2018), probable fossorial prolegs of nymphs as in Cicadoidea (Matsumura, 1927; Dietrich, 2003), metatibial apical teeth arranged in double rows as in Cercopoidea (Pulz and Carvalho, 1998; Burrows, 2006), tegminal veins bScP and Pc + CP distinct as in stem Cercopoidea (Wang et al., 2012; Chen et al., 2017, 2018).

The cicadomorph clade Clypeata has been well recorded in the Kachin amber biota: up to now, eleven genera and twelve species attributed to four families (Minlagerrontidae, Sinoalidae, Tettigarctidae and Cicadellidae) have been reported (Poinar and Kritsky, 2012; Chen et al., 2018, 2019a, b, c, d; Jiang et al., 2019; Fu et al., 2019; Wang et al., 2019). *Burmacicada protera* Poinar and Kritsky, 2012, erected on the basis of an early instar hatchling, was originally assigned to the singing cicada family Cicadidae, but its systematic position has been questioned by other authors (Moulds, 2018; Chen et al., 2019d).

Up to now, only one genus (*Minlagerron* Chen, Szwedo and Wang, 2019) with two species (*Minlagerron griphos* Chen, Szwedo and Wang, 2019 and *Minlagerron onyxos* Chen, Szwedo and Wang, 2019) assigned to the bizarre family Minlagerrontidae has been reported based on three fossil specimens in the mid-Cretaceous Kachin amber from northern Myanmar (Chen et al., 2019a). We here erect a new genus and species, *Megagerron zhuoi* gen. et sp. nov., on the basis of one specimen from the same amber biota, providing some novel information on the morphological and taxonomic diversity of this unusual Mesozoic cicadomorph lineage.

2. Geological context

The single fossil specimen described herein comes from amber mines situated in the Hukawng Valley of Kachin Province, northern Myanmar (see locality in Fig. 1 of Chen et al., 2019e). The rock containing the amber was determined to be 98.79 ± 0.62 Ma based on U-Pb dating of zircon crystals (Shi et al., 2012), corresponding to the early Cenomanian (mid-Cretaceous) according to the updated International Chronostratigraphic Chart (Cohen et al., 2018).

3. Material and methods

The fossil specimen, containing in a yellow and transparent amber piece and deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, was examined, photographed and measured using the VHX 5000 digital microscope platform, with incident and transmitted light used alternately. The line drawings and reconstructions were prepared in image-editing software CorelDraw X7 and Adobe Photoshop CS6. The venational terminology used in the present study is slightly modified from Nel et al. (2012) and Bourgoin et al. (2015) as in Chen et al. (2018, 2019a, b, c, d).

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:3D1631CF-4192-43E7-88F3-35343320A75F.

4. Systematic palaeontology

Class **Insecta** Linnaeus, 1758
Order **Hemiptera** Linnaeus, 1758
Suborder **Cicadomorpha** Evans, 1946
Family **Minlagerrontidae** Chen, Szwedo and Wang (2019)

Emended diagnosis. Head with postclypeus almost transversely rectangular in the middle, with basal half having a deep longitudinal groove medially; thorax with anterior part sharply constricted, forming unique 'neck' and 'shoulder' structures; prothoracic legs with strengthened femora with several lateral teeth and tibiae deviantly club-shaped; female pygofer completely wrapped by tergite VIII, with ovipositor short and reduced; tegmina with venation thick and reticular, multiple veinlets ending at anterior margin, and two crossveins *ir* and *rp-mp*.

Genus *Megagerron* gen. nov.
(urn:lsid:zoobank.org:act:79B95181-06CC-4DE5-90D9-F5C998F5A958)
Type species: *Megagerron zhuoi* gen. et sp. nov.; by present designation and monotypy.

Etymology. The name of the new genus is a combination of Greek "mega" (large) and "gerron" (suffix of the type genus of the family Minlagerrontidae), proposed to reflect some similarity between this new genus and *Minlagerron* and meanwhile the larger size of the former.
Diagnosis. Head with compound eyes relatively compressed (vs. distinctly protruding in *Minlagerron*); tegmen wide (vs. obviously narrower in *Minlagerron*), with basal part of costal area sclerotized and pitted, other parts membranous (vs. only clavus sclerotized in *Minlagerron*), CuA_2 short, not ending at the same point as CuA_1, apical cell C5 not closed by the two terminal branches of CuA (vs. CuA_2 long, nearly ending at the same point as CuA_1, leading to C5 almost closed by the two terminal branches of CuA in *Minlagerron*), stalk R + MP without veinlets (vs. with a single veinlet near its bifurcation in *Minlagerron*), veinlets of R and RA long and oblique (vs. relatively short and mostly nearly transverse in *Minlagerron*), CuP straight at connection with *cua-cup* (vs. distinctly geniculate at connection in *Minlagerron*); crossvein *cua-cup* long (vs. much shorter in *Minlagerron*).

Megagerron zhuoi gen. et sp. nov.
(urn:lsid:zoobank.org:act:16E6F179-409F-46D1-BD35-89EB5AC2313B)
Figs. 1–3

Material. Holotype: NIGP170723, an almost complete adult in an amber piece, six unknown.
Etymology. The specific epithet is in honor of Mr. De Zhuo, who assisted in collecting the Burmese amber piece.
Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; lowermost Cenomanian, Upper Cretaceous.
Diagnosis. Body relatively large, with length nearly 10.0 mm long and width about 5.0 mm; tegmen with wing apex acute, anterior margin smoothly curved, Cell C1 almost as long as C1′, and much longer than C1″, C2 about twice as long as C2′, C3 slightly wider, but shorter than C2′, veins with one row of regular pits each side, R + MP + CuA bifurcating into R + MP and CuA at basal 0.22 wing length, stalk R + MP very short, stem MP straight and forking into MP_{1+2} and MP_{3+4} at basal 0.77 wing length, stem CuA branching into CuA_1 and CuA_2 at basal 0.58 wing length, crossvein *mp-cua* connecting to stem CuA.
Description. Body dorsoventrally flat, including tegmina in repose 8.70 mm long, 5.11 mm wide. Right and left wings spreading, not tent-like over abdomen.

Head partly destroyed, with compound eyes in dorsal view 1.08 mm long, 1.34 mm wide as preserved. Vertex densely pitted. Compound eyes large, 0.70 mm long and 0.39 mm wide in dorsal view, not very protruding.

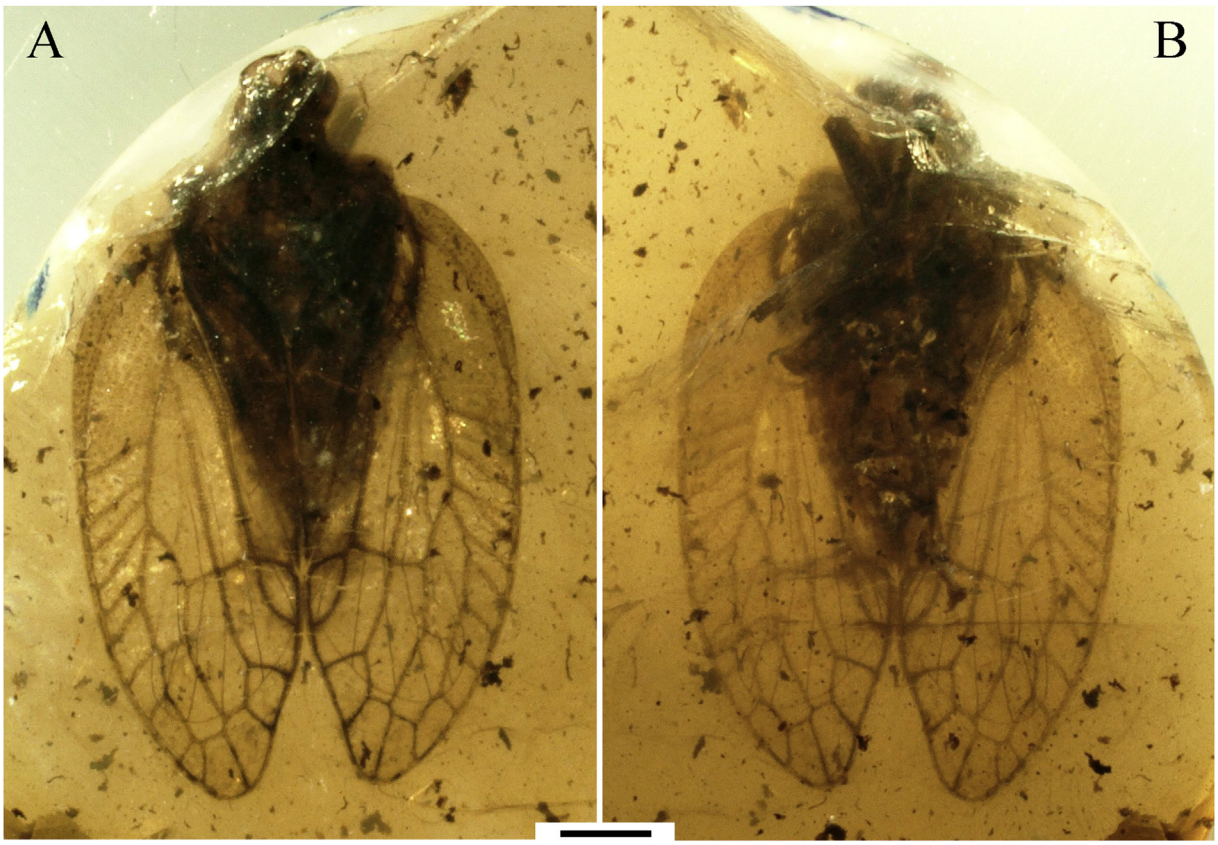

Fig. 1. Photographs of the holotype of *Megagerron zhuoi* gen. et sp. nov. (A), dorsal view; (B), ventral view. Scale bar = 1.0 mm.

Thorax much wider than head, with anterior part sharply constricted as narrow 'neck' region. Pronotum 0.95 mm long in the middle line, and 2.61 mm wide, with disc densely pitted; anterior margin short; anterolateral angles almost rectangular; anterolateral margins strongly concave in the middle, with anterior part constituting 'neck' and posterior part constituting 'shoulder'; lateral angles rounded; posterolateral margins long and nearly straight; posterolateral angles obtuse; posterior margin concave. Mesonotum large, 1.60 mm long, and 2.58 mm wide; disc pitted. Legs densely covered with short setae on surface. Prothoracic legs with femora very thick, sunken ventrally, with one row of strong lateral teeth on ventral margin; tibiae slightly longer than femora, club-shaped, with basal 2/3rds slender, apical 1/3rds slightly curved and inflated ventrally; tarsi with apical tarsomere swollen, much thicker than basi- and midtarsomere; two tarsal claws sharp apically. Mesothoracic legs poorly preserved, obscure. Metathoracic legs with femora slightly shorter than tibiae; tibiae slender but slightly thickened apically, with two rows of apical teeth (teeth of apical row with setae at apex); tarsi with apical tarsomere swollen, much thicker than basi- and midtarsomere; tarsal claws not well preserved, obscure.

Abdomen not well preserved, flat, widest near its middle; pygofer poorly preserved, obscure, gender unknown.

Tegmen wide, with length 6.67 mm, width 2.54 mm. Clavus and basal part of costal area sclerotized and pitted; other parts membranous. Anterior margin smoothly curved. Apical margin near terminal point of MP_{1+2} distinctly concave. Wing apex acute. Basal cell relatively broad, 1.42 mm long. Cell between CA and Pc + CP long and broad. Cell C1 almost as long as C1′, and much longer than C1''. C2 about twice as long as C2'. C3 slightly wider, but shorter than C2'. C4 long and sinuous. Apical cell C5 somewhat fusiform, not closed by two terminal branches of CuA. Veins thick, with one row of regular pits each side. Pc + CP long. bScP short, fusing with R + MP + CuA beyond middle of basal cell. R + MP + CuA bifurcating into R + MP and CuA at basal 0.22 wing length. Stalk R + MP very short, without veinlets. Veinlets of R and RA nine in number, long and oblique. R + MP branching into R and MP at basal 1/4 wing length. R bifurcating into RA and RP at basal 0.51 wing length; RP unbranched. Crossveins *ir* two in number. Stem MP straight, long, and bifurcating into MP_{1+2} and MP_{3+4} near wing apex, at basal 0.77 wing length; MP_{3+4} much shorter than MP_{1+2}. Crossveins *rp-mp* two in number, with the basal one connecting stem MP and the apical one connecting MP_{1+2}. Stem CuA branching into CuA_1 and CuA_2 apicad of bifurcation of stem R, at basal 0.58 wing length; CuA_2 much shorter than CuA_1, not ending at the same point as the latter. Crossvein *mp-cua* connecting stem MP, and connecting CuA instead of CuA_1. CuP long, straight at connection with crossvein *cua-cup*. Crossvein *cua-cup* long and straight. Pcu slightly curved. A_1 long, nearly straight.

Hind wing without appendix. Wing-coupling lobe on anterior margin prominent. Veins much thinner than tegminal veins. Longitudinal veins (RA, RP, MP and CuA_1) slightly geniculate at connection with crossveins (*ir*, *rp-mp*, *mp-cua*). Apical margin slightly concave at ending of longitudinal venis. Stalk R branching into RA and RP at wing incision of anterior margin. RA much

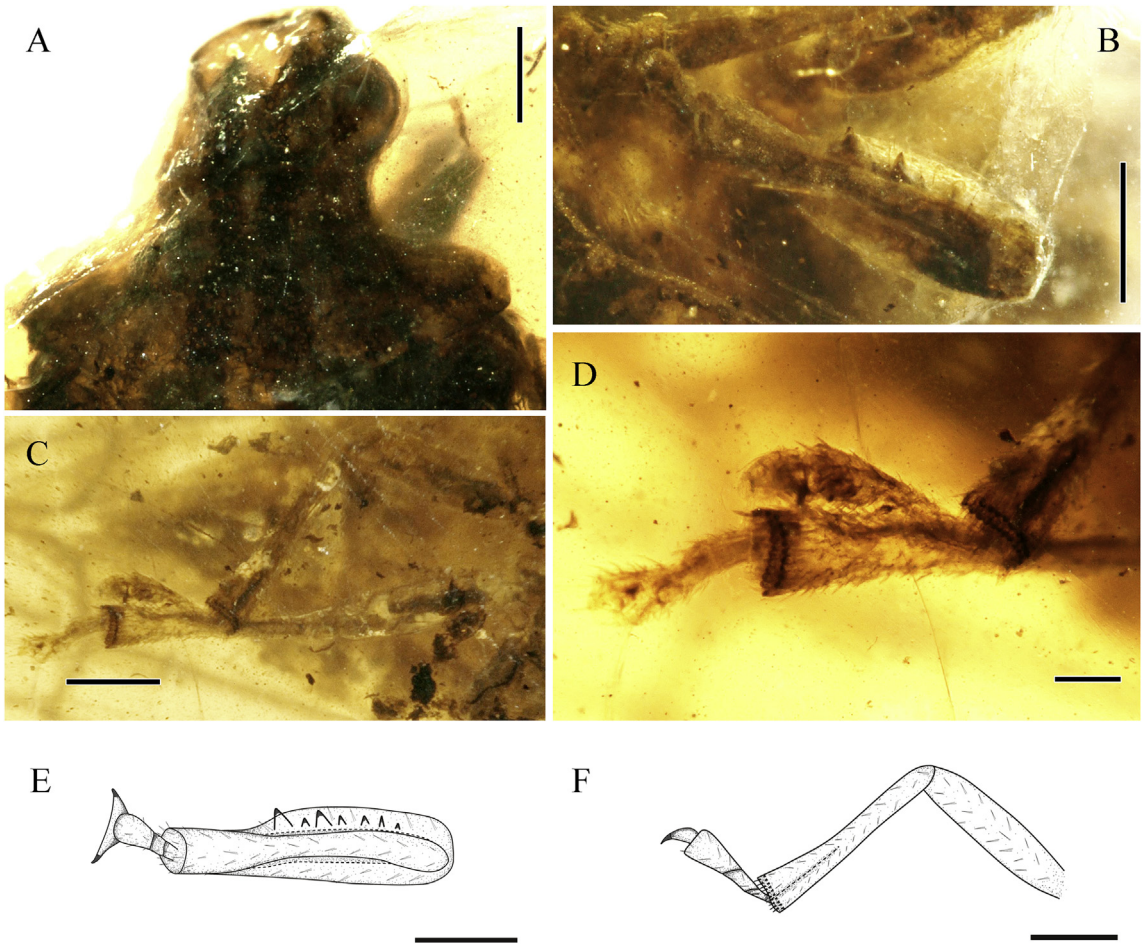

Fig. 2. Body structures of *Megagerron zhuoi* gen. et sp. nov. (A), head and pronotum in dorsal view; (B), left prothoracic leg; (C), metathoracic legs; (D), enlarged metathoracic tarsi and apical tibiae; (E), line drawing of left prothoracic leg; (F), line drawing of right metathoracic leg. Scale bars = 0.5 mm (A-C, E-F) and 0.2 mm (D).

longer than R, with basal part nearly fused with wing incision. RP longer than RA, connected to RA by crossvein *ir* and to MP by crossvein *rp-mp*. MP unbranched. CuA forking into CuA_1 and CuA_2 much apicad of bifurcation of R. CuA_1 connected to MP by crossvein *mp-cua*.

5. Discussion

Megagerron zhuoi gen. et sp. nov. in the Kachin amber from northern Myanmar undoubtedly belongs to the recently erected Clypeata family Minlagerrontidae Chen, Szwedo and Wang (2019) based on the following morphological characteristics: the pronotum with the anterior part sharply constricted, forming unique 'neck' and 'shoulder' structures; the prothoracic femora with ventral teeth in a row, tibiae club-shaped; the tegmen with thick venation reticular with multiple veinlets ending at anterior margin and two crossveins *ir* and *rp-mp* (Chen et al., 2019a).

The reported fossil cicadomorphs are mostly represented by isolated wings (see Carpenter, 1992), and thus the current systematic framework of extinct 'Homoptera' including the clade Clypeata is mainly based on isolated wings. As mentioned above, the genus *Minlagerron* shows a series of bizarre tegminal traits never recorded in other ancient Clypeata; however, some of these traits are absent in the new genus and species described herein. A single prenodal veinlet near the forking of R + MP is present in *Minlagerron* but absent from the new material, and thus this morphological character should not be treated as a diagnostic characteristic of Minlagerrontidae. Another grotesque venational character of *Minlagerron* is that vein CuA_2 is long and nearly ends at the same point as CuA_1, leading to apical cell C5 almost closed by the two terminal branches of CuA (Chen et al., 2019a), is also absent in *Megagerron* gen. nov., and so this character should be a diagnostic feature of the genus *Minlagerron* instead of the family Minlagerrontidae.

Minlagerrontidae derived a series of extremely unusual or even grotesque apomorphic characteristics, never recorded in other Clypeata, such as the specialized prolegs: the strengthened and ventrally sunken femora with one row of strong lateral teeth on ventral margin; the club-shaped tibiae with basal $^{2}/_{3}^{rds}$ slender, apical $^{1}/_{3}^{rds}$ slightly curved and inflated ventrally (Chen et al., 2019a). The modified prolegs in adult Minlagerrontidae were interpreted as 'grasping' legs to be used for clinging to the bark or foliage of the host plants, and/or grasping the mating partner (coordinated with the prothoracic 'neck' and 'shoulder' structure) in Chen et al. (2019a). Nevertheless, the prolegs of the three fossil specimens in Chen et al. (2019a) are all preserved in a somewhat stretched state. The new minlagerrontid fossil reported herein, with the left basal $^{2}/_{3}^{rds}$ protibia tightly folded to the ventrally sunken femur, and the club-shaped apical part of tibia and the ventral teeth of

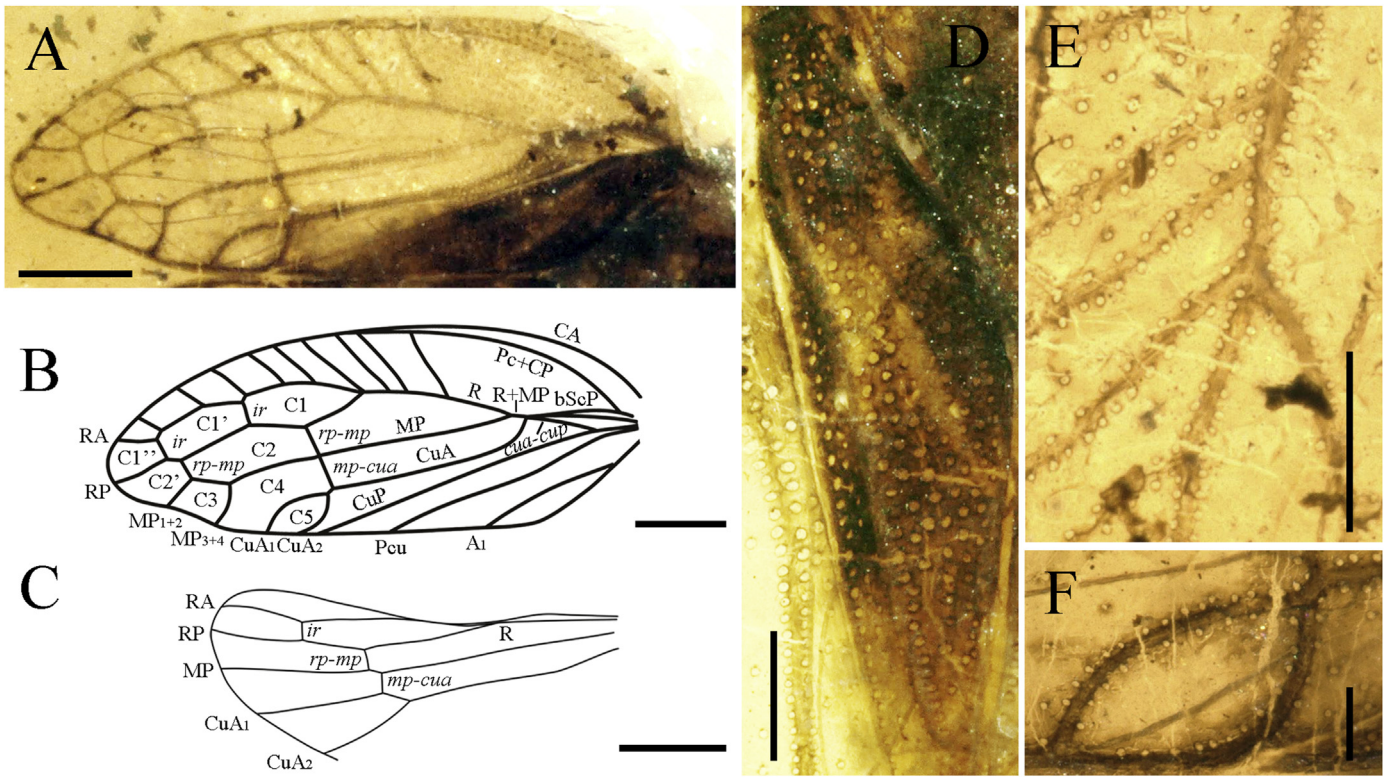

Fig. 3. Wings of *Megagerron zhuoi* gen. et sp. nov. (A), photograph of left tegmen and hind wing; (B), line drawing of left tegmen; (C), line drawing of left hind wing; (D), enlarged pitted and sclerotized clavus of left tegmen; (E), R and its branches of left tegmen, showing one row of regular pits each side; (F), CuA and CuP of left tegmen, showing one row of regular pits each side and open apical cell C5. Scale bars = 1.0 mm (A-C), 0.5 mm (D, E) and 0.2 mm (F).

femur tightly closed (Fig. 2B), further confirms that the prolegs of Minlagerrontidae are adapted at 'grasping'.

6. Conclusion

Amber affords exceptional preservation of insects and other microorganisms (Chen et al., 2016a). The mid-Cretaceous Kachin amber biota from northern Myanmar, as probably the most diverse Mesozoic paleo-biota (Shi et al., 2012; Kania et al., 2015; Dunlop et al., 2018), recorded many unique insect groups, providing novel insights in the evolution, ecology and behavior of late Mesozoic insects (e.g., Mey et al., 2017; Rasnitsyn et al., 2017; Liu et al., 2018). Discovery of the bizarre family Minlagerrontidae indicates that ancient Clypeata had diversified multi-dimensionally and evolved with high disparity (Chen et al., 2019a). The known Minlagerrontidae is only represented by one genus with two species based on three fossil specimens. *Megagerron zhuoi* gen. et sp. nov. described herein extends knowledge of morphology and taxonomic diversity of the recently erected family. However, it remains hard to infer the precise systematic position of this enigmatic family based on available data due to its highly modified body structures and limited data on the morphological characteristics (especially for body structures) of early Clypeata.

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