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Giants trapped in resin: new material of Sinoalidae in mid-Cretaceous Kachin amber from northern Myanmar (Insecta, Cicadomorpha)

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A B S T R A C T

The cicadomorph family Sinoalidae was documented in the late Middle to early Late Jurassic Yanliao Biota from northeastern China and mid-Cretaceous Kachin amber from northern Myanmar. The known sinoalid froghoppers contained in Kachin amber bear a much smaller body size than their Jurassic relatives. Herein, two new sinoalids trapped in Kachin amber, with a relatively large body size, are described and ascribed to *Makrosala elegans* Chen & Wang gen. et sp. nov. and *M. venusta* Chen & Wang gen. et sp. nov. The Burmese amber is now recognized as a significant window to the Cretaceous world, but taphonomical biases should be kept in mind when studying the ecology, biodiversity, and community composition and structure of this amber palaeo-biota.

1. Introduction

The Mesozoic hemipteran family Sinoalidae, with a mixture of ancestral morphological traits shared with Hylicelloidea and cercopoid Procercopidae as well as a series of unique autapomorphies, can be easily recognized by its metatibiae with two rows of well-developed lateral spines and tegmina with costal area and clavus more sclerotized and punctate (Wang et al., 2012; Chen et al., 2018, 2019a, c). This froghopper group, as the most recently erected family of Cicadomorpha: Cercopoidea (Wang et al., 2012), was firstly reported from the late Middle to early Late Jurassic Yanliao Biota in northeastern China, originally with four definite genera included (Hong, 1983; Wang et al., 2012). Subsequently, four additional genera from the Yanliao Biota were attributed to this family (Chen et al., 2017, 2019b; Fu et al., 2017; Fu and Huang, 2018, 2019a, b). Very recently, some sinoalids were recorded in mid-Cretaceous Kachin amber from northern Myanmar, with seven genera established (Chen et al., 2018, 2019a, c, d, e; Fu and Huang, 2019c, Appendix 1).

Sinoalid froghoppers are high in abundance, taxonomic diversity and morphological disparity in Kachin amber and they are all very small insects (shorter than 8 mm). We herein describe two new fossil sinoalids trapped in Kachin amber, *Makrosala elegans* Chen & Wang gen. et sp. nov. and *M. venusta* Chen & Wang gen. et sp. nov., bearing a much larger body than their confamilials in the same Lagerstätte.

2. Material and methods

The two new sinoalid specimens described herein, contained in two transparent and yellowish amber pieces, are now deposited in the Nanjing Institute of Geology and Palaeontology, Chinese

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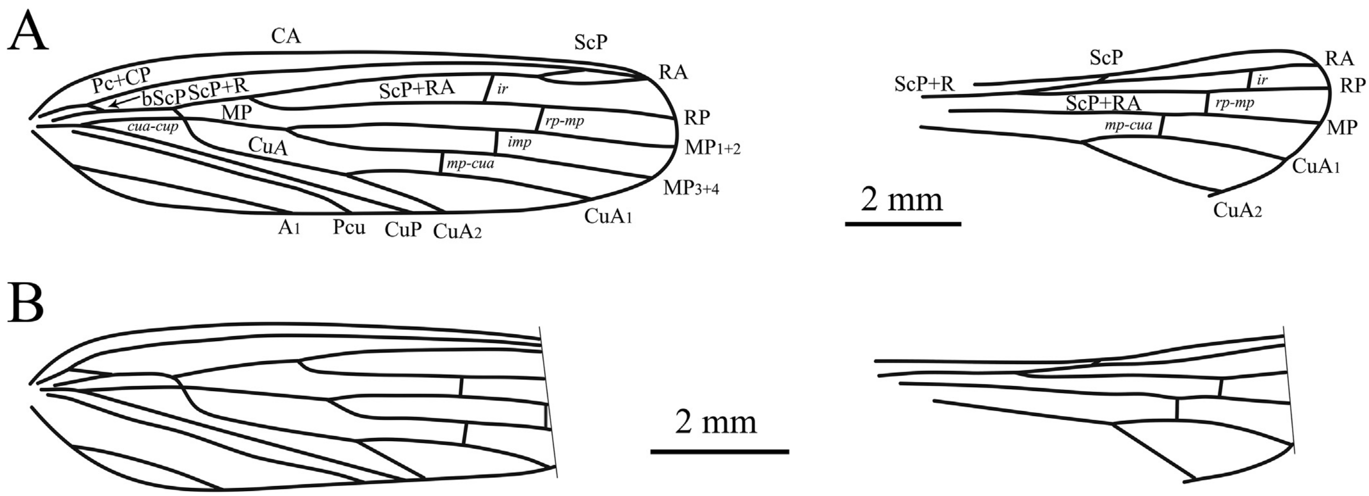

Fig. 1. Line drawings of wings of sinoalids described in this study. (A), *Makrosala elegans* Chen & Wang gen. et sp. nov., holotype, tegmen (left) and hindwing (right); (B), *Makrosala venusta* Chen & Wang gen. et sp. nov, holotype, tegmen (left) and hindwing (right). All to scale bars.

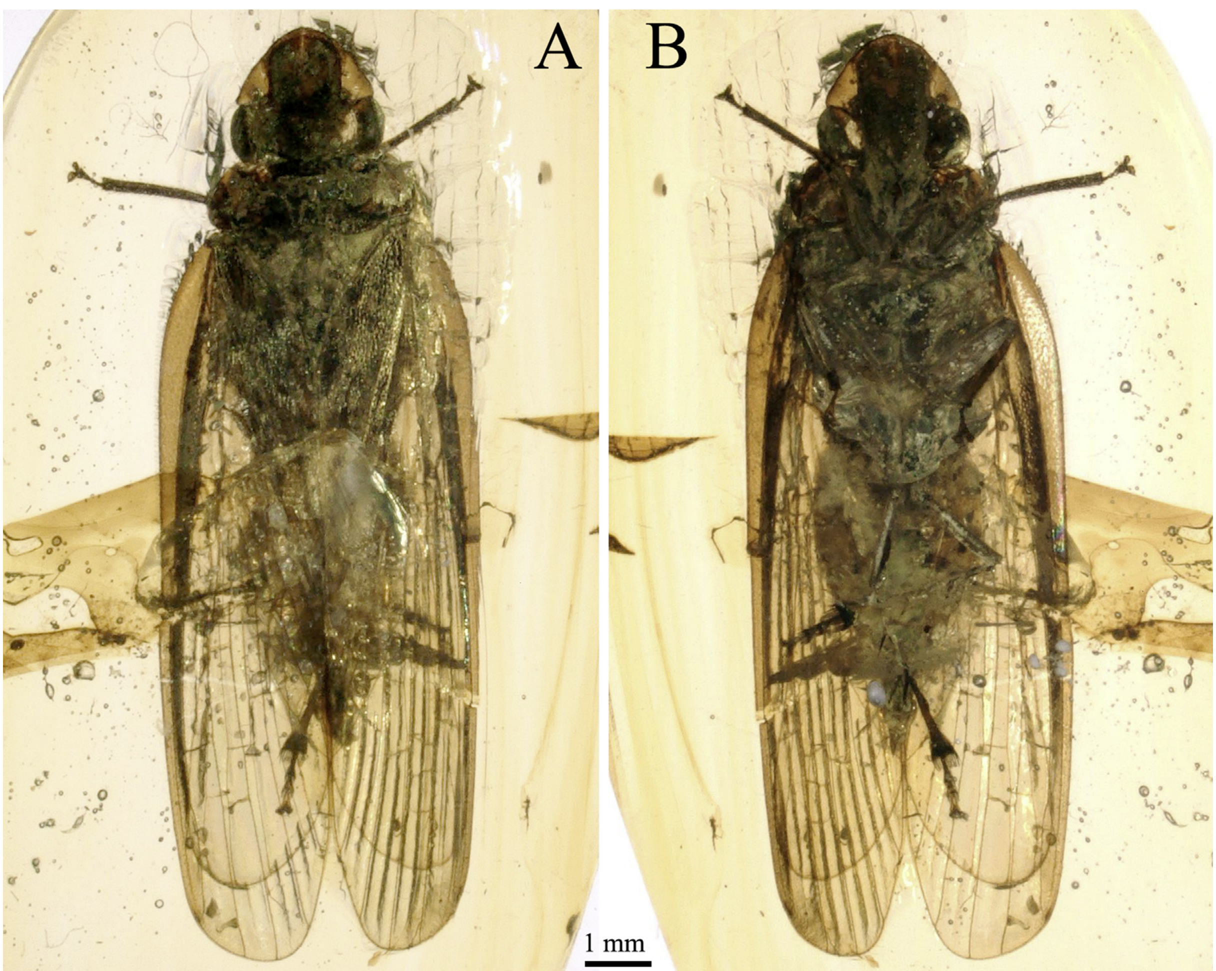

Fig. 2. Photos of holotype of *Makrosala elegans* Chen & Wang gen. et sp. nov. (A), dorsal view; (B), ventral view. All to scale bar.

Academy of Sciences. They were collected from the Hukawng Valley, Kachin State, northern Myanmar (see locality inChen et al., 2019d, fig. 1). The age of the rock yielding Kachin amber was determined to be 98.79 ± 0.62 Ma (earliest Cenomanian) based on U—Pb dating of zircon crystals (Shi et al., 2012), but its precise age may be older (close to the boundary between the Albian and Cenomanian or even the late Albian) because the amber displays traces of redeposition (Mey et al., 2018; Smith and Ross, 2018; Yu et al., 2019).

The two amber pieces were re-cut as thin as possible and then polished to show morphological details of the new sinoalid

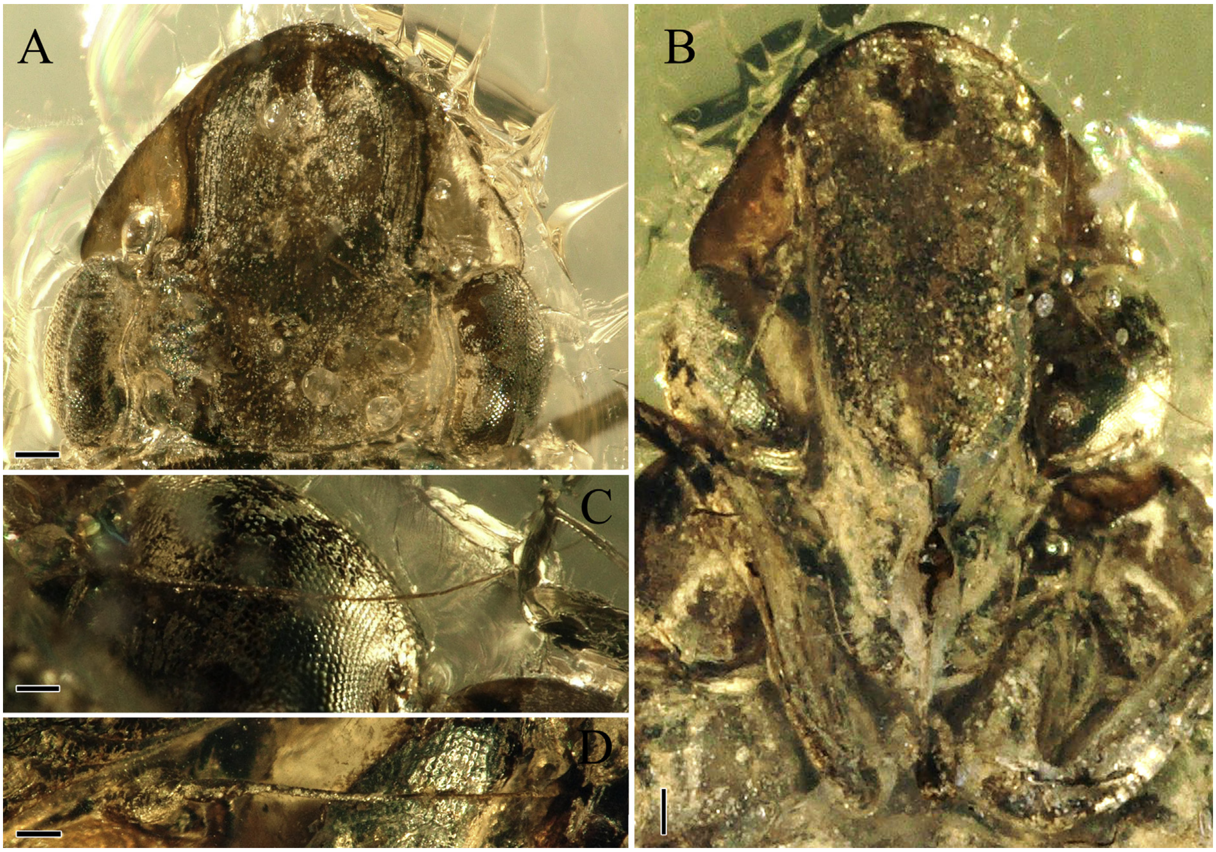

Fig. 3. Photos of head of *Makrosala elegans* Chen & Wang gen. et sp. nov., holotype. (A), dorsal view; (B), ventral view; (C), right antenna; (D), left antenna. Scale bars = 0.2 mm (A, B), 0.1 mm 0.1 (C, D).

specimens more clear. VHX 5000 digital microscope platform was used to photograph and measure the two fossil specimens, and image-editing software CorelDraw 12.0 and Adobe Photoshop CS3 were used to prepare the line drawings of the tegmina. Venational terminologies follow Nel et al. (2012) and Bourgoin et al. (2015), with slight modification, and the nomenclature of body structures mainly follows Evans (1966) and Moulds (2005).

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:6D0922EE-45A6-445B-9875-B1F61356AA18.

3. Systematic palaeontology

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

Genus ***Makrosala*** Chen & Wang gen. nov.
(urn:lsid:zoobank.org:act:AFED7589-6CCE-45EA-9408-B58F6C8E7ABF)
Type species: *Makrosala elegans* Chen & Wang gen. et sp. nov.; by present designation

Etymology. The generic name is formed by the combination of the Greek '*makros*' (long) and the Latin '*ala*' (wing), in reference to the long tegmina.

Diagnosis. Body medium-sized (vs. body size small for other sinoalid genera in Kachin amber). Pronotum with anterior margin strongly concave laterally and surrounding posterior margin of compound eyes (autapomorphy). Tegmen postcostal cell reduced (autapomorphy); MP_{1+2} and MP_{3+4} very long (MP_{1+2} and MP_{3+4} relatively short for other sinoalids); crossvein *cua-cup* connecting MP + CuA at its forking into MP and CuA (crossvein *cua-cup* connecting stem MP + CuA, far away from its forking for *Cretosinoala* and *Mesolongicapitis*).

Makrosala elegans Chen & Wang sp. nov.
(urn:lsid:zoobank.org:act:1653FF69-EEB6-4723-AC14-BA568EF66665)
Figs. 1A, 2–5

Material. Holotype: NIGP172741, a complete adult insect in an amber piece, with overlapped wings on top of body.
Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; mid-Cretaceous.
Etymology. The specific epithet is derived from the Latin "*elegans*" (meaning elegant).
Diagnosis. Crown with length/width ratio about 0.87 (vs. crown with length/width ratio about 0.71 for *M. venusta*). Compound eyes distinctly elongate, not produced, reniform, with inner margin concave (vs. compound eyes produced, elliptical, with inner margin not concave for *M. venusta*). Postclypeus long, with base almost reaching anterior margin of head (vs. postclypeus shortened, with base not reaching anterior margin of head for *M. venusta*).

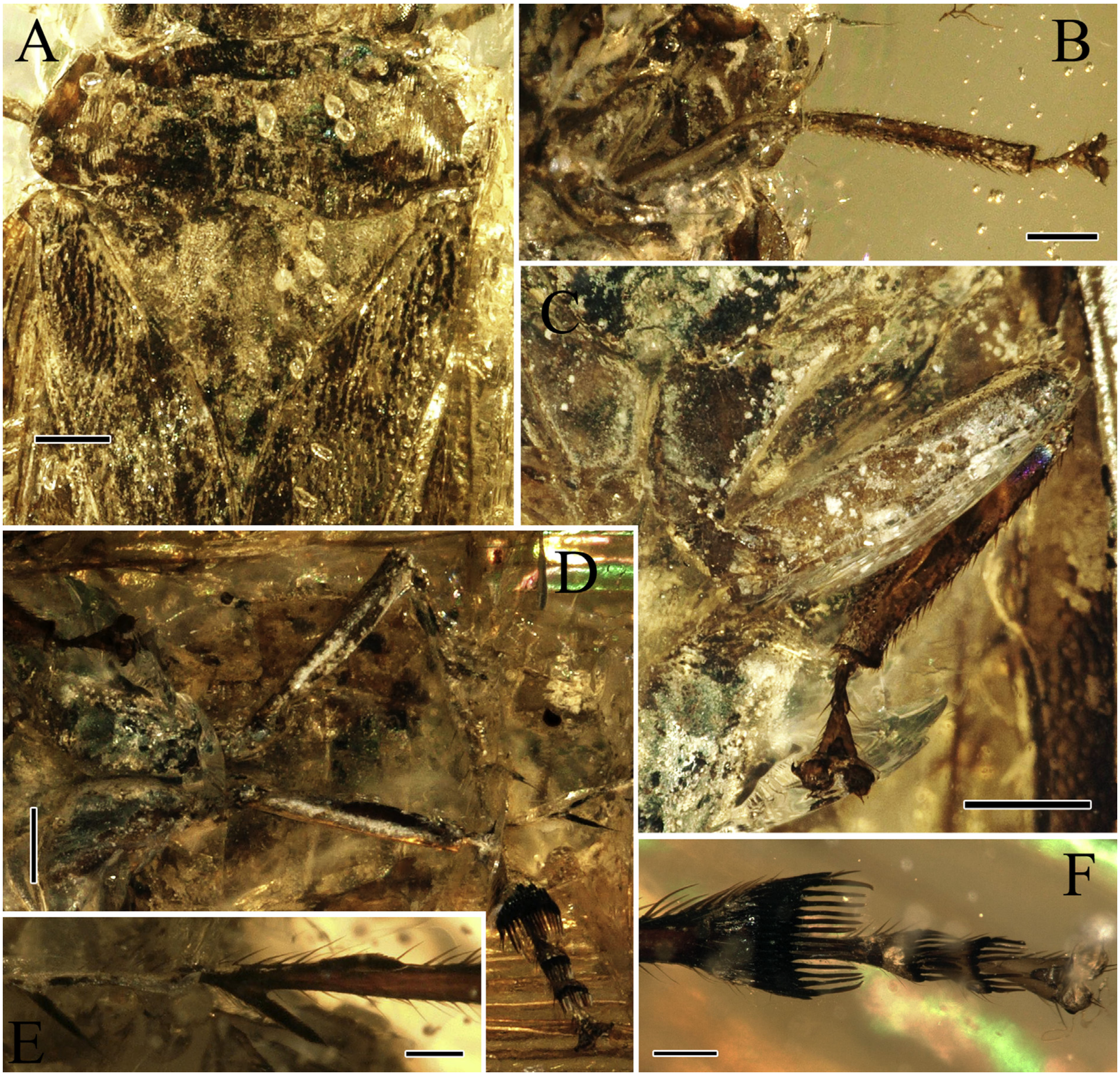

Fig. 4. Photos of thorax of *Makrosala elegans* Chen & Wang gen. et sp. nov., holotype. (A), pronotum and mesonotum; (B), left prothoracic leg; (C), left mesothoracic leg; (D), left metathoracic leg; (E), enlarged of part of right metatibia, showing three large lateral spines; (F), enlarged apical tibia and tarsus of right metathoracic leg. Scale bars = 0.5 mm (A–D), 0.1 mm 0.2 (E, F).

Mesonotum slighter wider than head (vs. mesonotum apparently narrower than head for *M. venusta*). Tegmen with postcostal cell narrower than cell between CA and Pc + CP; crossvein *ir* just basad of *imp*, and obviously apicad of *mp-cua*; crossvein *rp-mp* obviously apicad of *imp*; crossvein *mp-cua* almost at the same level of termination of CuA_2 (vs. tegmen with postcostal cell wider than cell between CA and Pc + CP; crossvein *ir* absent or distinctly apicad of *imp*; crossvein *rp-mp* obviously basad of *imp*; crossvein *mp-cua* apparently apicad of termination of CuA_2 for *M. venusta*).

Description. Body with wings in repose about 14.49 mm long, 4.88 mm wide.

Head with length about 2.04 mm, width with compound eyes about 2.34 mm, length/width ratio about 0.87. Crown broad, distinctly produced anteriorly; anterior margin rounded and angled medially; posterior margin smoothly convex; disc with tiny granules. Coronal margin thin and strongly expanded before compound eyes; coronal supraantennal ledges well expanded. Ocelli three in number; median ocellus much larger than lateral ones; distance between lateral two slightly shorter than that between ocellus and compound eye of the same side. Compound eyes large, distinctly elongate but not produced, reniform, with inner margin concave, with length/width ratio about 2.4 in dorsal view; posterior margin surrounded by anterior margin of pronotum. Genae relatively long. Lora relatively broad. Maxillary plates thin and relatively broad. Postclypeus long and broad, with base almost reaching anterior margin of head, length/width ratio about 2.0; somewhat depressed; transverse grooves and medial carina not distinct; lateral margin slightly concave in middle. Anteclypeus small and oval. Rostrum short and stout, just extending beyond procoxae. Antenna with antennal pit shallow; scape

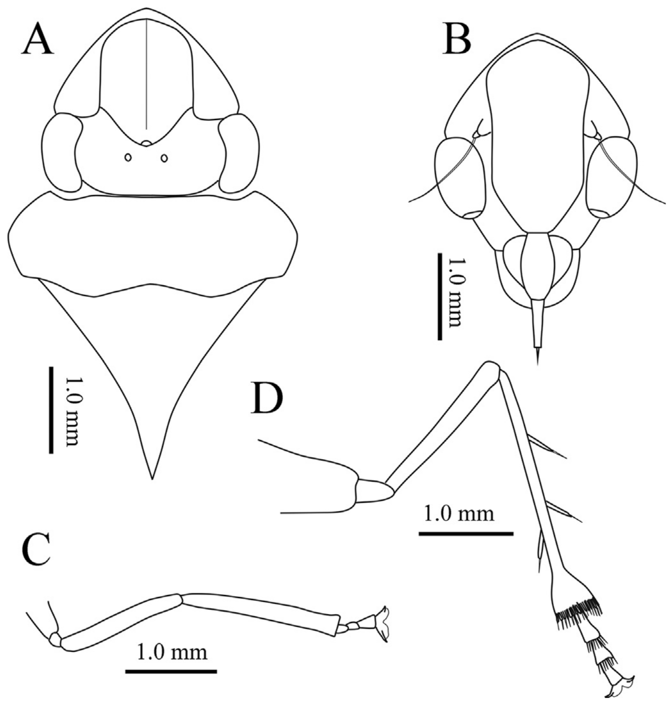

Fig. 5. Line drawings of *Makrosala elegans* Chen & Wang gen. et sp. nov., holotype. (A), head and thorax in dorsal view; (B), face; (C), left prothoracic leg; (D), left metathoracic leg. All to scale bars.

shorter and slenderer than pedicel; pedicel large, swollen; flagellum long, filiform, with basal segments much thicker than remaining ones, joints between segments obscure, but likely with at least seven segments.

Pronotum shortened, about 0.78 mm long in midline and about 3.22 mm wide, widest at its lateral angles, with length/width ratio about 0.24; disc with tiny granules; anterior margin nearly straight in middle, but strongly concave laterally and surrounding posterior margin of compound eyes; anterolateral angles rounded; anterolateral margins smoothly convex; lateral angles rounded; posterolateral margins smoothly concave, almost transverse, slightly shorter than anterolateral margins; posterolateral angles obtuse; posterior margin strongly concave, much shorter than anterior margin. Mesonotum large, about 2.15 mm long in midline, and 2.47 mm wide, with length/width ratio about 0.87, slighter wider than head; disc with tiny granules; lateral margin obviously concave near scutellum; posterior angle of scutellum very acute. Prothoracic legs with coxa thick; trochanter much slenderer than coxa; femur not very thick, about 2/3 length of tibia; tibia prismatic in cross section, densely covered with long setae; tarsus covered with long setae, with apical tarsomere enlarged apically and much longer than basi- and midtarsomere; tarsal claws large, arolium expanded, widely bilobate and deeply incised. Mesothoracic legs with coxae very large, subtriangular, and close to each other; trochanter slender; femur almost as long as tibia, much thicker than profemora; tibia densely covered with long setae; tarsus covered with long setae, with apical tarsomere distinctly enlarged apically, much longer than basi- and midtarsomere; tarsal claws large, arolium expanded, widely bilobate and deeply incised. Metathoracic legs with coxae very large, subtriangular, close to each other; trochanter slender; femur long but slender, about 2/3 length of tibia; tibia much slenderer than femur, covered with very long setae, lateral spines with long subapical hair arranged in two rows, with one and two in number for each row, double rows of about 15 apical teeth, with teeth in apical row with extremely strong subapical setae; tarsus ventrally with dense long setae, basitarsomere slightly longer than mid- and apical tarsomeres, and basi-and midtarsomeres with eight apical teeth with extremely strong apical setae arranged in one row; tarsal claws large, arolium well-developed, widely bilobate and deeply incised.

Abdomen not well preserved, with pygofer covered by metathoracic legs and wings, and genitals invisible.

Tegmen slender, with length about 11.62 mm, width about 2.77 mm, length/width ratio about 4.20. Clavus and costal area much more punctate and sclerotized than other parts. Tegminal apex somewhat truncate; costal margin smoothly arched at wing base, then almost straight; claval margin strongly arched; postclaval margin nearly straight. Cell between CA and Pc + CP relatively broad and very long, almost reaching wing apex. Postcostal cell long, but extremely narrow, even narrower than cell between CA and Pc + CP. Basal cell long but narrow, about 0.23 of tegminal length. Clavus relatively broad, with apex at about basal 0.59 of tegminal length. Pc + CP extremely long, reaching termination of RA. bScP fused with Pc + CP basally, independent bScP extremely short, migrated to R + MP + CuA and fused with the latter basad of middle of basal cell. ScP + R short, forking into ScP + RA and RP at basal 0.35 of tegminal length. ScP + RA long, slightly curved, subparallel to Pc + CP, forking into ScP and RA at basal 0.79 of tegminal length. ScP short, about half length of RA. RP long, distinctly curved at base and nearly straight for remaining part. Common stalk MP + CuA extremely short, bifurcating into MP and CuA at apex of basal cell. MP almost straight, slightly longer than ScP + R, branching into MP_{1+2} and MP_{3+4} at basal 0.41 of tegminal length. MP_{1+2} and MP_{3+4} very long, almost of equal length. CuA strongly curved at base, then nearly straight, branching into CuA_1 and CuA_2 at basal 0.49 of tegminal length; CuA_1 much longer than CuA_2. CuP nearly longitudinal, smoothly curved near its connection with crossvein *cua-cup*, then inclined and nearly straight. Pcu nearly straight, subparallel to CuP and obviously curved apically. A_1 long and nearly straight. Crossvein *cua-cup* connecting MP + CuA its forking into M and CuA. Crossvein *ir* just basad of *imp*, and obviously apicad of *mp-cua*. Crossvein *rp-mp* obviously apicad of *imp*. Crossvein *mp-cua* almost at the same level of termination of CuA_2.

Hind wing without distinct outer membrane. ScP + R not very long, shorter than RP. Independent ScP extremely short. RA and RP almost straight. MP unbranched, almost straight and subparallel to RP. CuA with preserved part straight, bifurcating into CuA_1 and CuA_2 almost at the same level of separation of ScP. CuA_1 and CuA_2 smoothly curved; CuA_1 about 2/3 length of CuA_2. Crossvein *ir* present, apicad of *rp-mp*, and the latter almost at the same level of termination of CuA_2, and apicad of *mp-cua*.

Makrosala venusta Chen & Wang sp. nov.

(urn:lsid:zoobank.org:act:F0F03065-D199-453E-9BCA-6336A7349FE9)
Figs. 1B, 6-10

Material. Holotype: NIGP172742, a female adult insect in an amber piece, with apical parts of wings and ovipositor destroyed.

Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; mid-Cretaceous.

Etymology. The specific epithet is derived from the Latin "*venusta*" (meaning charming), and also refers to "*Venus de Milo*", indicating the partly destroyed wings of the holotype.

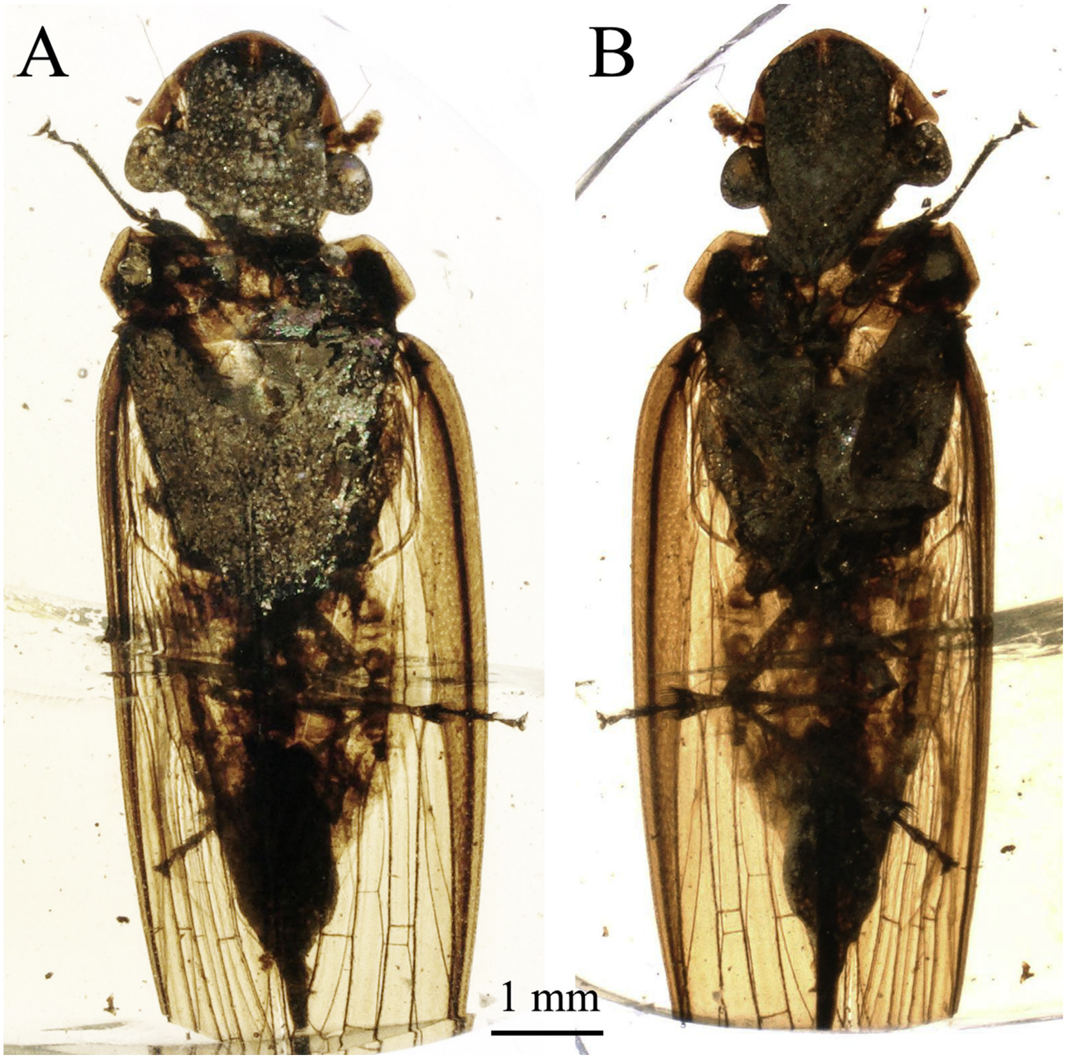

Fig. 6. Photos of holotype of *Makrosala venusta* Chen & Wang gen. et sp. nov. (A), dorsal view; (B), ventral view. All to scale bar.

Diagnosis. Crown with length/width ratio about 0.71 (vs. crown with length/width ratio about 0.87 for *M. elegans*). Compound eyes produced, elliptical, inner margin not concave (vs. compound eyes distinctly elongate, not produced, reniform, with inner margin concave). Postclypeus shortened, with base not reaching anterior margin of head (vs. postclypeus long, with base almost reaching anterior margin of head for *M. elegans*). Mesonotum apparently narrower than head (vs. Mesonotum slighter wider than head for *M. elegans*). Tegmen with postcostal cell wider than cell between CA and Pc + CP; crossvein *ir* absent or distinctly apicad of *imp*; crossvein *rp-mp* obviously basad of *imp*; crossvein *mp-cua* apparently apicad of termination of CuA_2 (vs. tegmen with postcostal cell narrower than cell between CA and Pc + CP; crossvein *ir* just basad of *imp*, and obviously apicad of *mp-cua*; crossvein *rp-mp* obviously apicad of *imp*; crossvein *mp-cua* almost at the same level of termination of CuA_2 for *M. elegans*).

Description. Body with wings in repose as preserved about 10.62 mm long in total (about 12 mm as estimated if complete), 3.98 mm wide.

Head with length about 1.84 mm, width with compound eyes about 2.59 mm, length/width ratio about 0.71. Crown broad, distinctly produced anteriorly; anterior margin rounded and angled medially; disc with tiny granules. Coronal margin before compound eyes thin and expanded; coronal supraantennal ledges well expanded. Ocelli obscure. Compound eyes large and produced, elliptical, inner margin not concave, with length/width ratio about 1.60 in dorsal view. Genae, lora and maxillary not very clear. Postclypeus shortened but broad, with base not reaching anterior margin of head, length/width ratio about 1.72; somewhat depressed; transverse grooves and medial carina not very distinct. Anteclypeus small and oval. Rostrum short and stout, just extending beyond procoxae; labium broken. Antenna with antennal pit shallow; scape shorter but obviously thicker than pedicel; flagellum long, filiform, with basal two segments much thicker than others, joints between other segments obscure.

Pronotum shortened, about 0.95 mm long in midline and about 3.32 mm wide, widest at its lateral angles, with length/width ratio about 0.29; disc with tiny granules; anterior margin slight concave in middle, but strongly concave laterally; anterolateral angles rounded; anterolateral margins smoothly convex; lateral angles obtuse; posterolateral margins slightly convex, oblique, slightly shorter than anterolateral ones; posterolateral angles obtuse;

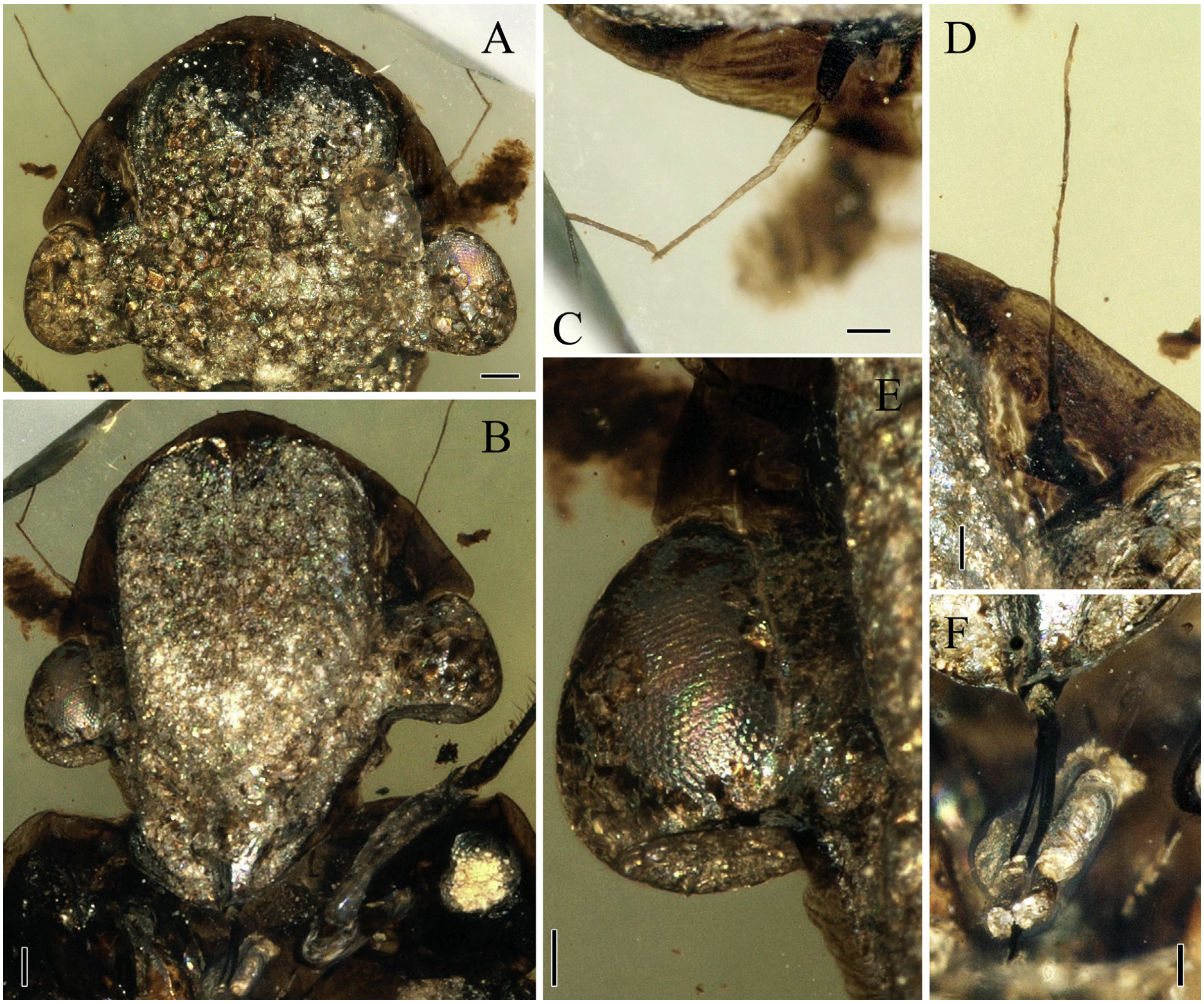

Fig. 7. Photos of head of *Makrosala venusta* Chen & Wang gen. et sp. nov., holotype. (A), dorsal view; (B), ventral view; (C), right antenna; (D), left antenna; (E), right compound eye; (F), rostrum. Scale bars = 0.2 mm (A, B), 0.1 mm (C–F).

posterior margin slightly concave, shorter than anterior one. Mesonotum large, about 1.54 mm long in midline, and 2.24 mm wide, with length/width ratio about 0.69, apparently narrower than head; disc with tiny granules; lateral margin obviously concave near scutellum; posterior angle of scutellum very acute. Prothoracic legs with coxa thick; trochanter much slenderer than coxa; femur not very thick, about 2/3 length of tibia; tibia densely covered with long setae; tarsus covered with long setae, with apical tarsomere enlarged apically and longer than basi- and midtarsomere; tarsal claws large, arolium not distinctly expanded, bilobate and shallowly incised. Mesothoracic legs with coxae very large, nearly triangular, and close to each other; trochanter slender; femur almost as long as tibia, much thicker than profemora; tibia densely covered with long setae; tarsus covered with long setae, with three tarsomeres not well preserved; tarsal claws large, arolium not distinctly expanded, bilobate and shallowly incised. Metathoracic legs with coxa very large, nearly triangular, right and left coxae close to each other; trochanter slender; femur long but slender, about 2/3 as long as tibia; tibia much slenderer than femur, covered with very long setae, lateral spines with long subapical hair arranged in two rows, with one and two in number for each row, double rows of about 15 apical teeth, with teeth in apical row with extremely strong subapical setae; tarsus ventrally with dense long setae, basitarsomere much longer than mid- and apical tarsomeres, and basi-and midtarsomeres with seven apical teeth with extremely strong apical setae arranged in one row; tarsal claws large, arolium well-developed, widely bilobate and deeply incised. Abdomen not well preserved. Pygofer extremely developed, long and swollen. Ovipositor very long and ensiform, with distal part destroyed, densely covered with long hairs. Anal tube and its apical process obscure.

Tegmen with distal part destroyed; length as preserved 7.41 mm (approximately 10 mm as estimated if complete), width 2.54 mm. Clavus and costal area much more punctate and sclerotized than other parts. Costal margin strongly arched at wing base, then almost straight; claval margin strongly arched; postclaval margin nearly straight. Cell between CA and Pc + CP relatively broad and very long. Postcostal cell long, narrow, but wider than cell between CA and Pc + CP. Basal cell long, relatively broad. Clavus relatively broad. Pc + CP extremely long. bScP fused with Pc + CP basally, independent bScP relatively long, migrated to R + MP + CuA and fused with the latter basad of middle of basal cell. ScP + R short, about 4/5 length of MP. ScP + RA long and slightly curved for preserved part, and gradually close to Pc + CP. RP long, distinctly

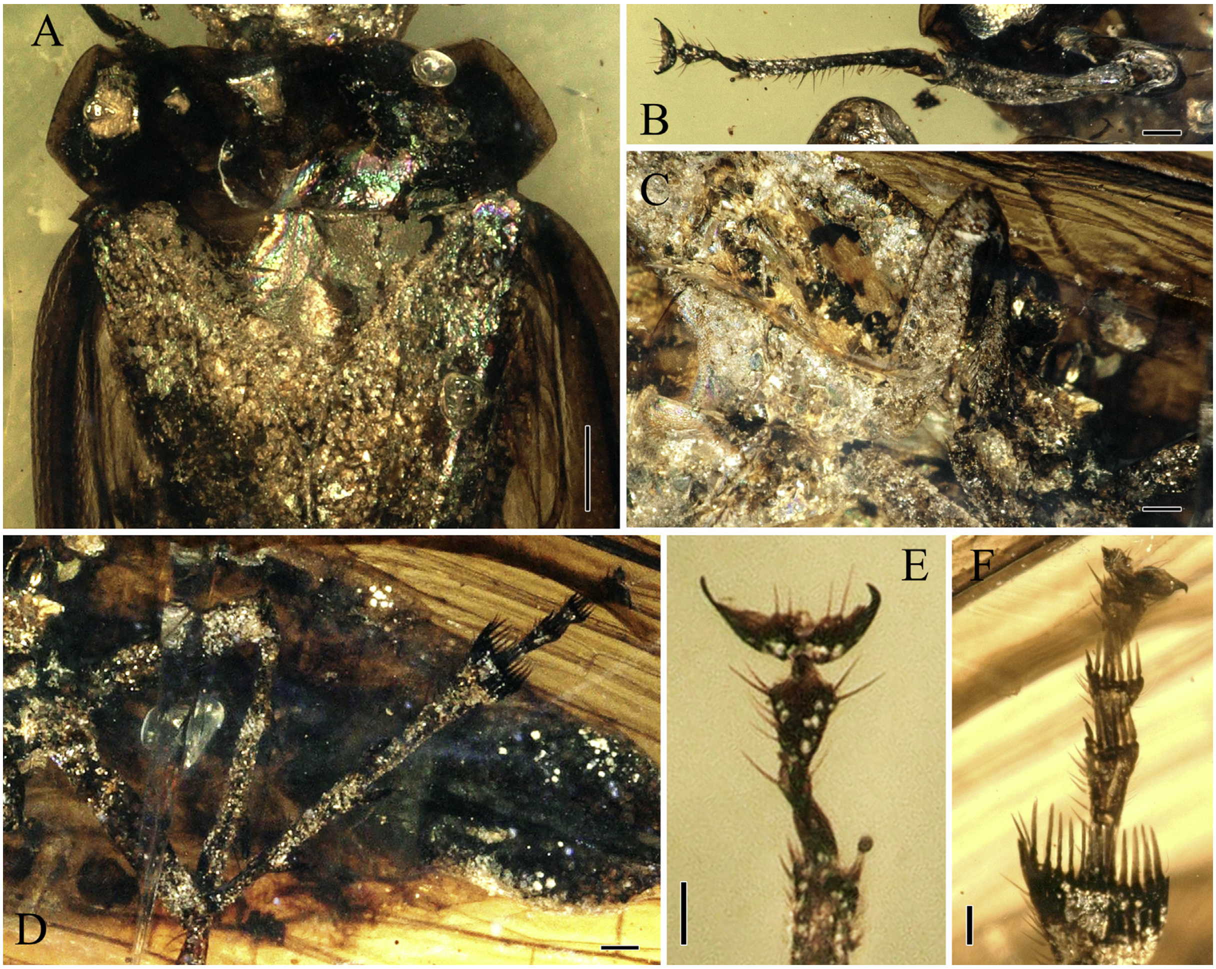

Fig. 8. Photos of thorax of *Makrosala venusta* Chen & Wang gen. et sp. nov., holotype. (A), pronotum and mesonotum; (B), left prothoracic leg; (C), left mesothoracic leg; (D), right metathoracic leg; (E), enlarged apical tibia and tarsus of right prothoracic leg; (F), enlarged apical tibia and tarsus of right metathoracic leg. Scale bars = 0.5 mm (A), 0.2 mm (B–D), 0.1 mm (E, F).

curved at base, and nearly straight for remaining part. Common stalk MP + CuA extremely short, bifurcating into MP and CuA at apex of basal cell. MP almost straight and longitudinal, slightly longer than ScP + R, branching into MP_{1+2} and MP_{3+4} apicad of bifurcation of ScP + R. MP_{1+2} and MP_{3+4} very long, and subparallel for preserved part. CuA strongly curved at base, then nearly straight, and branching into CuA_1 and CuA_2 apicad of bifurcation of MP; CuA_1 much longer than CuA_2. CuP nearly longitudinal, smoothly curved near connection with its crossvein *cua-cup*, then inclined and nearly straight. Pcu slightly sinuous, subparallel to CuP. A_1 long and nearly straight. Crossvein *cua-cup* connecting MP + CuA at its forking into M and CuA. Crossvein *ir* absent or distinctly apicad of *imp* (as estimated). Crossvein *rp-mp* obviously basad of *imp*. Crossvein *mp-cua* apparently apicad of termination of CuA_2.

Hind wing destroyed apically. ScP + R not very long, shorter than RP. Independent ScP extremely short. RA and RP slightly sinuous. MP slightly sinuous and subparallel to RP. CuA with preserved part straight, bifurcating into CuA_1 and CuA_2 slightly apicad of separation of ScP. CuA_1 smoothly curved and CuA_2 straight, CuA_1 about half length of the latter. Crossvein *ir* absent. Crossvein *rp-mp* slightly apicad of termination of CuA_2 and *mp-cua*.

4. Discussion

Sinoalidae, possessing a mixture of derived morphological characteristics and ancestral features shared with primitive Clypeata groups (Hylicelloidea and Jurassic Procercopidae), has been documented in the late Middle to early Late Jurassic Yanliao Biota and the mid-Cretaceous Kachin amber biota (Hong, 1983; Wang et al., 2012; Chen et al., 2017, 2018, 2019a). To date, with more than 15 genera included, this lineage is now the most diverse at generic level among the three extinct families (Sinoalidae, Procercopidae Handlirsch, 1906 and Cercopionidae Hamilton, 1990) of Cercopoidea. Sinoalids in Kachin amber likely constitute a monophyletic group with some derived features distinctly different from their Jurassic confamilials, such as the crown broad, produced anteriorly with its anterior margin possessing angular apex, coronal supraantennal ledges distinct, lateral spines on metatibiae reduced in number and piliferous, the pronotum commonly shortened, and tegmina with cell between Pc + CP broad and postcostal cell extremely long with apex at the same level or apicad of termination of CuA_2 (Chen et al., 2018, 2019b, c, d).

Makrosala elegans Chen & Wang gen. et sp. nov. and *M. venusta* Chen & Wang gen. et sp. nov. described herein bear a body size

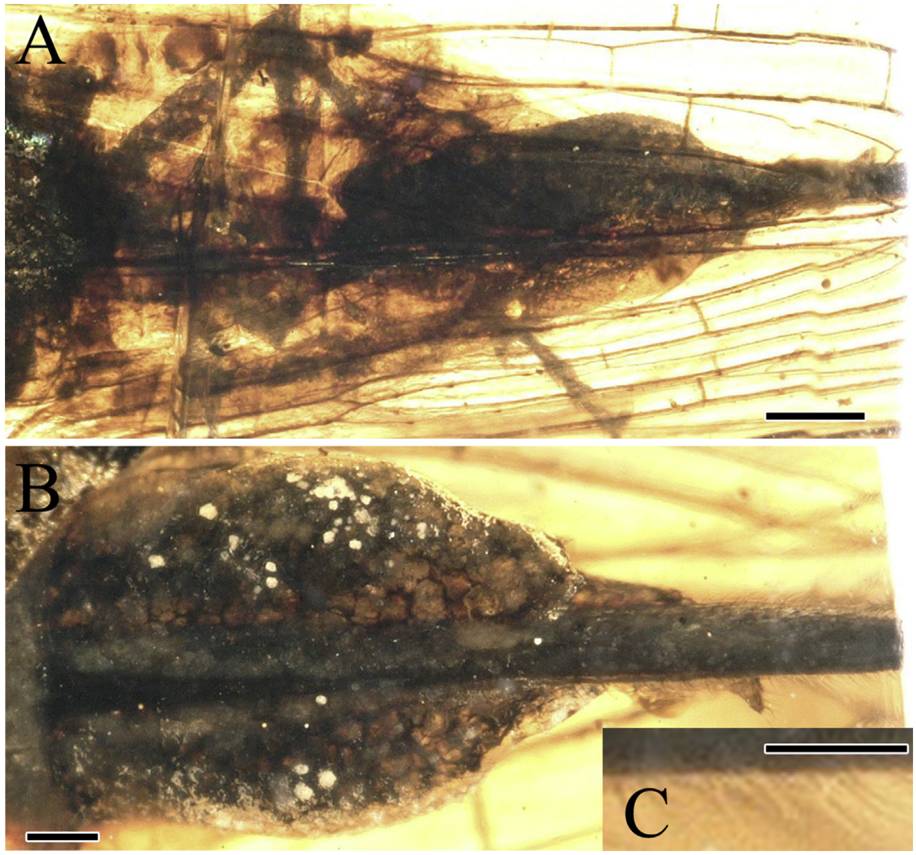

Fig. 9. Photos of abdomen of *Makrosala venusta* Chen & Wang gen. et sp. nov., holotype. (A), dorsal view; (B), pygofer in ventral view; (C), enlarged part of ovipositor, showing dense hairs. Scale bars = 0.5 mm (A), 0.2 mm (B), 0.1 mm (C).

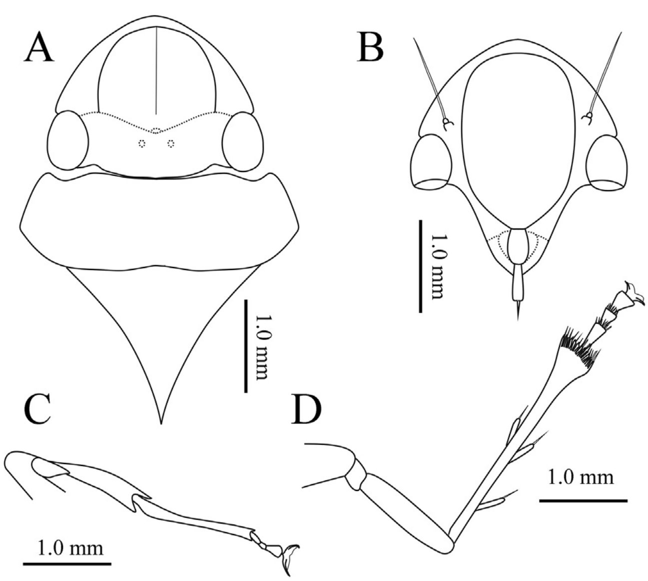

Fig. 10. Line drawings of *Makrosala venusta* Chen & Wang gen. et sp. nov., holotype. (A), head and thorax in dorsal view; (B), face; (C), left prothoracic leg; (D), right metathoracic leg. All to scale bars.

similar to most sinoalids in the Jurassic Yanliao Biota, which are much larger than known sinoalids trapped in Kachin amber (Fig. 11). The two new species share some common characteristics as mentioned above with the previously reported sinoalids in Kachin amber, but differs from the latter in the following characters: the body much large in size; the pronotum with anterior margin greatly concave laterally and surrounding posterior margin of compound eyes; tegmina long and slender, with cell between CA and Pc + CP extremely broad, postcostal cell extremely narrow, and bifurcation of longitudinal veins (ScP + R, MP and CuA) migrated to wing base, leading to very long veins ScP + RA, RP, MP_{1+2}, MP_{3+4}, CuA_1 and CuA_2. Hence, our finding provides some novel knowledge about the morphological diversity of Sinoalidae in mid-Cretaceous Kachin amber.

Up to now, seven sinoalid genera have been reported in Kachin amber (Appendix 1), making it the hitherto known most abundant and diverse cicadomorphan group in this amber biota. The new genus shares a series of critical features with *Fangyuania* Chen, Szwedo and Wang, 2018 (Chen et al., 2018), e.g., the crown very broad, with anterior margin relatively rounded, coronal supra-antennal ledges well expanded, the pronotum extremely shortened, and tegmina with the common stalk of MP + CuA present but very short and connecting crossvein *cua-cup* at its bifurcation, suggesting that these two genera might be closely related. However, the new genus can be discriminated from *Fangyuania* by a series of novel traits as mentioned above.

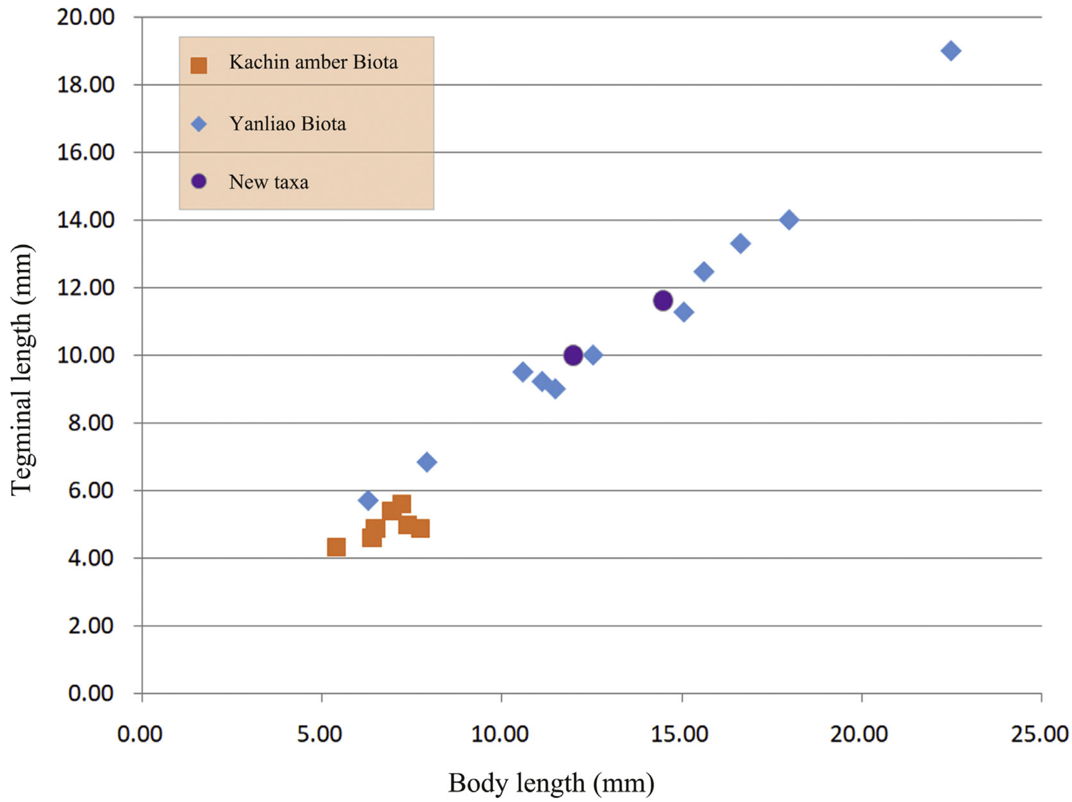

Fig. 11. Scatter plots showing average body and tegminal length of each sinoalid species. All sinoalids with data on both body and tegminal length available were included in the analysis, and the body and tegminal length of *Makrosala venusta* are estimated in complete length.

5. Conclusions

Amber affords exceptional preservation of insects and other microorganisms (Chen et al., 2016), and it is unsurprising that compared to their Jurassic relatives preserved in rock, sinoalids contained in Kachin amber generally bear much smaller body, since tree resin drops are commonly small and large insects could be strong and quick enough to escape (Ross, 1997; von Tschirnhaus and Hoffeins, 2009). *Makrosala* Chen & Wang gen. nov. described herein with a relatively large body suggests that all formerly reported sinoalid froghoppers in Kachin amber belonging to very small insects results from the taphonomical bias. Different factors, such as body size, behavior and habitat preferences, and resin chemistry and viscosity, may influence the preservation of insects in amber (Martínez-Delclòs et al., 2004). Recent trapping experiments in tropical forests suggested that composition of arthropods in modern resins and Miocene amber is mainly influenced by habitat and ecological biases (Solórzano Kraemer et al., 2015, 2018). However, compared to Cenozoic ambers, a predominance of smaller organisms was revealed in Cretaceous ambers (Poinar, 1992; Martínez-Delclòs et al., 2004). The Burmese amber is now recognized as a significant window to the Cretaceous world (Shi et al., 2012; Kania et al., 2015; Dunlop et al., 2018), and taphonomical biases should be kept in mind when studying the ecology, biodiversity, and community composition and structure of this amber palaeo-biota.

CRediT authorship contribution statement

Jun Chen: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **Bo Wang:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **Yan Zheng:** Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Hui Jiang:** Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Yuling Li:** Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Tian Jiang:** Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Haichun Zhang:** Conceptualization, Supervision, Visualization, Writing - original draft, Writing - review & editing.

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Appendix 1. Geographical and stratigraphic distribution of the family Sinoalidae. J2 Middle Jurassic; J3: Upper Jurassic; K2: Upper Cretaceous

Horizon	Locality	Taxon
Cenomanian (K2)	Hukawng Valley, Kachin, Myanmar	*Fangyuania xiai* Chen, Szwedo and Wang, 2018; *Jiaotouia minuta* Chen and Wang, 2019; *Ornatiala amoena* Chen, Wang and Zhang, 2019; *Ornatiala kachinensis* Chen, Zheng, Wei and Wang, 2020; *Mesolongicapitis peii* Chen, Zhang and Wang, 2019; *Mesodorus orientalis* Chen and Wang, 2019 *Paraornatiala daidaleos* Fu and Huang, 2019a, b, c; *Cretosinoala tetraspina* Fu and Huang, 2019a, b, c; *Makrosala elegans* Chen & Wang gen. et sp. nov.; *Makrosala venusta* Chen & Wang gen. et sp. nov.
Callovian-Oxfordian (J2-J3)	Daohugou, Ningcheng, Inner Mongolia, China	*Luanpingia daohugouensis* Fu et al, 2017; *Luanpingia youchongi* Fu and Huang, 2019a, b, c; *Sinoala parallelivena* Wang and Szwedo, 2012; *Jiania crebra* Wang and Szwedo, 2012; *Jiania gracila* Wang and Szwedo, 2012; *Shufania hani* Chen et al, 2017; *Stictocercopis wuhuaensis* Fu and Huang, 2018; *Juroala daohugouensis* Chen and Wang, 2019; *Juroala minuta* (Fu and Huang, 2019a, b, c); *Juroala daidaleos* (Fu and Huang, 2019a, b, c)
	Zhouyingzi, Luangping, Hebei, China	*Luanpingia longa* Hong, 1983; *Hebeicercopis triangulata* Hong, 1983; *Huabeicercopis yangi* Hong, 1983
	Xiaofanzhangzi, Chengde, Hebei, China	*Chengdecercopis xiaofanzhangziensis* Hong, 1983