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Short communication

The youngest record of the leafhopper family Archijassidae in Kachin amber from the lowermost Upper Cretaceous of northern Myanmar (Cicadomorpha, Cicadelloidea)

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ABSTRACT

The Mesozoic hemipteran family Archijassidae, known from the Late Triassic to the Early Cretaceous, is recorded as the ancestral group of mega-diverse leaf- and treehoppers. On the basis of a fossil contained in Kachin amber from the lowermost Upper Cretaceous of northern Myanmar, we herein erect a remarkably new taxon, *Formosixinia aeterna* Chen & Wang, gen. et sp. nov. The new genus and species can be assigned to Archijassidae based upon a series of body and wing characteristics, but also displays some unique traits, making it distinctly different from all known archijassids and even quite unique within Cicadelloidea. Our finding not only reveals the youngest record of Archijassidae but also the first representative of this family in amber, and it further provides some novel information on the morphological disparity and evolutionary history of early leafhoppers.

1. Introduction

Leafhoppers, treehoppers and relatives (Cicadomorpha: Membracoidea *s.l.*), with approximately 25,000 living species covering nearly one-third of hemipterans, constitute an extremely mega-diverse insect lineage (McKamey, 1998, 2002; Dietrich et al., 2017; Bartlett et al., 2018). With well-developed piercing-sucking mouthparts, leaf- and treehoppers are plant fluid (phloem, xylem and parenchyma) feeders, just as other true hoppers (Backus, 1988; Dietrich et al., 2017). This cicadomorph group distinctly differs from other insects in possessing specialized anointing behavior: It coats body integuments with Malpighian tubule secretion, using extremely long metathoracic legs with strong macrosetae arranged in comb-like rows on tibia (Rakitov, 2002; Shcherbakov, 2012; Rakitov and Gorb, 2013; Bartlett et al., 2018).

The Mesozoic family Archijassidae Becker-Migdisova, 1962, recorded as the most ancient group of Membracoidea *s.l.*, gradually transforms morphologically into modern leaf- and treehopper forms. This family was reviewed in details by Shcherbakov (2012), with three subfamilies recognized: Archijassinae Becker-Migdisova, 1962, possessing a series of primitive characters, was recorded from the Upper Triassic of Australia and the Lower-Middle Jurassic of Eurasia (Handlirsch, 1906–1908; Tillyard, 1916, 1919; Ansorge, 1996; Evans, 1956); Karajassinae Shcherbakov, 1992, displaying intermediate morphological features, was reported from the Jurassic to the Lower Cretaceous of Eurasia (Westwood, 1854; Shcherbakov, 1992, 2012); and Dellasharinae Shcherbakov, 2012, as the ancestral group of modern leaf- and treehoppers, was discovered from the Upper Jurassic of Asia and the Lower

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Cretaceous of Eurasia (Meunier, 1904; Handlirsch, 1907; Zhang, 1985; Shcherbakov, 1986, 2012).

We herein describe a new archijassid leafhopper, *Formosixinia aeterna* gen. et sp. nov., in Kachin amber from the lowermost Upper Cretaceous (~100 Ma) of northern Myanmar. The new genus and species, as the youngest record of Archijassidae as well as its first known representative in amber, shares a series of plesiomorphies with Archijassidae, displays some derived morphological characteristics as in modern leafhoppers, and also bears some intriguing unique autapomorphies, providing novel insights into the evolutionary history and morphological disparity of the stem group of leaf- and treehoppers.

2. Material and methods

The new archijassid leafhopper was trapped in a yellow and transparent Burmese amber piece from Kachin Province, northern Myanmar (See locality in Fig. 1 of Chen et al., 2019c). This specimen (NIGP171102) is housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences. Amber pieces, affording exceptional three-dimensional preservation of organisms, often provide more morphological details as well as more evidence on ephemeral behaviors than rock fossils (Chen et al., 2016). The Kachin amber biota has been a significant window to mid-Cretaceous ecosystems, with more than 1000 extinct species reported (Cruickshank and Ko, 2003; Shi et al., 2012; Kania et al., 2015; Ross, 2019; Chen et al., 2019b). The age of Kachin amber is now confirmed as mid-Cretaceous (earliest Cenomanian; 98.79 ± 0.62 Ma) on the basis of U-Pb zircon dating analysis, supported by biostratigraphical evidences (Grimaldi et al., 2005; Shi et al., 2012).

The amber piece was re-cut and polished to show more morphological details. A VHX 5000 digital microscope platform was used to check, photomicrograph and measure the specimen. Line drawings and illustrations of tegmen and hind wing were prepared using image-editing software CorelDraw 12.0 and Adobe Photoshop CS3.

The taxonomic framework employed herein follows Szwedo (2018), in which the updated higher-level systematics of fossil and living Hemiptera was provided: within Clypeata Qadri, 1967, Cicadelloidea Latreille, 1802 (leafhoppers) was resurrected as an independent superfamily, with extinct Archijassidae Becker-Migdisova, 1962 and extant Cicadellidae Latreille, 1802 included, and is treated to be independent of Membracoidea Rafinesque, 1815 *s.s.* (treehoppers) and Myerslopioidea Evans, 1957. Membracoidea *s.l.*, however, is used herein including Cicadelloidea, Myerslopioidea and Membracoidea *s.s.* in some sections for convenience of expression. It is worth mentioning that Ulopidae Le Peletier and Audinet-Serville, 1825, as an independent family of Membracoidea *s.s.* in Szwedo (2018), together with the leafhopper subfamily Megophthalminae Kirkaldy, 1906, is sister to or form a paraphyletic grade subtending the treehopper lineage (Membracoidea *s.s*) in the phylogenetic trees inferred from a recent phylogenomic analyses of Membracoidea *s.l.* (Dietrich et al., 2017); therefore, their classificational rank (two families of Membracoidea or Cicadelloidea, or two subfamilies of Cicadellidae) is pending further study.

Venational terminology used herein mainly follows Chen et al. (2018), which is slightly modified from Nel et al. (2012) and Bourgoin et al. (2015).

All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic

Fig. 1. Photographs of holotype of *Formosixinia aeterna* Chen & Wang, gen. et sp. nov. (NIGP171102). (A), dorsal view; (B), ventral view; (C), lateral view. Scale bars = 1.0 mm.

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3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Cicadomorpha Evans, 1946
Superfamily Cicadelloidea Latreille, 1802
Family Archijassidae Becker-Migdisova, 1962

Genus ***Formosixinia*** Chen & Wang, gen. nov
(urn:lsid:zoobank.org:act:C3C7BEBD-BBC3-4712-8201-306D05DFFF25).
Type species: *Formosixinia aeterna* Chen & Wang, sp. nov.; by present designation and monotypy.

Etymology. The generic name is from the Latin "*formosus*" (beautiful) and the Mandarin "*xin*" (heart), referring to the beautiful heart-shaped head in dorsal view; gender feminine.
Diagnosis. Head with a narrow and thin process anteriorly, heart-shaped in dorsal view. Mesonotum with five distinct longitudinal carinae; metalegs with tibia bearing with macrosetae arranged in AD and PD rows extremely strong and in AV and PV rows much slender. Tegmen with wing base contractive in width and petiole-like; bifurcation of MP and CuA almost at same level. Hind wing with Pcu and A_1 fused basally and connected to each other at a point after division from stem Pcu+A_1.

Formosixinia aeterna Chen & Wang, gen. et sp. nov.
(urn:lsid:zoobank.org:act:7A237B92-6117-4BB4-A5CD-01CCD88486AD).
Figs. 1–7.

Material. Holotype NIGP171102: an adult female insect trapped in an amber piece, with right tegmen and hind wing at top of body and left wings outspread.
Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; lowermost Cenomanian, lowermost Upper Cretaceous.
Etymology. The specific epithet is the Latin word "aeterna" (eternal).
Diagnosis. As for genus as it is the only so far included species.
Description. Body dark in colour, 8.99 mm long as preserved.
Head. Head 0.43 mm long in midline and 2.52 mm wide with compound eyes, heart-shaped in dorsal view, with a short and narrow head process anteriorly; disc rough; anterior margin strongly convex and posterior margin strongly concave. Ocelli? on vertex, two in number, very close to midline of crown and almost touching pronotum. Compound eyes large, surrounding antero-lateral angles of pronotum. Face somewhat obscure and slightly deformed. Antennal pit shallow; scape apparently thicker but shorter than pedicel; flagellum relatively short, somewhat filiform, with basal part thicker. Postclypeus not extending onto crown,

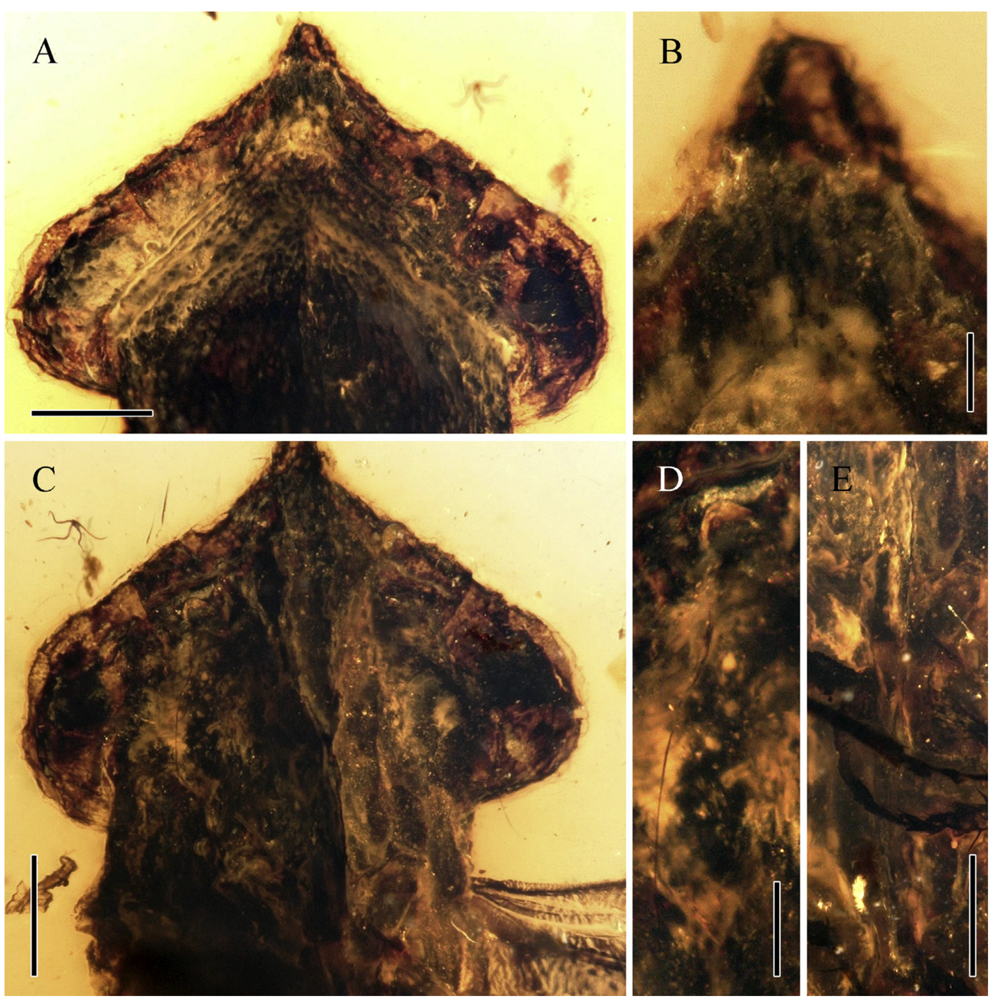

Fig. 2. Head of holotype of *Formosixinia aeterna* Chen & Wang, gen. et sp. nov. (NIGP171102). (A), crown in dorsal view; (B), face in ventral view; (C), enlarged head anterior process in dorsal view; (D), right antenna; (E), rostrum. Scale bars = 0.5 mm (A, C, E), 0.1 mm (B), and 0.2 mm (D).

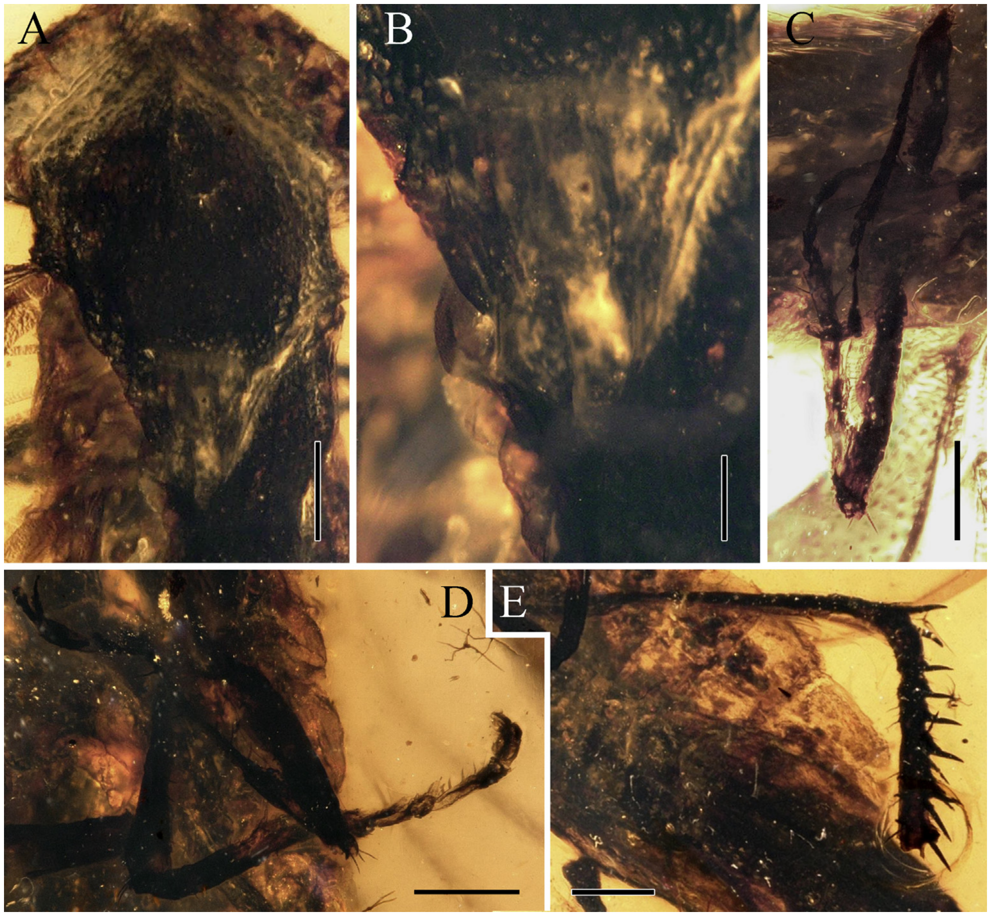

Fig. 3. Thorax of holotype of *Formosixinia aeterna* Chen & Wang, gen. et sp. nov. (NIGP171102). (A), pronotum and mesonotum; (B), enlarged mesonotum, showing longitudinal carinae; (C), prothoracic legs; (D), mesothoracic legs; (E), right metathoracic leg. Scale bars = 0.5 mm (A, C-E) and 0.2 mm (B).

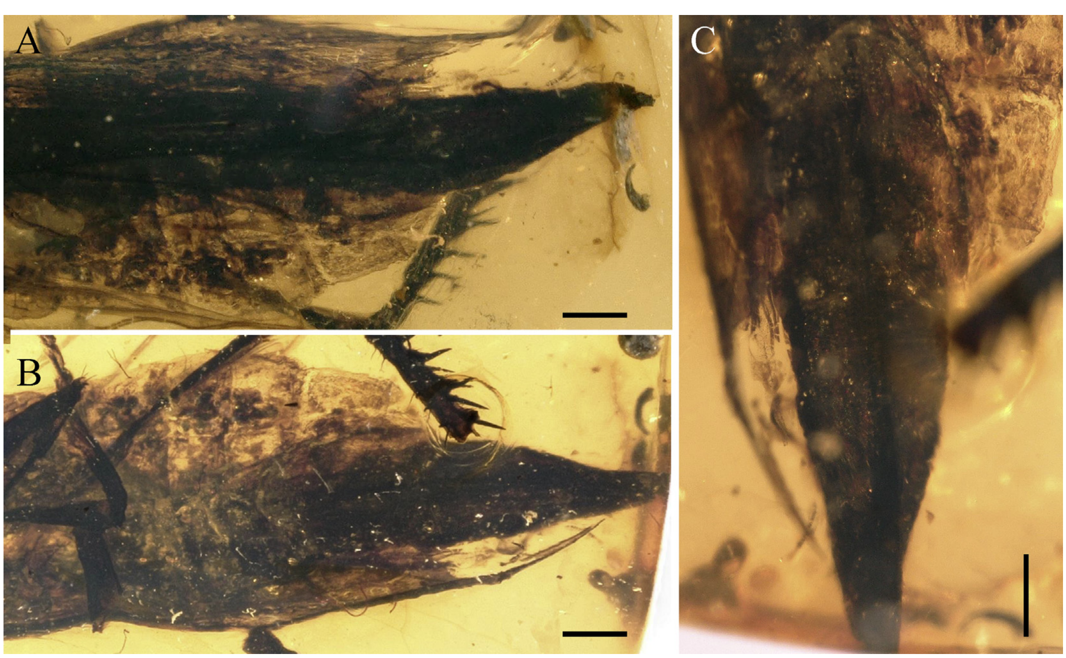

Fig. 4. Abdomen of holotype of *Formosixinia aeterna* Chen & Wang, gen. et sp. nov. (NIGP171102). (A), dorsal view; (B), ventral view; (C), enlarged pygofer in ventral view. Scale bars = 0.5 mm.

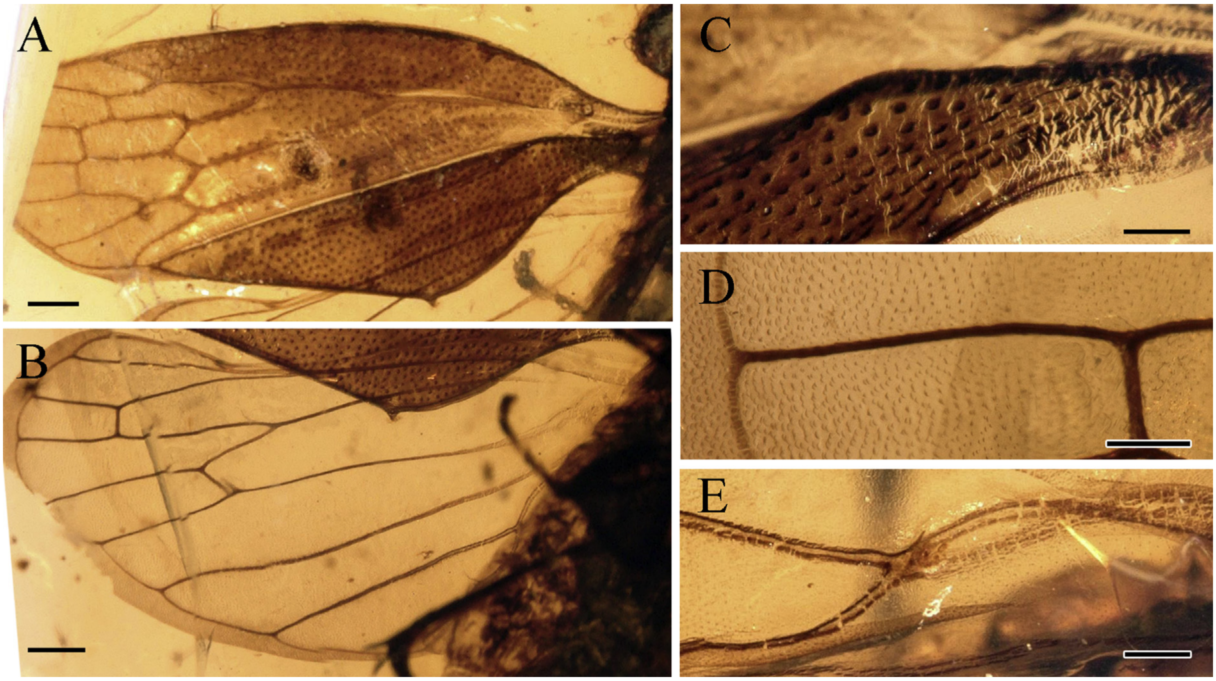

Fig. 5. Left tegmen and hind wing of holotype of *Formosixinia aeterna* Chen & Wang, gen. et sp. nov. (NIGP171102). (A), tegmen; (B), hind wing; (C), enlarged basal part of tegminal stem Pcu; (D), enlarged part of hind wing, showing granulated membrane; (E), enlarged part of hind wing, showing Pcu and A_1 connected at one point. Scale bars = 0.5 mm (A, B) and 2 mm (C–E).

broad, without distinct transverse grooves. Anteclypeus, genae and lora not very clear. Rostrum long, extending to hind coxae.

Thorax. Pronotum 1.99 mm long, 1.66 mm wide, longest at midline, narrower than head, extremely expanded, inflated; disc distinctly punctate; anterior margin strongly convex and embedded in crown, anterolateral angles round, surrounded by posterior part of inner margin of compound eyes; anterolateral margins slightly concave, short; lateral angles obtuse; posterolateral margins slightly longer than anterolateral margins, smoothly concave; posterolateral angles obtuse; posterior margin slightly concave,

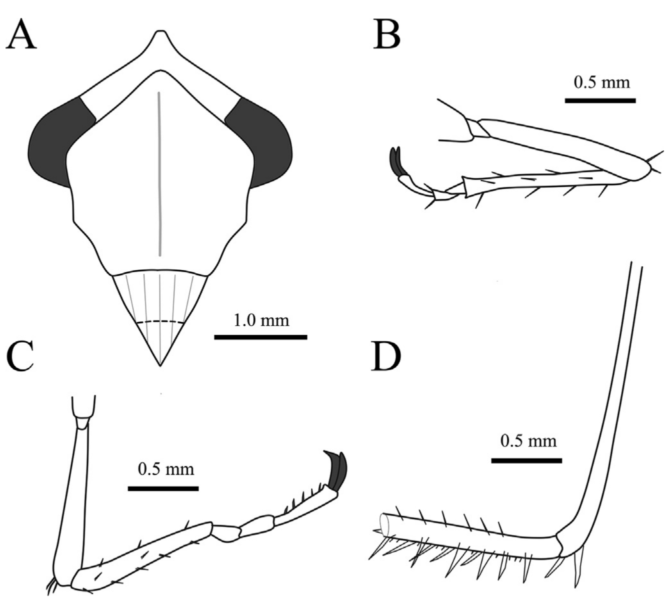

Fig. 6. Line drawings of body structures of holotype of *Formosixinia aeterna* Chen & Wang, gen. et sp. nov. (NIGP171102). (A), head and thorax in dorsal view; (B), left prothoracic leg; (C), right mesothoracic leg; (D), left metathoracic leg. All to scale.

nearly as long as anterolateral ones. Mesonotum largely covered by pronotum, 1.05 mm long with scutellum, 0.83 mm wide; disc with five distinct carinae, and extending to scutellum; mesoscutal sulcus not very distinct, depressed. Prothoracic legs with coxa strong; trochanter much slenderer; femur strong, with two strong apical macrosetae; tibia slenderer than femur, sparsely covered with lateral macrosetae; tarsus with apical tarsomere about twice as long as basi- and midtarsomere; tarsal claws extremely long, almost as long as apical tarsomere. Mesothoracic legs with coxa strong; trochanter much slenderer; femur strong, with three apical macrosetae; tibia slenderer than femur, sparsely covered with lateral macrosetae; tarsus with apical tarsomere covered with strong macrosetae, much longer than basi- and midtarsomere; tarsal claws well developed, about 2/3 as long as apical tarsomere. Metathoracic legs with only right one partly preserved, with coxa and trochanter obscure; femur relatively slender but very long, with two extremely strongly apical macrosetae as preserved; tibia with only basal part preserved, thicker than femur, possessing four rows of macrosetae with ones arranged in AD and PD rows extremely strong, and ones arranged in AV and PV rows much slenderer; tarsus and tarsal claws destroyed.

Abdomen. 4.48 mm in length as preserved, 2.28 mm in width, slightly wider than thorax and narrower than head. Pygofer long, about half of length of abdomen as preserved. Ovipositor well developed, ensiform, with apex slightly destroyed.

Tegmen (left). Tegminal apex destroyed, 6.83 mm in length as preserved, 2.66 mm in width, widest near middle of clavus. About basal 2/3rds part punctate and more sclerotized and apical 1/3rds part membranous. Basal cell narrow. Six apical cells present as preserved. Three subapical cells present. Wing base contractive in width, petiole-like, with distinct outer membrane at its posterior margin. Costal and claval margin arched and forming carinae. Narrow appendix present on apical margin, extending to apical part of clavus. Costal area long but narrow. Clavus slightly shorter but much broader than costal area. CP present. Stem R+MP long, about

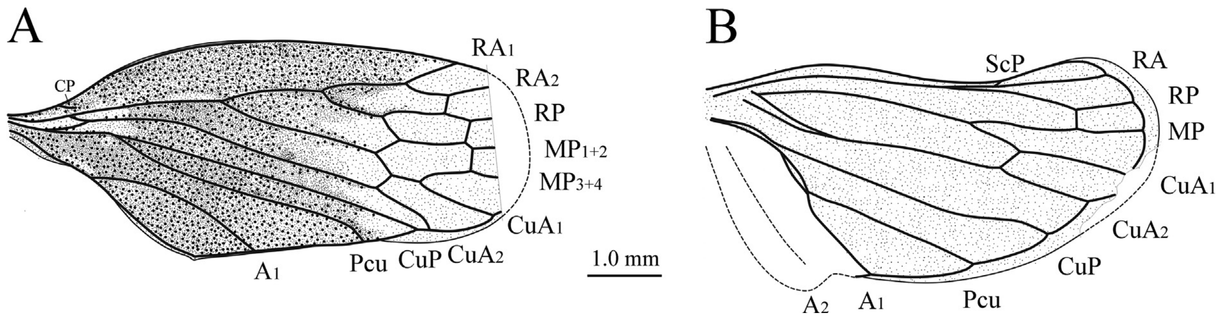

Fig. 7. Illustration of left tegmen and hind wing of holotype of *Formosixinia aeterna* Chen & Wang, gen. et sp. nov. (NIGP171102). (A), tegmen (reversed); (B), hind wing (reversed). All to scale.

twice as long as stem R. Stem R nearly straight, slightly longer than RA. RA_1 straight, shorter than RA and RA_2. RP sinuous, connected to RA_2 by crossvein *ir* and to MP_{1+2} by two *rp-mp* crossveins. Stem MP nearly straight, oblique, bifurcating into MP_{1+2} and MP_{3+4} almost at same level of connection of basal crossvein *r-mp* with RP. MP_{1+2} geniculate at its connection with crossveins. MP_{3+4} straight basally, subsequently fused with CuA_1 for long distance, and then becoming independent and connected to MP_{1+2} by crossvein *imp*. Stem CuA smoothly arched for basal half and, nearly straight for distal half, branching into CuA_1 and CuA_2 almost at same level of bifurcation of MP. CuA_1 much longer than CuA_2. CuP long and straight. Pcu strongly curved for about basal 3/10ths, greatly cocked, lamellar, covering basal part of CuP; smoothly curved for about middle 6/10ths; and strongly arched sub-apically. A_1 long, smoothly arched. Hind wing (left). Outer margins slightly destroyed, 6.48 mm in length, 3.86 mm in width as preserved. Appendix wide. Membrane densely covered with tiny granules. Peripheral vein distinctly concave at terminal points of longitudinal veins. Stem ScP+R long and smoothly arched, forking into ScP+RA and RP at basal 0.53 wing length. Independent ScP short. RA almost longitudinal and straight. RP geniculate at connection with crossvein *rp-mp*, longer than RA. MP fused with CuA basally, sinuous, connected to CuA_1 by crossvein *mp-cua*. CuA very broad for about basal 1/4th, bifurcating at basal 0.68 wing length. CuA_1 geniculate at connection with crossvein *mp-cua*, longer than CuA_2. CuP long and sinuous. Pcu fused with A_1 basally, connected to A_1 at point at basal 0.24 wing length after its separation from Pcu+A_1 at basal 0.20 wing length. A_1 shorter than Pcu.

4. Discussion

Archijassidae, as the most ancient group of Membracoidea *s.l.*, displays a series of gradual morphological transforms from plesiomorphies to derived traits shared with modern leaf- and treehoppers (Shcherbakov, 2012). Its subfamily Dellasharinae was considered by Shcherbakov (2012) to be the transitional unit from ancient archijassids to modern forms. *Formosixinia* gen. nov. can be compared to this subfamily with the following characteristics: the metatibia with well-developed macrosetae lacking prominent bases; the tegmen with a narrow costal area, at least (most probably) six apical cells, three subapical cells, and a distinct anastomosis replacing crossvein *mp-cua* in MP_{3+4} and CuA_1; the hind wing with RA long and MP_{3+4} completely fused to CuA_1, and five apical cells. However, the new taxon bears a series of deviant apomorphies, and also some derived characters as displayed in modern leafhoppers, e.g., the postclypeus not extending onto the crown and a long stalk of R+MP in tegmen; therefore, we tentatively treated it as subfamily *incertae sedis* in the present study. Further studies based on additional fossil materials are needed to determine whether the characters shared by the new taxon and modern leafhoppers are homologous or just the results of convergent evolution.

Although sharing a series of morphological features with other reported archijassids (Shcherbakov, 2012), *Formosixinia* gen. nov. shows some novel traits, making is distinctly different from know Archijassidae and even unique within all extinct and living leaf- and treehoppers. The most striking feature of the new taxon is the shortened head with a short process anteriorly, and heart-shaped in dorsal view (Fig. 2A); to our knowledge, the characteristic is at least unique in cicadomorph insects. The new genus bears another intriguing trait that the tegminal base is somewhat petiole-like (Figs. 5A, 6A), which is also not common among cicadomorphs. The novel morphological traits present in our new taxon indicate that stem Membracoidea *s.l.* likely evolved multi-dimensionally and showed high disparity in the Mesozoic.

A greatly expanded pronotum is not common within modern Membracoidea *s.l* except treehoppers. In the mega-diverse modern Cicadelloidea, the pronotum is generally shorter than its width. With a few exceptions, however, a quite long pronotum is present and even extended to the scutellar suture in the small subfamily Signoretiinae Baker, 1915, the Cicadellinae: Proconini *Tretogonia* Melichar, 1926 and Typhlocybinae: Dikraneurini *Sweta* Viraktamath & Dietrich, 2011 have a extremely long pronotum (Takiya et al., 2013). The new genus possesses an extremely expanded and inflated pronotum covering most of the mesonotum (Fig. 3A). The pronotum of basal Clypeata (Hylicelloidea, Tettigarctidae, Procercopidae, and Archijassidae) is generally enlarged, covering most of the mesonotum (Shcherbakov, 1988, 2012; Chen et al., 2014), and is likely reduced independently in modern cicadas, leafhoppers, and some froghopper groups.

Anointing, related to a series of specialized morphological, physiological and behavioural adaptations, is shared by modern leafhoppers, treehoppers and relatives, and is unique among insects (Dietrich et al., 2017; Bartlett et al., 2018). Long metathoracic legs with strong macrosetae arranged in comb-like rows on the tibia displayed in karajassines were argued to be correlated to the improvement of jumping abilities, but subsequently were interpreted as adaptations to anointing behavior (Shcherbakov, 1992, 2012). All reported archijassids are preserved as rock imprint fossils, and the holotype of *Formosixinia aeterna* gen. et sp. nov. is the first archijassid contained in amber and three-dimensionally preserved. The number and specialization of metathoracic tibia spines of the new taxon is not so developed as in modern leafhoppers, and the spinulation of prothoracic tibiae is also weak, suggesting that anointing behavior of Mesozoic archijassids was likely still at initial stage: these insects might be just smear body integuments with liquid produced from their Malpighian tubules, but without brochosome distribution as in modern leafhoppers.

5. Conclusions

Like the other two modern cicadomorph groups (i.e., Cicadoidea, Cercopoidea), Membracoidea *s.l.* is widely accepted to be derived from ancient Hylicelloidea in the Late Triassic (Shcherbakov and Popov, 2002; Wang et al., 2012; Chen et al., 2018). A recent anchored hybrid enrichment based phylogenomic analysis of Membracoidea *s.l.* showed that divergence events among most major leafhopper lineages (subfamily level) appeared in the Early to mid-Cretaceous, including the lineage comprising all the three recognized treehopper families (Dietrich et al., 2017). Unfortunately, this mega-diverse insect assemblage has a poor fossil record, with representatives of its modern groups in the Mesozoic still very scanty (Chen et al., 2019a). The Kachin amber biota, with unexpected palaeo-biodiversity, provides significant information about the morphology and evolution of Mesozoic insects. Leafhoppers are abundant and diverse in this amber biota; however, only four genera and species have been recognized by limited studies and attributed to Archijassidae, and Cicadellidae: Coelidiinae, Ledrinae and Signoretiinae, respectively (Poinar and Brown, 2017; Chen et al., 2019a; Wang et al., 2019; this study). With more leafhoppers reported, Kachin amber will add more significant information to the early evolution of this highly diverse insect lineage.

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