A new bizarre cicadomorph family in mid-Cretaceous Burmese amber (Hemiptera, Clypeata)

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ABSTRACT

As the most diversified organismal group, insects evolved countless structural innovations, and some unique ones have vanished in their geological history. We herein report a new true hopper family Minlagerrontidae Chen, Szwedo and Wang fam. nov. with two new species (*Minlagerron griphos* Chen, Szwedo and Wang gen. et sp. nov. and *Minlagerron onyxos* Chen, Szwedo and Wang gen. et sp. nov.) in mid-Cretaceous Kachin amber from northern Myanmar. The new family, tentatively attributed to Hylicelloidea (Clypeata), shares a series of plesiomorphies with ancient Clypeata, and also bears some extremely unusual or even grotesque morphological characteristics, never recorded in other Clypeata, Hemiptera, or even all fossil and living insects. This family possesses a greatly specialized head with tylus extremely broad, compound eyes produced, postclypeus almost transversely rectangular in the middle, with basal half having a deep longitudinal groove medially, and rostrum stout. The anterior part of minlagerrontid prothorax is sharply constricted, forming a unique 'neck' and 'shoulder' structures, and the prothoracic legs are also highly modified with strengthened femora with several lateral teeth and tibiae deviantly club-shaped. The female pygofer of the new family is completely wrapped by tergite VIII and its ovipositor is short and reduced. Additionally, minlagerrontids possess unique tegmina with C5 almost closed, surrounded by terminal branches of CuA, and thick venation reticular with multiple ambient veins ending at anterior margin and crossveins *ir* and *rp-mp* diploid. The new highly specialized family erected herein suggests that in the Mesozoic, to reduce mutual competition, ancient Clypeata had diversified multi-dimensionally and so possibly evolved with high disparity to occupy a wide range of ecotypes.

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1. Introduction

The Hemiptera, one of the Big Five insect orders comprising over 100,000 known species, is an unbelievably successful insect group (Beutel et al., 2014; Gullan and Cranston, 2014; Szwedo, 2018). The high species diversity of hemipterans is believed to correspond to the evolutionary transition from chewing mouthparts of the stem Acercaria to stylet-like sucking-piercing rostrum, allowing them to uptake variable food (Shcherbakov and Popov, 2002; Grimaldi and Engel, 2005; Huang et al., 2016; Szwedo, 2018). The phytophagous 'homopterans' (true hoppers, i.e. planthoppers, froghoppers, singing cicadas, leafhoppers and their extinct allies; sternorrhynchans, i.e. aphids, scale insects, whiteflies, psyllids and their extinct allies) were treated as an independent order or as a suborder within the Hemiptera up to 1990s. However, this taxonomic

name is now generally abandoned because Heteroptera (true bugs) is considered to be derived from the early Cicadomorpha, rendering 'Homoptera' paraphyletic (Shcherbakov and Popov, 2002; Forero, 2008). The Hemiptera is now divided into six suborders (Paleorrhyncha, Fulgoromorpha, Cicadomorpha, Sternorrhyncha and Coleorrhyncha and Heteroptera) (Szwedo, 2018). Although the traditional 'Auchenorrhyncha' (true hoppers; Bartlett et al., 2018), consisting of two monophyletic suborders Cicadomorpha and Fulgoromorpha, shares some morphological characters and ecological habits, its monophyly remains disputed (Sorensen et al., 1995; Cryan and Urban, 2012; Song et al., 2012; Beutel et al., 2014).

The clade Clypeata, constituting all living Cicadomorpha (Cercopoidea, Cicadoidea, Myerslopioidea and Membracoidea *s.l.*) and their common stem group (the extinct superfamily Hylicelloidea), bears a striking feature: 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 (Shcherbakov and Popov, 2002; Wang et al., 2012; Chen et al., 2014; Bartlett et al., 2018). The Clypeata firstly appeared in the terminal Permian, represented by the superfamily Hylicelloidea, and in the early Mesozoic modern cicadomorphan lineages rose in succession and then continued to flourish (Shcherbakov and Popov, 2002; Szwedo, 2018).

Whether it is from the ecological or taxonomic perspective, insects are overwhelmingly more diverse than any other group of organisms on this planet, due to countless structural innovations to adapt to different functional contexts (Stork et al., 2015; Bai et al., 2018). In the present study, we report a weird true hopper family, Minlagerrontidae fam. nov., with its monobasic genus and two new species. The novel extinct family erected herein is from mid-Cretaceous Kachin amber of northern Myanmar and tentatively attributed to Hylicelloidea (Clypeata). The new family displays a series of extremely specialized morphological structures indicating its specific ecological habits and life histories.

2. Material and methods

Three yellow and transparent amber pieces, containing the new fossil Clypeata specimens, were collected from the Hukawng Valley of Kachin Province in northern Myanmar (Kania et al., 2015: fig. 1; Chen et al., 2019). Although Kachin amber has been mined and traded for thousand years (Laufer, 1906; Zherikhin and Ross, 2004; Poinar et al., 2008), most organismal inclusions with valuable scientific significance were described in recent years (Guo et al., 2017; Ross, 2018). With many new groups of plants, fungi, invertebrates and even vertebrates reported in Burmese amber, this amber biota, as one of the most diverse Mesozoic palaeobiotas, is now recognized as a significant window to the mid-Cretaceous ecosystems (Cruickshank and Ko, 2003; Poinar et al., 2008; Shi et al., 2012; Kania et al., 2015; Szwedo and Nel, 2015).

Now, Burmese amber from Kachin Province is biostratigraphically considered to be mid-Cretaceous (e.g., Cruickshank and Ko, 2003; Grimaldi et al., 2005; Ross et al., 2010) and the earliest Cenomanian (98.79 ± 0.62 Ma) based on a recent U-Pb zircon dating study (Shi et al., 2012). However, a slightly older age, late Aptian, was recently postulated (Zheng et al., 2018a) due to the fact that the amber shows evidence of redeposition (Grimaldi and Ross, 2017).

Recently, a new unique amber biota about 72.1 Ma (latest Campanian of the Late Cretaceous; dated using U−Pb zircon geochronology) was reported from Tilin, central Myanmar with chemical components and organismal inclusions quite different from those from Kachin amber, showing a biotic change from the mid-Cretaceous to the Late Cretaceous (Zheng et al., 2018b).

The amber specimens described herein are deposited in the Lingpoge Amber Museum in Shanghai, China (BA16001) and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP0001; NIGP0002). 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:E9E6E246-610C-4672-861E-E36FD15C4C4A. The fossil specimens studied herein were examined and photomicrographed using the Zeiss Axio Zoom.V16 microscope system with Axiocam 512 colour camera under control of Zen software, multilayered images were composed with Helicon Focus 6 software package, and VHX 5000 digital microscope platform, with incident and transmitted light used simultaneously in most instances. The measurements were executed using the VHX 5000 digital microscope platform. The line drawings and reconstructions were prepared in two image-editing softwares (CorelDraw X7 and Adobe Photoshop CS6).

The venational terminology used herein mainly follows Chen et al. (2018), which is modified from Nel et al. (2012) and Bourgoin et al. (2015). The taxonomic framework employed herein follows Szwedo (2018), in which the higher-level systematics and classification of fossil and living Hemiptera was updated: within Clypeata, Cicadelloidea (leafhoppers and close relatives) was resurrected as an independent superfamily, with extinct Archijassidae and extant Cicadellidae included, and is treated to be independent of Membracoidea *s.s.* (treehoppers and close relatives). Nevertheless, for convenience of expression, we use Membracoidea *s.l.* as a taxon including Cicadelloidea and Membracoidea *s.s.* in some sections.

3. Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Suborder Cicadomorpha Evans, 1946
Clade Clypeata Qadri, 1967

Family Minlagerrontidae Chen, Szwedo and Wang, fam. nov. (urn:lsid:zoobank.org:act:A9F3BAF0-6862-46E4-A415-27ED3FB1A4F8).
Type genus: *Minlagerron* Chen, Szwedo and Wang, gen. nov.

Diagnosis. Anterodorsal portion of postclypeus strongly developed, but not incised into vertex (autapomorphy); pronotum divided into two sections, with anterior section narrower, protruded anteriad, and posterior one distinctly wider (autapomorphy); tegmen with CA and Pc+CP slightly separated at base (as in Hylicelloidea), with basal cell very narrow, elongate, terminals of stem MP reaching margin basad of apex of tegmen (autapomorphy), basal portion of CuA leaving basal cell strongly curved mediad, towards claval suture (as in Hylicelloidea), terminal CuA$_2$ strongly curved at level of claval apex, subparallel to CuP, areola postica short (autapomorphy).

Description. Head with strongly developed postclypeus, extending to crown, not incised in the vertex; postclypeus in dorsal view shallowly concave at anterior margin, in frontal view concave medially; traces of salivary pump muscles attachments visible; vertex with distinct ocelli on elevation, ocelli separated from each other by ridge. Compound eyes large, with postocular eminences. Pronotum about as long in mid line as mesonotum, divided in two sections with anterior distinctly narrower than head with compound eyes, protruding anteriad, and forming a 'neck'; posterior section wide, wider than head with compound eyes, and expanded laterally; posterior margin of pronotum with wide triangular incision. Mesonotum with mesoscutellum separated. Tegmen with

costal complex veins CA and Pc+CP separated at base; long and very narrow basal cell; bScP slightly shifted from common stem R+MP+CuA, fused to stem R+MP+CuA at basal cell; stem ScP+R+MP leaving basal cell at point with stem CuA; prenodal branchings of ScP+R+MP, and ScP+R present; ScP+R forked basad of apex of clavus; MP forked near apical margin; CuA distinctly curved at base, forked on nodal line; nodal veinlets rp-mp and mp-cua basad of claval apex, veinlet ir on membrane, apicad of claval apex; second veinlet ir and veinlet rp-mp_{1+2} distinctly apicad on membrane, apical veinlet mp-cua or partial fusion of MP_{3+4} and CuA (or CuA_1) absent; appendix absent. Hindwing with ScP+R forked well basad of wing coupling apparatus; terminals RA and RP single, vein MP single, stem CuA forked apicad of stem ScP+R forking; apical ir veinlet present, veinlet rp-mp apicad of veinlet mp-cua; appendix very narrow. Profemora with a row of spines ventrally; protibiae and mesotibiae widened apically; metatibiae without lateral spines, with apical double rows of teeth and long subapical setae. Male genitalia with enlarged pygofer fused with genital valve, genital plates fused with genital valve; gonostyles elongate. Anal tube long. Female genitalia with 8th abdominal tergite dorsally elongate, pygofer barrel-shaped, ovipositor of piercing-sawing type, short, not longer than apex of pygofer. Anal tube shorter than in male.

Genus *Minlagerron* Chen, Szwedo and Wang, gen. nov. (urn:lsid:zoobank.org:act:2DA06D6E-D18A-4D8D-8E2F-077D70AD7183).
Type species: *Minlagerron griphos* Chen, Szwedo and Wang, gen. et sp. nov.; by present designation and monotypy.

Etymology. The generic name is derived from the Kachin word 'minla' meaning ghost and Ancient Greek word gerron, ~to (γέρρον, γέρροντό), meaning an oblong shield, covered with ox-hide, such as the Persians used, indicating its specialized characters of the pronotum. Gender: neuter.

Diagnosis. Head with compound eyes about ¾ of width of pronotum. Disc of crown subquadrate, anterior margin of crown shallowly incised, and coronal suture present. In lateral view postclypeus with distinct ventral angulation; antclypeus carinate medially. Pronotum with anterior margin narrow, about $^1/_3$ of pronotum width; posterior margin widely arcuately W-shaped. Disc of crown, pronotum, and mesonotum punctate. Profemur with eight ventral teeth in a row. Protibiae club-shaped, with basal $^2/_3^{rd}$ slender, apical $^1/_3^{rd}$ slightly curved and inflated ventrally; apical portion covered with longer and stiff setae ventrally. Metatibiae without lateral spines, double row of nine apical teeth with long subapical setae. Tarsal claws large, widely inserted, with widely bilobed arolium in between. Tegmen with carinate costal margin in basal portion; single prenodal veinlet near forking of ScP+R+MP, and additional two or three prenodal veinlets, RP single and MP with two terminals. Male genital valve rounded, convex, fused with pygofer, genital plates triangular; pygofer with lateral process; genital styles elongate, widened apically. Male anal tube elongate, about four times as long as wide. Female pygofer barrel-shaped, ventral slit narrow, gonapophyses VIII and IX about half as long as pygofer. Female anal tube short, slightly longer than wide.

Description. Head with compound eyes narrower than pronotum, compound eyes large, spherical, with distinct postocular tumosities continued on ventral side of compound eye; crown distinct, with anterior part formed by flattened postclypeus, possessing a slightly sinuate anterior margin, and rounded anterolateral angles; vertex possessing a median eminence, with median and lateral ocelli placed on; ocelli distinct, distributed tightly in middle of crown. Postclypeus very swollen, with median concavity, about twice as long in mid line as wide at dorsal margin, wider and sinuose on dorsal margin, narrower on basal margin, lateral margins converging ventrad; in lateral view with distinct ventral angular eminence; muscle traces parallel, distinct. Anteclypeus separated from postclypeus by distinct groove, about $^1/_3$ of postclypeal length, narrow, about 2.5 times as long as wide, with median carination. Clypellus short. Loral plates semilunar, about 3.5 times as long as wide, dorsal angle reaching basal ¼ of postclypeus, ventral angle slightly exceeding ½ of anteclypeal length basad. Maxillary plates narrow, genae widened, subgenal suture present but indistinct. Antennal ridges carinate, base of antenna in shallow pit, scapus short, pedicel about three times as long as wide, flagellomeres elongate. Rostrum short, thick, reaching mesocoxae, apical segment about 1.5 times longer than wide, and longer than subapical one.

Procoxa elongate, tapering apicad, protrochanter distinctly longer than wide, profemora slightly flattened laterally, carinate ventrally with row of eight ventral teeth, protibiae longer than profemora, widened apicad, covered with short setae, apex of profemur with bunches of longer setae; basiprotarsomere cymbiform, medioprotarsomere short; distiprotarsomere long, its length exceeding combined length of basi- and medioprotarsomeres, tarsal claws large, arolium bilobate. Mesobasisternum large, subpentagonal. Mesocoxa elongate, subconical and flattened, with base shifted posteriad from procoxa base; metafemur without ventral row of teeth, metatibia and metatarsus similar to protibia and protarsus. Metacoxa with base close to mesocoxa base; bases of metacoxae close to each other, metacoxa without lateral expansion, metatrochanter short; metafemur shorter than metatibia, subquadrangular in cross-section; metatibia long, widening apicad, subquadrangular in cross-section, covered with short setae, without lateral spines, two rows of apical teeth, nine teeth each, apical one with long subapical thick setae; basimetatarsomere cymbiform, about as long as median one, with plantar surface with row of setae, distimetatarasomere longer than combined length of basi- and mediometatasomeres; tarsal claws very large, inserted widely, with large, bilobed arolium.

Tegmen about three times as long as wide, with costal margin curved strongly at base, carinate; venation distinct, veins pitted medially, with two rows of tiny hairs; costal margin (CA) shifted mediad from Pc+CP, Pc+CP distinct, continued towards apex of clavus; clavus long, exceeding $^2/_3$ of tegmen length; basal part of clavus punctate, corium and membrane membranous, transparent; appendix absent; basal cell very narrow, about ten times as long as wide; bScP slightly shifted from common stem R+MP+CuA at basal cell, fused with it at basal cell; stem R+MP slightly shorter than basal cell, forked at about ½ of clavus length, branch R forked at level of claval apex, terminal $ScP+RA_1$ at level of nodal transverse veinlets rp-mp and mp-cua, four terminals of RA reaching margin basad of tegminal apex; branch RP single, reaching margin at tegmen's apex; branch MP curved at base, forked distad of claval apex on membrane, with two terminals MP_{1+2} and MP_{3+4}, reaching margin on tornus; branch CuA leaving basal cell at point with R+MP stem, strongly curved mediad, forked mearly basad of claval apex, terminal CuA_1 short, reaching margin slightly apicad of claval apex, branch CuA_2 ungulate, reaching tornus close to ending of CuA_1; CuP distinct, parallel to claval suture, claval vein Pcu subparallel to claval suture, claval vein A_1 slightly arcuate; posterior margin of clavus distinctly delimited by A_2, very narrow jugal part present; prenodal veinlets on costal cell distinct, nodal veinlets rp-mp and mp-cua at same level; membrane with single ir veinlet and more apicad with ir and rp-mp_{1+2} veinlets; costal cell wide, about as wide as radial cell; cell C1 subpentagonal, about twice as long as wide; cell C3 subquadrate, cell C5 subtriangular; cells C2 and C4 adhering to each other. Hindwing with costal lobe at base, anteroapical angle widely angulate, apical margin widely arcuate; ScP+R forked at level of wing coupling apparatus, ScP+R forked

distinctly basad, well before wing coupling apparatus, ScP+RA$_1$ short, oblique, RA$_2$ reaching margin before hindwing apex, RP reaching margin at hindwing apex; MP single; CuA forked slightly basad of level of wing coupling apparatus; ambient vein present; *ir* veinlet distinctly apicad of *rp-mp* veinlet; *rp-mp* veinlet slightly apicad of wing coupling apparatus level, apicad of *mp-cua* veinlet.

Male terminalia with genital valve, genital plates and pygofer fused; genital valve (IXth sternite) roundly convex, with basal margin rounded, incised in VIIIth sternite; genital plates short, subtriangular, with acute apices; median fissure between genital plates narrow; pygofer with wide, rounded lateral process in dorsal part; genital styles elongate, with triangularly expanded apical portions; aedeagus narrow, tube-like, forked in apical part; anal tube long, widening caudad, with epiproct and anal style distinct.

Female terminalia: posterior margin of VIIth sternite roundly convex; VIIIth tergite expanded, wrapping pygofer; pygofer barrel-shaped, with narrow ventral slit; ovipositor short, gonapophyses VIII and IX with apices reaching ¾ of pygofer length; anal tube short, slightly longer than wide; anal style triangular.

Minlagerron griphos Chen, Szwedo and Wang, gen. et sp. nov. (urn:lsid:zoobank.org:act:95A10C03-BAC1-4FBB-8094-F4D0E783BA15).
Figs. 1–6

Material. Holotype: BA16001, a complete male adult insect in an amber piece; paratype: NIGP0001, a complete female adult insect in an amber piece.

Etymology. The specific epithet is derived from Ancient Greek word griphos (γρῖφος), meaning literally a fishing-basket, but metaphorically anything intricate, a dark saying, riddle, and refers to the peculiar character of the fossil.

Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; uppermost Albian/lowermost Cenomanian, uppermost Lower Cretaceous/lowermost Upper Cretaceous.

Diagnosis. Anterolateral angles of crown roundly angulate (widely angulate in *M. onyxos*), lora long but relatively narrow; abdomen relatively wide and nearly widest at middle, with anal tube slender, aedeagus short, just extending beyond apex of genital styles; tegmen with cell C1 shorter than C1′, C4 very broad, much wider than C5; stem ScP+R forking into ScP+RA and RP nearly at same level of bifurcation of stem CuA; first prenodal veinlet basad of stem ScP+R+MP forking.

Description. Holotype (BA16001) male. Body somewhat dorsoventrally flat, tegmina held tectiform at repose. Length including tegmen in repose about 6.7 mm, width about 3.2 mm. Head with compound eyes in dorsal view about 0.8 mm long, and 1.0 mm wide. Pronotum about 0.8 mm long in middle line, and 1.5 mm wide, with disc densely pitted, wider than head, with anterior part
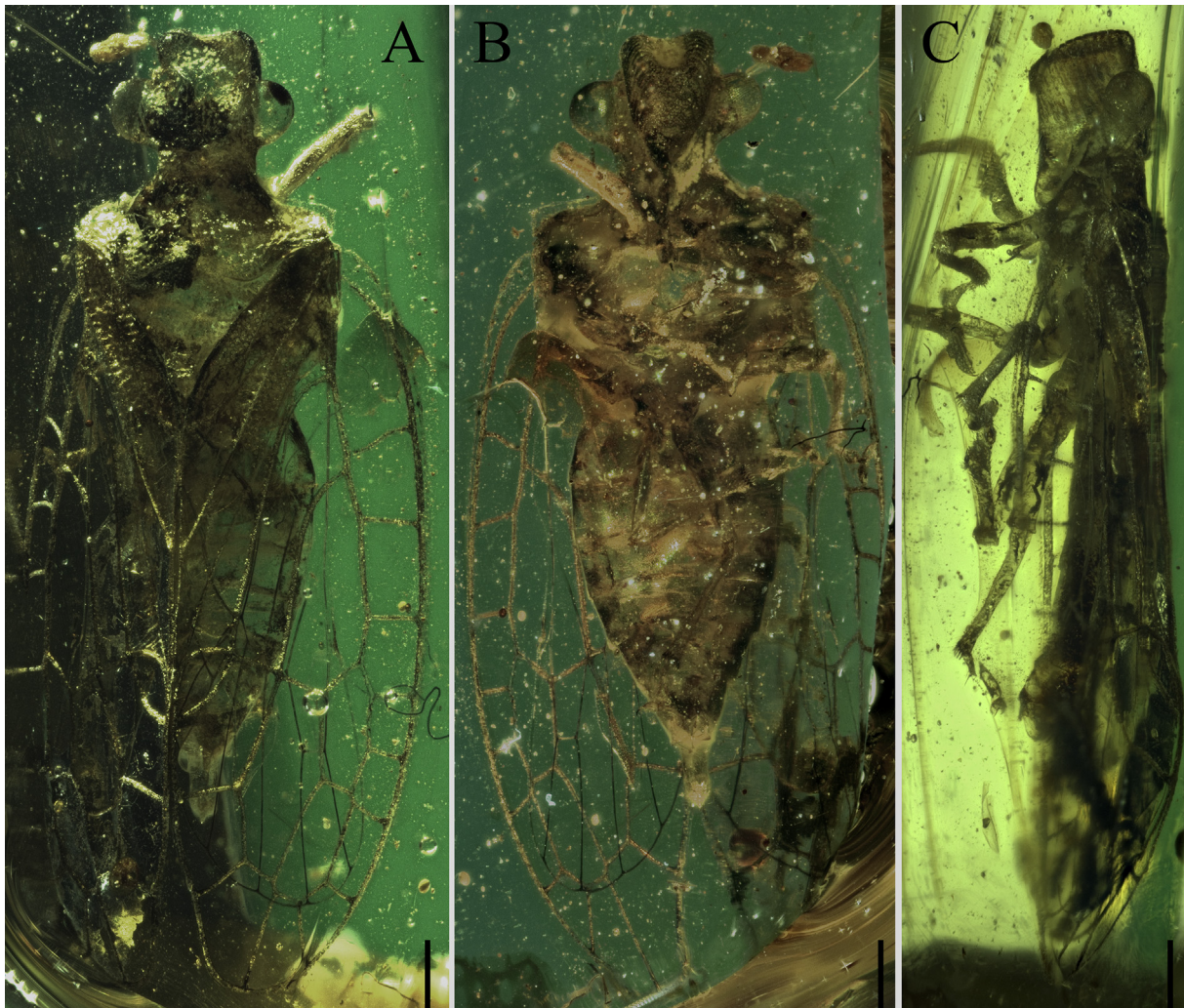

Fig. 1. Holotype of *Minlagerron griphos* Chen, Szwedo and Wang, gen. et sp. nov. (A), dorsal view; (B), ventral view; C, lateral view. Scale bars = 0.5 mm.
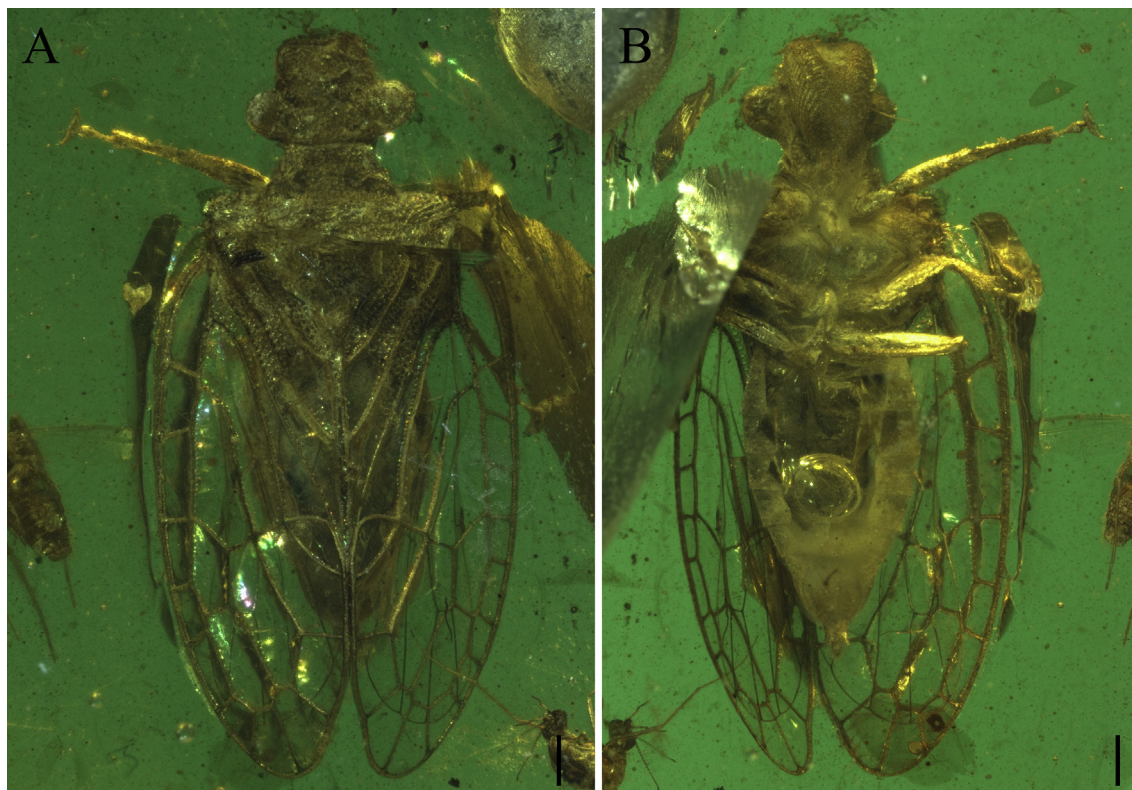
Fig. 2. Paratype of *Minlagerron griphos* Chen, Szwedo and Wang, gen. et sp. nov. (A), dorsal view; (B), ventral view; C, lateral view. Scale bars = 0.5 mm.

sharply constricted as narrow 'neck' region; anterior margin short, slightly concave; anterolateral angles almost rectangular; anterolateral margins strongly concave in the middle, with anterior part constituting 'neck' and posterior part constituting 'shoulders'; lateral angles rounded; posterolateral margins long and nearly straight; posterolateral angles obtuse; posterior margin strongly concave. Mesonotum with scutellum about 1.0 mm long, and 1.1 mm wide; disc pitted; mesoscutal sulcus not well expressed. Aedeagus short, with apex just extending to apex of genital styles. Tegmen with length about 5.3 mm, width about 1.7 mm. Cell C1 shorter than C1′. Apical cell C5 almost closed by two terminal branches of CuA, much smaller than C4. ScP+R+MP+CuA forking at basal 0.17 of wing length. Stem R+MP, stem R and vein RA totally with eight terminal branches ending at anterior margin. Stem R+MP branching into R and MP at basal 0.3 of wing length. R bifurcating into RA and RP at basal 0.55 of wing length; Stem MP forking into MP_{1+2} and MP_{3+4} at basal 0.72 of wing length; MP_{3+4} much shorter than MP_{1+2}. Stem CuA branching into CuA_1 and CuA_2 at same level of bifurcation of stem ScP+R; two terminal branches of CuA almost with equal length and almost ending at the same point. CuP geniculate at very apex. Hind wing with membrane with tiny grains; appendix extremely narrow; wing-coupling lobe on anterior margin prominent, just basad of free terminal part of $ScP+RA_1$. Longitudinal veins (RA, RP, MP and CuA_1) slightly geniculate at connection with crossveins (*ir, rp-mp, mp-cua*).

Paratype (NIGP0001) female. Morphological characteristics in general as in holotype. Body length including tegmen in repose about 6.8 mm long, about 3.3 mm wide. Tegmen about 5.1 mm long, about 1.8 mm wide. Stalk R+MP, stem R and vein RA totally with nine and seven terminal branches in right and left tegmina respectively.

Minlagerron onyxos Chen, Szwedo and Wang, gen. et sp. nov. (urn:lsid:zoobank.org:act:6FE6AE57-CCD8-4288-94BC-53EA00A1AC71).
Figs. 7—9

Material. Holotype: NIGP0002, a complete male adult insect in an amber piece.
Etymology. The specific epithet is derived from Ancient Greek onyx, onyxos (ὄνυξ, ὄνυχος), and refers to large claws presented by this insect.
Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; uppermost Albian/lowermost Cenomanian, uppermost Lower Cretaceous/lowermost Upper Cretaceous.
Diagnosis. Anterolateral angles of crown widely angulate (more angulate in *M. griphos*), lora short but broad; abdomen relatively narrow, with anal tube somewhat stout, genital styles heavily sclerotized, aedeagus long, apparently extending beyond apex of genital styles; tegmen with cell C1 much longer than C1′, C4 relatively narrow, stem ScP+R bifurcating into ScP+RA and RP much basad of bifurcation of stem CuA; first prenodal veinlet at level of ScP+R+MP forking.
*Description.* Body somewhat dorsoventrally flat, tegmina hold tectifom at repose. Length including tegmen in repose about 7.0 mm, width about 3.3 mm. Head with compound eyes in dorsal view about 1.0 mm long, and 1.3 mm wide. Anterior margin of crown strongly concave. Genae reduced and extremely narrow. Lora extended, very broad, flat. Pronotum about 0.7 mm long in middle line, and 1.2 mm wide; anterior margin short, slightly concave. Mesonotum with scutellum about 1.2 mm long, and mm 1.4 wide; posterior angle of scutellum very sharp. Abdomen flat, long but relatively narrow. Male anal tube long and relatively stout; anal style not subuliform. Genital plates small, sharp apically. Genital styles broad, dark, heavily sclerotized. Aedeagus long, apparently
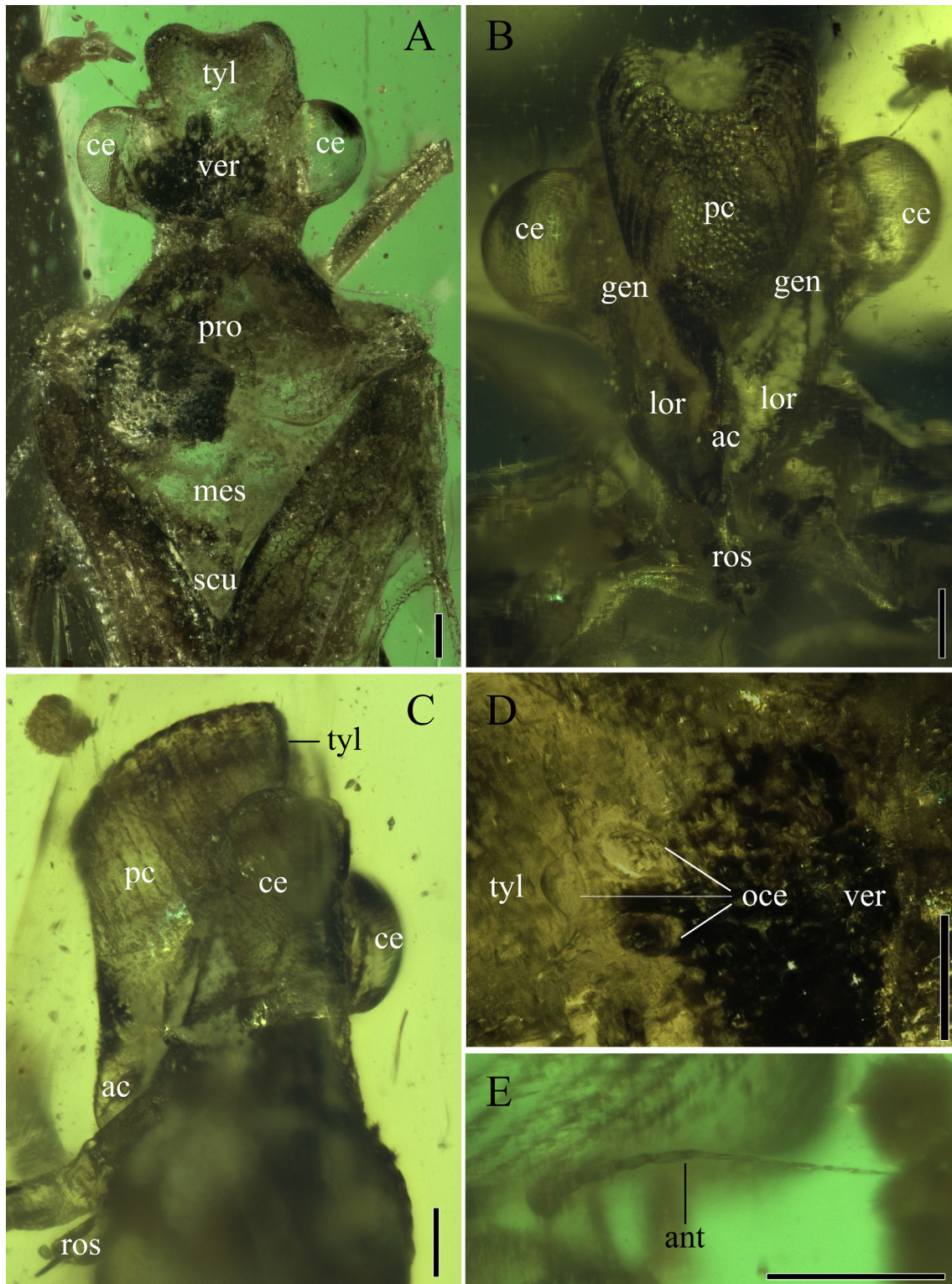
Fig. 3. Head and thorax of holotype of *Minlagerron griphos* Chen, Szwedo and Wang, gen. et sp. nov. (A), head and thorax in dorsal view; (B), head in ventral view; (C), head in lateral view; (D), detail of ocelli; (E), enlarged left antenna. Annotations: ac, anteclypeus; ant, antenna; ce, compound eye; gen, gena; lor, lorum; mes, mesonotum; oce, ocellus; pc, postclypeus; pro, pronotum; ros, rostrum; scu, scutellum; tyl, tylus; ver, vertex. Scale bars = 0.2 mm.

extending to apex of genital styles. Tegmen with length about 5.4 mm, width about 2.0 mm. Basal cell extremely narrow. Cell C1 much longer than C1′. Apical cell C4 relatively narrow, just slightly wider than C5. Stem ScP+R+MP+CuA forked into ScP+R+MP and CuA at basal 0.15 wing length. Stalk ScP+R+MP, branch R and branch RA totally with ten and nine terminal branches ending at anterior margin for right and left tegmina respectively. Stalk ScP+R+MP branching into ScP+R and MP at basal 0.28 wing length.
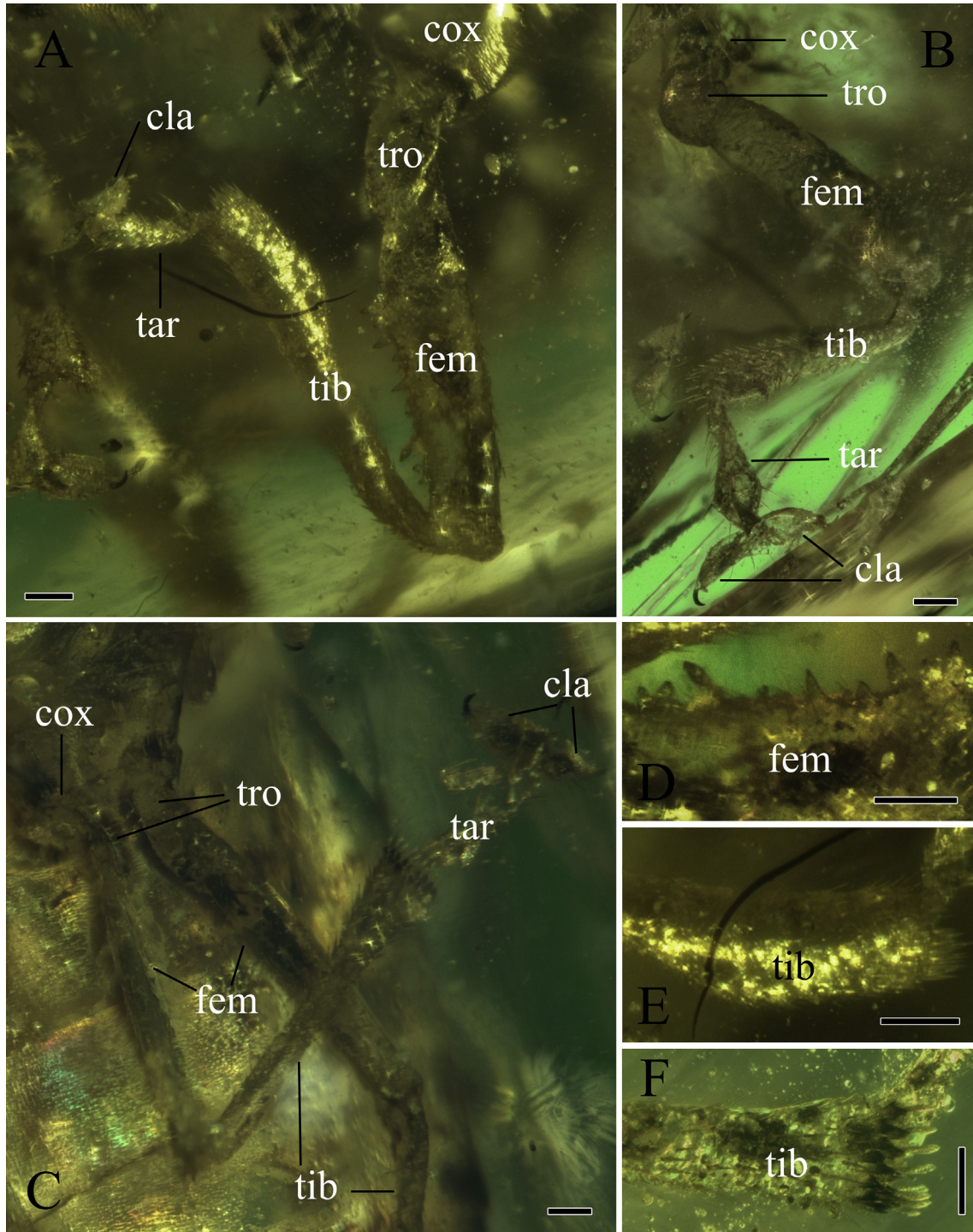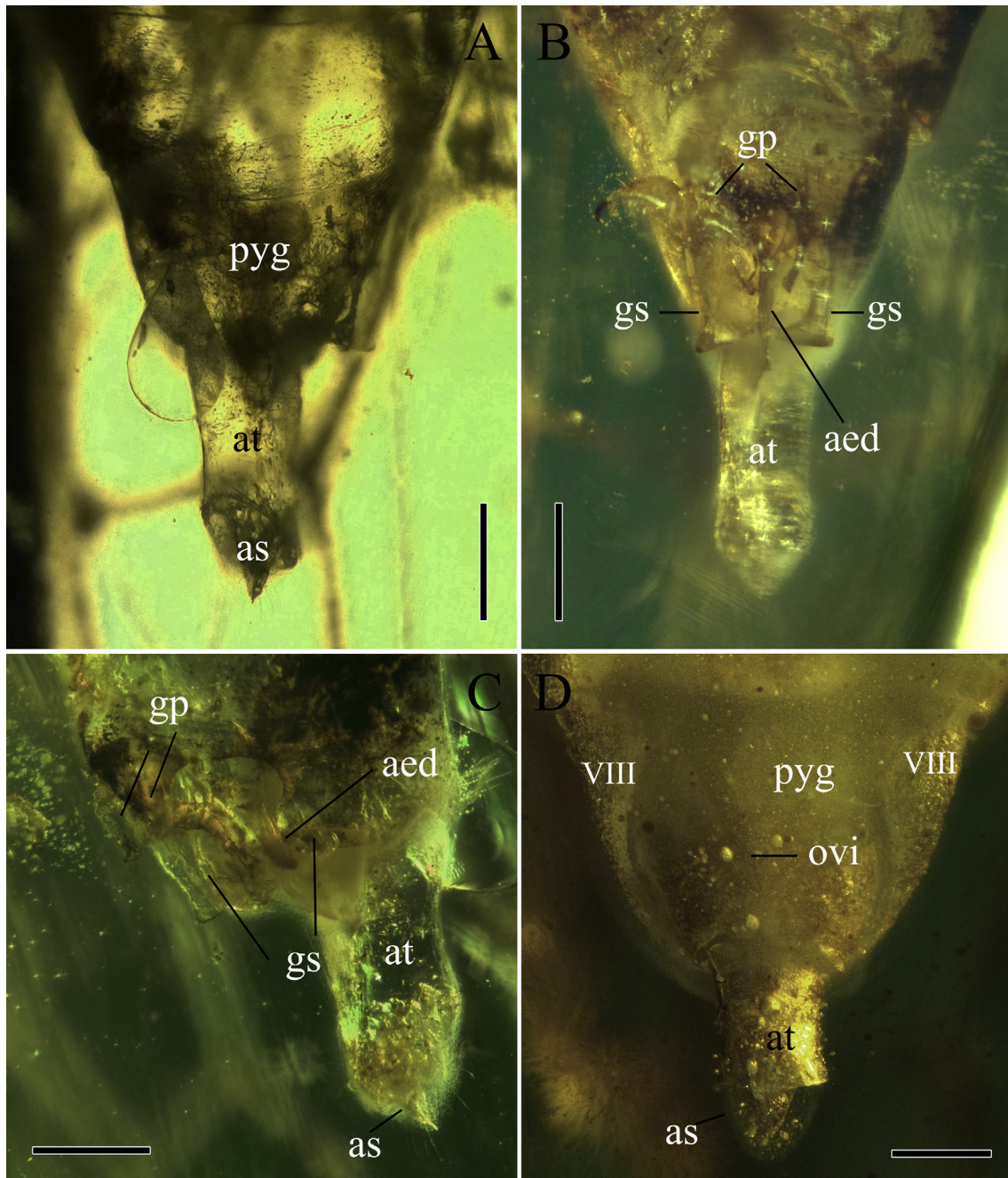
Fig. 4. Legs of holotype of *Minlagerron griphos* Chen, Szwedo and Wang, gen. et sp. nov. (A), left prothoracic leg; (B), left mesothoracic leg; (C), right metathoracic leg; (D), lateral teeth on left prothoracic femur; (E), inflated apical part of left prothoracic tibia; F, apical teeth on left metathoracic tibia. Annotations: cla, claw; cox, coxa; fem, femur; tar, tarsus; tib, tibia; tro, trochanter. Scale bars = 0.1 mm.

ScP+R bifurcating into ScP+RA and RP near middle of wing; branch MP strongly curved at base, long, and bifurcating into MP_{1+2} and MP_{3+4} at basal 0.74 wing length; MP_{3+4} much shorter than MP_{1+2}. Branch CuA branching into CuA_1 and CuA_2 at basal 0.55 wing length, apparently apicad of bifurcation of stem R; two terminal branches of CuA almost with equal length and almost ending at same point. CuP long, geniculate terminally. Hind wing with wing-coupling lobe on anterior margin prominent, just basad of free terminal part of $ScP+RA_1$. Longitudinal veins slightly geniculate at connection with crossveins.

Remarks. Minlagerron onyxos gen. et sp. nov. resembles *Minlagerron griphos* gen. et sp. nov. with a similar body size and shape, but can be easily distinguished from the latter in the following body structures: postclypeus much shorter, lora short but broad, abdomen narrow, anal tube stout, genital styles heavily sclerotized, aedeagus apparently extending beyond apex of genital styles, as

Fig. 5. Pygofer of *Minlagerron griphos* Chen, Szwedo and Wang, gen. et sp. nov. (A), holotype in dorsal view; (B), holotype in ventral view; (C), holotype in lateral view; (D), paratype in ventral view. Annotations: aed, aedeagus; as, anal style; at, anal tube; gp, genital plate; gs, genital style; ovi, ovipositor; pyg, pygofer; VIII, tergite VIII. Scale bars = 0.2 mm.

well as a series of tegminal characteristics: cell C1 much longer than C1′, cell C4 narrow, stem R bifurcating into RA and RP apparently basad of bifurcation of stem CuA. The difference of the new species from that of *Minlagerron griphos* gen. et sp. nov. in the male genital confirms that these two new taxa are independent biological species.

4. Discussion

Minlagerrontidae fam. nov. can be undoubtedly attributed to Cicadomorpha: Clypeata based on the following morphological characters: the antenna located between the compound eye and the postclypeus with pedicel not bulbous; postclypeus hypertrophied, with transverse grooves (muscle attachments), occupying the largest portion of the face and reaching the crown, longitudinal veins on the clavus (Pcu and A_1) independent, not fused apically in form of 'Y' vein (Dietrich, 2005; Wang et al., 2012; Bartlett et al., 2018).

The clade Clypeata Qadri, 1967 (Hemiptera: Cicadomorpha) appeared in the fossil record in the terminal Permian, but subsequent radiations had resulted in a successful group in the early and middle Mesozoic, represented by some stem groups: Hylicelloidea: Chiliocyclidae (Triassic Carnian), Mesojabloniidae (Triassic Carnian) and Hylicellidae (Triassic Ladinian to Cretaceous Aptian); Cercopoidea: Procercopidae (Jurassic Hettangian to Cretaceous Turonian)
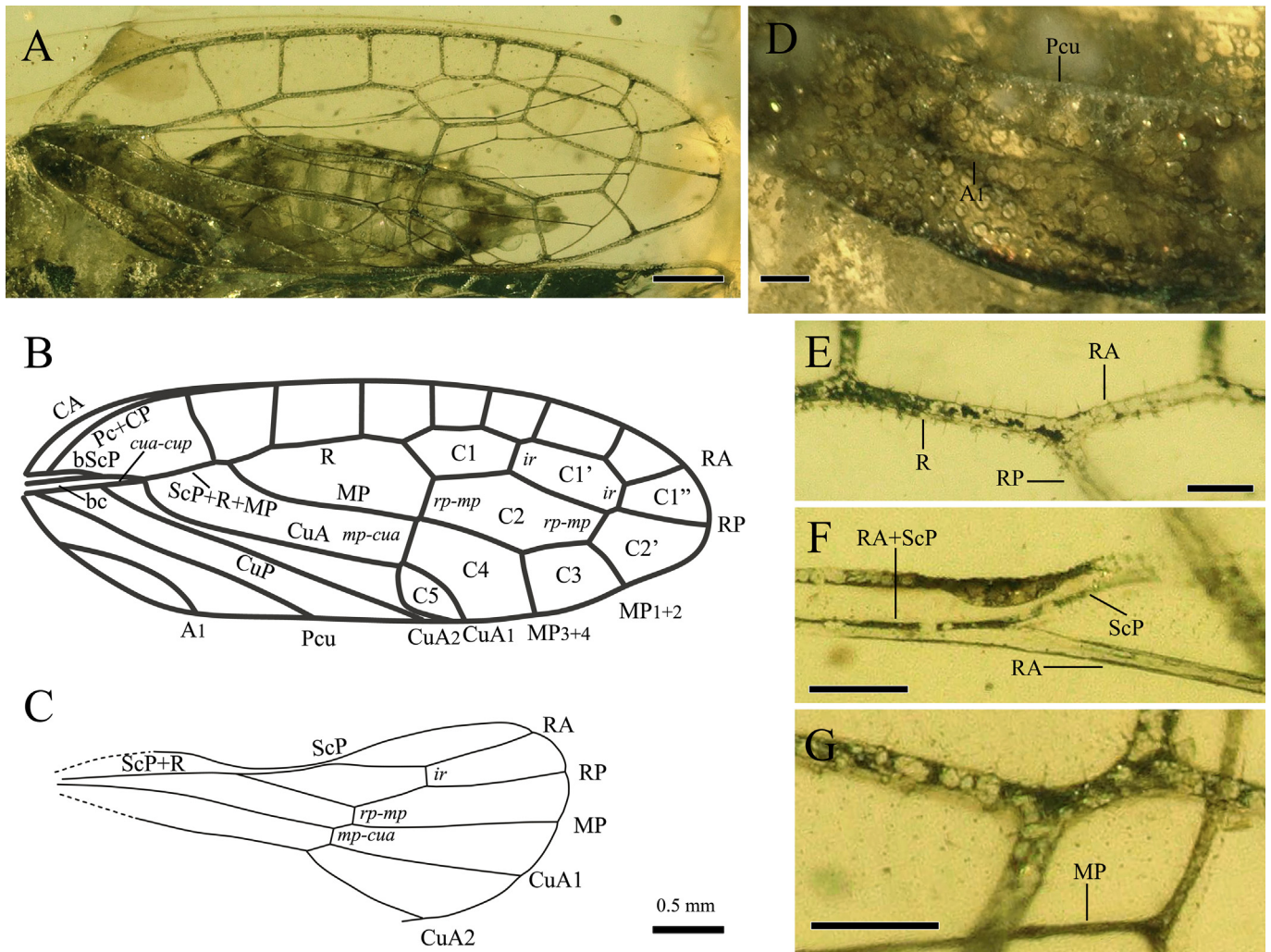
Fig. 6. Right wings of holotype of *Minlagerron griphos* Chen, Szwedo and Wang, gen. et sp. nov. (A), photograph of tegmen and hindwing; (B), line drawing of tegmen; (C), line drawing of hindwing; (D), enlarged pitted and sclerotized clavus of tegmen; (E), enlarged part of longitudinal veins R, RA and RP of tegmen, showing pits and two rows of tiny hairs; (F), enlarged wing-coupling lobe on anterior margin of hindwing; (G), details of part of hindwing, showing narrow appendix on apical margin and punctate membrane. Annotation: bc, basal cell. Scale bars = 0.5 mm (A–C), 0.1 mm (D–G).

and Sinoalidae (Jurassic Callovian-Oxfordian to Cretaceous Cenomanian); Cicadoidea: Tettigarctidae (Triassic Rhaetian to Recent); Cicadelloidea: Archijassidae (Triassic Carnian to Jurassic Tithonian). By the early Cretaceous, representatives of modern Clypeata lineages became to radiate rapidly (Shcherbakov and Popov, 2002; Wang et al., 2012; Chen et al., 2015; Szwedo, 2018).

Minlagerrontidae fam. nov. described above from the mid-Cretaceous of Kachin represents an extinct offshoot of Clypeata, and probably is the latest representative of Hylicelloidea. There are several morphological features in Minlagerrontidae fam. nov. suggesting its placement within Hylicelloidea; alas, many of them seem to be symplesiomorphies, present also in representatives of Cicadoidea or Cercopoidea. The enlarged, swollen postclypeus is a general character of all Clypeata, retained in Cicadoidea, and most groups of Cercopoidea, but is just recognizable among a few Membracoidea *s.l.* (Dmitriev, 2010; Wang et al., 2012). The enlargement is related to adaptation of the Clypeata to intake of xylem sap from plants, the sap which is under negative pressure, and on thermodynamic grounds, energy must be used to power the cibarial pump which extracts the xylem sap (Raven, 1983; Zimmerman et al., 1994). Another disadvantage of xylem fluid is its extreme poorness in nutrients (amino acids, sugars) as well as

containing also some ions and minerals (Terra, 1990; Novotný and Wilson, 1997). Therefore, a shift to xylem as a source of food was a major evolutionary effort leading to a high level of Clypeata specialization. Minlagerrontidae fam. nov. retained an primitive condition of Hylicelloidea in the structure of the antenna, with short scapus, slightly elongate pedicel and seven segments, which is a condition retained also in modern Cicadoidea: Tettigarctidae and Cicadidae as well as in Myerslopioidea (Myers, 1928; Evans, 1941; Anufriev and Emeljanov, 1988; Hamilton, 1999). The head capsule structure is very conservative in Minlagerrontidae, resembling the basal model proposed for Clypeata (Dmitriev, 2010), but some modifications separate it from general patterns in Cicadoidea, Cercopoidea or Cicadelloidea. One of these pecularities is the well developed dorsal part of the postclypeus, placed in front of the vertex, but not embraced by it, not incised into the vertex as it is observable in Cercopoidea. This portion is sometimes named the tylus in modern Cercopoidea; however, the tylus *s. str.* is only part of the crown, the ovoid or bean-shaped plate, formed by the outer surface of the sucking pump, instead of the whole dorsal part of the postclypeus (Hamilton, 1982; Pulz and Carvalho, 1998). Another peculiarity is the median eminence of the vertex, with the median ocellus directed anteriad, and lateral ocelli directed laterad,
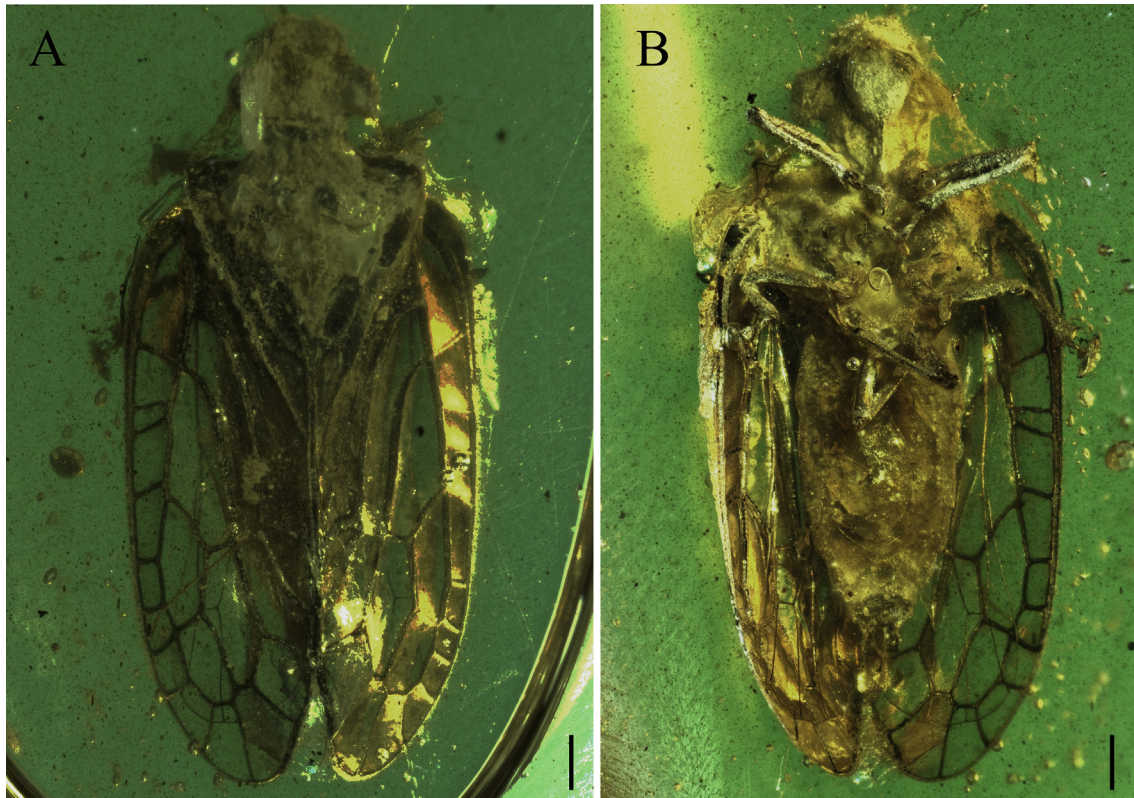
Fig. 7. Holotype of *Minlagerron onyxos* Chen, Szwedo and Wang, gen. et sp. nov. (A), dorsal view; (B), ventral view. Scale bars = 0.5 mm.

distinctly elevated over the crown disc. A similar situation is present in Cicadoidea, the only Recent Clypeata group retaining three ocelli (Moulds, 2005). the presence of three ocelli is a trait shared by basal Clypeata–Hylicelloidea, ancient groups of Cercopoidea (Procercopidae and Sinoalidae) and stem Cicadelloidea (Shcherbakov, 1996, 2012b; Dietrich, 2005; Wang et al., 2012; Chen et al., 2018). The bulging eyes of Minlagerrontidae fam. nov., post-ocular eminences, long and narrow maxillary plates, reaching to the tip of the anteclypeus also resemble those in Cicadoidea; semilunar loral plates are a typical feature of the Clypeata head. In Minlagerrontidae fam. nov. the genal suture is weak but visible, a character sometimes present in some Cicadelloidea (Dmitriev, 2010). A short rostrum in *Minlagerron* gen. nov. suggests it fed on twigs and branches similar to modern Cicadellidae.

Division of the pronotum into two sections, with different sculptures, is observed in Jurassic Hylicellidae, and also is retained in extinct and Recent Tettigarctidae and Cicadidae; however, the narrower 'neck' and wider 'shoulders' of Minlagerrontidae fam. nov. are exceptional characters, highly apomorphic for this family. In detail, the anterior part of pronotum is sharply constricted and much narrower than the head, with anterior part of anterolateral margins of pronotum longitudinal, forming a 'neck' region; moreover, the anterolateral margins of the pronotum are strongly curved, leading to their posterior part being almost transverse, forming a prominent 'shoulder' structure; the grotesque structure adapt to prothorax has never been recorded in other insect groups. The shape and structures of thorax are highly plastic for insects to adapt some special functional contexts, such as hunting behavior for praying mantises (Corrette, 1990) and mantispids (Kral, 2013), and mimicry for stick and leaf insects (Wedmann et al., 2007). It is speculative to address the function of this weird configuration that is unknown in living insects; however, acquisition of broader field

of vision and facility for holding during copulation are two potential alternative interpretations.

The mesonotum of *Minlagerron* gen. nov. is typical for Clypeata, with no exceptional characters. In Tettigarctidae, it is much more covered by an enlarged pronotum; in Cicadidae, mesonotum is enlarged, with a cruciform elevation of metascutellum, and is more or less exposed in Cercopoidea.

The prothoracic legs of Minlagerrontidae fam. nov. are highly modified: profemora strengthened, sunken ventrally, with one row of strong lateral teeth on ventral margin; pro- and mesotibiae club-shaped, with basal $2/3^{rds}$ slender, apical $1/3^{rds}$ slightly curved and inflated ventrally. Strengthened profemora with strong lateral teeth indicate that *Minlagerron* gen. nov. was probably fossorial in juvenile stages like modern Cicadoidea. The modified profemur (strong and with lateral teeth) is easily recognizable in adult individuals for certain cicadas, e.g. *Cryptotympana* Stål, 1861 (Matsumura, 1927), so enlarged and armed profemora of Minlagerrontidae fam. nov. are likely the result of retention of nymphal characters like in living Cicadoidea. The three adult fossil specimens of the new family described above possess well-developed eyes and ocelli, and fully developed tegmina and hind wings, suggesting that they are not subterranean and so the fossorial prolegs of nymphs likely transformed into 'grasping' legs for adults. Protibiae of the *Minlagerron* gen. nov. are club shaped, with basal $2/3^{rds}$ slender, apical $1/3^{rds}$ slightly curved and inflated ventrally, provided with longer stiff setae, so combined with armed femora suggests that the prolegs could be used for clinging to the bark or foliage of the host plants (as it could be observed e.g. in some Coleoptera – Crowson, 1981), and/or to grasp the mating partner (coordinated with the prothoracic 'neck' and 'shoulder' structure). Row of ventral spines on ventral surface of profemora, retained in imagines, could be interpreted as vestigial, as
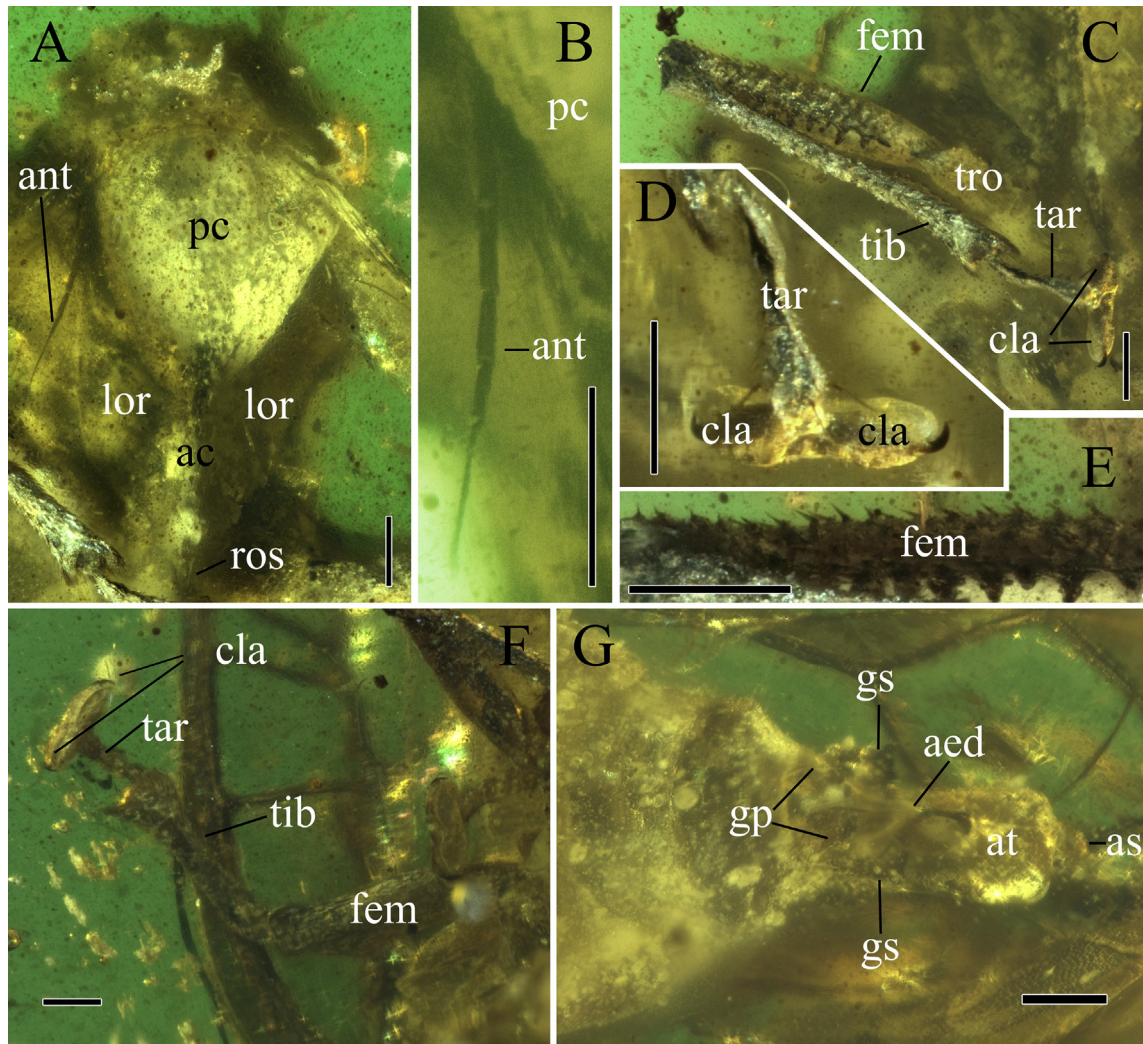
Fig. 8. Body structures of *Minlagerron onyxos* Chen, Szwedo and Wang, gen. et sp. nov. (A), head in ventral view; (B), enlarged right antenna; (C), right prothoracic leg; (D), enlarged right prothoracic tarsus and claws (mirrored); (E), enlarged right femur, showing lateral teeth and row of strong setae; (F), right mesothoracic leg; (G), pygofer. Annotations: ac, anteclypeus; aed, aedeagus; ant, antenna; as, anal style; at, anal tube; cla, claw fem, femur; gp, genital plate; gs, genital style; lor, lorum; pc, postclypeus; ros, rostrum; tar, tarsus; tib, tibia; tro, trochanter. Scale bars = 0.2 mm.
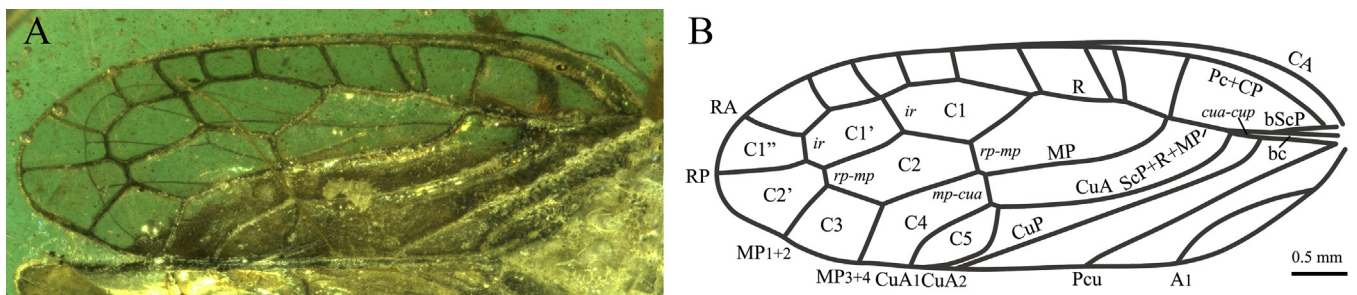
Fig. 9. Left wings of *Minlagerron onyxos* Chen, Szwedo and Wang, gen. et sp. nov. (A), photograph of tegmen and hindwing; (B), line drawing of tegmen. Annotation: bc, basal cell. All to scale bar.

indicated by similar structures observed in subterranean nymphs of modern Cicadidae (Moulds, 2005; Bartlett et al., 2018). Subterranean and accordingly root-sucking nymphs were postulated for Hylicelloidea (Shcherbakov, 1989; Shcherbakov and Popov, 2002). This remarkable behavior is also present in modern Tettigarctidae and Cicadidae. Juvenile cercopoids, known as spittlebugs, hide themselves with foaming spittle or in sap-filled tubes to provide protection from predation, parasitism and desiccation (Rakitov, 2002; Cryan and Svenson, 2010). Nymphs of Membracoidea *s.l.* are commonly free living with a rich behavioral diversity, and some groups (treehoppers) even possess various forms of parental care and ant mutualism (Wood and Dowell, 1984; Masters et al., 1994; Lin, 2006). The alternative conclusion that the nymphs were free living with their prothoracic legs

modified for grasping just like their adults, however, should not be completely rejected.

Metatibia without lateral spines or rows of enlarged setae vs. lateral spines well developed for Cercopoidea and Cicadoidea and rows of strong setae present in Cicadelloidea and Membracoidea (Wang et al., 2012; Chen et al., 2018) is another plesiomorphic condition shared by Minlagerrontidae fam. nov. with Hylicellidae (Shcherbakov, 1989). As mentioned above, the metatibia of Minlagerron gen. nov. lack lateral spines, contrary to situation observed among Cercopoidea and Cicadoidea, with lateral spines well-developed, or highly specialized rows of strong setae present in Membracoidea s.l. (Wang et al., 2012; Chen et al., 2018). Double apical row of teeth is well developed in Minlagerron gen. nov., with the apical row provided with long subapical setae. This situation is similar to that in Cercopoidea (Pulz and Carvalho, 1998; Burrows, 2006), and it seems that development of apical rows of teeth is plesiomorphic condition in Clypeata, related to the improvement of jumping abilities (Dietrich, 2002; Burrows, 2006).

The striking feature of Minlagerron gen. nov. is conformation of the tarsal claws and arolium − the tarsal claws are large, curved and sharp, widely inserted on tip of distitarsomere, and the arolium is widely bilobate and deeply incised, and covers bases of claws. Arolii are present in superfamilies of Clypeata, except singing cicadas Cicadoidea. Arolium of recent Clypeata contains a gland, but its exact function is not entirely clear. The secretion probably plays a role in adhesion to smooth surfaces. These structures in Minlagerron gen. nov. differ from the pattern observed in Recent clypeatans (Friedemann et al., 2014; Friedemann and Beutel, 2014). The secondarily bilobed arolium is present in various Cicadelloidea and Membracoidea, but absent in Cicadoidea; in Cercopoidea it is present in form of a single eversible lobe. Apart from Membracoidea s.l., the bilobed arolium is also present in unrelated Sternorrhyncha: Psylloidea, and it seems that it was developed independently. The question whether the conformation of claws and arolium in Minlagerrontidae fam. nov. is plesiomorphic or highly specialised (apomorphic) remains open.

In Hylicelloidea, there are several venational patterns. A peculiar one is found in Triassic Mesojabloniidae Storozhenko, 1992, originally described as Grylloblattodea and then transferred to Hylicelloidea (Storozhenko, 1992; Shcherbakov, 2011). The tegmina of Mesojabloniidae were weakly sclerotized and bear little, if any, surface sculpture, with modifications of shape and postnodal part to strengthen them. It was postulated by Shcherbakov (2011) that the tegmina were held in repose shallowly tectiform, distally almost flat, with a slight overlap. Such conformation of tegmina closely resembles that in the extant planthopper family Achilidae. By analogy with these planthoppers' behavior, it was hypothesized that at least some mesojabloniids were associated with arboreal hosts and spent much time on their bark, with tegmina minimizing their shadows (Shcherbakov, 2011).

Position and content of Chiliocyclidae Evans, 1956 are disputable. Shcherbakov (1992, 1996) placed the family within Hylicelloidea, which was followed by Szwedo (2018). Martins-Neto et al. (2003) listed Chiliocyclidae in Scytinopteroidea, but gave no explanation for such an action. This placement was followed recently by Lara and Wang (2016). Also the taxonomic content of the Triassic family Chiliocyclidae is not stabilized. The genus Chiliocycla Tillyard, 1919 is weakly known, based on fragmentary tegmen, with basal portion poorly preserved, making difficult the interpretation of venation. The special feature of Chiliocycla is the strongly punctate sculpture of basal ¾ths of tegmen with more membranous apical portion. Such sculpture of tegmina is present in various degrees among other Clypeata as well. Position of the other genera placed in Chiliocyclidae: Tipuloidea Wieland, 1925 and Argentinocicada Martins-Neto et Gallego, 1999 must be

reconsidered; these genera used to be placed in Scytinopteridae (Martins-Neto and Gallego, 1999; Martins-Neto et al., 2008). These genera share a number of tegminal features with Hylicellidae (bScP distinct, separated from stem R+MP+CuA at level of basal cell, narrowed apicad basal cell, small cell C3), but bear tegmina with veinlet cua-cup of the basal cell very weak and relatively long, straight and oblique stem ScP+R+MP, stem CuA forked basad of claval apex, cell C5 elongated, distinguishing them with most other Hylicellidae.

The new family Minlagerrontidae fam. nov. clearly differs from Mesojabloniidae and Chiliocyclidae in venational characters of the tegmen; it differs also from Hylicellidae by wing being membranous, punctate only in the claval portion, stronger curve of the basal section of CuA leaving the basal cell, very late forking of MP, with cell C3 open to the tegminal margin. The costal complex of Minlagerron gen. nov. is clearly different from that in Hylicellidae: costal margin is narrow, blade-like, Pc+CP is thickened and extending beyond level of nodal line, and the free branch of CP is absent. Long CA shifted from Pc+CP is present in Hylicellidae, but at least fragmentary free branch of CP is present (Evans, 1956; Shcherbakov, 1989, 2012a). The tegmen of Minlagerrontidae fam. nov. has bScP distinct, separated from stem R+MP+CuA but not reaching to the apex of basal cell, the character present also in Hylicellidae: Conjucellinae. Long and straight common stem ScP+R+MP leaving basal cell is a unique feature of Minlagerontidae fam. nov., short common stem is present in Hylicellidae: Conjucellinae, but not among other Hylicellidae, when at least short common stem MP+CuA is present, at least closing basal cell. Presence of two veinlets rp-mp is another feature of above described new family common with Hylicellidae. Prenodal branchings of ScP, as in Milagerrontidae fam. nov., are present also in Hylicellidae: Vietocyclinae, but these are more oblique (Shcherbakov, 1989). In all Hylicellidae cell C3 is closed with imp veinlet (Evans, 1956; Shcherbakov, 1989, 2012a); the unique feature of Minlagerrontidae fam. nov. is cell C3 open, reaching margin of tegmen and then cells C2 and C4 adjoining each other. The cell C5 in Minlagerrontidae fam. nov. is peculiarly small, lenticular, with delimiting branch CuA2 geniculate. The hind wing of Minlagerron gen. nov. clearly differs from Hylicellidae hind wing. In Minlagerron gen. nov. the branches of RP and MP are connected with transverse veinlet, not fused for a distance as in Vietocycla Shcherbakov, 1989 or Cycloscytina Martynov, 1927. The hind wing stem MP is single in Minlagerrontidae fam. nov., while it is (multi)branched in Hylicellidae (Shcherbakov, 1989). The terminals of vein CuA in Hylicellidae are close to each other near the margin, while in Minlagerrontidae fam. nov. the terminals of CuA are widely diverging towards the margin. In at least some Hylicellidae, narrow appendix is present on the hind wing, while it is absent in Minlagerron gen. nov.

Male terminalia in Minlagerrontidae fam. nov. are superficially similar to those of Cercopoidea: pygofer is elongated, in form of ring, with pygofer and genital valve fused; genital styles are fused with genital valve, but the vestigial suture is marked. In Cicadoidea, the pygofer lacks valves, but reduced genital plates are sometimes retained (lateral lobes), and the anal tube is supplied with lateral hooks and posterior lobe; anal tube usually envelops shaft of penis (Myers, 1928; Anufriev and Emeljanov, 1988). Genital styles are distinct, also resembling these structures present in Cercopoidea and Membracoidea s.l., and the simple, tubular aedeagus seems to be primitive condition in Minlagerrontidae fam. nov. One peculiar feature of Minlagerron gen. nov. is the long, tubular anal tube, distinctly extending beyond the tip of male genitalia. Such a long anal tube is not observed among recent Clypeata, but it seems rather to be a specialisation, not a plesiomorphic condition. An elongated anal tube is also observed among Kachin amber

inclusions of various unrelated Fulgoromorpha, as well as in some Cicadellidae inclusions in Burmese amber. The female pygofer of Minlagerrontidae fam. nov. is unusual for true hoppers: shortened, completely wrapped by tergite VIII and with a very short ovipositor. The morphology of the ovipositor could be indicative of the egg deposition. In planthoppers (Fulgoromorpha) the ovipositor may be strongly modified, to lay eggs in ground or glue them to the host plant surface; these ovipositor of orthopteroid type usually lay eggs inside host plant tissues. Females of Cicadoidea and Membracoidea *s.l.* have a long pygofer and ovipositor to insert eggs into host plant tissues (Caceres-Sanchez et al., 2017; Bartlett et al., 2018). The shortened pygofer and ovipositor possessed by the new family indicate that this extinct true hopper group probably inserted eggs into shallow topsoil, on or near the roots, or just deposited them on soil surface, and hatchling nymphs dug deep into soil by themselves.

The highly apomorphic and specialized Minlagerrontidae fam. nov. erected from mid-Cretaceous Kachin amber is apparently an extinct offshoot of Clypeata, and might belong to the stem group of Clypeata, as possibly the latest representative of Hylicelloidea. Based on available fossil evidence, Minlagerrontidae fam. nov., is tentatively attributed to Hylicelloidea herein; however, the extremely specialized body structures of this new family and the fragmentary nature of the fossil record of early Clypeata prevent us from strictly reconstructing the phylogenetic relationships between this family and the other ancient Clypeata lineages.

It is a difficult issue to reconstruct the life cycle and style of extinct organisms, and a series of highly modified and unique characteristics of Minlagerrontidae fam. nov. make this task even harder. However, available morphological evidence allows some plausible interpretations. Nymphs were probably subterranean with digging prolegs and therefore root-sucking like modern cicadas and some other stem Hylicelloidea (Shcherbakov, 1989; Shcherbakov and Popov, 2002; Bartlett et al., 2018). Adults might live on trees and bushes, using their specialized 'grasping' prolegs to anchor themselves to the bark or foliage, and possibly grasp the prothoracic 'shoulder' of the partner to facilitate mating. The hypertrophied postclypeus, with traces of strong muscles of salivary pump, indicate that these minlarerrontid insects were xylem-feeders (Shcherbakov and Popov, 2002; Dietrich, 2002; Wang et al., 2012; Chen et al., 2014; Bartlett et al., 2018), like other ancient and contemporary representatives of the Clypeata lineages. Females very probably laid eggs in shallow topsoil or on soil surface close to the host plants. However, we add a proviso, that reconstruction of the ecology and behavior of the Minlagerrontidae fam. nov. here presented is tentative, based on interpretation of their morphology and knowledge of the related Clypeata lineages.

5. Conclusions

Fossiliferous amber pieces afford exceptional preservation of insects and other microorganisms, providing more details than rock fossils about morphology, ecology, ethology and evolutionary history (Chen et al., 2016). The Kachin amber, as one of the most diverse Mesozoic palaeobiotas (Cruickshank and Ko, 2003; Poinar et al., 2008; Shi et al., 2012; Kania et al., 2015), give us a rare opportunity to glimpse the unique insect assemblage in the mid-Cretaceous when the revolution of terrestrial ecological system was burgeoning (Lloyd et al., 2008; Herendeen et al., 2017). The new family Minlagerrontidae fam. nov. erected on the basis of the Kachin amber inclusions bears some plesiomorphies as well as a series of unusual or even grotesque derived characteristics, indicating that in the Mesozoic, ancient Clypeata had diversified multi-dimensionally and so occupied a wide ranges of ecotopes to reduce mutual competition. Nevertheless, true hoppers are generally monophagous or narrowly oligophagous (Bartlett et al., 2018). The rapid floristic shifting from gymnosperms to angiosperms in the late Early to Late Cretaceous probably resulted in the extinction of ancient groups like Hylicellidae, Procercopidae, Sinoalidae, Cercopionidae, Archijassidae, and Minagerrontidae fam. nov., but also likely led to the subsequent appearance of modern lineages of the Clypeata.

References

Anufriev, G.A., Emeljanov, A.F., 1988. Podotryad Cicadinea (Auchenorrhyncha) — Tsikadovye [Suborder Cicadinea (Auchenorrhyncha)]. In: Ler, P.A. (Ed.), Keys to the insects of the Far East of the USSR. Homoptera and Hetroptera. Nauka, Leningrad, pp. 12—495.

Bai, M., Beutel, R.G., Zhang, W., Wang, S., Hörnig, M., Gröhn, C., Yan, E., Yang, X., Wipfler, B., 2018. A new Cretaceous insect with a unique cephalo-thoracic scissor device. Current Biology 28, 438—443.

Bartlett, C.R., Deitz, L.L., Dmitriev, D.A., Sanborn, A.F., Soulier-Perkins, A., Wallace, M.S., 2018. The diversity of the true hoppers (Hemiptera: Auchenorrhyncha). In: Foottit, R.G., Adler, P.H. (Eds.), Insect Biodiversity: Science and Society, vol. 2, pp. 501—590.

Beutel, R.G., Friedrich, F., Ge, S., Yang, X., 2014. Insect Morphology and Phylogeny. A Textbook for Students of Entomology. Walter de Gruyter, Berlin-Boston.

Bourgoin, T., Wang, R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroinski, A., Yap, S., Szwedo, J., 2015. From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). Zoomorphology 134, 63—77.

Burrows, M., 2006. Morphology and action of the hind-leg joints controlling jumping in froghopper insects. Journal of Experimental Biology 209, 4622—4637.

Caceres-Sanchez, L., Torrico-Bazoberry, D., Cossio, R., Reque, K., Aguilar, S., Niemeyer, H.M., Pinto, C.F., 2017. Biology, ecology and demography of the tropical treehopper *Ennya maculicornis* (Hemiptera: Membracidae): relationships between female fitness, maternal care and oviposition sites. Ecological Entomology 42, 477—483.

Chen, J., Wang, B., Zhang, H., Wang, X., 2014. A remarkable new genus of Tettigarctidae (Insecta, Hemiptera, Cicadoidea) from the Middle Jurassic of northeastern China. Zootaxa 3764, 581—586.

Chen, J., Wang, B., Zhang, H., Wang, X., Zheng, X., 2015. New fossil Procercopidae (Hemiptera: Cicadomorpha) from the Middle Jurassic of Daohugou, Inner Mongolia, China. European Journal of Entomology 112, 373—380.

Chen, J., Wang, B., Jarzembowski, E.A., 2016. Palaeontology: benefits of trade in amber fossils. Nature 532, 441.

Chen, J., Szwedo, J., Wang, B., Zheng, Y., Wang, Y., Wang, X., Zhang, H., 2018. The first Mesozoic froghopper in amber from northern Myanmar (Hemiptera, Cercopoidea, Sinoalidae). Cretaceous Research 85, 243—249.

Chen, J., Wang, B., Zheng, Y., Jiang, H., Jiang, T., Zhang, J., Zhang, H., 2019. A new sinoalid froghopper in mid-Cretaceous Burmese amber, with inference of its phylogenetic position (Hemiptera, Cicadomorpha). Cretaceous Research 95, 121—129.

Corrette, B.J., 1990. Prey capture in the praying mantis *Tenodera aridifolia sinensis*: coordination of the capture sequence and strike movements. Journal of Experimental Biology 148, 147—180.

Crowson, R.A., 1981. The Biology of the Coleoptera. Academic Press Inc.(London) Ltd., London, 802 pp.

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21, 441—455.

Cryan, J.R., Svenson, G.J., 2010. Family-level relationships of the spittle bugs and froghoppers (Hemiptera: Cicadomorpha: Cercopoidea). Systematic Entomology 35, 393–415.

Cryan, J.R., Urban, J.M., 2012. Higher-level phylogeny of the insect order Hemiptera: is Auchenorrhyncha really paraphyletic? Systematic Entomology 37, 7–21.

Dietrich, C.H., 2002. Evolution of Cicadomorpha (Insecta, Hemiptera). Denisia 4, 155–170.

Dietrich, C.H., 2005. Keys to the families of Cicadomorpha and subfamilies and tribes of Cicadellidae (Hemiptera: Auchenorrhyncha). Florida Entomologist 88, 502–517.

Dmitriev, D.A., 2010. Homologies of the head of Membracoidea based on nymphal morphology with notes on other groups of Auchenorrhyncha (Hemiptera). European Journal of Entomology 107, 597–613.

Evans, J.W., 1941. The morphology of Tettigarcta tomentosa White, (Homoptera, Cicadidae). Proceedings of the Royal Society of Tasmania 35–49.

Evans, J.W., 1946. A natural classification of leaf-hoppers (Homoptera, Jassoidea). Part 1. External morphology and systematic position. Transactions of the Royal Entomological Society of London 96, 47–60.

Evans, J.W., 1956. Palaeozoic and Mesozoic Hemiptera (Insecta). Australian Journal of Zoology 4, 165–258.

Forero, D., 2008. The systematics of the Hemiptera. Revista Colombiana de Entomologia 34, 1–21.

Friedemann, K., Beutel, R.G., 2014. Morphology of Arolia in Auchenorrhyncha (Insecta, Hemiptera). Journal of Morphology 275, 1217–1225.

Friedemann, K., Spangenberg, R., Yoshizawa, K., Beutel, R.G., 2014. Evolution of attachment structures in the highly diverse Acercaria (Hexapoda). Cladistics 30, 170–201.

Grimaldi, D., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, New York, p. 755pp.

Grimaldi, D.A., Ross, A.J., 2017. Extraordinary Lagerstätten in amber, with particular reference to Cretaceous of Burma. In: Fraser, N., Sues, H.D. (Eds.), Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land. Dunedin Academic Press, Edinburgh, pp. 287–342.

Grimaldi, D., Zhang, J., Fraser, N.C., Rasnistyn, A., 2005. Revision of the bizarre Mesozoic scorpionflies in the Pseudopolycentropodidae (Mecopteroidea). Insect Systematics and Evolution 36, 443–458.

Gullan, P.J., Cranston, P.S., 2014. The Insects: An Outline of Entomology, fifth ed. Wiley-Blackwell, Oxford. 595 pp.

Guo, M., Xing, L., Wang, B., Zhang, W., Wang, S., Shi, A., Bai, M., 2017. A catalogue of Burmite inclusions. Zoological Systematics 42, 249–379.

Hamilton, K.G.A., 1982. The spittlebugs of Canada (Homoptera: Cercopidae). Insects and Arachnids of Canada 10, 1–102.

Hamilton, K.G.A., 1999. The ground-dwelling leafhoppers Myerslopiidae, new family, and Sagmatiini, new tribe (Homoptera: Membracoidea). Invertebrate Taxonomy 13, 207–235.

Herendeen, P.S., Friis, E.M., Pedersen, K.R., Crane, P.R., 2017. Palaeobotanical redux: revisiting the age of the angiosperms. Nature Plants 3, 17015.

Huang, D., Bechly, G., Nel, P., Engel, M.S., Prokop, J., Azar, D., Cai, C., van de Kamp, T., Staniczek, A., Garrouste, R., Krogmann, L., dos Santos Rolo, T., Baumbach, T., Ohlhoff, R., Shmakov, A.S., Bourgoin, T., Nel, A., 2016. New fossil insect order Permopsocida elucidates major radiation and evolution of suction feeding in hemimetabolous insects (Hexapoda: Acercaria). Scientific Reports 6, 23004.

Kania, I., Wang, B., Szwedo, J., 2015. Dicranoptycha Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Upper Cretaceous Burmese amber. Cretaceous Research 52, 522–530.

Kral, K., 2013. Vision in the mantispid: a sit-and-wait and stalking predatory insect. Physiological Entomology 38, 1–12.

Lara, M.B., Wang, B., 2016. New hemipteran insects (Eoscarterellidae, Scytinopteridae, and Protopsyllidiidae) from the Upper Triassic Potrerillos Formation of Mendoza, Argentina. Paläontologisches Zeitschrift 90, 49–61.

Laufer, B., 1906. Historical jottings on amber in Asia. Memoirs of the American Anthropological Association 1, 215–244.

Lin, C., 2006. Social behaviour and life history of membracine treehoppers. Journal of Natural History 40, 1887–1907.

Linnaeus, C., 1758. Systema naturae per regni tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, tenth ed. Laurentius Salvius, Stockholm.

Lloyd, G.T., Davis, K.E., Pisani, D., Tarver, J.E., Ruta, M., Sakamoto, M., Hone, D.W.E., Jennings, R., Benton, M.J., 2008. Dinosaurs and the Cretaceous Terrestrial Revolution. Proceedings of the Royal Society, B 275, 2483–2490.

Martins-Neto, R.G., Gallego, O.F., 1999. The Triassic insect fauna from Argentina. I. Auchenorrhyncha, Miomoptera and Ensifera. Revista Espanola de Paleontologia 14, 191–202.

Martins-Neto, R.G., Gallego, O.F., Melchor, R.N., 2003. The Triassic insect fauna from South America (Brazil, Argentina and Chile): a checklist (except Blattoptera and Coleoptera) and descriptions of new taxa. Acta Zoologica Cracoviensia 46, 229–256.

Martins-Neto, R.G., Gallego, O.F., Zavattieri, A.M., 2008. The Triassic insect fauna from Argentina: Coleoptera, Hemiptera and Orthoptera from the Potrerillos Formation, south of Cerro Cacheuta, Cuyana basin. Alavesia 2, 47–58.

Martynov, A.V., 1927. Jurassic fossil insects from Turkestan. 6. Homoptera and Psocoptera. Izvestiya Akademii Nauk SSSR 20, 1349–1366, 1926.

Masters, K.L., Masters, A.R., Forsyth, A., 1994. Female-biased sex ratio in the neotropical treehopper Umbonia ataliba (Homoptera/Membracidae). Ethology 96, 353–366.

Matsumura, S., 1927. New species of Cicadidae from the Japanese Empire. Insecta Matsumurana 2, 46–58.

Moulds, M.S., 2005. An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. Records of the Australian Museum 57, 375–446.

Myers, J.G., 1928. The morphology of the Cicadidae. Proceedings of the Zoological Society of London 365–472, 1928.

Nel, A., Prokop, J., Nel, P., Grandcolas, P., Huang, D., Roques, P., Guilbert, E., Dostal, O., Szwedo, J., 2012. Traits and evolution of wing venation pattern in paraneopteran insects. Journal of Morphology 273, 480–506.

Novotný, V., Wilson, M.R., 1997. Why are there no small species among xylem-sucking insects? Evolutionary Ecology 11, 419–437.

Poinar, G.O., Buckley, R., Brown, A.E., 2008. The secrets of burmite amber. Mid-America Paleontological Society Digest 20, 21–29.

Pulz, C.E., Carvalho, G.S., 1998. Morfologia do adulto de Deois flexuosa Walker, 1851 (Insecta, Hemiptera, Cercopidae). Biociências 6, 95–117.

Qadri, M.A.H., 1967. Phylogenetic Study of Auchenorrhyncha, vol. 4. University Studies (Karachi), pp. 1–16.

Rakitov, R.A., 2002. Structure and function of the Malpighian tubules, and related behaviors in juvenile cicadas: evidence of homology with spittlebugs (Hemiptera: Cicadoidea and Cercopoidea). Zoologischer Anzeiger 241, 117–130.

Raven, J.A., 1983. Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. Advances in Ecological Research 13, 135–234.

Ross, A.J., 2018. Burmese (Myanmar) Amber Taxa, On-line Checklist v.2018.1. https://www.nms.ac.uk/media/1157149/burmese-amber-taxa-v2018_1.pdf.

Ross, A., Mellish, C., York, P., Crighton, B., 2010. Chapter 12. Burmese amber. In: Penney, D. (Ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, pp. 208–235.

Shcherbakov, D.E., 1989. New cicadas (Cicadina) from the later Mesozoic of Transbaikalia. Paleontological Journal 4, 52–63, 1988.

Shcherbakov, D.E., 1992. The earliest leafhoppers (Hemiptera: Karajassidae n. fam.) from the Jurassic of Karatau. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 39–51, 1992.

Shcherbakov, D.E., 1996. Origin and evolution of the Auchenorrhyncha as shown by the fossil record. In: Schaefer, C.W. (Ed.), Studies on Hemipteran Phylogeny. Thomas Say Publications in Entomology. Entomological Society of America, Lantham, MD, pp. 31–45.

Shcherbakov, D.E., 2011. New and little-known families of Hemiptera Cicadomorpha from the Triassic of Central Asia—early analogs of treehoppers and planthoppers. Zootaxa 2836, 1–26.

Shcherbakov, D.E., 2012a. A new subfamily of Mesozoic Hylicellidae (Homoptera: Cicadomorpha). Russian Entomological Journal 21, 441–444.

Shcherbakov, D.E., 2012b. More on Mesozoic Membracoidea (Homoptera). Russian Entomological Journal 21, 15–22.

Shcherbakov, D.E., Popov, Y.A., 2002. Superorder Cimicidea Laicharting, 1781 order Hemiptera Linné, 1758. The bugs, cicadas, plantlice, scale insects, etc. In: Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), History of Insects. Kluwer Academic Publisher, Dordrecht, pp. 152–155.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Wang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163.

Song, N., Liang, A., Bu, C., 2012. A molecular phylogeny of Hemiptera inferred from mitochondrial genome sequences. PLoS One 7, e48778.

Sorensen, J.T., Campbell, B.C., Gill, R.J., Steffen-Campbell, J.D., 1995. Non-monophyly of Auchenorrhyncha ("Homoptera"), based upon 18S rDNA phylogeny: eco-evolutionary and cladistic implications within pre-heteropterodea Hemiptera (s. l.) and a proposal for new monophyletic suborders. Pan-Pacific Entomologist 71, 31–60.

Stål, C., 1861. Genera nonnulla nova Cicadinorum. Annales de la Société Entomologique de France 1, 613–622.

Stork, N.E., McBroom, J., Gely, C., Hamilton, A.J., 2015. New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. Proceedings of the National Academy of Sciences 112, 7519–7523.

Storozhenko, S., 1992. New Mesozoic grylloblattid insects (Grylloblattida) from Middle Asia. Paleontologicheskiï Zhurnal 1, 67–75, 1992.

Szwedo, J., 2018. The unity, diversity and conformity of bugs (Hemiptera) through time. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 107, 109–128.

Terra, W.R., 1990. Evolution of digestive systems of insects. Annual Review of Entomology 35, 181–200.

Tillyard, R.J., 1919. Mesozoic Insects of Queensland. No. 7 Hemiptera Homoptera; with a note on the phylogeny of the suborder. Proceedings of the Linnean Society of New South Wales 44, 857–896.

Wang, B., Szwedo, J., Zhang, H., 2012. New Jurassic Cercopoidea from China and their evolutionary significance (Insecta: Hemiptera). Palaeontology 55, 1223–1243.

Wedmann, S., Bradler, S., Rust, J., 2007. The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior. Proceedings of the National Academy of Sciences 104, 565–569.

Wieland, G.R., 1925. Rhaetic crane flies from South America. American Journal of Science 9, 21–28.

Wood, T.K., Dowell, R., 1984. Sex ratio in Umbonia crassicornis Amyot and Serville (Homoptera, Membracidae). American Midland Naturalist 112, 58–66.

Zheng, D., Nel, A., Chang, S.C., Jarzembowski, E.A., Zhang, H., Wang, B., 2018a. A well-preserved true dragonfly (Anisoptera: Gomphides: Burmagomphidae fam. nov.) from Cretaceous Burmese amber. Journal of Systematic Palaeontology 16, 881–889.

Zheng, D., Chang, S., Perrichot, V., Dutta, S., Rudra, A., Mu, L., Kelly, R.S., Li, S., Zhang, Q., Wang, J., Wang, H., Fang, Y., Zhang, H., Wang, B., 2018b. A Late Cretaceous amber biota from central Myanmar. Nature Communications 9, 3170.

Zherikhin, V.V., Ross, A.J., 2004. A review of the history, geology and age of Burmese amber (Burmite). Bulletin of the Natural History Museum (Geology) 56, 3–10.

Zimmermann, U., Meinzer, F.C., Benkert, R., Zhu, J.J., Schneider, H., Goldstein, G., Kuchenbrod, E., Haase, A., 1994. Xylem water transport: is the available evidence consistent with the cohesion theory? Plant, Cell and Environment 17, 1169–1181.