

## Short communication

# A representative of the modern leafhopper subfamily Ledrinae in mid-Cretaceous Burmese amber (Hemiptera, Cicadellidae)

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## ABSTRACT

The Cicadellidae, one of largest insect families, is highly diversified in its living groups; fossils of this family, however, are poorly documented. Up to now, only three modern cicadellid subfamilies have been reported from the late Mesozoic, represented by five monotypic genera. We herein erect a new taxon, *Qilia regilla* gen. et sp. nov., from mid-Cretaceous Burmese amber, and tentatively ascribe it to Ledrinae: Paracarsonini. The new genus differs distinctly from other Paracarsonini from the Crato Formation of Brazil in having the head with the apex of the anterior margin acute; the antennae located relatively far away from the postclypeus; crossveins from RA to the anterior margin of the wing absent, resulting in a long and unbroken anterior cell; the terminal branches of RA and MP reduced in number; and crossveins (*ir* and *rp-mp*) weakly expressed. The results of the present study greatly expand the paleogeography of modern Ledrinae in the late Mesozoic, and also add some significant information to our knowledge of the diversity, distribution and evolution of early leafhoppers.

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## 1. Introduction

The hitherto earliest Cicadelloidea Latreille, 1802 (leafhoppers and their relatives) were recorded in the Upper Triassic of Australia, represented by the extinct Archijassidae Becker-Migdisova, 1962; this family flourished in the Jurassic, and became extinct in the Early Cretaceous likely due to replacement by its derived descendants (i.e. Cicadellidae Latreille, 1802, Membracoidea Rafinesque, 1815 and Myerslopioidea Evans, 1957) in the Cretaceous Terrestrial Revolution, as in other Clypeata groups (i.e. Cercopoidea Leach, 1815 and Cicadoidea Latreille, 1802) (Shcherbakov and Popov, 2002; Zherikhin, 2002; Szwed, 2005, 2018; Lloyd et al., 2008; Wang et al., 2010;

Shcherbakov, 2012; Chen et al., 2015; Chen and Wang, 2016; Herendeen et al., 2017; Katz, 2017). The Cicadellidae (leafhoppers), as one of the 10 largest insect families, displays extreme taxonomic richness in its recent groups. Fossil records of this family, however, are poorly documented. Up to now, fewer than 100 confirmed fossil species have been erected, with most of them from the Cenozoic (Poinar and Brown, 2017; Bartlett et al., 2018; Dietrich and Thomas, 2018).

Just a few cicadellids have been recorded from the Cretaceous (Oman, 1937; Zhang, 1985; Shcherbakov, 1986; Hamilton, 1990, 1992; Ross and Cook, 1995; Menon et al., 2007; Poinar and Brown, 2017). Based on tegminal venation patterns, *Mesojassoides gigantea* Oman, 1937 from the Maastrichtian (Upper Cretaceous) of Colorado, U.S.A. was assigned to Cicadellinae Latreille, 1802: Bathysmatophorini Anufriev, 1978 (Szwed, 2005). *Priscacutius denticulatus* Poinar and Brown (2017; just online, not printed yet) from the Cenomanian (lowermost Upper Cretaceous) Burmese amber was treated as the earliest representative of Signoretinae Baker,

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1915: Phlogisini Linnavuori, 1979 on the basis of an enlarged and punctate pronotum that extends to the scutellar suture, the ocelli being distant from the anterior margin, and the carinae on crown and face being reduced (Dietrich and Thomas, 2018). *Proerrhomus rugosus* Hamilton, 1990, along with several other fossil specimens without formal description from the well-known Aptian (Lower Cretaceous) Crato Formation of Brazil, was ascribed to Cicadellinae: Proerrhomini Hamilton, 1990 (Menon et al., 2007).

The Jascopidae Hamilton, 1971, originally considered to represent a transitional form combining characteristics of Cercopidae and Cicadellidae, was erected by Hamilton (1971) based on a hemipteran nymph from Campanian (Upper Cretaceous) Canadian amber. Additional taxa from the Triassic to the Cretaceous of Australia and Eurasia were later attributed to the family (Hamilton, 1990, 1992). This family was treated as a synonym of Cicadellidae, and most 'jascopid' genera were ascribed to other cicadomorph families, by subsequent authors (Evans, 1972, 1988; Shcherbakov, 1992, 1996; Shcherbakov and Popov, 2002; Menon et al., 2007; Shcherbakov, 2012). The tribe Paracarsonini Hamilton, 1990, with two monotypic genera *Paracarsonus* Hamilton, 1990 and *Platyjassites* Hamilton, 1990 from the Crato Formation of Brazil, originally placed in Jascopidae, was transferred to Cicadellidae: Ledrinae Fairmaire, 1855 (Shcherbakov, 1996; Shcherbakov and Popov, 2002; Menon et al., 2007; Dietrich and Thomas, 2018). Its phylogenetic position was also carefully discussed (but not analyzed) by Jones and Deitz (2009), in their cladistic analysis of the Ledrinae.

We herein report a new leafhopper fossil, referable to the subfamily Ledrinae, from mid-Cretaceous Burmese amber. The new taxon, displaying a combination of several ancestral characteristics and a series of unique morphological traits, sheds new light on the diversification, radiation and evolution of early leafhoppers in the late Mesozoic.

## 2. Geological context

The amber piece, with the new leafhopper specimen included, was collected from the Hukawng Valley of Kachin Province in northern Myanmar (Fig. 1). Burmese amber, designated as Burmite

by Helm (1893) due to its remarkable distinctiveness relative to other amber types, has been mined for thousands of years (Poinar et al., 2008). The Burmese amber biota, as probably the most diverse Mesozoic palaeobiota (Shi et al., 2012), is now recognized as a significant window to the Cretaceous biosphere (Cruckshank and Ko, 2003; Poinar et al., 2008; Kania et al., 2015).

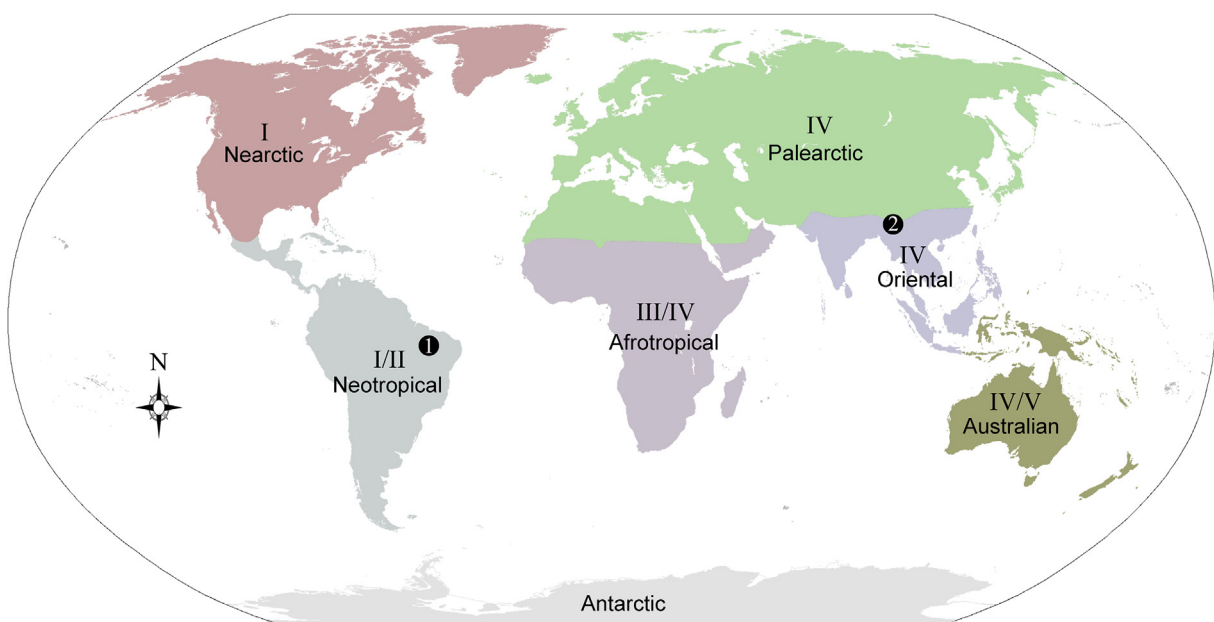
The age of Burmese amber had been obscure for a long time, even briefly considered as young as the Miocene (Grimaldi et al., 2005). Now, Burmese amber is biostratigraphically considered to be mid-Cretaceous (e.g., Cruckshank and Ko, 2003; Grimaldi et al., 2005; Ross et al., 2010) earliest Cenomanian (ca.  $98.79 \pm 0.62$  Ma) in age, based on a recent U–Pb zircon dating study (Shi et al., 2012).

Leafhoppers are relatively abundant and highly diverse in Burmese amber; only one taxon, *Priscacutius denticulatus*, however, has been formally described and illustrated. The taxon was originally treated as subfamily *incertae sedis* within Cicadellidae, but subsequently ascribed to the modern subfamily Signoretinae based on the enlarged and punctate pronotum that extends to the scutellar suture (Dietrich and Thomas, 2018). The new taxon erected herein, referable to the modern subfamily Ledrinae, is the second representative of Cicadellidae.

## 3. Material and methods

The amber piece containing the fossil leafhopper is yellow and transparent. The fossil specimen was examined, photomicrographed and measured using the VHX 5000 digital microscope platform, with incident and transmitted light used alternately or sometimes simultaneously. The line drawings and reconstructions were prepared in two image-editing softwares (CorelDraw X7 and Adobe Photoshop CS6). The amber specimen is deposited in Linyi University (LYU-MD-YC001). All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoo-bank.org:pub:B1F6EBA0-1155-4EC7-BE8A-CE3D6D0CD988.

The venational terminology used herein mainly follows Chen et al. (2018), which is modified from Nel et al. (2012) and Bourgoïn et al. (2015). Wing abbreviations are as follows: RA,



**Fig. 1.** The location of fossil deposits and distribution of modern tribes of Ledrinae. 1, the Lower Cretaceous Crato Formation of northeastern Brazil; 2, The Upper Cretaceous Burmese amber. I, Xerophloeiini; II, Hespenerini; III, Afrorubriini; IV, Ledrini; V, Rubrini.

anterior branch of radial vein; RP, posterior branch of radial vein; MP, posterior branch of medial vein; CuA<sub>1</sub>, first branch of anterior branch of cubital vein; CuA<sub>2</sub>, second branch of anterior branch of cubital vein; CuP, posterior branch of cubital vein; Pcu, postcubital vein; A<sub>1</sub>, first branch of anal vein; *ir*, crossvein connecting anterior and posterior branches of radial vein; *rp-mp*, crossvein connecting posterior branch of radial vein and posterior branch of medial vein; *mp-cua*, crossvein connecting posterior branch of medial vein and anterior branch of cubital vein; *cua-cup*, crossvein connecting anterior and posterior branches of cubital vein.

The higher-level systematics and classification of fossil and living Hemiptera was recently updated by Szwedo (2018). In that study, the Cicadelloidea (leafhoppers and close relatives) was resurrected as an independent superfamily, with extinct Archijassidae and extant Cicadellidae included, and is independent of the Membracoidea (treehoppers and close relatives). The taxonomic framework employed herein follows Szwedo (2018).

#### 4. Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Cicadomorpha Evans, 1946

Family Cicadellidae Latreille, 1802

Subfamily Ledrinae Fairmaire, 1855

Tribe Paracarsonini Hamilton, 1990

Genus *Qilia* Chen, Wang and Jones, gen. nov.

(urn:lsid:zoobank.org:act:BF0719A2-3174-400E-A741-69756833CEB2)

Type species: *Qilia regilla* Chen, Wang and Jones, gen. et sp. nov.; by present designation and monotypy.

*Etymology.* Named in honor of Professor Qi Li, the Ph.D. supervisor of the first author (J. Chen).

*Diagnosis.* Head wider than pronotum; with coronal margin wrapping around compound eyes. Lateral ocelli extremely near posterior margin of crown, and closer to one another than to eyes. Postclypeus with base almost reaching coronal margin. Metathoracic legs with tibiae long, row II with four large lateral spines. Tegmen with base almost touching compound eyes; appendix narrow; crossveins from RA to the anterior margin of the wing absent, resulting in a long, continuous, and unbroken anterior cell.

*Qilia regilla* Chen, Wang and Jones, gen. et sp. nov.

(urn:lsid:zoobank.org:act:3D7E1A19-D9BA-410E-A270-280BD05EC798)

Figs. 2–6

*Etymology.* The specific epithet is derived from the Latin “regilla” (honorable and distinguished), in praise of Professor Q. Li.

*Holotype.* LYU-MD-YC001, adult with gender unknown, right tegmen outspread, abdomen and hindwings not preserved; deposited in Linyi University in Linyi, China.

*Locality and horizon.* Hukawng Valley, Kachin Province, Myanmar; lowermost Cenomanian, Upper Cretaceous (Shi et al., 2012).

*Diagnosis.* Size small. Pronotum with posterior margin curved. Tegmen well sclerotized and punctate, with RA and MP unbranched and crossveins (*ir* and *rp-mp*) reduced in number and weakly expressed.

*Description.* Measurements (in mm). Body including tegmen in repose length 5.05; head with compound eyes length 1.07, width 1.82; compound eye in dorsal view length 0.53, width 0.25; postclypeus length 0.99, width 0.62; anteclypeus length 0.61, width 0.28; rostrum length 0.82; lorum length 0.47, width 0.19; pronotum length 0.94, width 1.64; mesonotum with scutellum and post-scutellum included length 0.54, width 0.69; scutellum + post-scutellum length 0.35, width 0.29; fore coxa length 0.43, trochanter length 0.22, femur length 0.66, tibia length 0.72, tarsus length 0.48; middle trochanter length 0.18, femur length 0.66, tibia length 0.84, tarsus length 0.32; hind femur length 0.90, tibia length 1.52, tarsus length 0.72; right tegmen length 3.51, width 1.49.

*Head.* (Figs. 2, 3A–C, 4). Head with compound eyes conspicuously wider than pronotum. Coronal margin wrapping around compound eyes. Anterior margin foliaceous; apex acute. Crown slightly concave, with a distinct medial carina; disc with tiny granules. Compound eyes large, somewhat ovaloid. Two lateral ocelli near posterior margin of crown, closer to one another than to eyes. Face heavily pitted. Postclypeus about one-third as wide as head, broad, slightly inflated, widest at its middle, transverse grooves not distinct; base almost reaching coronal margin. Anteclypeus somewhat flat at base. Rostrum moderately long, extending to hind coxae. Antenna with flagellum filiform, slender.

*Thorax.* (Figs. 2, 3D, 5). Pronotal disc with tiny granules; medial carina distinct; anterior margin long, somewhat arcuate; anterolateral margins reduced, very narrow; lateral angles very acute; posterolateral margin slightly concave; posterior margin distinctly

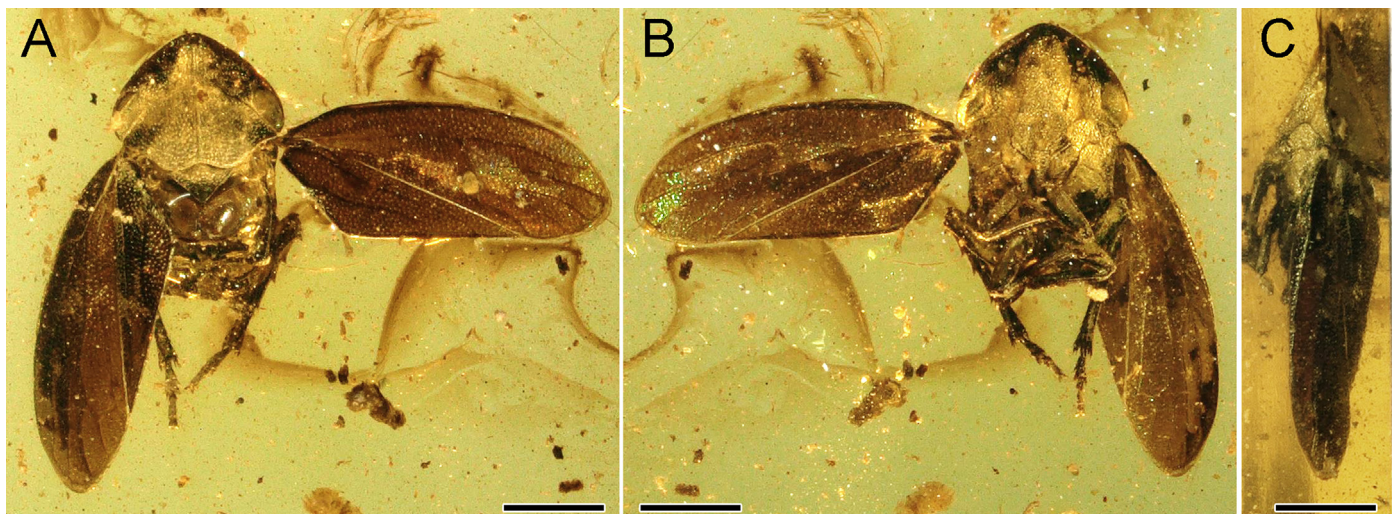
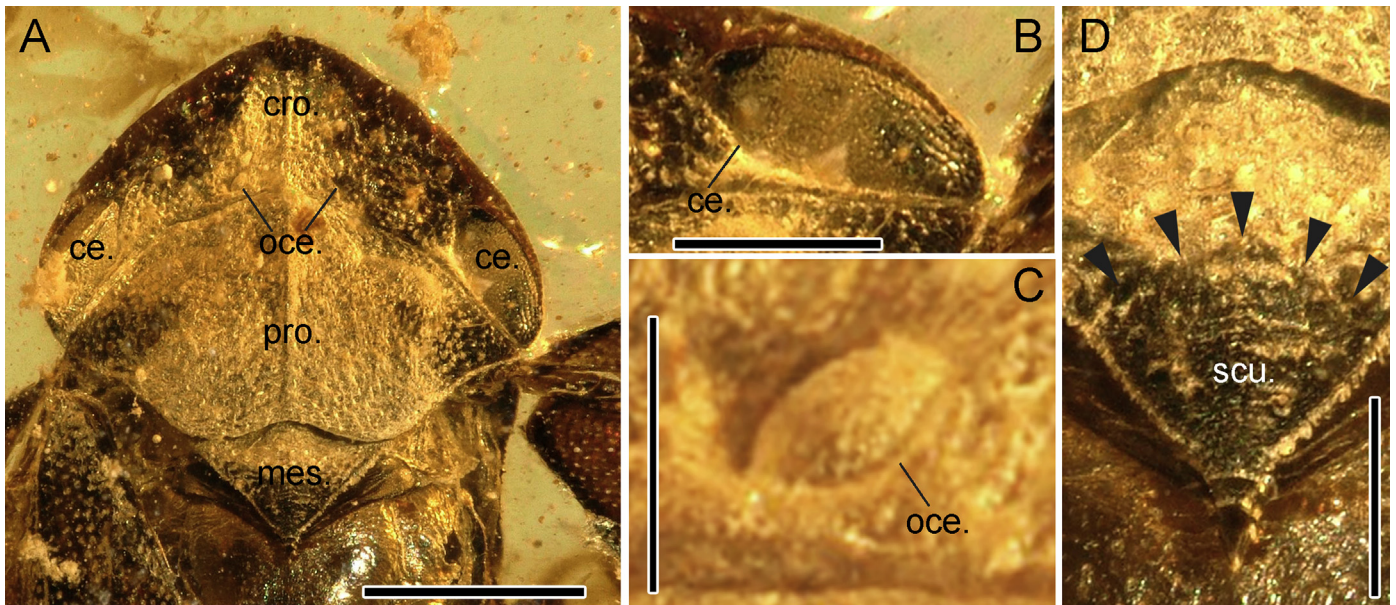


Fig. 2. Photographs of holotype of *Qilia regilla* gen. et sp. nov. (A), dorsal view; (B), ventral view; (C), lateral view. Scale bars = 1 mm.





**Fig. 3.** Head and thorax of *Qilia regilla* gen. et sp. nov. in dorsal view. (A), overview of head and thorax; (B), right compound eye; (C), left ocellus; (D), mesonotum. Annotations: cro., crown; ce., compound eye; oce., ocellus; pro., pronotum; mes., mesonotum; scu., scutellum. Triangles in (D) indicate mesoscutal sulcus. Scale bars = 1 mm (A), 0.5 mm (B), 0.1 mm (C), 0.2 mm (D).

concave and bilobed. Mesonotum apparently smaller than pronotum; medial carina not distinct; mesoscutal sulcus smoothly curved; scutellum transversely rugose; post-scutellar apex forming a long spine, spear-like. Proepisternum large. Prothoracic legs with coxae strong; femora with distinct marginal carina; tibiae slightly longer than femora, with some long setae; basi- and midtarsomere of similar length, apical tarsomere obviously longer; tarsal claws reduced. Mesothoracic legs with trochanters well developed; femora thick, slightly shorter than tibiae; tibiae setose; tarsi setose, with basitarsomere apparently shorter than mid- and apical tarsomeres; two tarsal claws visible. Metathoracic legs with femora strong; metatibiae much longer than fore- and middle tibiae, densely covered with setae; cucullae of row II large; apical teeth arranged in two rows; tarsi with midtarsomere much shorter than basi- and apical tarsomeres, and basi- and midtarsomeres with well-developed apical teeth; two tarsal claws large.

**Tegmen.** (Figs. 1, 6). Tegmen broad, sclerotized and punctate; base almost touching compound eyes. Appendix present at anterior and apical margin, narrow. Anterior margin smoothly curved; apical margin acute; claval margin strongly arched. Clavus long and broad, with apex reaching 3/4 of tegmen length. RA+MP bifurcating at basal 0.27 of wing length. Stem R long, branching into RA and RP at basal 0.74 of wing length; RA and RP long, unbranched. MP slightly sinuous, unbranched. CuA divided from R+MP+CuA at wing base, connected to CuP by a short common stalk instead of crossvein *cua-cup*, branching into CuA<sub>1</sub> and CuA<sub>2</sub> at basal 0.68 of wing length; CuA<sub>1</sub> long, geniculate at its connection with crossvein *mp-cua*; CuA<sub>2</sub> short, slightly curved. CuP curved at its fusion with CuA and then straight. Pcu sub-parallel to CuP. A<sub>1</sub> sinuous, with apical part weak. Crossveins *ir*, *rp-mp* weak, and *rp-mp* two in number; crossvein *mp-cua* oblique.

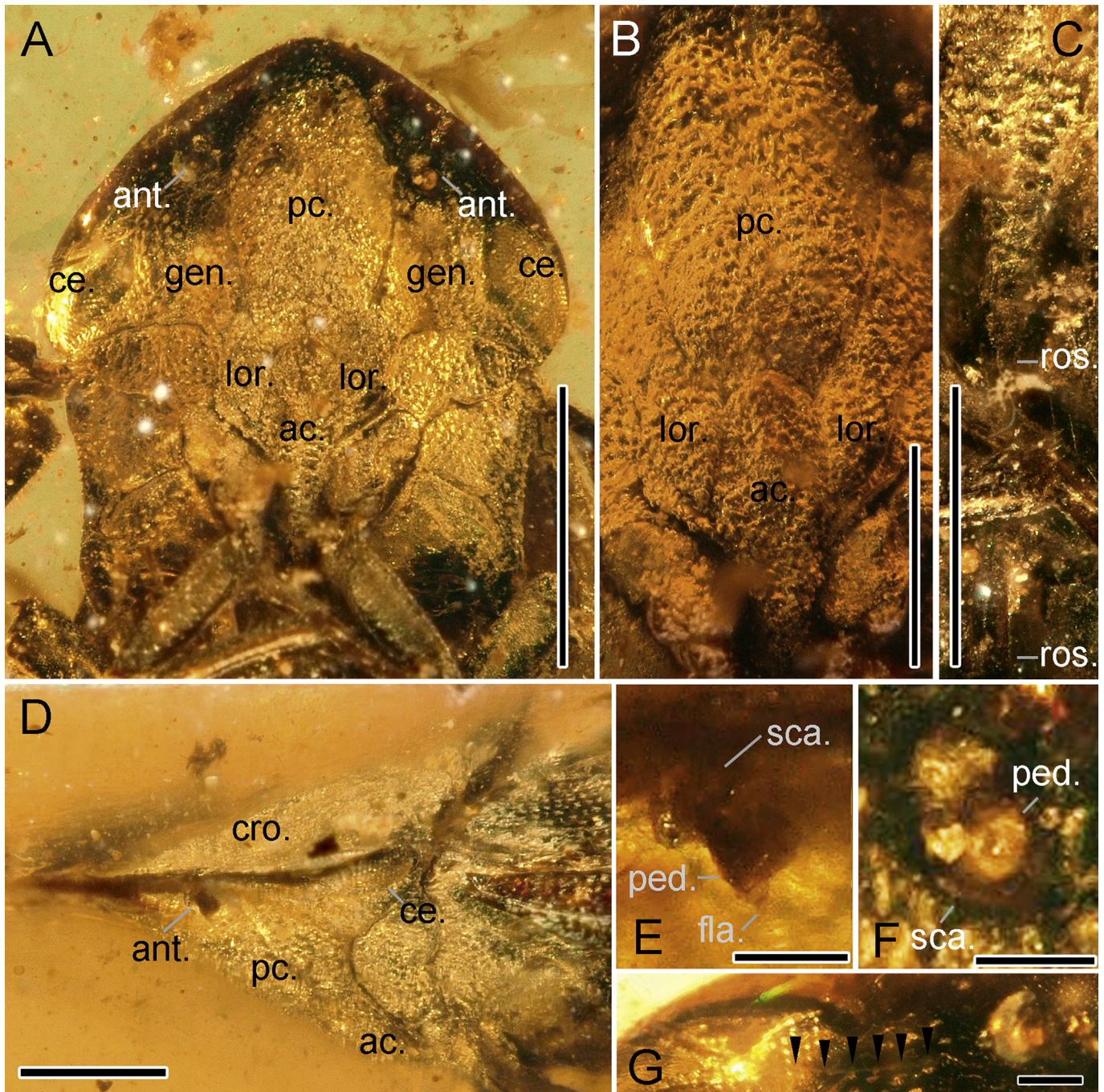
## 5. Discussion

The remarkable new leafhopper described herein from mid-Cretaceous Burmese amber can be attributed to Ledorinae: Paracarsonini on the following morphological characteristics:

integument heavily pitted; head large; coronal margin wrapping around compound eyes; postclypeus one-third as wide as head; tegmen with base extremely close to compound eyes; appendix of forewing present, at least apically, but narrow; metathoracic tibia row II with cucullae and their corresponding subtending macrosetae reduced or absent (5 or fewer). Jones and Deitz (2009: 60) transferred *Paracarsonus* Hamilton, 1990 to Xerophloeini, and considered that *Platyjassites* Hamilton, 1990 might belong within the *Petaloccephala* genus group of Ledorini. However, *Paracarsonus*, *Platyjassites*, and *Qilia* gen. nov. share some common traits separating them from recent Ledorinae, including Xerophloeini and the *Petaloccephala* genus group, and even most Cicadellidae (e.g., coronal margin wrapping around at least part of compound eyes, tegmen with base extremely close to compound eyes, metathoracic tibia row II with macrosetae number reduced), suggesting that the Paracarsonini might be a monophyletic group. We tentatively treat Paracarsonini as a valid tribe in the present study, closely related to Xerophloeini. However, the systematic position of these Mesozoic ledrine leafhoppers should be tested in a phylogenetic framework in a future study.

Amber affords exceptional three-dimensional preservation of insects as well as other tiny organisms (Chen et al., 2016), often providing more details than imprint fossils (e.g., Wang et al., 2016; Wichard et al., 2018). The known records of Paracarsonini were previously reported exclusively from the Crato Formation of Brazil based on imprint fossils, with some key diagnostic features obscured or even not preserved (Jones and Deitz, 2009). Compared with materials from the Crato Formation, the Paracarsonini in Burmese amber provide some new information on the diagnostic traits of the tribe. For example, the tegmen with the base very close to the compound eyes is a common character shared by the known Paracarsonini genera. *Qilia* gen. nov. further shows this character is likely accompanied by extreme reduction of the anterolateral margins of the pronotum, and this character is unique within Ledorinae. Hamilton (1990) ascribed Paracarsonini to Jascopidae based on the metathoracic leg with the tibia very short, the basitarsomere extremely enlarged and the claws small, which are





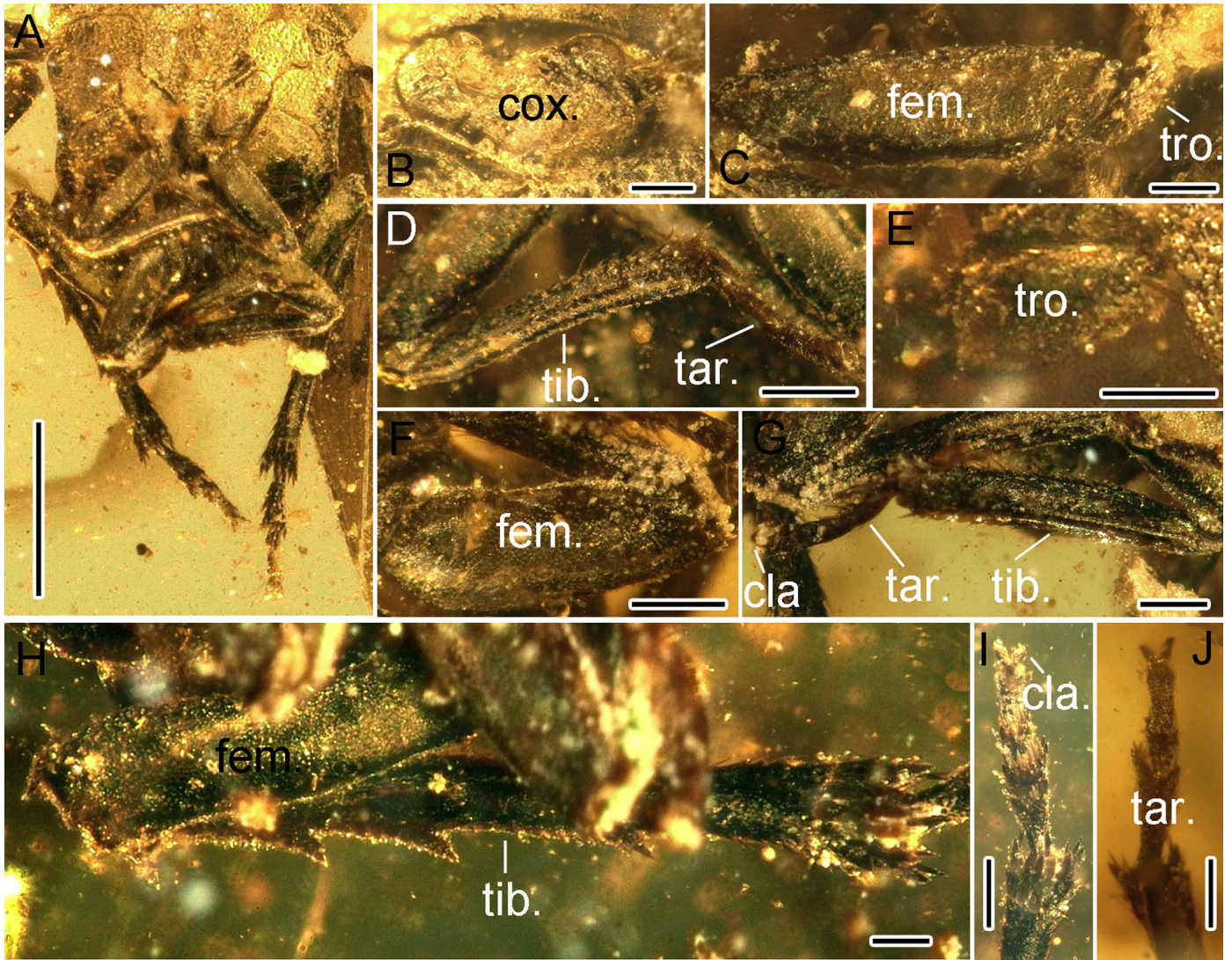
**Fig. 4.** Head of *Qilia regilla* gen. et sp. nov. in ventral and lateral view. (A), overview of head in ventral view; (B), postclypeus, anteclypeus and lorum; (C), rostrum; (D), overview of head in lateral view; (E), left antenna in lateral view; (F), left antenna; (G), right antenna. Annotations: gen., gena; lor., lorum; ce., compound eye; pc., postclypeus; ac., anteclypeus; ros., rostrum; cro., crown; ant., antenna; sca., scape; ped., pedicel; fla., flagellum. Triangles in (G) indicate flagellum. Scale bars = 1 mm (A), 0.5 mm (B, C, D), 0.1 mm (E, F, G).

similar to its type genus; however, the assertions and illustrations of these characters in Hamilton (1990) were considered to be misinterpretations of the fossil material (Shcherbakov, 1992; Jones and Deitz, 2009). Our new fossil leafhopper, bearing hind legs with a long tibia, regular basitarsomere, and well-developed tarsal claws, confirms that Paracarsonini is apparently different from the type genus of Jascopidae and should not be assigned to the family. Besides, some special morphological traits, present in the new leafhopper but not revealed in fossils from the Crato Formation, might be synapomorphies of Paracarsonini, such as the post-

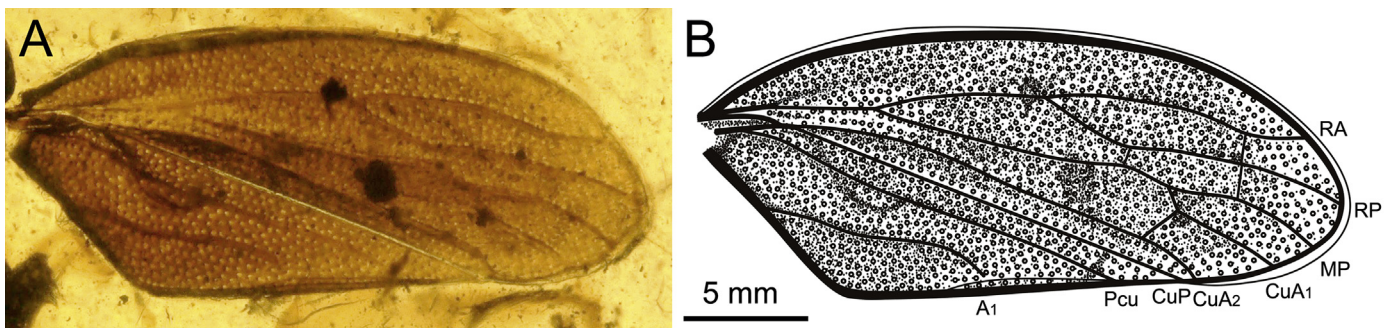
scutellum apex being spear-like. However, the question as to whether these characters are tribe-level diagnostic traits or just autapomorphies of *Qilia* gen. nov. is open until more fossil material becomes available.

Although Ledrinae is a small subfamily of Cicadellidae, with only approximately 300 living species attributed to 38 genera, modern ledrine leafhoppers are widespread, with the Xerophloeini being Nearctic and Neotropical, Hespenerdrini Neotropical, Afrorubriini Afrotropical, Rubriini Australian, and the Ledrini widespread in the Afrotropical, Palearctic, Oriental and Australian regions (Fig. 1;





**Fig. 5.** Legs of *Qilia regilla* gen. et sp. nov. (A), overview of legs; (B), left fore coxa; (C), right fore trochanter and femur; (D), right fore tibia and tarsus; (E), left middle trochanter; (F), right middle femur; (G), left middle tibia and tarsus; (H), right hind femur and tibia; (I), right hind tarsus in ventral view; (J), right hind tarsus in dorsal view. Annotations: cox., coxa; tro., trochanter; fem., femur; tib., tibia; tar., tarsus; cla. claw. Scale bars = 1 mm (A), 0.1 mm (B, C, E, H), 0.2 mm (D, F, G, I, J).



**Fig. 6.** Right tegmen of *Qilia regilla* gen. et sp. nov. (A), photograph; (B), drawing. All to scale bar.

Jones and Deitz, 2009). According to the phylogenetic analysis of Jones and Deitz (2009), the higher level evolutionary relationships within Ledorinae are as follows: (Xerophloeini + Afrorubriini) + (Rubrini + (Hespenedrini + Ledorini)). The phylogeographic patterns of modern ledorines support the view that this subfamily

represents an ancestral lineage of Cicadellidae (Evans, 1951, 1958; Ross, 1957; Shcherbakov, 1992; Dietrich et al., 2005; Jones and Deitz, 2009). Our find of a new fossil in Burmese amber expands the paleogeography of Ledorinae in the late Mesozoic, confirming that Ledorinae is an old leafhopper group, and further suggesting



that this subfamily had probably distributed worldwide at the latest in the mid-Cretaceous.

## 6. Conclusions

With the current study, three modern leafhopper subfamilies (Cicadellinae, Signoretinae and Ledorinae) with two extant (Bathysmatophorini and Phlogisini) and two extinct (Proerrhomini and Paracarsonini) tribes have now been reported from the Cretaceous. Some other Cretaceous cicadellids have been placed as subfamily *incertae sedis*, mostly due to absence of diagnostic characters as a result of poor preservation. Although the record of Mesozoic Cicadellidae remains scarce and extremely fragmentary, it has revealed high morphological and taxonomical diversification. Our new fossil, tentatively assigned to Paracarsonini of Ledorinae, adds some significant information to our knowledge of diversity, distribution and evolution of early leafhoppers.

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