

The first representative of Progonocimicidae (Hemiptera: Coleorrhyncha) from mid-Cretaceous Burmese amber

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ABSTRACT

Gakasha calcaridentata gen. et sp. nov. representing Progonocimicidae: Cicadocorinae (moss bugs) is described. It is the first record of Coleorrhyncha in mid-Cretaceous Burmese amber and the second in fossil resins from the Cretaceous. The taxonomic position of some taxa placed in the genus *Mesocimex* is analysed and new placements proposed. The fossil record of Cicadocorinae is discussed.

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1. Introduction

The hemipteran suborder Coleorrhyncha Myers et China, 1929 is known in the fossil record since the Permian. These Hemiptera, also known as ‘moss bugs’, contains four families: the only extant family Peloridiidae Breddin, 1897 (Holocene-recent); and extinct families Karabasiidae Yu. Popov, 1985 (Jurassic, Sinemurian-Tithonian), Hoploridiidae Yu. Popov et Shcherbakov, 1991 (Cretaceous, Aptian) and Progonocimicidae Handlirsch, 1906 (Permian (Changhsingian)–Cretaceous (Aptian)) (Dong et al., 2014; Szwedo, 2018).

The extant Peloridiidae comprises 17 genera and 38 described species, distributed in temperate and subantarctic rain forests of eastern Australia, New Zealand, New Caledonia and Patagonia, in the Southern Hemisphere, with a classical southern Gondwanan

distribution (Burckhardt, 2009; Burckhardt et al., 2011; Shcherbakov, 2014; Ye et al., 2018). Mainly found in damp moss or on decaying mossy trunks and twigs of *Nothofagus* trees, almost all extant species of Peloridiidae lack hind wings and are unable to fly. They occasionally feed on moss rhizoids, or even on wood-destroying fungi or on lichens (Evans, 1982; Popov and Shcherbakov, 1996; Szwedo, 2011; Shcherbakov, 2014).

The family Hoploridiidae was previously considered to be one of the subfamilies of Karabasiidae (Popov and Shcherbakov, 1991) but recently, Dong et al. (2014) suggested they to be raised to family rank. Species of Hoploridiidae are characterized by the large and flattened body, and distinguished from Karabasiidae by the reticulate venation and wide paranota lacking areolation, two-segmented hind tarsi without an apical pecten of teeth. The family Karabasiidae was considered to be a transitional group between Progonocimicidae and Peloridiidae (Popov and Shcherbakov, 1991, 1996; Wang B. et al., 2009; Szwedo, 2011; Jiang J.Q. et al., 2016).

The more ancient family Progonocimicidae was widespread in Eurasia, Australia, and South America from the Late Permian to Late

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Cretaceous with more than 20 genera, consisting of two sub-families: Progonocimicinae Handlirsch, 1906 and Cicadocorinae Becker-Migdisova, 1958 (Popov and Shcherbakov, 1991, 1996; Wang B. et al., 2009; Szwedo, 2011; Jiang J.Q. et al., 2016). This statement was undermined by Dong et al. (2014), but based on weak premises. Progonocimicinae was considered to derive from the Ingruoidae (Ingruomorpha Szwedo, 2018) in the late Permian, and consists the ancestors of Cicadocorinae and Karabasiidae (Popov and Shcherbakov, 1996). Members of this subfamily were widely dispersed in the Triassic (eastern part of Australia, Kazakhstan, Kyrgyzstan; the taxa from Argentina need revision, most probably representing Heteroptera: Archegocimicidae), while in the Jurassic their records are limited to Europe (Germany, Belgium). Cicadocorinae appeared in the fossil record in the early Jurassic and persisted at least to mid-Cretaceous.

According to previous studies, the Progonocimicinae: Cicadocorinae only occurred during the Cretaceous in the United Kingdom, Russia (Transbaikalia Krai), Mongolia and in Lebanon in the southern hemisphere, with 6 genera and 10 species (Figs 1, 7, Table 1).

2. Material and method

The amber under study was from an amber mine located near Noije Bum Village, Tanaing (Tanai) Town, Kachin State, Myanmar (Kania et al., 2015: fig. 1A–D; Jiang T. et al., 2018: fig. 1A–C). The U-Pb dating of zircons from the volcanoclastic matrix of the amber has provided a refined age estimate of 98.79 ± 0.62 Ma for the deposit (Shi et al., 2012), although some traces of re-deposition suggested that the amber might be reworked and the age of the amber should be older than the deposits (Ross, 2015; Wang B. et al., 2016, 2015; Zhang et al., 2017). Domichnia (crypts) of martesiine bivalves (Pholadidae: Martesiinae) boring into amber pieces suggested that the age of the amber is older than the deposit, but recent study of bivalves has shown that some of them were boring into the resin while it was still soft indicating that the amber is contemporaneous with the age of the deposit (Ross, 2018; Smith and Ross, 2018).

The amber deposit is located in the West Burma terrane, which collided with the Sibumasu terrane in the Eurasian continental margin at around 80 Ma, in the low latitude tropical zone (Heine and Müller, 2005; Seton et al., 2012; Broly et al., 2015). This suggests some island or archipelago environments for at least part of the amberiferous area at time of resin formation and deposition (Jiang et al., 2018; Rasnitsyn and Öhl-Kühlme, 2018). The depositional environment was suggested to be a nearshore marine setting close to deltas, with marine fossils found in the deposits (Cruickshank and Ko, 2003; Thu and Zaw, 2017).

The specimen was prepared in the Laboratory of Evolutionary Entomology and Museum of Amber Inclusions, University of Gdańsk, Poland, and was observed under a stereoscopic microscope with varying illumination and filters to increase contrast of pigmentation and morphological details. Drawings were prepared under a Nikon microscope (SMZ1000) with a drawing tube attached, and photographs were taken using a Zeiss AXIO Zoom.V16 microscope system, in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. Photographs and drawings were adjusted using CorelDraw X8 and CorelPhoto-Paint X8 packages. All taxonomic acts established in the present work have been registered in ZooBank.

The nomenclature of the wing venation used in this paper is based on the general scheme for Paraneoptera (Nel et al., 2012), modifying the interpretations of Kukulová-Peck (1991), Popov and Shcherbakov (1991) and Szwedo (2011). Cell nomenclature is adopted from Bourgoin et al. (2015). Abbreviations:

- PC – precosta
- CA – costa anterior
- CP – costa posterior
- bScP – basal portion of subcosta posterior
- dScP – distal portion of subcosta posterior
- dScP+RA₁ – common branch of distal portion of subcostal posterior fused with first branch of radius anterior; Popov and Shcherbakov (1991) interpreted this vein as free distal portion of subcosta
- R – radius

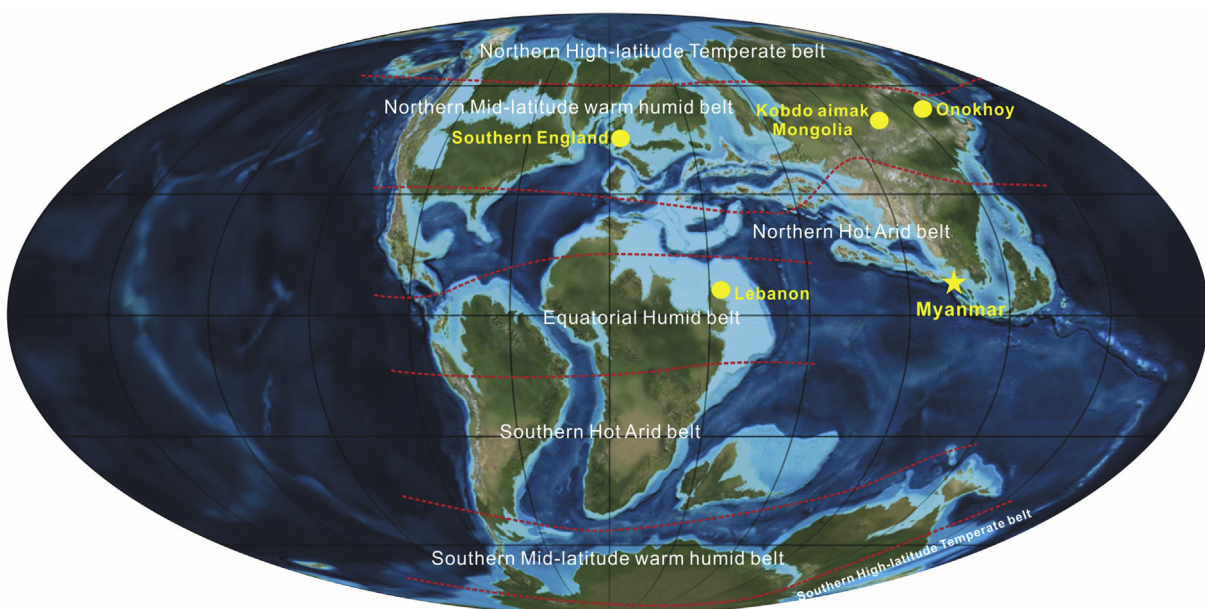


Fig. 1. Distribution map of known Cretaceous Progonocimicinae: Cicadocorinae, palaeogeographic reconstruction for 105 Ma, courtesy of Professor Ron Blakey (Colorado Plateau Geosystems, Inc.); climatic belts after Skelton (2003) and Chumakov (2004).

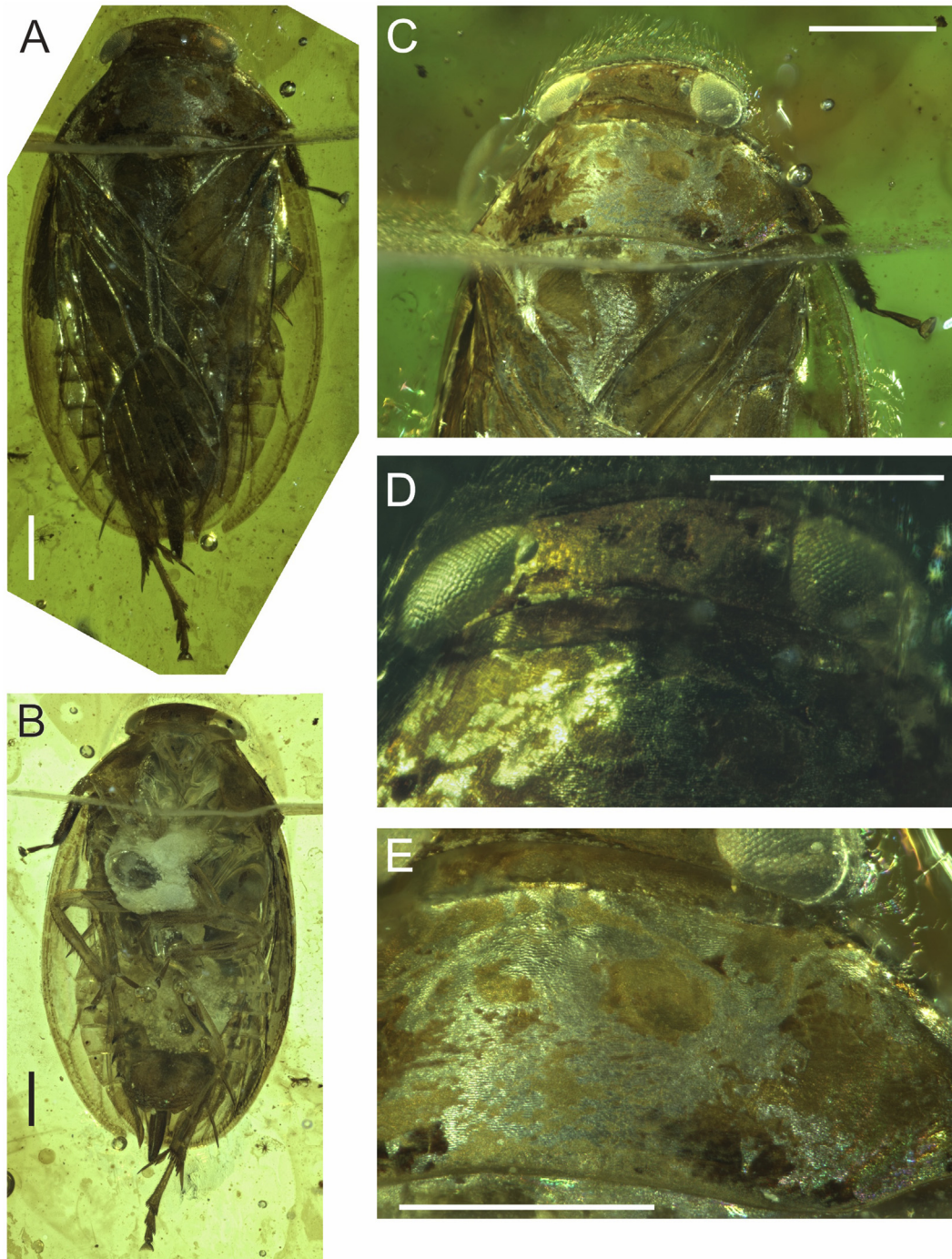


Fig. 2. *Gakasha calcaridentata* gen. et sp. nov. A. General dorsal view of the specimen. B. Ventral view of the specimen. C. Anterior portion of body. D. Head in dorsal view. E. Sculpture of pronotum. Scale bars: 0.5 mm.

RA – radius anterior

RP – radius posterior; RS according to [Popov and Shcherbakov \(1991\)](#)

MP – media posterior; according to [Kukalová-Peck \(1991\)](#) vein MA in Paraneoptera is completely fused with R

MP₁₊₂ – common stalk of MP₁ and MP₂

MP₁ – first terminal of Media posterior

MP₂ – second terminal of media posterior

MP₃₊₄ – common terminal of third and fourth branch of media posterior

CuA – cubitus anterior

CuA₁ – first terminal of cubitus anterior

CuA₂ – second terminal of cubitus anterior; ambient vein according to [Popov and Shcherbakov \(1991\)](#)

CuP – cubitus posterior (claval fold, claval suture is parallel and adjacent to CuP; in former papers these two structures were treated as “claval fracture”; claval fracture according to [Popov and Shcherbakov, 1991](#))

Pcu – postcubitus

A₁ – first anal vein; veins Pcu and A₁ are fused at apical portion of clavus forming common stalk Pcu+A₁

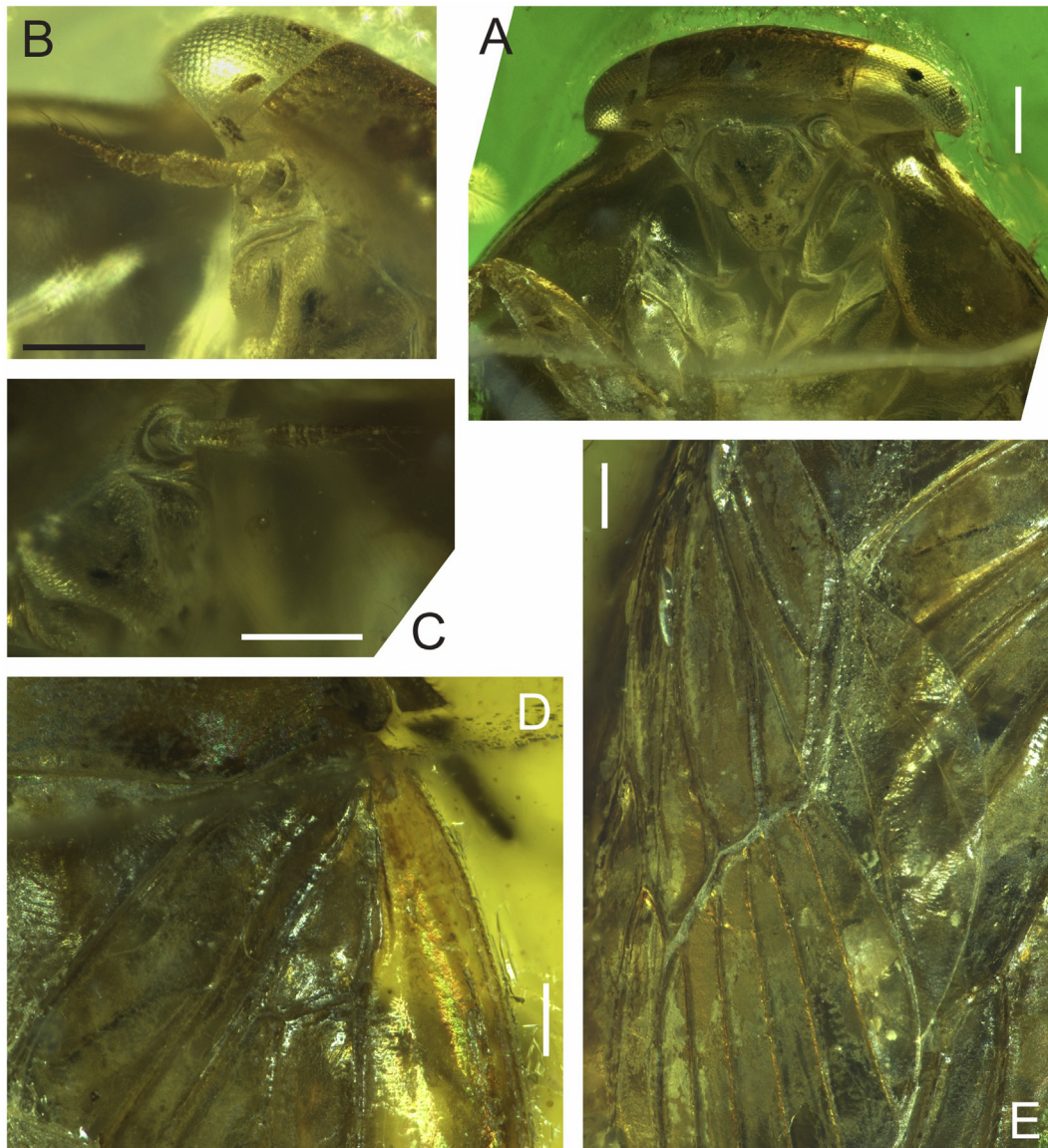


Fig. 3. *Gakasha calcaridentata* gen. et sp. nov. A. Head in ventral view. B. Right antenna. C. Left antenna. D. Basal cell of right tegmen. E. Claval margin, tornus, nodal line of left tegmen and posterior part of left hind wing.

rp-mp – transverse veinlet connecting radius posterior and media posterior

mp-cua – transverse veinlet connecting media posterior and cubitus anterior

icu – veinlet connecting cubitus posterior with claval margin or tornus

costal area – area between veins of costal complex, i.e. CA and PC+CP (veins of costal complex are termed precostal carina by Popov and Shcherbakov, 1991)

costal cell – area of corium between costal complex and stem ScP+R

radial cell – area of corium between stems ScP+R and MP

medial cell – area of corium between stems MP and CuA

cubital cell – area of corium between stem CuA and claval suture (CuP)

Cell C0 – area delimited by forking of ScP+RA₁ and RA₂ ('stigmal area' in Sternorrhyncha and Fulgoromorpha)

Cell C1 – area delimited by forking of RA and RP

Cell C2 – area between branches RP and MP/MP₁₊₂, proximally and distally delimited by radiomedial transverse veinlet *rp-mp*₁

Cell C3 – area between first fork of stem MP, i.e. between branches MP₂ and MP₃₊₄

Cell C3a – area between branches MP₁ and MP₂

Cell C4 – area between branches MP₃₊₄ and CuA₁

Cell C5 – the areola postica, the cell delimited by the first fork of stem CuA, i.e. branches CuA₁ and CuA₂.

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Coleorrhyncha Myers et China, 1929

Superfamily Progonocimicoidea Handlirsch, 1906

Family Progonocimicidae Handlirsch, 1906

Subfamily Cicadocorinae Becker-Migdisova, 1958

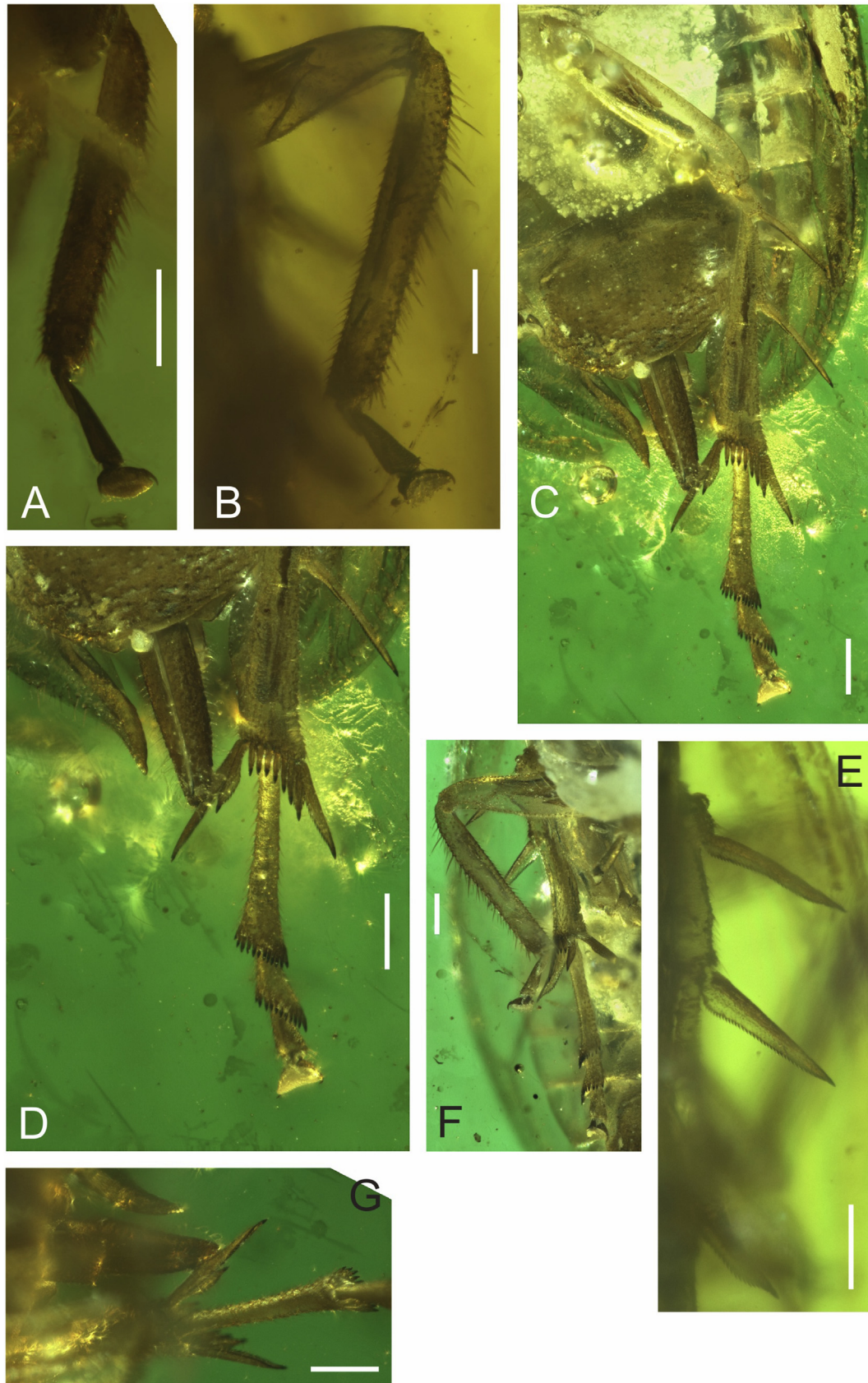


Fig. 4. *Gakasha calcaridentata* gen. et sp. nov. A. Protibia and protarsus. B. Mesofemur, mesotibia and mesotarsus; C. Left metatibia. D. Left metatarsus, female genital plate, ovipositor and anal tube, ventral view. E. Lateral spurs of left metatibia. F. Right metatarsus, ventral view. G. Anal tube, ovipositor and left metatarsus, dorsal view through the tegmen membrane.

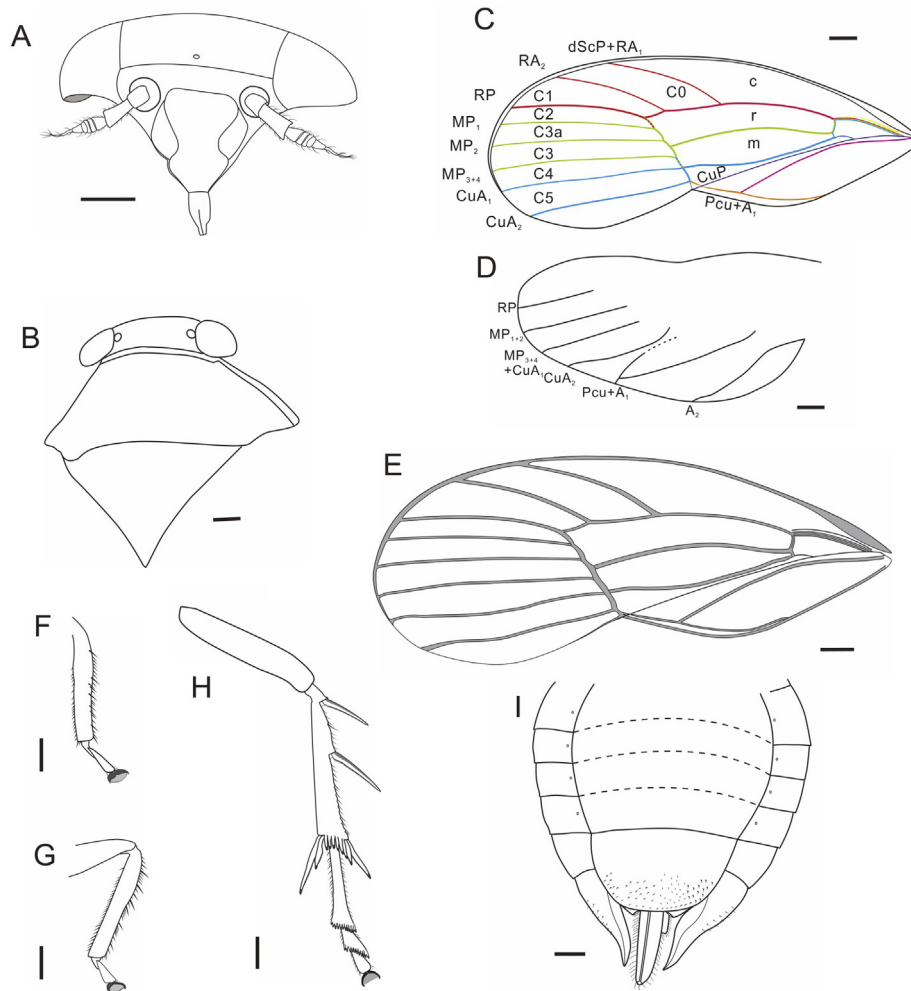


Fig. 5. *Gakasha calcaridentata* gen. et sp. nov. A. Head in anteroventral view. B. Outline of head, pronotum and mesonotum, dorsal view. C. Left tegmen, pattern of venation and cell nomenclature, c – costal cell, r – radial cell; m – median cell. D. Hindwing venation pattern. E. Left tegmen. F. Protibia and protarsus; G. Mesoleg. H. Metaleg. I. Female abdomen and genital structures, ventral view. Scale bars: 0.2 mm.

2012 Ciadococinae [sic!] Becker-Migdisova, 1958: Dong et al., p. 74
2013 Ciadococinae [sic!] Becker-Migdisova, 1958: Dong et al., p. 34

Genus ***Gakasha*** gen. nov.

Type species: *Gakasha calcaridentata* sp. nov., by present designation and monotypy

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Etymology. Generic name is derived from the word ‘ga kasha’ meaning “a minute insect” in Kachin language. Gender: feminine
Diagnosis. In general shape of tegmen resembling Cretaceous genera *Onokhoia* Yu. Popov, 1988 and *Ilahulgalbus* Szwedo, Azar et Ziadé, 2011 (tegmen elongated, not broadly rounded as in Yuripopovia Jarzembowski, 1991, Valdiscytina Yu. Popov, 1993 in Klimaszewski and Popov, 1993, *Ildavia* Yu. Popov, 1993 in Klimaszewski and Popov, 1993 and *Popovus Özdikmen et Demir, 2007*). Posterior margin of tegmen rounded (more truncate in *Onokhoia* and *Ilahulgalbus*); bScP reaching nearly to apex of basal cell (bScP not reaching half of basal cell in *Ilahulgalbus*); dScP+RA₁ separating from stem R at level of Pcu+A₁ intersection with claval fold and CuP (dScP+RA₁ separating from stem R at level of claval veins Pcu and A₁ junction in *Onokhoia*; dScP+RA₁ separating from stem R slightly apicad of claval veins junction in *Ilahulgalbus*); basal cell closed with longer stalk of MP+CuA, and shorter CuA stalk (basal cell closed by

subequal stalks MP+CuA and CuA in *Onokhoia*; basal cell closed at point by stalk MP+CuA in *Ilahulgalbus*); short, oblique veinlet *rp-mp*₁ present (absent in *Onokhoia* – branches RP and MP₁ connected at point; longer, not so oblique veinlet *rp-mp* in *Ilahulgalbus*). Hind wing with a short common terminal CuP+Pcu (similar to *Absoluta* Becker-Migdisova, 1962; common terminal CuP+Pcu longer in *Ilahulgalbus*). Metatibia with two movable lateral spurs (no armature of metatibia in *Onokhoia*; single movable lateral spur in *Ilahulgalbus*), and four apical spurs (two external ones longer).

Description. Head with compound eyes narrower than pronotum (ca. 0.61), about 4 times as wide as long in midline. Vertex between compound eyes about twice as wide as long in mid line, wider at anterior and posterior margins; anterior margin slightly arcuate, posterior margin subparallel, elevated; disc of vertex with delicate puncturation. Lateral ocelli distinct, at half of compound eyes length, adpressed to compound eyes. Supraantennal ridge straight; median ocellus just above the ridge. Postclypeus slightly swollen, longer in mid line than wide at base, subtriangular, wider in upper margin, tapering ventrad; anteclypeus shorter than postclypeus, convex, subtriangular, about as long in mid line as wide; lorai plates semilunar, with upper angles reaching upper margin of postclypeus, lower angles at level of lower margin of postclypeus, reaching lateral margins of anteclypeus at about its upper 1/5. Maxillary plate and genae narrow. Clypellus about three times as

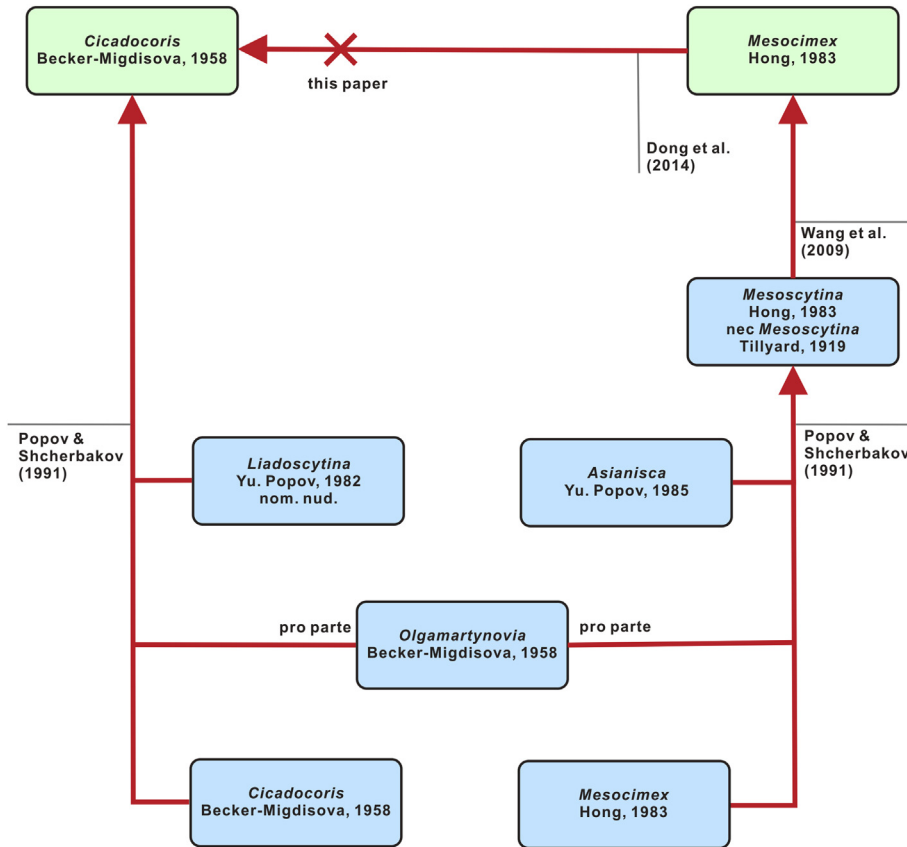


Fig. 6. Graphical summary of taxonomic decisions and synonyms of the genera *Cicadocoris* and *Mesocimex*.

long as wide at base. Bases of antennae between margin of clypeus and lower margin of compound eyes; antenna 3-segmented, scapus short, pedicel twice as long as wide, flagellum longer than pedicel, thick, tapered, annulate, with 7 annuli, each annulus provided with two longer and thicker setae (some shorter, irregular setae present on basal annuli), three basal pairs about as long as annulus width, apical with setae longer than length of annulus, terminal one with four longer apical setae, two apical and two subapical ones. Rostrum with basal segment short, apical segment reaching mesocoxae.

Pronotum subhexagonal, wider than mesonotum, about 2.5 times as wide as long in midline; anterior margin arcuate; anterolateral angles widely angulate; posterior margins straight, diverging posteriad, posterolateral margins acutely angulate, posterolateral margin arcuate, posterior margin shallowly arcuately concave. Disc of pronotum delicately transversely wrinkled. Lateral margin of pronotum carinate, lateroventral lobes tuck, reaching prothoracic katapisternum.

Mesonotum triangular, about 1.5 times as wide as long in mid line. Disc of mesonotum delicately transversely wrinkled.

Left tegmen overlapping right tegmen. Tegmen membranous, with venation distinct, nodal line thick, oblique, veins on corium thickened, to less extent on membrane, elevated. Tegmen about 3.25 times as long as wide at claval apex, about 2.3 times as long as maximal width. Apex of clavus slightly distad of $\frac{1}{2}$ of tegmen length. Costal margin arcuate, anterolateral angle widely arcuate, apex between terminals RP and MP₁, posterior margin slightly arcuate, posterolateral margin broadly rounded, tornus and claval margin arcuate. Costal area narrow, distinctly narrower than costal

cell (less than $\frac{1}{5}$ th), thickened, slightly widened at very base, horizontally carinate, reaching MP₃₊₄. Basal cell about 2.5 times as long as wide, closed posteriorly by stalks MP+CuA and CuA; bScP slightly shifted from main stem R+MP+CuA, reaching nearly to apex of basal cell. Stem R arcuate, subparallel to costal margin, longer than dScP+RA₁ branch; dScP+RA₁ oblique, reaching costal margin posteriad of claval apex; terminal RA₂ slightly longer than terminal ScP+RA₁, subparallel to terminal RP; terminal RP slightly arcuate anteriad, as prolongation of nodal line. Stem MP leaving basal cell separately, arcuate, subparallel to stem R; first fork at nodal line, stalk MP₁₊₂ short, in nodal line, terminal MP₁ thinner than stem MP and MP₁₊₂ stalk, straight, shorter than terminal MP₂; terminal MP₂ straight, thinner, parallel to terminal MP₁; terminal MP₃₊₄ longest, longer than MP₂, straight, thinner, parallel to terminal MP₂. Stem CuA leaving basal cell separately, arcuate, adhering to claval suture (CuP) in basal portion, then directed mediad, forked at nodal line; terminal CuA₁ in line prolonging stem CuA, straight reaching margin posteriad of tegmen apex; terminal CuA₂ straight, subparallel to CuA₁. Claval veins Pcu and A₁ fused at about $\frac{2}{3}$ rd of claval suture length, in apical portion of clavus; free portion of A₁ about $\frac{1}{3}$ rd of claval suture length. Veinlet *rp-mp*₁ short, oblique, thickened, placed at nodal line; veinlet *mp*₃₊₄-*cua*₁ subperpendicular to CuA, about as long as stalk MP₃₊₄, thickened, placed at nodal line; very short *icu* intersecting the prolongation of CuP on thickened margin of tornus. Costal cell at widest point about as wide as radial cell; radial cell longer than medial cell, acute at apex, closed by RP stalk, *rp-mp*₁, MP₁ stalk and MP₁₊₂ stalk; medial cell lanceolate, closed obtusely apicad by MP₃₊₄ stalk and *mp*₃₊₄-*cua* veinlet, slightly narrower than radial cell. Costal cell at widest point as wide as radial cell at widest point. Cell C0 elongate, obliquely diamond-shaped; longer than cell C1, about as long as cell

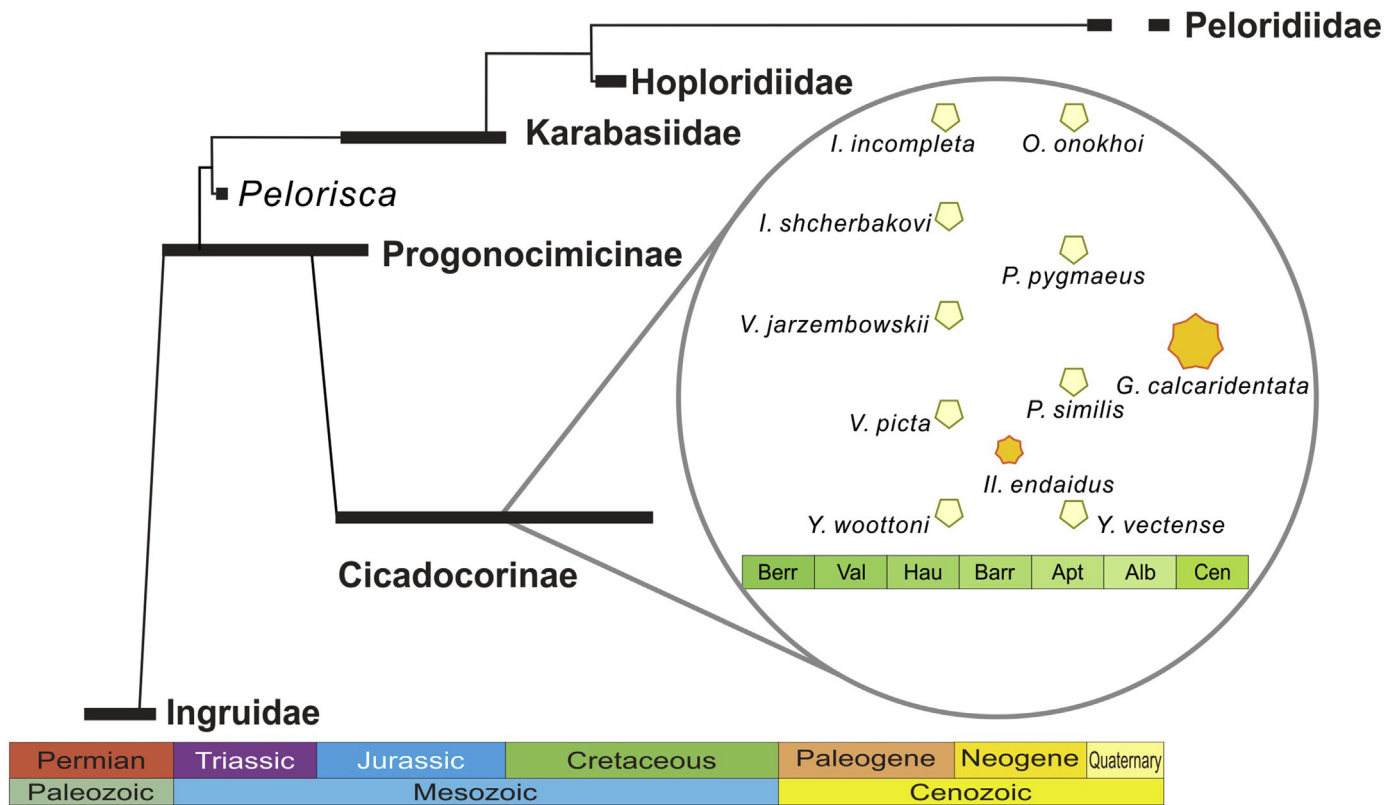


Fig. 7. Evolutionary outline of main Coleorrhyncha lineages with more detailed reference to the Cretaceous Cicadocorinae. Note that Progonocimicinae as recently understood seems not to form a monophyletic lineage.

Table 1
List of species of Progonocimicidae in Cretaceous.

Species	Locality	Geological age
<i>Gakasha calcaridentata</i> gen. et sp. nov.	Noije Bum Hill, Burmese amber	Cenomanian (ca. 99.8 Ma)
<i>Onokhoia onokhoiensis</i> Yu. Popov, 1988	Onokhoy, Transbaikial Krai, Russia	Aptian (125.45–112.6 Ma)
<i>Popovus pygmaeus</i> (Yu. Popov, 1986)	Kobdo aimak, Mongolia	Aptian (125.5–112.6 Ma)
<i>Popovus similis</i> (Yu. Popov, 1986)	Kobdo aimak, Mongolia	Aptian (125.5–112.6 Ma)
<i>Yuripopovia vectense</i> Heads, 2008	Atherfield, Isle of Wight, United Kingdom	Aptian (125.45–122.46 Ma)
<i>Ilahulgabalus endaidus</i> Szwedo, Azar et Ziadé, 2011	Daychouniyeh, Lebanon	Barremian (130–125.45 Ma)
<i>Ildavia incompleta</i> Yu. Popov, 1993	Keymer Tile Works, United Kingdom	late Hauterivian (136.4–130 Ma)
<i>Valdiscytina picta</i> Yu. Popov, 1993	Keymer Tile Works, United Kingdom	late Hauterivian (136.4–130 Ma)
<i>Ildavia shcherbakovi</i> Yu. Popov, 1993	Clockhouse Brickworks, United Kingdom	late Hauterivian (136.4–130.0 Ma)
<i>Valdiscytina jarzembowskii</i> Yu. Popov, 1993	Clockhouse Brickworks, United Kingdom	late Hauterivian (136.4–130.0 Ma)
<i>Yuripopovia woottoni</i> Jarzembowski, 1991	Clockhouse Brickworks, United Kingdom	late Hauterivian (136.4–130.0 Ma)

C3a; cell C3 subrectangular, longer than cell C3a and cell C5; cell C5 subrectangular, merely wider apically, about as wide as appendix.

Hindwing with short common terminal of CuP+Pcu.

Procoxa slightly elongate, protrochanter elongate, subconical. Proleg short, profemur shorter than protibia; protibia subquadrangular in cross section, with rows of short setae along margins and at apex; basiprotarsomere shorter than apical one, elongately cup-shaped; apical protarsomere about twice as long as basiprotarsomere, tarsal claws distinct, arolium fan-shaped, wide. Mesoleg short; mesofemur shorter than mesotibia; mesotibia slightly longer than protibia, subquadrangular in cross section, with rows of short setae along margins; mesotarsus two-segmented. Metacoxae conical, adpressed to each other, metatrochanters ring-like. Metatibia elongated, with two movable lateral spurs, first subbasal and second slightly basad of half of metatibia's length, and row of apical teeth and four movable spurs. Lateral spurs narrow

basally, rounded at anterior margin, flattened at posterior margin, with row of about 30 small spinules; two external apical spurs almost as long as lateral spurs, slightly flattened at internal margins, provided with row of small spinules ventrally, third and fourth spurs (subexternal ones) shorter, about half of lateral spur length, elongately leaf-shaped, with lateroventral carinations provided with row of six spinules; row of apical teeth between spurs composed of 6 elongate ones; metatarsus long, about 0.8 of metatibia length; basimetatarsomere longer than combined length of mid- and apical metatarsomeres, widening apicad, with row of 11 apical teeth; midmetatarsomere about as long as apical metatarsomere, with oblique row of 11 apical teeth. Tarsal claws distinct, arolium fan-shaped, wide.

Abdomen wide, flattened, 4th abdominal segment the widest, subsequent segments narrowing posteriad, hypopleurites 3rd to 7th distinct, spiracles placed in middle of their length, shifted mediad towards sternites; female 7th sternite large with distinctly arcuate

posterolateral margin, anterior margin straight; hypopleurite 8th (paratergite) distinctly elongate caudally, with tapered process, not exceeding tip of ovipositor, with rows of short setae dispersed along mediolateral carination. Anal tube short, about as long as wide, covered with short setae. Gonoplasts tube-like, elongate, opened ventrally, covering gonapophyses VIII and IX and covered with row of elongate setae; in ventral view exceeding length of anal tube about 3 times.

***Gakasha calcaridentata* sp. nov.**

(Figs 2–5)

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Etymology. Specific epithet is derived from Latin calcar (spur) and dens, -tis (tooth), and refers to row of small denticles on posterior margin of metatibial lateral and lateroapical spurs.

Material. Holotype, female. Burmese amber, oval piece, 19 × 16 × 3.5 mm, weight 0.88 g. The inclusion of the taxon described here was cut out from the lump, polished and preserved as a microscopic slide in Canada balsam. Specimen No. NIGP154576, deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing.

Dorsal side well displayed, ventral side partly visible, obscured by cracks filled with hard sediment (partly removed) and internal impurities (decay gases) and resin layers. Syninclusions: an unidentified Cixiidae-like planthopper (Hemiptera: Fulgoromorpha); Hymenoptera Apocrita, Hymenoptera Apocrita Parasitica; Coleoptera; Diptera Nematocera.

Diagnosis. Vertex between compound eyes twice as wide as long in mid line. Pronotum in mid line 2.5 times as long as vertex in mid line, about 2.8 times as long as wide. Tegmen membranous, transparent. Stem CuA at base very close to claval suture; segment between first fork of ScP+R and RA₂ fork about ½ as long as stem ScP+R. Cell C0 elongately diamond-shaped, more than 3 times as long as wide; apical cells elongate, cell C1 about 7 times as long as wide; cell C3 longer than median cell. Appendix as wide as cell C5. Angle between claval margin and tornus (tangents) ca. 135°. Metatibio-metatarsal formula 2+2+6: 11: 11. Anal tube in female about as long as wide.

Description. Body total 4.16 mm long, 2.32 mm wide. Head transverse, distinctly shorter (0.28 mm) in mid line than wide with compound eyes (1.13 mm), about ½ as wide as pronotum. Lateral ocelli distinct, on the crown, adhering compound eyes, median ocellus adjacent to supraantennal ledge. Pronotum 1.8 mm wide and 0.65 mm long in mid line. Mesonotum about 1.26 mm wide at base and 0.85 mm long in mid line. Tegmen 3.27 mm long, about 1 mm wide at claval apex, maximal width 1.37 mm, veins on corium thickened, carinate, nodal line veins thick, carinate, terminal RP thick, terminals of MP and CuA thinner, not distinctly carinate. Cubital cell very narrow at base then widening to nodal line. Vein Pcu at base adhering claval suture, then diverging, vein A₁ and Pcu+A₁ shifted from claval margin. Margin of tornus arcuate, strengthened at very base by prolongation of CuP (fused with Pcu+A₁?).

Protibia setigerous, 0.55 mm long, external rows of setae longer than internal ones; protarsus two-segmented, 0.37 mm long. Mesotibia 0.84 mm long, mesotarsus 0.37 mm long. Metatibia about 1.1 mm long, with 2 long lateral spurs, first slightly basad of knee, second, slightly apical of ½ of metatibia length, lateral spurs ca. 0.38 mm long; basimetatarsomere 0.57 mm long, mid-metatarsomere 0.28 mm long, apical metatarsomere 0.28 mm long, 0.33 mm long with tarsal claws.

Anal tube of female ca. 0.18 mm long (dorsal view). Ovipositor (portion visible in ventral view, gonoplasts) ca. 0.35 mm long.

4. Discussion

4.1. Taxonomic and nomenclatorial problems within Cicadocorinae

The oldest members of Cicadocorinae come from the Late Triassic deposits of England (Popov et al., 1994), and they were considered to originate from some early Progonocimicinae. Cicadocorinae diversified markedly in the Jurassic and distributed worldwide in the Early Cretaceous (Bechly and Szwedo, 2007; Szwedo, 2011). The subfamily Cicadocorinae comprises the genera *Absoluta* Becker-Migdisova, 1962, *Archiceropsis* Handlirsch, 1939, *Cicadocoris* Becker-Migdisova, 1958, *Mesocimex* Hong, 1983, *Illahulgabalus* Szwedo, Azar et Ziadé, 2011, *Ildavia* Yu. Popov, 1993, *Onokhoia* Yu. Popov, 1988, *Valdiscytina* Yu. Popov, 1993 and *Yuripopovia* Jarzembowski, 1991 (Popov and Shcherbakov, 1991; Heads et al., 2018). After synonymisation of most of the species of the genus *Olgamartynovia* Becker-Migdisova, 1958 by Popov and Shcherbakov (1991), *Cicadocoris* and *Mesocimex* became the largest genera of Cicadocorinae. They have been suggested to be synonyms by most of the former studies (Dong et al., 2014; Jiang J.Q. et al., 2016), but this synonymisation seems to be premature. Popov and Shcherbakov (1991) presented sets of characters separating these genera, based mainly on venational characters; however, some species can present transitional combinations. Most of the species ascribed to these two genera are in need of urgent revisionary studies to resolve their taxonomic position. A graphical summary of generic synonymies is presented on figure 6. One of the obstacles hampering the clarification of taxonomy and classification within Cicadocorinae is dissymmetry of some veins on left and right tegmina, and a new approach to this problem, already addressed by Popov and Shcherbakov (1991), is necessary.

The genus *Olgamartynovia* Becker-Migdisova, 1958, *sensu stricto* was synonymized under *Cicadocoris* (Popov and Shcherbakov, 1991), with some species moved to *Cicadocoris*, other to *Mesoscytina* Hong, 1983, and a few remaining of uncertain position (Fig. 6). Thus the genus *Cicadocoris* comprises the type species and some five more. Some of the species placed in *Cicadocoris* should be synonymized, because the differences between left and right tegmina were formerly interpreted as specific ones (Popov and Shcherbakov, 1991). A provisional list of species comprised in the genus is as follows: *Cicadocoris kuliki* Becker-Migdisova, 1958 (type species) stat. resurr. and *C. affinis* (Yu. Popov, 1982) stat. resurr., *C. arcuatus* (Yu. Popov, 1982) stat. resurr., *C. assimilis* Dong, Yao et Ren, 2013, *C. frater* (Yu. Popov, 1982) stat. resurr. The taxonomic placement of the following species is not certain, and these are only tentatively placed within the genus *Cicadocoris*: ?*C. admotus* (Yu. Popov, 1982), ?*C. complexus* (Yu. Popov, 1982), ?*C. confinis* (Yu. Popov, 1982), ?*C. conjunctus* (Yu. Popov, 1982), ?*C. distans* (Yu. Popov, 1982), ?*C. ignoratus* (Yu. Popov, 1982), ?*C. parallelus* (Yu. Popov, 1982), ?*C. similis* (Yu. Popov, 1982), ?*C. sogjutensis* (Yu. Popov, 1982), ?*C. turanicus* (Becker-Migdisova, 1958).

Venational characters of *Cicadocoris parvus* Jiang et Huang, 2017 match to the set proposed by Popov and Shcherbakov (1991) for the genus *Mesocimex*, therefore we propose a new combination *Mesocimex parvus* (Jiang et Huang, 2017) comb. nov. Jiang J-Q. and Huang (2017) suggested that *Cicadocoris varians* Dong, Yao et Ren, 2012 is probably a junior synonym of *Mesocimex sinensis* because of taphonomic deformation; therefore we propose a new combination *Mesocimex varians* (Dong, Yao et Ren, 2012) comb. nov. The other species originally described in *Olgamartynovia* merit generic separation: '*Olgamartynovia rigida* Yu. Popov, 1982 = '*Olgamartynovia paula* Yu. Popov, 1982; '*Olgamartynovia beckermigdisovae* Yu.

Popov, 1982, '*Olgamartynovia*' *nana* Yu. Popov, 1982; '*Olgamartynovia*' *transbaikalia* Yu. Popov, 1985; '*Olgamartynovia*' *distincta* Yu. Popov, 1982 as already suggested by Popov and Shcherbakov (1991), and sustained by Dong et al. (2013), and Heads et al. (2018). This action is not followed here, as the original material needs to be revised prior to taxonomic decisions, and more substantiated characters and data on the diversity and disparity within Cicadocorinae should be gathered. Therefore, we propose to conserve the formal generic name '*Olgamartynovia*' for these taxa with: ?'*Olgamartynovia*' *rigida* Yu. Popov, 1982; ?'*Olgamartynovia*' *beckermigdisovae* Yu. Popov, 1982; ?'*Olgamartynovia*' *nana* Yu. Popov, 1982; ?'*Olgamartynovia*' *transbaikalia* Yu. Popov, 1985 and ?'*Olgamartynovia*' *distincta* Yu. Popov, 1982.

The generic name *Mesocimex* Hong, 1983 was resurrected from synonymy for the reasons given in Wang B. et al. (2009). Jiang et al. (2016) proposed to synonymise *Mesocimex lini* Wang, Szwedko et Zhang, 2009 under *Mesocimex brunneus* (Hong, 1983), referring to text-figure 51 (Hong, 1983: p. 66) and figures 1 and 2 of plate 11. However, these photos are a taxon named *Mesocimex sinensis* Hong, 1983. A photograph of *M. brunneus* is presented on plate 11, figure 3. According to this photo *M. brunneus* is characterised by vertex in mid line about as long as wide, and in *M. lini* it is $\frac{1}{2}$ of vertex width; the same ratio is visible in specimens figured by Jiang et al. (2016: Fig. 2A, B, C) as *C. brunneus*. Before this problem will be solved, we propose to treat *Mesocimex lini* Wang, Szwedko et Zhang, 2009 stat. resurr. as a valid name.

A nomenclatorial combination *Cicadocoris sinensis* (Hong, 1983) was proposed first by Dong et al. (2014); Jiang et al. (2016), referring to the original description of *Mesocimex sinensis* and fig. 50 in Hong (1983: p. 65), but mistakenly listed fig. 3 of plate 11; the original paper refers to figs. 1 and 2 of plate 11. Jiang et al. (2016) proposed to synonymise *Cicadocoris anisomeridis* Dong, Yao et Ren, 2014 under *C. sinensis*. The venation of *C. anisomeridis* is very close to specimens identified as *C. sinensis* by Jiang et al. (2016, fig. 3 B, C, D, fig. 4), but according to a photo of *C. anisomeridis* in Dong et al. (2014: fig. 1A–D) the head of it presents a vertex about as long as wide, while in some *C. sinensis* specimens figured in Jiang et al. (2016, fig. 3A, B) the vertex is about twice as wide as long in mid line. According to Hong (1983) *M. sinensis* had 'head small', and any other details could be found in descriptions and inferred from photos. Venational characters in Cicadocorinae species seem to be very conservative or could be homoplastic, so probably not very informative for nomenclatorial purposes. Therefore the above mentioned synonyms should be treated with some reservations and they need to be revised. Hence, we propose the names *Mesocimex sinensis* Hong, 1983 stat. resurr. and *Cicadocoris anisomeridis* Dong, Yao et Ren, 2014 stat. resurr. as valid until the material will be checked.

The genus *Cicadocoris* comprises 14 (to 19) currently recognised species level taxa, distributed mainly in Kyrgyzstan and north China in the Early and Middle Jurassic (Dong et al., 2012). The *Mesocimex* species come also from the Early to Middle Jurassic, and mainly occur in Kyrgyzstan, Russia, north China and the United Kingdom (Wang B. et al., 2009; Dong et al., 2013).

4.2. Morphological features and peculiarities of *Gakasha* gen. nov.

The above described genus *Gakasha* gen. nov. can be placed in Cicadocorinae by the following characters: tegmen with costal area horizontal, base of costal area narrow; stem R continued by branch RP, dScP+RA₁ convex and free portion of A₁ shorter than half of claval suture. It is the second genus known from the fossil resins of the Cretaceous, differing from *Ilahulgabalus* by characters of the tegmen venation, armature of metatibia and metatarsus. Regarding the tegmen shape and ratio, it resembles the genus *Onokhoia* from

Transbaikalia, but differs in details of venation and metatibia armature. *Gakasha* gen. nov. is for the moment the most completely preserved specimen, presenting much more details, often not available from compression/impression fossils. The newly described genus presents a number of peculiar features, not known up to date among Cicadocorinae and Progonocimicidae. For the first time, the lateral ocelli are clearly observed – Popov and Shcherbakov (1991) mentioned that ocelli were untraceable among known fossils, with supposed position at anterior margin of the head. In *Gakasha* gen. nov., ocelli are placed on the crown, adhering compound eyes, but more posteriad, not on the margin. In Peloridiidae, ocelli are small, sometimes inconspicuous, placed at anterior margin of the head, close to compound eye (Popov and Shcherbakov, 1996; Spangenberg et al., 2013). Another feature of *Gakasha* gen. nov. is presence of 3-segmented antennae, with terminal segment slightly incrassate, tapering apicad. This character is characteristic for Peloridioidea Breddin, 1897; Progonocimicoidea are characteristically with antennae 4–7 segmented, setaceous or incrassate (Popov and Shcherbakov, 1991). The flagellum of the antenna in *Gakasha* gen. nov. is annulate, with seven recognisable annuli, each provided with some setae, shorter at base, but distinctly longer in apical annuli, with the longest setae on the terminal one. In *Hackeriella veitchi*, the scapus is longer than pedicel (in *Gakasha* gen. nov. it is opposite, scapus is short, and pedicel distinctly longer) and flagellum not annulated, and lacks setae (Spangenberg et al., 2013); a similar, non-annulate, and lacking distinct setae, flagellum is present in other Peloridiidae (Burckhardt, 2009). The postclypeus and anteclypeus in *Gakasha* gen. nov. seem to be fused, but separated by a groove. The postclypeus is more inflated, anteclypeus convex and loreal plates wide, resembling the situation present in *Mesocimex*. The general venation pattern of *Gakasha* gen. nov. is typical of Cicadocorinae; it differs clearly from *Ilahulgabalus* by the shape of the nodal line and width of appendix; the nodal line of *Gakasha* gen. nov. is formed by terminal RP, oblique veinlet *rp-mp*₁, stalk of MP₁, stalk of MP₁₊₂, stalk of MP₃₊₄; veinlet *mp*₃₊₄-*cu*₁, stalk CuA₂ and veinlet *icu*. Such a model is unique among Cicadocorinae genera; in *Onokhoia*, the anterior portion of the nodal line is formed by fused veins RP and MP₁; in the other genera by terminal MP₁. Two lateral movable spurs are present in *Mesocimex* and *Cicadocoris*, at least in some species ascribed to the genus *Mesocimex* (*M. lini* stat. resurr.); in this species, the base of the spur seems to be distinctly wider than in *Gakasha* gen. nov. and there are no elongated spurs/teeth at the metatibial apex (Wang B. et al., 2009). The genus *Onokhoia* is characteristically lacking lateral movable spurs; in *Ilahulgabalus* there is a single lateral spine and four of the apical teeth are enlarged. Four distinct lateral (movable) spurs, provided with row of denticles, at the tip of the metatibia seem to be a unique feature of *Gakasha* gen. nov. The basimetatarsomere and midmetatarsomere in *Gakasha* gen. nov. are provided with an apical row of teeth, similar to most Cicadocorinae – in *Ilahulgabalus*, the basimetatarsomere is provided with a row of small apical teeth and the midmetatarsomere is spatulate, elongate in the middle, with a lateral tooth (or two lateral teeth). The midmetatarsomere is about as long as the apical metatarsomere in *Gakasha* gen. nov., while in *Ilahulgabalus* it is shorter. These differences could be related to the jumping abilities of these Cicadocorinae. Strongly armed metatibiae, with long lateral spurs and four apical spurs, together with long tarsus with apical teeth on basi- and midmetatarsomeres of *Gakasha calcaridentata* gen. et sp. nov. infer advanced jumping abilities in this species (Burrows, 2007a,b, 2009b; Bonsignori et al., 2013; Clemente et al., 2017). A single apical metatibial spur is a unique feature of the planthopper family Delphacidae Leach, 1815 (Fulgoroidea Latreille, 1807) (Asche, 1985; Wilson, 2005; Bartlett et al., 2014). According to Metcalfe (1969), it appears to have

developed from an apical tibial spine, and represents a sequence of primitive to advanced states, i.e., thick and spike-like to thin and flattened, which is also reflected in the ontogeny of delphacids, and is of evolutionary and classification importance (Wilson and McPherson, 1981). The exact role of this spur during jumping is not studied yet, but it could be assumed that it prevents legs from slipping on the surface when preparing to jump on the one hand, and on the other, could serve as part of a sensory mechanism responsible for jump mechanics and co-ordination. Membranized episterna in front of the metacoxae and legs modified for jumping, with apical pectens of macrosetae bearing teeth on the metatibia and on enlarged basi- and midmetatarsomeres, were postulated as symplesiomorphies of Coleorrhyncha (Popov and Shcherbakov, 1996). Cicadocorinae are believed to be the best hoppers among the Coleorrhyncha, their decline in the mid-Cretaceous being synchronous with the rise of another groups of small, jumping Hemiptera (Popov and Shcherbakov, 1996), the modern planthoppers (Fulgoroidea Latreille, 1807) and leafhoppers (Cicadelloidea Latreille, 1802); probably also the first jumping psyllids (Psylloidea Latreille, 1807). The modern Peloridiidae are also able to jump (Burrows et al., 2007), but their metatibia lack any lateral spurs or enlarged apical teeth, so the jumping mechanism in Cicadocorinae was probably different. The only family in which the apical movable spur on the metatibia is developed is Delphacidae: alas the exact jumping mechanics of these planthoppers is still unknown. Data about jumping abilities in representatives of Fulgoromorpha Evans, 1946 (Burrows, 2009a,b, 2014a,b) and Cicadomorpha Evans, 1946 – froghoppers (Burrows, 2003, 2006a,b; Gorb, 2004; Sutton and Burrows, 2010), leafhoppers (Burrows, 2007a,b) and treehoppers (Burrows, 2013) suggest some similarities and differences in structure of body parts engaged in jumping, power amplification mechanisms, neural control and jumping mechanisms (Bräunig and Burrows, 2008; Burrows, 2006a,b, 2007c, 2009b, 2010, 2013, 2014a,b; Burrows and Bräunig, 2010; Burrows and Sutton, 2013; Burrows et al., 2008, 2011, 2014; Siwanowicz and Burrows, 2017; Sutton and Burrows, 2010). In recent Peloridiidae, the hind coxae are set more closely together, and may touch each other towards their most dorsal medial edges where some tubercles (microtrichia) are present (Burrows et al., 2007). They are not tightly linked together by attachment devices in contrast to the situation in froghoppers (Gorb, 2004; Burrows, 2006b) or leafhoppers (Burrows, 2007a). The metacoxae of Cicadocorinae are tightly placed close to each other, similar to the situation in Cicadomorpha, and probably present some attachments. In the Heteroptera Latreille, 1810 (Saldidae Amyot et Audinet-Serville, 1843 and Hahn, 1831) two distinct jumping strategies are used (Burrows, 2009a; Burrows and Dorosenko, 2017), and it seems that in the case of Cicadocorinae, in which the hindwings are well developed, but metatibiae not extremely elongated, the addition of wing movements to the propulsive movements of the legs has made their jumping performance more effective.

Jumping ability is often treated as a single character (Hennig, 1981; Shcherbakov and Popov, 2002); however, this ability was actually achieved by a combination of many structural modifications of the legs and thorax, including those of muscles, muscle attachments, and associated sclerites involving energy storage and the locking system, among others (Gorb, 2004). Ogawa and Yoshizawa (2017), after detailed studies of metathoracic muscular characters suggested that almost all apomorphic conditions associated with jumping ability evolved independently in Cicadomorpha and Fulgoromorpha. Thus, regarding particular morphological structures in Cicadocorinae, i.e. closed metacoxae, elongated metatibiae, presence of apical spurs preventing slipping, elongate tarsal segments with apical rows of teeth, we can also assume that jumping mechanisms and adaptation details in

Cicadocorinae could differ from those observed in modern hemipterans.

The abdomen of *Gakasha* gen. nov. differs from females of other Cicadocorinae with the 3rd abdominal segment being longer laterally than the following segments 4th to 7th (the abdominal segments are homonomous in lateral length). In this, it more resembles the situation in the female abdomens of modern Peloridiidae (Sweet, 1996; Burckhardt, 2009) with the first two abdominal segments narrowed and diminished. Distinct hypopleurites (3rd to 7th) with spiracle placed mediad and close to the margin also resemble the situation in Peloridiidae. A unique feature of *Gakasha* gen. nov. is the enlarged female 7th abdominal sternite, covering the base of the ovipositor, as it is observable among Cicadellidae. Another peculiar feature of *Gakasha* gen. nov. is the presence of the enlarged 8th hypopleurites (paratergites) forming the elongate, tapered caudal processes. An ovipositor with gonoplags fused dorsally, covering the 8th and 9th gonapophyses, with a ventral slit, is peculiar and also resembles more the so-called saw-case present in Cicadellidae. In known Cicadocorinae, the 9th abdominal segment of the females seems to be rather barrel-shaped, with obtuse posterior margin; it is small in *Gakasha* gen. nov., flattened, only with posterolateral angles visible. Karabasiidae have a 9th abdominal segment broadly emarginate apically, embracing the base of anal tube; in Hoploridiidae, the 9th segment is wider than long, with distinctly truncate lateral lobes (Popov and Shcherbakov, 1991). Unlike in Peloridiidae, in *Gakasha* gen. nov. the base of anal tube of the female is not concealed by lateral lobes of the 9th abdominal segment. The details of the genital and paragenital structures of Cicadocorinae are still poorly known, but seem to be variable, and could provide important phylogenetic information.

Morphology-based cladistic analyses, with revised morphological observations and including Coleorrhyncha, supported the relationship of Coleorrhyncha+Heteroptera (Friedemann et al., 2014) as clade Prosorrhyncha (Szwedo, 2018); this opinion was also supported by molecular phylogenetic studies based on 18S rRNA (Wheeler et al., 1993; Campbell et al., 1995; Ouvrard et al., 2000) and multiple gene regions (Cryan and Urban, 2012). Recent phylogenomic study of Hexapoda that incorporated data from >1400 gene regions (Misof et al., 2014) casted doubt on this view. A sister group relationship between Coleorrhyncha and Heteroptera was also refuted by recent mitochondrial phylogenomic analyses (Cui et al., 2013; Wang Y. et al., 2015). Moreover, recent studies of wing base structure (Yoshizawa et al., 2017) suggested that Coleorrhyncha could be more closely related to Cicadomorpha and Fulgoromorpha than to Heteroptera. Therefore, an apparent conflict between various morphological and molecular data and their interpretations has arisen in the placement of Coleorrhyncha. Regarding the fossil record of the group, the Coleorrhyncha appeared in the Late Permian, as descendants of Ingrididae (Fig. 7) – the group close to highly diversifying early Cicadomorpha during the Permian (Popov and Shcherbakov, 1996; Shcherbakov and Popov, 2002; Szwedo, 2018). Coleorrhyncha is monophyletic lineage, divided into two main clades. The family Progonocimicidae seems not to be a monophylum, contrary to the opinion of Dong et al. (2014), based on a very limited number of taxa examined. Cicadocorinae seems to form a single lineage, but the status of Progonocimicinae is not clear. Placement of the genus *Pelorisca* Popov et Shcherbakov, 1991 in this subfamily is controversial (Popov and Shcherbakov, 1991). The family Karabasiidae seems to be the monophyletic sister group to Hoploridiidae + Peloridiidae (Fig. 7). The ancient history of the Coleorrhyncha, together with the high specialization and relictual character of its recent representatives could be one of the sources of incongruences in phylogenetic proposals.

4.3. Distributional pattern of Cretaceous Cicadocorinae

The Cretaceous representatives of Cicadocorinae present interesting distributional pattern, with *Ildavia*, *Yuripopovia* and *Valdisicytina* from the Lower Cretaceous deposits of the United Kingdom, *Popovus* from the Lower Cretaceous of western Mongolia, *Onokhoia* from the Lower Cretaceous of Transbaikalia (Russia), and two genera from more southern latitudes – *Ilahulgabalus* from the Lower Cretaceous amber of Lebanon and *Gakasha* gen. nov. from mid-Cretaceous Burmese amber (Table 1; Figs. 1 and 7). According to palaeoclimatic reconstructions for the Early Cretaceous (Skelton, 2003; Chumakov, 2004), Cicadocorinae were mainly distributed in the temperate warm humid zone (Hauterivian to Aptian), except *Ilahulgabalus*, present much more south in the tropical equatorial dry zone in the lower Barremian (Maksoud et al., 2017), but with the climate more mild and humid (Azar et al., 2003, 2010). *Gakasha* gen. nov. dates from earliest Cenomanian times, from the equatorial humid zone, but according to palaeotopographic data, with arid influence caused by elevated areas nearby (Skelton, 2003; Wu et al., 2017; Li et al., 2018). By the mid Cretaceous, extensive outgassing of carbon dioxide due to magmatic eruptions at oceanic ridges and vast outpourings of lava and volcanic activity, rising sea level (lowering albedo), and the continuing breakup of Pangea had led to long-term global warming (~20°–22 °C). Therefore the global climate was one of the warmest in Earth's history (Hay and Floegel, 2012; Hay, 2017). The data from palaeoclimatic reconstructions (Chumakov, 1995, 2004; Chumakov et al., 1995; Zhou et al., 2012) suggest that the Equatorial-Tropical arid belts associated with the descending limbs of the Hadley cells were extensive in the Early Cretaceous, becoming more restricted in the warmer Late Cretaceous, and that vegetation spread to warm high latitudes and cool low latitudes in a warm climate with a high level of CO₂ (Zhou et al., 2012), similar to the pattern of modern vegetation (Bonan, 2008). The find of Cicadocorinae in Burmese amber put a new question to the reconstruction of Burmese amber forests biota, as the Cicadocorinae more probably inhabited rather humid environments. Palaeoenvironmental details and palaeoecological reconstructions for the Burmese amber forest have not been fully elaborated yet. Palynological study suggests a humid warm temperate climate (Cruickshank and Ko, 2003) for resin production and amber deposition. Both pollen and plant fossils identified so far, suggest that the amberiferous forest was placed in the equatorial floristic realm (Vakhrameev, 1988).

5. Concluding remarks

Summary of taxonomic changes: *Mesocimex lini* Wang, Szwedlo et Zhang, 2009 stat. resurr. from *Cicadocoris brunneus* (Hong, 1983); *Cicadocoris kuliki* Becker-Migdisova, 1958 stat. resurr. from *Mesocimex kuliki* (Becker-Migdisova, 1958); *Cicadocoris affinis* (Yu. Popov, 1982) stat. resurr. from *Mesocimex affinis* (Yu. Popov, 1982); *Cicadocoris arcuatus* (Yu. Popov, 1982) stat. resurr. from *Mesocimex arcuatus* (Yu. Popov, 1982). *Cicadocoris frater* (Yu. Popov, 1982) stat. resurr. from *Mesocimex frater* (Yu. Popov, 1982). Incertae sedis taxa within the genus *Cicadocoris*: ?*C. admotus* (Yu. Popov, 1982), ?*C. complexus* (Yu. Popov, 1982), ?*C. confinis* (Yu. Popov, 1982), ?*C. conjunctus* (Yu. Popov, 1982), ?*C. distans* (Yu. Popov, 1982), ?*C. ignoratus* (Yu. Popov, 1982), ?*C. parallelus* (Yu. Popov, 1982), ?*C. similis* (Yu. Popov, 1982), ?*C. sogjutensis* (Yu. Popov, 1982), ?*C. turanicus* (Becker-Migdisova, 1958). Conserved collective 'Olgamartynovia' with 'Olgamartynovia' *rigida* Yu. Popov, 1982; 'Olgamartynovia' *beckermigdisovae* Yu. Popov, 1982; 'Olgamartynovia' *nana* Yu. Popov, 1982; 'Olgamartynovia' *transbaikalica* Yu. Popov, 1985 and 'Olgamartynovia' *distincta* Yu. Popov, 1982. Incertae sedis taxa within the genus *Mesocimex*: ?*M. admotus* (Yu.

Popov, 1982) stat. resurr., ?*M. complexus* (Yu. Popov, 1982) stat. resurr., ?*M. confinis* (Yu. Popov, 1982) stat. resurr., ?*M. conjunctus* (Yu. Popov, 1982) stat. resurr., ?*M. distans* (Yu. Popov, 1982) stat. resurr., ?*M. ignoratus* (Yu. Popov, 1982) stat. resurr., ?*M. parallelus* (Yu. Popov, 1982) stat. resurr., ?*M. parvus* (Jiang et Huang, 2017) comb. nov., ?*M. similis* (Yu. Popov, 1982) stat. resurr., ?*M. sogjutensis* (Yu. Popov, 1982) stat. resurr., ?*M. turanicus* (Becker-Migdisova, 1958) stat. resurr., ?*M. varians* (Dong, Yao et Ren, 2012) comb. nov.

Gakasha calcaridentata gen. et sp. nov. described above is the first representative of Cicadocorinae: Progonocimicidae found in Burmese amber. It is the second known taxon in amber, the latest known representative of the family, and the second known cicadocorine from the equatorial belt. *Gakasha calcaridentata* gen. et sp. nov. is very peculiar in morphological features, presenting a high level of morphological specialization. Apart generally uniform body structure and venation shared by most of Cicadocorinae, the new taxon presents specialized form in the antennae, highly modified armature of the hind legs (probably related to its jumping ability), and specialized female genital structures (with tubular ovipositor). *Gakasha calcaridentata* gen. et sp. nov., with its morphological peculiarities also casts some light on the taxonomic and nomenclatorial problems within Cicadocorinae, giving new pointers to the disparity of Cicadocorinae.

The relationships within the group and systematics of Cicadocorinae remain obscure. The venational characters of the genera and species seem to be reliable only to some extent, so new characters and a new approach to the available data are necessary to resolve nomenclatorial and systematic problems within Cicadocorinae and Progonocimicidae. Finding a well-preserved specimen entombed in amber gives a new opportunity to better understand the evolutionary history of the group including its diversity and morphological disparity.

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