

A new planthopper family Katlasidae fam. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea) from mid-Cretaceous Kachin amber

Cihang Luo ^{a, b}, Tian Jiang ^c, Jacek Szwedo ^{d, **}, Bo Wang ^b, Chuantao Xiao ^{a, *}

^a School of GeoSciences, Yangtze University, Wuhan 430100, Hubei, China

^b State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China

^c State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Beijing), Beijing 100083, China

^d Laboratory of Evolutionary Entomology and Museum of Amber Inclusions, Department of Invertebrate Zoology and Parasitology, Faculty of Biology, University of Gdańsk, 59, Wita Stwosza Street, PL80-308 Gdańsk, Poland

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ABSTRACT

A new planthopper family Katlasidae fam. nov. is described based on a well-preserved specimen from mid-Cretaceous Kachin amber (Burmese amber). It is characterized by vertex separated from frons with two parallel, transverse carinae; antenna with pedicel densely covered with sensory lentiform flattened plaque organs; pronotum with elevated disc, complete median carina and incomplete lateral carinae; mesonotum in shape of transverse lozenge, without median and lateral carinae; tegmen widened at membrane and with dense venation on it, costal area absent, stigma area without sclerotization or veinlets, clavus closed, terminals of MP multiplied, transverse veinlets not regular, not forming distinct rows; hind wing veinlets scarce, two transverse veinlets *rp-mp*; male pygofer elongate, tubular, ventrally carinate, genital styles exposed beyond ventral margin of pygofer. Only one genus and species *Katlasus xiai* gen. et sp. nov. has been discovered. The new family's morphological combination of characters reach beyond the known disparity of the Fulgoroidea. Important morphological characters of new taxa as antennal plaque organs, head and thorax structures, tegmen and wing structure and venation, and terminalia, as well as relationships of Katlasidae fam. nov. with other Fulgoroidea are discussed. Environmental changes, palaeoclimatic and palaeogeographical factors influencing diversification and evolutionary processes of planthoppers during the period of formation of modern faunistic complexes at mid-Cretaceous biotic re-organization times and documented in Kachin amber biota are discussed.

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1. Introduction

The order Hemiptera has the biggest number of families among any insects, with more than three hundred extant and extinct families as far as we know, inhabiting all terrestrial and some marine habitats (Szwedo, 2018). Fulgoromorpha (planthoppers) is a suborder of the Hemiptera and subdivided into three superfamilies: two extinct ones – Permian Coleoscytoidea Martynov, 1935 and Triassic Surijokocixioidea Shcherbakov, 2000 – and another superfamily Fulgoroidea Latreille, 1807, known in fossil record since the Jurassic (Szwedo, 2018). To date, the superfamily Fulgoroidea

contains 31 families, including 10 extinct families and 21 extant families (Bourgoin, 2020). Extinct families comprise two Jurassic families: Fulgoridiidae Handlirsch, 1939 (Handlirsch, 1939) and Qiyangiricaniidae Szwedo, Wang & Zhang, 2011 (Szwedo et al., 2011); seven Cretaceous families: Dorytocidae Emeljanov & Shcherbakov, 2018 (Emeljanov and Shcherbakov, 2018), Jubisentiidae Zhang, Ren & Yao, 2019 (Zhang et al., 2019), Lalacidae Hamilton, 1990 (Hamilton, 1990), Mimarachnidae Shcherbakov, 2007b (Shcherbakov, 2007b), Neazoniidae Szwedo, 2007 (Szwedo, 2007), Perforissidae Shcherbakov, 2007a (Shcherbakov, 2007a), Yetkhatidae Song, Szwedo & Bourgoin, 2019 (Song et al., 2019); and one Eocene family: Weiwoboidae Lin, Szwedo, Huang & Stroiński, 2010 (Lin et al., 2010). Extant families contain Achilidae Stål, 1866 + Achilixiidae Muir, 1923, Caliscelidae Amyot & Audinet-Serville, 1843, Cixiidae Spinola, 1839, Delphacidae Leach, 1815, Derbidae Spinola, 1839, Dictyopharidae Spinola, 1839,

* Corresponding author;

** Corresponding author.

E-mail addresses: jacek.szwedo@biol.ug.edu.pl (J. Szwedo), ctxiao@yangtzeu.edu.cn (C. Xiao).

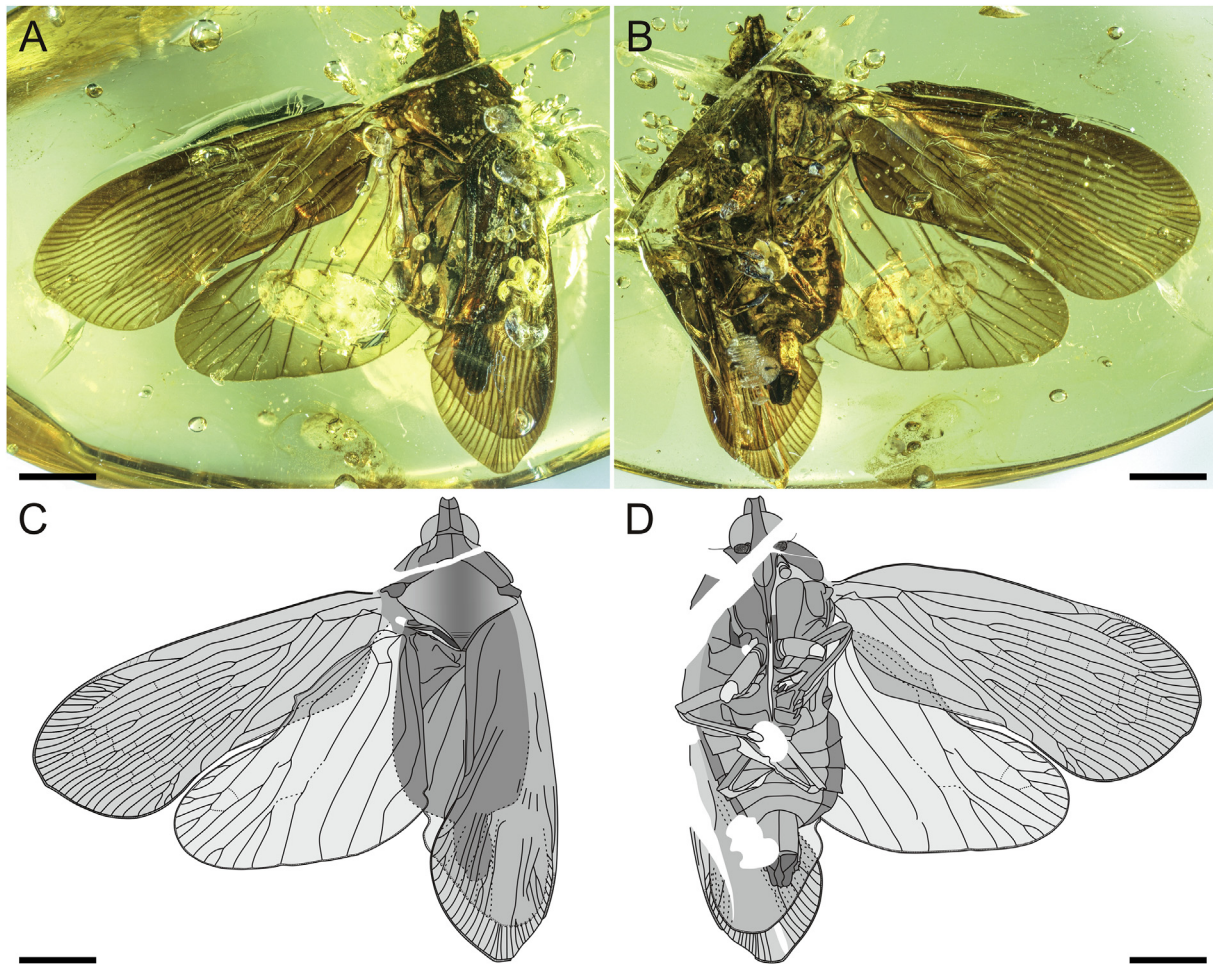


Fig. 1. Holotype of *Katlasus xiai* gen. et sp. nov. (NIGP172209). A, the photograph of the dorsal view. B, the photograph of the ventral view. C, line drawing of the dorsal view D, line drawing of the ventral view. Scale bars = 2 mm.

Eurybrachidae Stål, 1866 + Gengidae Fennah, 1949, Flatidae Spinola, 1839 + Hypochthonellidae China & Fennah, 1952, Fulgoridae Latreille, 1807, Issidae Spinola, 1839 + Acanaloniidae Amyot & Audinet-Serville, 1843, Lophopidae Stål, 1866, Meenoplidae Fieber, 1872 + Kinnaridae Muir, 1925, Nogodinidae Melichar, 1898, Ricaniidae Amyot & Audinet-Serville, 1843, Tettigometridae Germar, 1821 and Tropiduchidae Stål, 1866 (Lin et al., 2010; Szwedo et al., 2013; Zhang et al., 2019; Brysz and Szwedo, 2019).

Although ten families have been reported from Cretaceous, including three extant families Achilidae (Cockerell, 1917; Szwedo, 2004), Cixiidae (Fennah, 1961, 1987; Szwedo, 2001), Dictyopharidae (Emeljanov, 1983) and seven extinct Cretaceous families as mentioned above, our understanding of the phylogeny of basal planthopper lineage is still unclear (Song et al., 2019; Brysz and Szwedo, 2019). A few molecular attempts (Bourgoin and Campbell, 2002; Urban and Cryan, 2007; Song and Liang, 2013) are difficult to associate with reliable comparative morphology framework, and further morphological investigations at the higher levels of the planthopper classification are still needed (Song et al., 2019; Brysz and Szwedo, 2019).

Herein we describe a unique new planthopper specimen from the mid-Cretaceous Kachin amber, which cannot be attributed to any known extant and extinct families of Fulgoromorpha. This specimen has combined peculiar morphological characters in body structures and venation, clearly separating it from known

planthopper families, deserving its placement in a new fossil planthopper family.

2. Material and methods

The studied specimen originates from the Cretaceous deposits in the Hukawng Valley of Myanmar. The amber mine located near Danai (Tanai) Town (26° 21' 33.41" N, 96° 43' 11.88" E; palaeolatitude $5.0 \pm 4.7^\circ$ S) (Kania et al., 2015; Thu and Zaw, 2017; Westerweel et al., 2019; see the locality in Fig. 1 of Jiang et al., 2019). Over the last 100 years, and particularly in the past two decades, Kachin amber has received worldwide scientific interest; nearly 600 families of invertebrates, vertebrates, protists, plants, and fungi have been reported (Ross, 2019, 2020a, b; Yu et al., 2019). The Burma Terrane was part of a Trans-Tethyan island arc and stood at a near-equatorial southern latitude at about 95 Ma, suggesting island endemism for the Kachin amber biota (Westerweel et al., 2019), but Kachin amber still gives us new insights into the very important period of formation of modern faunistic complexes at mid-Cretaceous biotic re-organization times (Szwedo and Nel, 2015) and they are the ideal materials for studying the Cretaceous Terrestrial Revolution, which is marked by the radiation of angiosperms, social insects, and early mammals (Lloyd et al., 2008; Jiang et al., 2018; Bao et al., 2019). Radiometric U–Pb zircon dating from the volcanoclastic matrix of the amber constrained a refined

age of 98.79 ± 0.62 Ma (earliest Cenomanian) (Shi et al., 2012), but slightly older age was then proposed (late Albian by Zheng et al., 2018; Albian-Cenomanian boundary by Rasnitsyn et al., 2016).

Observations were performed using a Zeiss Stemi 508 microscope. The photographs were taken with a Zeiss Stereo Discovery V16 microscope system, in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, and measurements were taken using Zen software. Photomicrographic composites of 50 individual focal planes were digitally stacked as obtained using the software HeliconFocus 6.7.1 for a better illustration of 3D structures. Because of the amber thickness, some of the pictures were taken when ambers' surface covered by a sugary liquid to improve their light transmission and remove optical distortions. Photographs were adjusted using Adobe Lightroom Classic and line drawings were prepared by using CorelDraw 2019 graphic software.

The venational nomenclature follows the proposals presented by Bourgoïn et al. (2015). Vein abbreviation: CA, costal margin (costa anterior); Pc+CP, precosta + costa posterior; ScP+R, subcosta posterior + radius; RA, radius anterior branch; RP, radius posterior branch; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; Pcu, postcubitus; A₁, first anal vein; A₂, second anal vein.

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758.

Suborder Fulgoromorpha Evans, 1946.

Superfamily Fulgoroidea Latreille, 1807.

Family **Katlasidae** Luo, Jiang et Szwedo fam. nov.

urn:lsid:zoobank.org:act:D0EB751B-2406-40CF-B1EC-B160012D9D09.

Type genus. *Katlasus* gen. nov.

Diagnosis. Head with compound eyes distinctly narrower than pronotum. Vertex subrectangular, separated from frons with two parallel, transverse carinae; trigons not visible in dorsal view. Frons with single, weak, incomplete median carina extending to postclypeus; median ocellus vestigial (?); anteclypeus with distinct median carina extending to clypellus, and lateral carinae. Antenna with pedicel densely covered with sensory lentiform flattened plaque organs. Rostrum with apical segment slightly shorter than subapical one. Pronotum wide, with disc elevated, with complete median carina; lateral carinae not reaching posterior margin, diverging posteriad. Mesonotum in shape of transverse lozenge, without median and lateral carinae. Tegulae present. Tegmen with costal area absent (veins of costal complex fused); stigma area without sclerotization or veinlets; clavus closed; tornus long, tegmen widened at membrane. Tegmen with dense venation on membrane, terminals of MP multiplied, tightly packed, subparallel to longitudinal axis of tegmen; median sector occupying prevailing portion of membrane; nodal line absent, transverse veinlets not regular, not forming distinct rows. Hind wing with RP few terminals reaching margin; MP with few terminals reaching margin; two transverse veinlets *rp-mp*; veinlet *mp-cua* very short; veinlets scarce, not arranged in line; margin of hind wing with short, thick setae. Mesotibia subquadrate in cross section; with rows of dense, thick setae along margins; metatibia subquadrate in cross section; with lateral spines, one near knee and single (?) lateral spine. Male pygofer elongate, tubular, ventrally carinate; genital styles exposed beyond ventral margin of pygofer.

Remarks. Head capsule with double carina separating frons and vertex seems to be plesiomorphic condition, present also in Fulgoridiidae, Lalacidae, some Cixiidae and Delphacidae. This will

place the new family in 'basal' group of Fulgoroidea. Wide and relatively large pronotum, with separated and elevated median section (disc) is to be found among various planthoppers, e.g., in Kinnaridae, also wide and transverse mesonotum is similar to pattern observed in some Kinnaridae. Tegmen with widened membrane is more common in Achilidae, Achilixiidae and some Derbidae, however venation pattern in a new family is different. Stigmal area is triangularly elongated and lacking sclerotization or transverse veinlets. Closed clavus is present among most of planthoppers, this condition seems to be plesiomorphic. Multiplication of terminals on membrane is present in some families, superficially resembles some Fulgoridae, but such pattern is observed e.g. in Achilidae: Rhotalini, Lalacidae: Ancoralini; as well as in some 'higher' Fulgoroidea, e.g. some Lophopidae and Eurybrachidae. Hind wing venation pattern resembles (superficially?) some Achilidae and Dictyopharidae. Metalegs are not preserved enough details for discussion. The structure of male terminalia resembles the model present e.g., in Cixiidae, or Dictyopharidae, with lobate genital styles.

Genus **Katlasus** Luo, Jiang et Szwedo gen. nov.

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Type species. *Katlasus xiai* sp. nov.; by present designation and monotypy.

Etymology. The generic name is derived from the combination of two words from Jinghpo language spoken in the Kachin State – 'kat' meaning 'to be close fitting' and 'läsa' – meaning 'vein' and refers to the tegminal veins pattern. Gender: masculine.

Included species. Type species only.

Diagnosis. Head with compound eyes about half as wide as pronotum. Vertex double trapezoid, lateral margins converging anteriorly, carinate; anterior margin angulately concave, carinate, posterior margin widely angulate concave; median carina complete; disc of vertex concave. Frons narrow, widening in lower portion with lateral margins carinate; frontoclypeal suture arcuate; median ocellus vestigial (?); anteclypeus convex, distinctly longer than wide. Antennal scape short, pedicel barrel-like, about twice as long as wide, sensory plaque organs densely packed on whole surface; arista about twice as long as pedicel. Rostrum reaching metacoxae. Pronotum with median carina reaching posterior margin; lateral carinae diverging posteriad, postocular carinae present. Mesonotum wider than long in mid line, delicately transversely wrinkled, mesoscutellum not clearly separated, transversely wrinkled. Tegulae wide, not carinate. Tegmen macropterous, membranous, with dense venation and narrow appendix; tornus long slightly arcuate, membrane widened; basal cell long; stems ScP and MP leaving basal cell at the same point; stem ScP+R with a very short common stalk, branch ScP+RA subparallel to costal margin; terminal ScP+RA₁ distinctly oblique, separated at level of claval apex; RA with numerous terminals on membrane; branch RP not forked before membrane; reaching margin with two terminals; stem MP forked on corium, distinctly basad of stem CuA first forking, stem MP shorter than basal cell length; branch MP₁₊₂ forked several times on corium, basad of apex of clavus, then forking on membrane; branch MP₃₊₄ forked slightly basad of claval apex; branch MP₃ single, branch MP₄ forking on membrane; stem MP reaching margin with more than dozen terminals; stem CuA forked at basal 1/3 of tegmen length, basad of claval veins junction; branch CuA₁ single, branch CuA₂ forked on corium, basad of branch ScP+RA forking; branch CuA_{2a} forked basad of claval apex; branch CuA_{2b} forked on membrane, apicad of claval apex. Clavus long, reaching 3/5 of tegmen length, closed, CuP reaching margin at about distance of claval veins common stalk Pcu+A₁; claval veins Pcu and A₁ distinctly Y-shaped, fused very late, slightly basad of

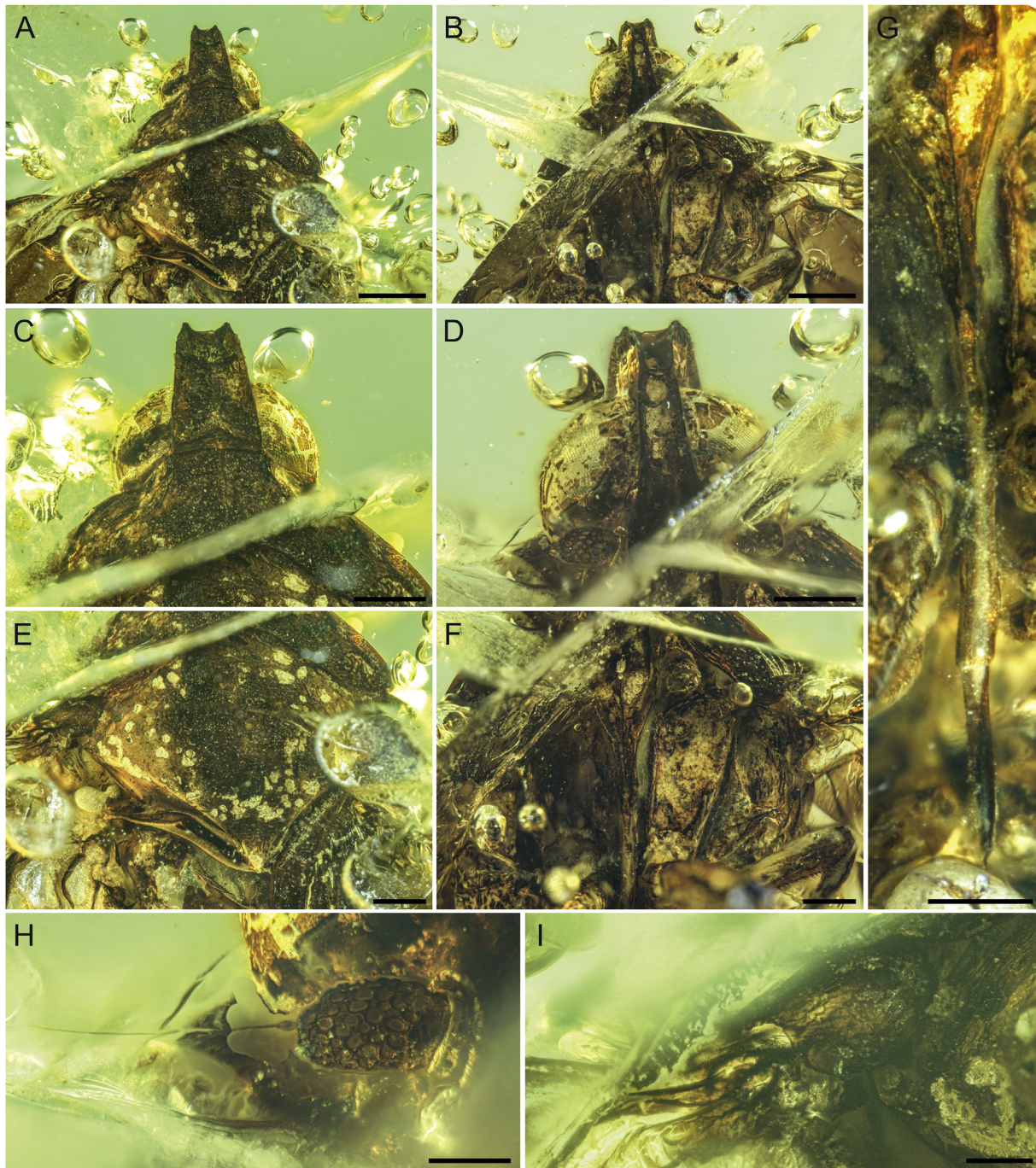


Fig. 2. Detailed photographs of the head, pronotum and mesonotum of *Katlasus xiai* gen. et sp. nov. A, head, pronotum and mesonotum in dorsal view. B, head, pronotum and mesonotum in ventral view. C, head and pronotum in dorsal view. D, head in ventral view. E, mesonotum in dorsal view. F, mesonotum in ventral view. G, rostrum in ventral view. H, antenna in ventral view. I, tegula in dorsal view. Scale bars for A-B = 1 mm, C-G = 0.5 mm, H-I = 0.2 mm.

branch ScP+RA forking, common stalk short, reaching margin (vein A₂) at level of ScP+RA forking. Hind wing with branch RA and RP forked at apical section; two veinlets *rp-mp* present, veinlet *mp-cua* very short, intersected by distinct fold, subparallel to stem MP at base and branch MP₃₊₄ in apical section. Procoxae long, flattened, with carinate margins. Mesotibia subquadrate in cross section, with densely packed rows of thick setae along margins, tarsomeres subequal in length. Metatibia subquadrate in cross section, basal (knee) lateral spine distinct, and probably single lateral spine at about half of metatibia length. Male pygofer tubular, slightly longer than wide in ventral view, ventral carina reaching posterior margin;

lateral sides elongate posteriad; male styles elongate, widened at base, rounded apically; male anal tube not distinctly exceeding apices of genital styles.

Katlasus xiai Luo, Jiang et Szwedo sp. nov.

(Figs. 1–5).

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Etymology. The specific name is dedicated to Mr. Fangyuan Xia, Director of the Lingpoge Amber Museum in Shanghai, for his contribution to the study of this amber specimen.

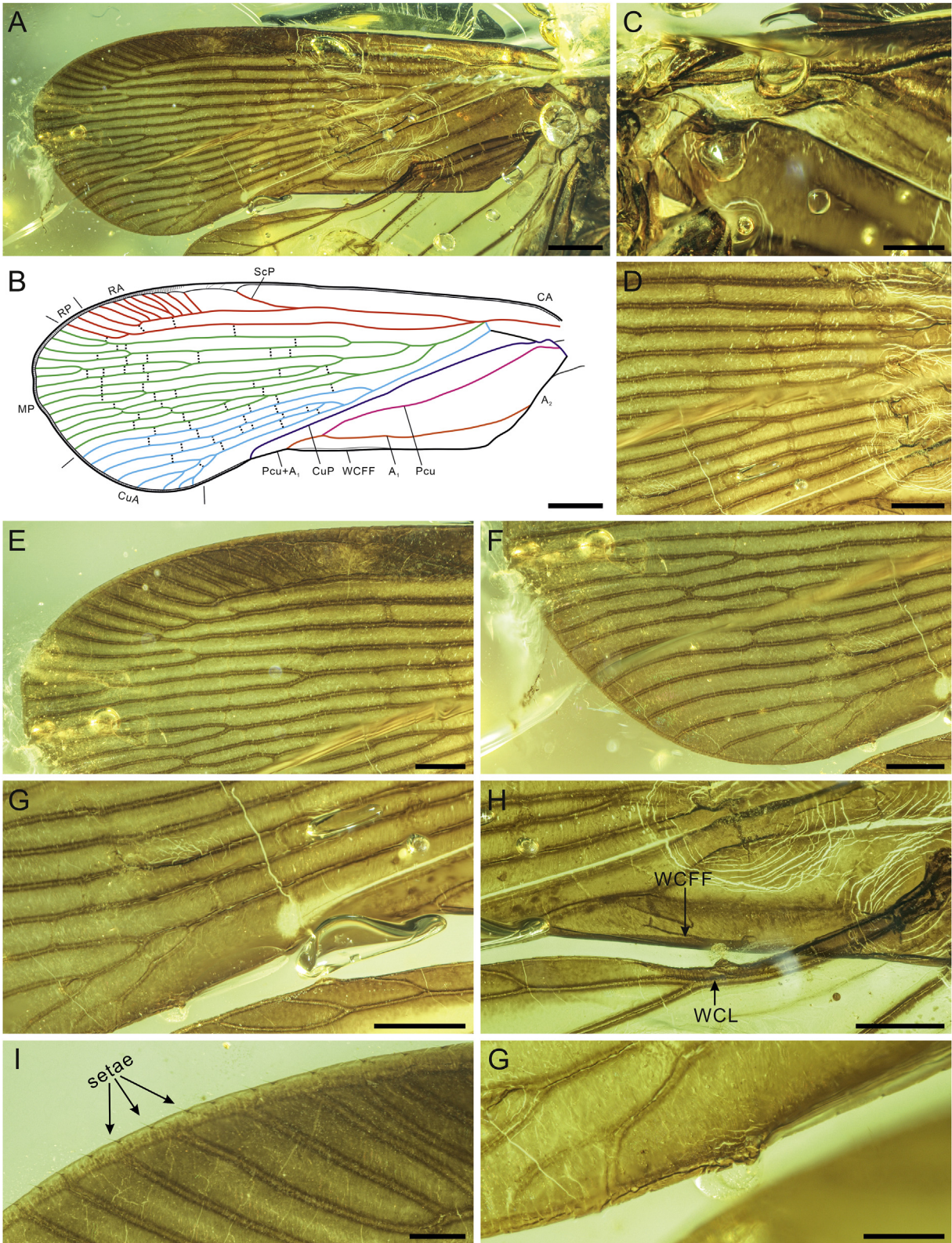


Fig. 3. Detailed photographs and line drawing of the tegmen of *Katlasus xiai* gen. et sp. nov. A, left tegmen in dorsal view. B, line drawing of the left tegmen in dorsal view. C, basal part of the left tegmen in ventral view. D-G, higher magnification of the left tegmen in dorsal view. Scale bars for A-B = 1 mm, C-H = 0.5 mm, I-G = 0.2 mm. Abbreviation: WCL, wing-coupling lobe; WCFF, wing-coupling fore fold.

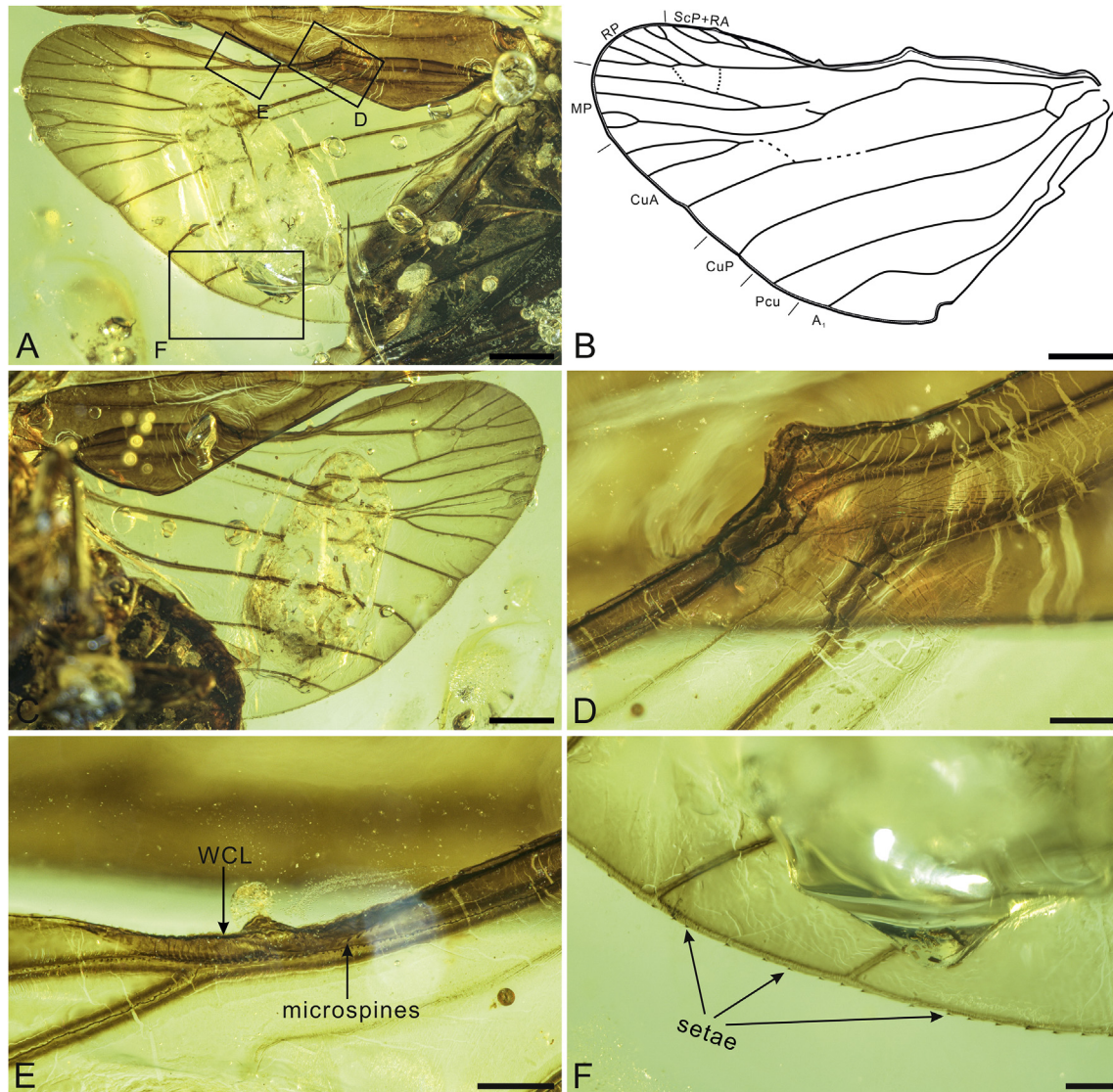


Fig. 4. Detailed photographs and line drawing of the hind wing of *Katlasus xiai* gen. et sp. nov. A, left hind wing in dorsal view. B, line drawing of the left hind wing in dorsal view. C, left hind wing in ventral view. D–F, higher magnification of the left tegmen in dorsal view. Scale bars for A–C = 1 mm, D–F = 0.2 mm. Abbreviation: WCL, wing-coupling lobe.

Material. Holotype. Specimen No. NIGP172209, deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing. Burmese amber, piece of oval shape, $25 \times 16 \times 4$ mm, weight 0.9 g. Holotype inclusion incomplete: legs partly preserved; the whole specimen was cut by a few fissures.

Locality and horizon. Burmese amber, from deposits near the Tanai town in the Hukawng Valley of northern Myanmar, upper Albian to lower Cenomanian (mid-Cretaceous).

Diagnosis. Frons about twice as wide in lower portion as at margin with vertex. Trigons absent. Mesonotum in mid line 3 times as long as pronotum in mid line. Tegmen with costal cell about as wide as cell C1; cell C1 more than 1.5 times as long as cell C3; main stems forking pattern sequence: ScP+R → MP → CuA; branch RA on membrane with 8(9) terminals; branch RP with 2 terminals, stem MP with 14 terminals, branch CuA₂ with 7 terminals on membrane. Hind wing with basal cell distinct, with 3 terminals of RA basad of apex; 3 terminals of RP, 4 terminals of MP and 3 terminals of CuA. Male genital styles widened at base, then narrowed and again roundly widened apically, slightly wrenched in apical portion, with ventral keel-like eminence.

Description. Adult, male. Total length ca. 13 mm, body (Fig. 1) 9.5 mm long. Head with compound eyes 1.54 mm wide, $\frac{1}{2}$ as wide as pronotum; 1.42 mm long in total (Fig. 2A, B, C). Double carina separating vertex and frons visible from above. Trigons and areolets absent. Vertex converging anteriorly, double trapezoid, about 1.1 times as long (0.72 mm) in as wide at base (0.66 mm); anterior margin carinate, 0.51 mm wide, angulately incised, lateral margins elevated, carinate, posterior margin widely angulately concave, 0.72 mm wide (Fig. 2A, C); disc of vertex sunken; median carina complete. Frons separated from vertex by double carina, no areolets, somewhat drop shape, elongate, strongly inward concave but slightly bulged below compound eyes; lateral carinae slightly elevated, gradually diverging downwards and slightly expanded outward below antennae; median carina incomplete, sharply ridged, extending almost to postclypeus. Frontoclypeal suture arcuate, indistinct. Postclypeus elongate, convex, with median carina distinct, lateral carinae slightly elevated, extending to anteclypeus. Anteclypeus narrow, about twice as long as wide, with median carina, clypellus elongately triangular (Fig. 2B, F, G). Rostrum long (in total 2.63 mm), reaching metacoxae, apical

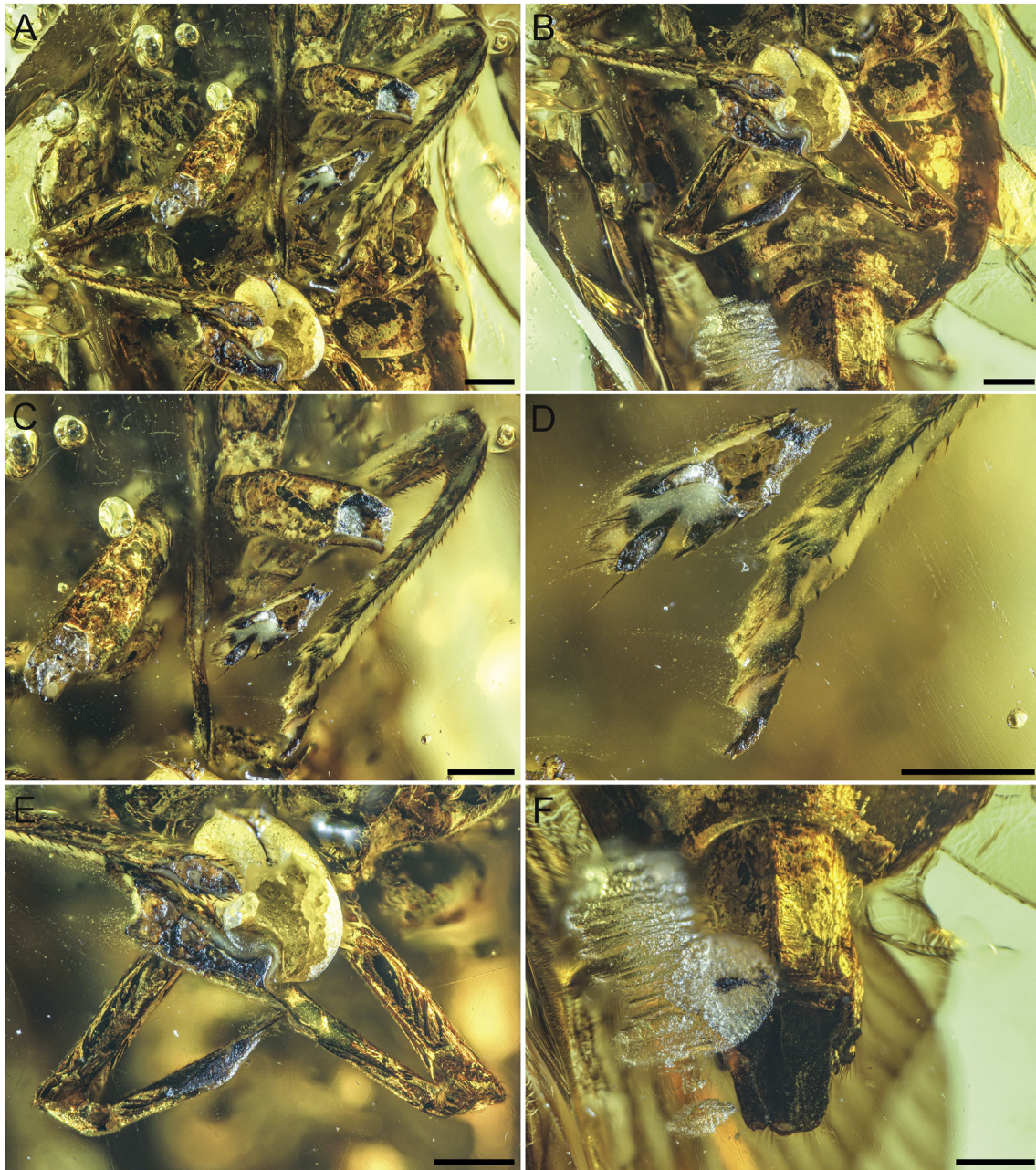


Fig. 5. Detailed photographs of legs and abdomen of *Kattalus xiai* gen. et sp. nov. A, fore leg, mid leg and abdomen. B, hind leg and abdomen. C, fore leg and mid leg. D, higher magnification of mid leg and tarsal claws and arolium. E, hind leg. F, male terminalia. Scale bars = 0.5 mm.

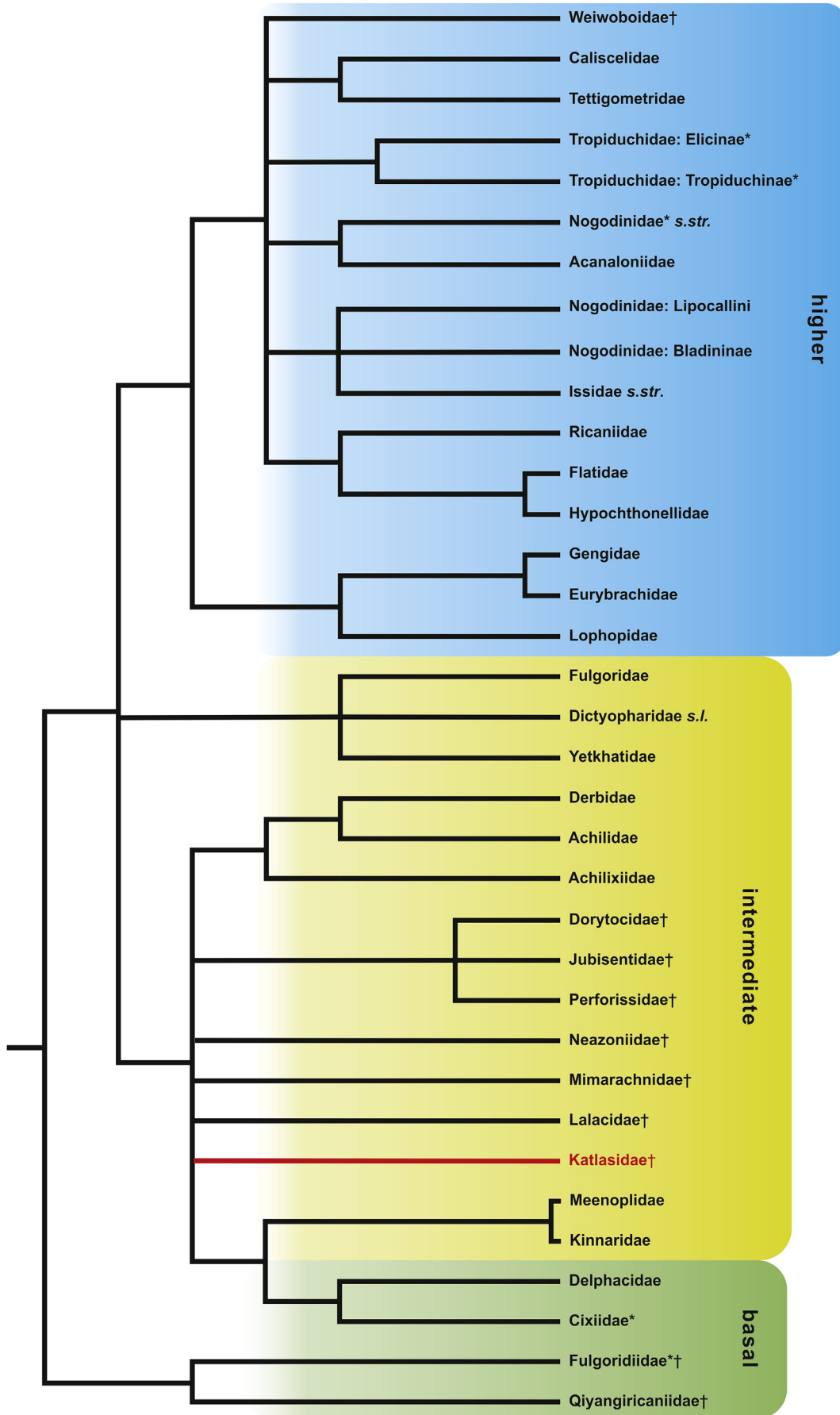
segment about as long as subapical one, with acute apex (Fig. 2G). Compound eyes large, bulging laterally, anterior margin distinctly exceeding half of the head length, 1.05 mm long and 0.61 mm wide (Fig. 2C, D). Median ocellus vestigial. Lateral ocelli distinct, in front of compound eyes. Antennal foveae elevated, ring-like; scape very short, ring-like, about 0.06 mm long; pedicel barrel-like, with more than 30 distinct sensory lentiform flattened plaque organs, 0.36 mm long and 0.23 mm wide; flagellum swelled at basal part, then whip-like, about 0.69 mm long (Fig. 2H).

Pronotum (0.58 mm long in mid line, 3.57 mm wide) with a complete median carina and incomplete, diverging posteriad lateral carinae on each side, delimiting pronotal disc; postocular carinae present, widely diverging behind compound eyes; pronotal disc

elevated, anterior margin almost straight, posterior margin strongly arcuately concave. Mesonotum transversely lozenge-shaped, convex, slight wrinkled on its surface, without intermediate and median carinae, scutellum transversely wrinkled (Fig. 2A, C, E).

Tegula relatively large (0.51 mm long, 0.39 mm wide from the dorsal view), strongly arched (Fig. 2I).

Tegmen (Fig. 3) macropterous, membranous, translucent, unicolorous, broadest at about 3/5 of its length, about 2.8 times as long as wide (10.65 mm long, 3.75 mm wide at broadest part). Costal margin slightly arcuate at the base, then almost straight; anteroapical angle widely rounded, posteroapical angle rounded, apical margin mildly rounded, tornus arcuate, claval margin almost straight, postclaval margin arcuate at the base, then almost straight,



then curved. Margin of the tegmen surrounded by ambient vein from the basal part of the costal margin to claval apex, with densely transverse veins between ambient and margin from the distal end of the costal area to claval apex; tegmen margin surrounded by very small setae from the distal end of the costal area to claval apex; clavus closed with claval apex at about 3/5 of the tegmen length. Basal cell elongated, about three times as long as wide (1.38 mm long and 0.69 mm wide). Tegmen with a large number of veins, most of the tegmen veins parallel to each other. Stems ScP+R and MP leaving basal cell from the same point (terminal of the basal cell). Stems ScP+RA and RP with a very short common stalk, then forked; stem ScP+RA slightly sinuate, subparallel to the costal margin, then forked at about 1/2 of the tegmen length; branch ScP merely arcuate, gradually closing to the tegmen margin; branch RA slightly sinuate, with 9 terminals reaching margin basad of anteroapical angle; branch RP slightly sinuate, subparallel to the costal margin, forked at about 5/6 (0.83) of the tegmen length, reaching margin with 2 terminals, at about anteroapical angle. Stem MP leaving basal cell with a short stalk, about 2/3 as long as basal cell, reaching margin with 14 terminals; stem MP curved at base, then forked at about 1/4 of the tegmen length; branch MP₁₊₂ forked slightly apical of stem MP forking; MP₁ slightly arched, then almost straight, then forked again at about 2/5 of the tegmen length; MP_{1a} slightly arched, then almost straight, subparallel to branch RP, reaching margin with 2 terminals forking on membrane, apical of MP_{1b} forking; MP_{1b} slightly curved, then almost straight, subparallel to branch MP_{1a}, reaching margin with 2 terminals forking on membrane; MP₂ slightly curved, then almost straight, then forked slightly apical of branch MP₁ forking; MP_{2a} slightly arched, then almost straight, reaching margin with 3 terminals; MP_{2b} slightly curved at base, then slightly curved, then forked, reaching margin with 3 terminals; branch MP₃₊₄ curved, then almost straight, then forked slightly basad of branch MP₁ forking; MP₃ single; MP₄ forked before apex of clavus, slightly sinuated, reaching margin with 3 terminals. Stem CuA with 8 terminals in total, CuA₁ single and CuA₂ with 7 terminals reaching margin; stem CuA almost straight, then forked at about 1/3 of the tegmen length; branch CuA₁ strongly arched mediad after forking, then slightly sinuate, parallel to MP₄, reaching margin with single terminal; branch CuA₂ slightly sinuate, then forked on corium, slightly apical of MP₂ forking; CuA_{2a} strongly arched after forking, then forked again, reaching margin with 2 terminals; CuA_{2b} almost straight, then forked on membrane, reaching margin with 5 terminals. Stem CuP strongly sinuate at the base, then almost straight, then strongly arcuated distally, reaching margin at about 3/5 of the tegmen length. Claval veins Pcu and A₁ fused slightly basad of 1/2 of the tegmen length, common portion Pcu+A₁ distinctly shorter (ca. 1/6) than free portion of Pcu; Pcu strongly arched at base, then slightly sinuate; A₁ slightly curved before forking; common portion Pcu+A₁ slightly sinuate, reaching claval margin (vein A₂) at distance about common part Pcu+A₁. Postclaval lobe distinct, with wing-coupling fore fold (WCFF) well developed, subparallel to the postclaval margin, reaching terminus of Pcu+A₁ at slightly more than half of the tegmen length. Nodal line absent, transverse veinlets in apical half of tegmen do not arranged in regular lines, apical line indistinct. Costal area absent, costal cell about as wide as cell C1; cell C1 the longest (5.42 mm long and 0.29 mm wide), about 4.5 times as long as the basal cell, delimited posteriorly by a transverse veinlet *ir*; cell C3 (3.33 mm long and 0.37 mm wide at widest point) about 1.5 times as long as the basal cell; cell C5 short (0.65 mm long and 0.31 mm wide), slightly less than the half length of the basal cell, delimited posteriorly by a transverse veinlet *icua*.

Hind wing (Fig. 4) membranous, transparent, subtriangular, shorter than tegmen, about twice as long as wide (8.13 mm long and 4.34 mm wide at broadest part). The costal margin strongly arched at the base, then slightly sinuate, then strongly arched again, then curved with a small arch; anteroapical angle widely rounded, posteroapical angle rounded, apical margin mildly rounded, tornus curved, postclaval margin slightly curved at base, then almost straight with a small arch. The margin of the hind wing surrounded by ambient vein from the basal part of the costal margin to the distal end of the postclaval margin, with densely transverse wrinkles between ambient and margin from anteroapical angle to the distal end of the postclaval margin; the hind wing margin surrounded by very small setae from anteroapical angle to the distal end of the postclaval margin. Basal cell present, subquadrangular. Stem ScP+R strongly arched at base, then almost straight, then sinuate, forked at about 3/5 of the hind wing length; stem ScP+RA subparallel to margin, reaching margin basad of the anteroapical angle with 3 terminals; branch RP almost straight, then forked at about 4/5 of the hind wing length, reaching margin at the apical angle with 5 terminals. Stem MP slightly arched at the base, then almost straight, then arched, forked slightly basad of ScP+R forking; MP₁₊₂ forked at about 7/10 of the hind wing length, reaching margin with 2 terminals; MP₃₊₄ do not fork until close to the margin, reaching margin with 2 terminals. Stem CuA straight, forked at about 2/3 of the hind wing length; branch CuA₁ arched, then forked at about 3/4 of the hind wing length, reaching margin with 2 terminals; branch CuA₂ almost straight, single. Stem CuP slightly sinuate, single. Stem Pcu strongly curved, single. Stem A₁ almost straight with a small arch, then strongly sinuate, single. Transverse veinlets sparse, two veinlets *rp-mp*, veinlet *mp-cua* very short; distinct fold along stem MP, intersecting *mp-cua* and apical cell. Wing-coupling lobe (WCL) present, slightly apical of the half of the hind wing length, darker than the hind wing, with several microspines on its lower edge.

Fore leg (Fig. 5A, C) coxa subcylindrical, carinate; profemur partly preserved, narrow and long, margins carinate, covered with numerous short setae, subquadrangular in cross section. Apex of middle protarsomere with row of setae, dorsally deeply incised, base of apical protarsomere sunken in this incision (Fig. 5D). Mid leg (Fig. 5A, C, D) mesofemur narrow and long (2.23 mm long, 0.37 mm wide), margins carinate, ventral margins with numerous short setae, mesotibia narrow and long (2.46 mm long, 0.22 mm wide), margins carinate, covered with numerous short setae; length of mesotarsomeres: I 0.29 mm, II 0.47 mm, III 0.39 mm, covered with short setae; basimesotarsomere and midmesotarsomere triangular, dorsally incised, ventrally with bunch of setae; apical mesotarsomere narrow. Hind leg (Fig. 5B, E) with metafemur narrow and long, margins carinate, covered with numerous short, indistinctive setae, metatibia partly preserved, narrow and long, margins carinate, covered with numerous short setae, basal (knee) lateral spine visible, lateral spine (not clearly preserved), at about middle of metatibia.

Abdomen wide, flattened (Fig. 5B), about 4.03 mm long with male terminalia, two flanks flatten, the center part arched; pregenital segments gradually contracted; posterior margin of pregenital segment widely arcuately curved. Male terminalia (Fig. 5F) 2.08 mm long, 0.94 mm wide. Pygofer tubular, elongate, distinctly narrower than abdomen, lateral sides elongate posteriad, with apical setae, ventral side with a distinctive median carination. Male genital styles elongate, widened at base, rounded apically; slightly wrenched in apical section, setose apically. Male anal tube elongate, not distinctly exceeding apices of genital styles, anal style rounded apically, with short setae.

Female unknown.

4. Discussion

Katlasidae fam. nov. can be referred to the superfamily Fulgoroidea based on the combination of these characters: head capsule with carinae; antennae base situated below the eyes, pedicel with lentiform flattened plaque sensory organs and whip-like flagellum, tegulae present, tegmen with ambient vein transversely wrinkled and 'Y-shape' veins on clavus (Pcu and A₁). But the new family does not match any known planthoppers and its morphological characters reach far beyond the known disparity of the group. Katlasidae fam. nov. can superficially resemble some members of the Cretaceous family Lalacidae by the shared characters: similar body size (5.9–18.5 mm in Lalacidae), head narrow, mesonotum without carinae in some genera (e.g., *Protodelphax* Hamilton, 1990, *Kinnarocixius* Hamilton, 1990, *Lalax* Hamilton, 1990, *Patulopes* Hamilton, 1990, *Carpopodus* Hamilton, 1990, *Psestocixius* Hamilton, 1990 and *Vulcanoia* Martins-Neto, 1988), tegmen margin surrounded by ambient vein, with densely transverse veins (but not as wide as in Lalacidae), hind wing with *rp-mp* crossveins and more vein branches. Head capsule of the new family retains plesiomorphic conditions, shared with Jurassic Fulgoridiidae, Cretaceous Lalacidae and some recent Cixiidae, viz. double transverse carina separating disc of vertex and frons, median ocellus present (at least vestigial). Median carina of vertex could be developed variously among representatives of various Fulgoroidea families, as well as median carina of frons, so these characters even believed to be 'basal' seems to be secondary and variable, therefore difficult in interpretation of their phylogenetic value (Bourgoin, 1986; Emeljanov, 1987; Anufriev and Emeljanov, 1988). The most striking feature on the head is the antennal pedicel covered with numerous sensory plaque organs. These are not star-shaped, forming a rosette containing two concentric fields like the petals and surrounding sepals of a flower (Bourgoin, 1985; Bourgoin and Deiss, 1994; Hamilton, 2011; Wang et al., 2018), the state most common among modern Fulgoroidea, but seems to represent the circular flattened plate model as defined by Bourgoin (1985). Such model of sensory lentiform flattened plaques in modern planthoppers is present in representatives of the family Tettigometridae (Bourgoin, 1985; Bourgoin and Deiss, 1994; Cheng and Yang, 1996). Bourgoin and Deiss (1994) discussed the various interpretations and possible ways of evolutionary changes in pedicellar sensory plates. Lewis and Marshall (1970) suggest that fulgoroid plate organs have evolved from a cluster of basiconic receptors, which have lost their separate identities. Therefore, the primitive conformation of the planthopper plate organ may be closer to a digitated or ridged type. Several observations and modifications of this most probable plesiomorphic condition were discussed by Bourgoin and Deiss (1994). However, even if some special conformations seem to be characteristic of some taxa, it is clear that structural variations of plate organs have taken place several times independently (Bourgoin and Deiss, 1994; Stroński et al., 2011). Bourgoin and Yap (2010) have reviewed the taxonomic distribution of different morphological types of sensory plaque organs and they recognized 5 main types: 1) the setae-like projected plate (e.g., Delphacidae, Kinnaridae, Tropiduchidae); 2) the flattened star-shaped plate (e.g. Cixiidae, Kinnaridae + Meenoplidae, Achilixiidae); 3) the crenellated plate (linear, U or Y shaped ridges) (Cixiidae, Dictyopharidae, Fulgoridae, and partly Ricaniidae); 4) the folded flattened plate (often clover leaf-like) (Flatidae, Lophopidae); 5) the circular flattened plate (Tettigometridae); and the family Katlasidae **fam. nov.** described above presents also this type. The structure of the pronotum, with elevated disc is shared with representatives of several other planthopper families, e.g., Delphacidae and Kinnaridae; postocular carinae are present also in some Cixiidae, Delphacidae and

Kinnaridae. Wide and transversely lozenge-shaped mesonotum is similar to pattern observed in some Kinnaridae and Fulgoridae (O'Brien and Wilson, 1985; Wilson, 2005). Tegmen of Katlasidae fam. nov. presents number of features shared with other planthoppers, but in unique combination. Widened membrane is shared with Achilidae + Achilixiidae and some Derbidae, also present in extinct Yetkhatidae; however widened membrane is present also in some Dictyopharidae and Fulgoridae (Bourgoin and O'Brien, 1994; Constant, 2015; Constant and Pham, 2017; O'Brien and Wilson, 1985; Song et al., 2019; Wilson, 2005). Dense venation of tegmen observed in *Katlasus* gen. nov. is not a unique feature among planthoppers, similar patterns of multiforked veins are observed e.g. in extinct Lalacidae: Ancoralini (Hamilton, 1990), not yet described fossils from Lowermost Eocene of France, also in modern Achilidae: Rhotalini, some extinct and extant Fulgoridae and Lophopidae and modern Eurybrachidae (Emeljanov, 1992; Fennah, 1950; O'Brien and Wilson, 1985; Wilson, 2005). Pattern of venation with unforked (or scarcely forked) CuA₁ and multiforked CuA₂ is to be found in some genera of Rhotalini (Achilidae); interestingly in most of modern planthoppers in which multiforking of CuA is observed both branches are secondarily forked, with branch CuA₁ often with more furcations and terminals. In *Katlasus* gen. nov. stigmal area is developed, delimited by distinctly oblique vein ScP anteriorly and less oblique terminal of RA posteriorly. This resemble the pattern of stigma area observed in Achilidae: Myconini (Fennah, 1950; Emeljanov, 1992). Clavus in *Katlasus* gen. nov. is closed, but the claval fold is slightly prolonged to membrane. Such prolongation of claval fold is observed in Achilidae, some Cixiidae, Derbidae and Dictyopharidae; this feature and its possible importance for classification and phylogenetic reconstructions needs to be further investigated. Claval veins are fused far from their bases – this pattern resembles Lalacidae, e.g., the genus *Ancorale* Hamilton, 1990, but such late fusion is present also in Jurassic Fulgoridiidae, Cretaceous Perforissidae, extinct, Cretaceous Cixiidae, therefore it could be regarded as plesiomorphic condition. Presence of short setae surrounding margin of tegmen is weakly investigated feature, often overlooked, but such setae are present in various groups of planthoppers, e.g., in Cixiidae and Tropiduchidae. Hind wing venation pattern resembles (superficially?) some Achilidae and Dictyopharidae. Two *rp-mp* veinlets and a fold intersecting weakened *mp-cua* is observed in Rhotalini (Achilidae), but also in some Dictyopharidae. Setae on the margin of hind wing is another character often overlooked, but variously developed setae are present at planthoppers' hind wings, not only at margin, but in some groups also along veins. Procoxae of *Katlasus* gen. nov. do not present any particular features, these are very similar to these in Cixiidae or Delphacidae. Pro- and mesofemora are bearing ventral row of setae – this character is also present in other planthoppers, however in *Katlasus* gen. nov., the setae seem to be short, thick and densely packed. Quadrangular in cross-section pro- and metatibiae are present in various groups of planthoppers, also emargination of the margins with rows of setae is a quite common feature. However, such combination of characters is not present in Lalacidae: Ancoralini. Metatibia is distinctly longer than metafemur, relatively slender, subquadrangular in cross-section, widened apically, it bears a single spine at base (knee spine), probably also single lateral spine, and a row of a few apical teeth. This character separates *Katlasus* gen. nov. from Lalacidae: Ancoralini – in the latter, metatibia is more robust, distinctly widened apically, without lateral spines and with apical row of teeth composed of more than dozen teeth (Hamilton, 1990). In general structure of male terminalia, *Katlasus* gen. nov. presents the model found in some Cixiidae, but also in Achilidae, Dictyopharidae and Fulgoridae, with widened abdomen and more or less tubular

pygofer. In Cixiidae apices of male genital styles are usually widened, making them more or less L-shaped, without additional subapical processes; it seems that similar conformation is present in Lalacidae. In Achilidae male genital structures are modified, genital styles are lobate apically, but usually with additional processes subapically. Such conformation is present also in Dictyopharidae and Fulgoridae. New genus described above *Katlasus* gen. nov. presents male genital styles lobate and slightly wrenched in apical portion, with ventral keel-like eminence, and any additional subapical processes are visible.

The question raises where to place the new family Katlasidae fam. nov. in phylogenetic framework of Fulgoroidea? It presents unique combination of plesiomorphic and apomorphic features. At first glance Katlasidae fam. nov. resembles some Lalacidae. Lalacidae is a small extinct group, including only 9 genera and 17 species (Martins-Neto, 1988; Hamilton, 1990; Zhang, 2002; Bourgoïn, 2020), and they are all described by Hamilton (1990) from the Lower Cretaceous Santana Formation of Brazil, except *Cretocixius stigmatus* Zhang, 2002 was discovered from Lower Cretaceous Lushangfen Formation located in Fangshan district of Beijing, China (Zhang, 2002). This family was placed into the 'Cixiidae-like' planthoppers group, together with Achilidae, Achilixiidae, Cixiidae, Delphacidae, Derbidae, Fulgoridiidae, Kinnaridae, Meenoplidae, Mimarachnidae, Neazoniidae (Bourgoïn and Szwedó, 2008; Jiang et al., 2018; Brysz and Szwedó, 2019). Venation pattern of vast majority of Lalacidae resembles some Cretaceous Cixiidae (Fennah, 1961, 1987; Szwedó, 2001), except its veins not forking before the nodal line and wide, transversely wrinkled appendix, resembling Kinnaridae-Meenoplidae (Bourgoïn, 1997). Within Lalacidae, one genus is quite exceptional, viz. *Ancorale* Hamilton, 1990 placed as sole genus of tribe Ancoralini Hamilton, 1990 (together with Kinnarocixiini Hamilton, 1990) in subfamily Ancoralinae Hamilton, 1990 (Hamilton, 1990). It is characteristic of dense, parallel venation and narrow appendix, similar to this in *Katlasus* gen. nov., but differs from it by characters of head capsule (elevated posteriad disc of vertex; presence of trigons; mesonotum with median groove; metatibia unarmed, with more than dozen apical teeth; veins of tegmen elevated with helical sculpture; hind wing venation proliferous). However, numerous crucial details of *Ancorale* morphology are actually weakly preserved (Hamilton, 1990), and we cannot exclude that *Ancorale* could be another genus to be included in the newly described family Katlasidae fam. nov.

It could be preliminarily stated that Katlasidae fam. nov. should be placed close to Lalacidae in 'intermediate' informal group of Fulgoroidea (Brysz and Szwedó, 2019, Fig. 6). As the eleventh planthoppers' family reported from Cretaceous and the eighth planthoppers' family from mid-Cretaceous Burmese amber (Ross, 2019, 2020a, b), these planthoppers' lineages have shown amazing morphological diversity, which probably linked with their successful co-evolution with plants (Li et al., 2017; Szwedó, 2018; Song et al., 2019). The Jurassic family Fulgoridiidae was considered as the ancestor of these high diversified extinct and recent planthopper family (Szwedó et al., 2011; Zhang et al., 2019), but Fulgoridiidae is a paraphyletic group (Szwedó and Żyła, 2009; Li et al., 2011), with numerous taxa known from isolated tegmina only, with other body structures weakly known (Jiang et al., 2018). Moreover, the Cretaceous families Dorytocidae, Jubisentidae and Perforissidae are probably not direct descendants of Jurassic 'Fulgoridiidae' (Zhang et al., 2019). Szwedó (2009) and Brysz and Szwedó (2019) considered that 'Cixiidae-like' families should be treated rather as sister-groups in respect to 'Fulgoridiidae'. The Cixiidae reaches with fossil record to the Lower Cretaceous, also

Achilidae, and extinct families Lalacidae, Mimarachnidae, Neazoniidae, and Perforissidae are present among Lower Cretaceous fossils. By the border of Lower and Upper Cretaceous several other families also placed in 'intermediate' Fulgoroidea appeared in fossil record: Dorytocidae, Jubisentidae, Yetkhatidae and above described Katlasidae fam. nov., and Dictyopharidae in Upper Cretaceous (Szwedó, 2018; Brysz and Szwedó, 2019). The knowledge on early stages of planthoppers evolution are still full of unresolved questions, and this unique new planthopper family Katlasidae fam. nov. raises more questions about the phylogeny of Fulgoroidea.

Finding of a new planthopper family gives us new insights into the very important period of formation of modern faunistic complexes at mid-Cretaceous biotic re-organization times. Katlasidae fam. nov. seems to be one more group diversified during the Cretaceous, than gone extinct as some others, viz. Dorytocidae, Jubisentidae, Lalacidae, Neazoniidae, Mimarachnidae, Perforissidae and Yetkhatidae (Szwedó, 2018; Brysz and Szwedó, 2019). Such diversification could be result of pressure of environmental changes. The Cretaceous has often been described as period of 'warm and equable' climate (Hay, 2016), with the average global temperature near to 18 °C. However, more recent refined work shows that climates during the 79 myrs of the Cretaceous were not quite so unvarying as originally thought (Holz et al., 2015; Huber et al., 2018; Vickers et al., 2019). Increasingly high sea levels in the epicontinental seas (up to 250 m above today's sea-level), fluctuating within tens of millions of years or in shorter cycles, was caused by slow geodynamic processes associated with changes in plate tectonics, and only in fraction by a lack of glaciated regions (Sames et al., 2020; Wagreich et al., 2020). The breakup of Pangea is linked to high activity of the mid-ocean ridges, especially mid-Cretaceous peak in oceanic crust production rates, widening them, causing cascading effects (Racki, 2020). Greenhouse gases from the high magmatic-volcanic activity and several interwoven feedback mechanisms, resulted in major perturbations of the global carbon cycle with repercussions on the Earth's climate and ocean circulation, observed as Oceanic Anoxic Events (e.g., Jenkyns, 2010; Beil et al., 2019). In terrestrial environments, angiosperms gradually increased their diversity and abundance throughout the Cretaceous, and by the Maastrichtian, they surpassed other plant groups in diversity, including cycadophytes, pteridophytes (ferns), and Coniferales (Jaramillo, 2019). This shift, related to changes of atmospheric CO₂ content and angiosperm plants physiology and morphology (de Boer et al., 2012; Jaramillo, 2019; Klein and Ramon, 2019; Yiotis and McElwain, 2019), resulted in their rapid radiation during the Cretaceous (Berendse and Sheffer, 2009; Bateman, 2020; Janssens et al., 2020). These changes affected the phytophagous insects, resulting in their adaptation and diversification. Larger meridional heat transport by atmospheric and/or oceanic circulation, shaping the mid-Cretaceous "supergreenhouse" period (Hasegawa et al., 2012) could be of importance for understanding of taxonomic diversity and composition of Kachin amber biota. Climatic and topographic factors in the area of Kachin amber formation and deposition in the mid-Cretaceous times, as it is considered to be an island or archipelago (Rasnitsyn and Öhm-Kühnle, 2018; Xing et al., 2018; Westerweel et al., 2019; Morley et al., 2020) could be responsible for magnification of evolutionary rate of planthoppers in this area. The observed distributional pattern of Cretaceous planthoppers, with some families represented in fossil record since the Lower and Upper Cretaceous of both hemispheres (viz. Achilidae, Cixiidae, Lalacidae, Mimarachnidae, Neazoniidae, Perforissidae) and the other exclusively found in mid-Cretaceous Kachin amber (viz. Dorytocidae, Yetkhatidae, Jubisentidae, and the newly described Katlasidae fam. nov.) needs to be further investigated.

5. Conclusion

A new planthopper family Katlasidae put one more pebble to the mosaic of Cretaceous stage of Fulgoroidea evolution and diversification. It is another peculiar group reported for the moment exclusively from Burmese amber from Kachin. This finding expands known taxonomic diversity and morphological disparity of Fulgoroidea, and raises more questions about the diversification and relationships of basal planthoppers' lineages.

CRedit authorship contribution statement

Cihang Luo: Writing - original draft. **Tian Jiang:** Writing - original draft. **Jacek Szwedo:** Writing - review & editing. **Bo Wang:** Writing - original draft. **Chuantao Xiao:** Methodology.

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