

Short communication

A new genus and species of Perforissidae (Hemiptera: Fulgoromorpha) from mid-Cretaceous Kachin amber

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ABSTRACT

A new genus and species of planthopper, *Lanlakawa changdaensis* gen. et sp. nov., is described based on a well-preserved specimen from mid-Cretaceous Kachin (Burmese) amber. This is the ninth genus of the extinct family Perforissidae and the sixth genus of the subfamily Cixitettignae. The new genus mainly differs from the five previously described genera in tegmen venation and the number of teeth in tibial pectens. Previous researches of sensory pits and wing-coupling apparatus are briefly reviewed.

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1. Introduction

Planthoppers (Fulgoromorpha) is one of six Hemiptera suborders, constituting a large group of oophagous, phytophagous insects known in fossil record since the Permian. It covers three superfamilies: two extinct – Permian Coleoscytoidea Martynov, 1935, Permian and Triassic Surijokocixioidea Shcherbakov, 2000 and Fulgoroidea Laterille, 1807, known in fossil record since the Jurassic (Szwedo, 2018).

Record of Fulgoroidea as inclusions in amber reaches early Cretaceous, twelve of 20 recent families are known as inclusions in various fossil resins as well as six extinct families (Table 1; Szwedo et al., 2004; Bourgoin, 2020).

The extinct Fulgoromorpha family Perforissidae Shcherbakov, 2007b is one of the groups known only from the Cretaceous (Shcherbakov, 2007b; Peñalver and Szwedo, 2010; Szwedo et al., 2013; Szwedo, 2018). This peculiar group presents a combination of particular morphological characters not to be found among either extinct or extant Fulgoroidea (Szwedo et al., 2013; Zhang et al., 2017) and can be placed among the 'Cixiidae-like' planthoppers due to characters like reduction of number of apical teeth and subapical setae and simplified venation (Szwedo, 2009; Szwedo et al., 2013; Zhang et al., 2017; Brysz and Szwedo, 2019). Up to now, the family includes two subfamilies, eight genera and nine species (Bourgoin, 2020): subfamily Perforissinae, including *Perforissus muiri* Shcherbakov, 2007b from the Upper Cretaceous of New Jersey (about 92 Ma) and *Cretargus emeljanovi* Shcherbakov, 2007b from the Upper Cretaceous of Taimyr (about 85 Ma) (Shcherbakov, 2007b); subfamily Cixitettignae, comprising *Cixitettix yangi* Shcherbakov, 2007b from the Upper Cretaceous of Taimyr (about 85 Ma), *Foveopsis fennahi* Shcherbakov, 2007b and *F. heteroidea* Zhang, 2017 from the mid-Cretaceous of Myanmar

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Table 1
Chronological account of first records of Fulgoroidea species as inclusions.

family	Species	Reference	fossil resin
Cixiidae Spinola, 1839	<i>Cixius vitreus</i> Germar et Berendt, 1856	Germar and Berendt, 1856 ^a	Baltic amber, Gulf of Gdańsk; Eocene (Lutetian-Bartonian)
Issidae Spinola, 1839	<i>Bolbossus bervoetsi</i> Gnezdilov et Bourgoïn, 2016	Bervoets, 1910 ^b	Baltic amber, Eocene (Lutetian-Bartonian)
Achilidae Stål, 1866	<i>Protepiptera kaweckii</i> Usinger, 1940	Usinger, 1940 ^c	Baltic amber, Gulf of Gdańsk; Eocene (Lutetian-Bartonian)
Dictyopharidae Spinola, 1839	<i>Netutela annunciator</i> Emeljanov, 1983	Emeljanov, 1983	Taimyr amber, Yantardakh; Upper Cretaceous (Santonian)
Derbidae Spinola, 1839	<i>Positrona shcherbakovi</i> Emeljanov, 1994	Emeljanov, 1994	Baltic amber, Gulf of Gdańsk; Eocene (Lutetian-Bartonian)
Kinnaridae Muir, 1925	<i>Oeclidius salaco</i> Emeljanov et Shcherbakov, 2000	Emeljanov and Shcherbakov, 2000 ^d	Dominican amber; Miocene (Burdigalian)
Nogodinidae Melichar, 1898	<i>Tonacatecutlius gibsoni</i> Stroiński et Szwedó, 2002	Stroiński and Szwedó, 2000 ^e	Mexican amber, Chiapas; Miocene (Burdigalian)
Tropiduchidae Stål, 1866	<i>Jantaritabia serafini</i> Szwedó, 2000	Szwedó, 2000 ^f	Baltic amber, Gulf of Gdańsk; Eocene (Lutetian-Bartonian)
Delphacidae Leach, 1815	<i>Serafinana perperunae</i> Gębicki et Szwedó, 2000	Gębicki and Szwedó, 2000	Baltic amber, Gulf of Gdańsk; Eocene (Lutetian-Bartonian)
Ricaniidae Amyot et Audinet-Serville, 1843	<i>Acroprieva msandarusi</i> Stroiński et Szwedó, 2002	Stroiński and Szwedó, 2002	East African copal; Pleistocene (Pliocene-Holocene?)
Perforissidae Shcherbakov, 2007b	<i>Perforissus muiri</i> Shcherbakov, 2007b	Shcherbakov, 2007b ^g	Raritan amber, New Jersey; Upper Cretaceous (Turonian)
Neazoniidae Szwedó, 2007	<i>Neazonia tripleta</i> Szwedó, 2007	Szwedó, 2007 ^h	Lebanese amber, Hammana/Mdeyrij; Lower Cretaceous (Barremian)
Lophopidae Stål, 1866	<i>Ordralfabetix sirophatanis</i> Szwedó, 2011	Szwedó, 2011	Oise amber, Paris basin; Eocene (Ypresian)
Caliscelidae Amyot & Audinet-Serville, 1843	<i>Quizqueiplana alexbrowni</i> Bourgoïn et Gnezdilov, 2016	Bourgoïn et al., 2016	Dominican amber, La Búcara mine, Cordillera Septentrional; Miocene (Burdigalian)
Mimarachnidae Shcherbakov, 2007c	<i>Burmessus raunoi</i> Shcherbakov, 2017	Shcherbakov, 2007c	Burmese amber, Kachin; mid-Cretaceous (Aptian/Cenomanian)
Dorytocidae Emeljanov et Shcherbakov, 2018	<i>Dorytocus ornithorhynchus</i> Emeljanov et Shcherbakov, 2018	Emeljanov, and Shcherbakov, 2018	Burmese amber, Kachin; mid-Cretaceous (Aptian/Cenomanian)
Jubisentidae Zhang, Ren et Yao, 2019	<i>Jubisentis hui</i> Zhang, Ren et Yao, 2019	Zhang, Ren and Yao, 2019	Burmese amber, Kachin; mid-Cretaceous (Aptian/Cenomanian)
Yetkhatidae Song, Szwedó et Bourgoïn, 2019	<i>Yetkhata jiangershii</i> Song, Szwedó et Bourgoïn, 2019	Song et al., 2019 ⁱ	Burmese amber, Kachin; mid-Cretaceous (Aptian/Cenomanian)

^a Germar and Berendt (1856) ascribed several fossils from Baltic amber to the genus *Cixius* Latreille, However, some of them are now moved to another genera and families (see Szwedó et al., 2004; Bourgoïn, 2020).

^b Since the name *Issus reticulatus* Bervoets, 1910 was the primary homonym of *Issus reticulatus* Herrich-Schäffer (1835) (Herrich-Schäffer, 1835), a new name was proposed (Gnezdilov and Bourgoïn, 2016).

^c Some of species described by Germar and Bervoets (1856) are to be placed in Achilidae (see Brysz and Szwedó, 2017; Bourgoïn, 2020).

^d The second species of Kinnaridae describe in this paper is *Quillessa stolidi* Emeljanov et Shcherbakov, 2000.

^e *Tritophania patruelis* Jacobi, 1938 described originally in Ricaniidae, later moved to Nogodinidae is placed now in Tropiduchidae (see Szwedó and Stroiński, 2017; Bourgoïn, 2020).

^f Shcherbakov (2007a) proposed transfer to Tropiduchidae some of Germar and Berendt's fossils resulting in *Jantaritambia oculata* (Germar et Berendt, 1856), and discussed placement of '*Cixius succineus* Germar and Berendt, 1856 in Tropiduchidae: Jantaritambiini.

^g Other species described from fossil resins there are: *Cretargus emeljanovi* Shcherbakov, 2007b; *Cixitettix yangi* Shcherbakov, 2007b and *Foveopsis fennahi* Shcherbakov, 2007b (Shcherbakov, 2007b).

^h Other species described there are: *Neazonia immatura* Szwedó, 2007 and *Neazonia imprinta* Szwedó, 2007.

ⁱ Second species described in this family is *Parwaina liuyei* Song, Szwedó et Bourgoïn (Song et al., 2019).

(about 98 Ma), *Tsaganema oshanini* Shcherbakov, 2007b from the Lower Cretaceous of Mongolia (about 125–112 Ma), *Iberofoveopsis migulelesi* Peñalver and Szwedó, 2010 from the Lower Cretaceous of Spain (about 125–113 Ma) and *Aafrita biladalshama* Szwedó et al., 2013 from the Lower Cretaceous of Lebanon (about 140–129 Ma) (Shcherbakov, 2007b; Peñalver and Szwedó, 2010; Szwedó et al., 2013; Zhang et al., 2017); and another species *Aonikenkissus zamunerae* Petrulevičius, Varela, Iglesias and Poiré, 2014 from the Upper Cretaceous of Argentina (about 96 Ma) whose subfamily remains unknown (Petrulevičius et al., 2014). Nymphs of this family were also recorded in the Lower Cretaceous Jordanian amber (Kaddumi, 2005; Zhang et al., 2017).

Herein we describe a new genus and species of cixitettigine Perforissidae, *Lanlakawa changdaensis* gen. et sp. nov. from mid-Cretaceous Burmese amber from Kachin.

2. Material and methods

The studied specimen originates from the Cretaceous deposits in the Hukawng Valley of Myanmar. The mining area was located at Noije Bum, close to Tanai Township (26°21'33.41" N, 96°43'11.88" E;

palaeolatitude 5.0 ± 4.7° S) (Kania et al., 2015; Thu and Zaw, 2017; Westerweel et al., 2019; see locality in Fig. 1 of Jiang et al., 2019), which is the main source of amber in the country until 2017. It is the most productive source of Cretaceous amber inclusions, preserving an enormous diversity of plants, invertebrates and vertebrates (Ross, 2019). The Burma Terrane was part of a Trans-Tethyan island arc at about 95 Ma, suggesting island endemism for the Burmese amber biota (Jiang et al., 2018; Rasnitsyn & Öhm-Kühnle, 2018; Xing et al., 2018; Westerweel et al., 2019). The fossils resins of Myanmar (mid-Cretaceous Kachin amber - burmite, weakly known Hkamti amber and Upper Cretaceous Hti Lin amber) still give us new insights into the very important period of formation of modern faunistic complexes at mid-Cretaceous biotic re-organization times (Szwedó 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, diversification of parasitic and especially parasitoid insect lineages, and early mammals (Lloyd et al., 2008; Jiang et al., 2018; Schachat 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 using the software HeliconFocus 6.7.1 for a better illustration of 3D structures. 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 Szwedo and Żyła (2009) and Nel et al. (2012) and Bourgoïn et al. (2015). Vein abbreviation: CA, costal margin; 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 Perforissidae Shcherbakov, 2007b

Subfamily Cixitettiginae Shcherbakov, 2007b

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

urn:lsid:zoobank.org:act:A389B6E7-62B2-448D-B99D-25DBBA9A605D.

Etymology. The generic name is derived from the Kachin language words 'lanlak' meaning numerous and 'awa' meaning tooth; generic name refers to a large number of teeth of the tibial pectens. Gender: feminine.

Type species: *Lanlakawa changdaensis* Luo, Jiang et Szwedo, sp. nov.; by original designation and monotypy.

Included species. Type species only.

Diagnostic. Costal margin slightly sinuate subbasally, gibbous slightly proximad of midlength (costal margin gibbous about midlength in *Foveopsis* Shcherbakov, 2007b); branches ScP + RA and RP leaving basal cell from the same point (terminal of basal cell) (short common stalk ScP + R + MP leaving basal cell in *Foveopsis*); ScP + RA shifted median in distal portion (RA subparallel to costal margin in distal portion in *Foveopsis*); RP single (as in *Foveopsis*), but not distinctly curved in apical section; MP + CuA leaving basal cell with a common stalk; MP with two terminals, MP₁₊₂ almost in line with stem MP, MP₃₊₄ shifted mediad (two terminals of MP in *Foveopsis*, distinctly curved anteriorly); stalk CuA about four times as long as common stalk MP + CuA; CuA forked distinctly anteriorly of claval veins fusion (CuA forked at level of claval veins fusion in *Foveopsis*); clavus open; claval vein CuP curved terminally at level of fusion with Pcu + A₁ (no such curve in *Foveopsis*); claval veins Pcu and A₁ fused in apical fourth of clavus length (claval veins fusion at apical third of clavus in *Foveopsis*); apical section of A₁, before fusion with Pcu close to the claval margin (A₂); fused veins CuP + Pcu + A₁ close and parallel to tornus, reaching posteroapical angle of tegmen. Hind wings with transverse veinlets *rp-mp* and *mp-cua* on line (veinlet *mp-cua* shifted slightly basad of veinlet *rp-mp* in *Foveopsis*). Metatibia, metatarsomere and metatarsomere widened apically (metatibia and first two metatarsomeres slender, weakly widened apically in *Foveopsis*); metatibial apical row with more than 10 teeth, with subapical setae.

Age and occurrence. Mid-Cretaceous amber from Kachin (terminal Albian/Cenomanian); Kachin State; Myanmar.

Lanlakawa changdaensis Luo, Jiang et Szwedo, sp. nov. (Figs. 1–4)

urn:lsid:zoobank.org:act:531780AB-E597-4A40-A082-065B70D2700F.

Etymology. The specific epithet is derived from 'changda', which is the abbreviation of 'Yangtze University' in Chinese.

Material. Holotype. Burmese amber, oval shape, 14.5 × 7 × 2 mm, weight 0.2 g. Specimen No. NIGP172208, deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing. Holotype inclusion incomplete: dorsal view of head partly obscured; dorsal view of pronotum, mesonotum and abdomen completely obscured by large bubbles; ventral view of abdomen hard to observe because of large bubbles, with ovipositor poorly preserved; right tegmen partly preserved; hind wing partly obscured; left mesoleg and metaleg partly covered with gas bubbles.

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

Diagnosis. Tegmen with contrasting pale and dark patterns; ScP + RA with two terminals; terminal ScP + RA₁ about half as long as terminal RA₂; cell C1 about twice as long as cell C5; cell C3 about as long as apical cells, about ¾ of cell C5 length; metatibio-tarsal formula 13(13): 10(10): 5(5).

Description. Adult. Body without wings 3.76 mm long, 0.91 mm wide, gradually converging posteriorly (Fig. 1). Head including compound eyes 1.01 mm long and 1.30 mm wide in ventral view (0.74 mm wide without compound eyes). Vertex short, posteriorly covered by the anterior margin of pronotum, visible portion 0.08 mm long, total length 0.62 mm; lateral edges carinate, slightly converging anteriorly. Frons subrectangular, almost as long as wide at mid line; median carina complete, distinct and protruded, slightly arched in lateral view; lateral margins of frons forming a marked keel; 17 large sensory pits present on each half of frons. The junction between frons and clypeus distinctly curved; lateral carinae present on postclypeus and extending to anteclypeus; total length of clypeus and rostrum 1.36 mm; apex of rostrum reaching metacoxae. Compound eyes large, bulging laterally. Lateral ocelli present and distinct, adjacent to the lateral carinae of frons; median one lacking. Antennal foveae elevated, scape very short, ring-like, about 0.04 mm long; pedicel subcylindrical, 0.15 mm long; sensory plaques large, denser in dorsal part of pedicel; flagellum whip-like, with base shifted slightly to ventral portion of apical apex; about 0.33 mm long (Fig. 2).

Pronotum and mesonotum damaged; anterior margin of pronotum arcuate.

Tegula small, partly obscured, merely carinate.

Tegmen (Fig. 3) about 3.2 times as long as wide (3.70 mm long and 1.16 mm wide), with contrasting pale and dark pattern; membrane finely granulate; tegmen widen beyond basal cell, costal margin shallowly sinuate subbasally, gibbous slightly proximad of mid-length, veins with tubercles; margin of tegmen from claval apex to distal end of costal area transversely wrinkled; clavus open, with fused claval veins reach 6/7^{ths} of tegmen length. Costal margin slightly widened at base, basal cell elongated, about 3.9 times as long as wide (0.43 mm long, 0.11 mm wide). Branches ScP + RA and RP leaving basal cell from the same point (terminal of basal cell), branch ScP + RA carinate, arcuately curved, subparallel to costal margin, forked at about 0.7 of tegmen length, reaching margin with 2 terminals; terminal ScP + RA₁ oblique, about half of length of terminal RA₂; branch RP single, slightly curved from basal to transverse veinlet *ir*, then strongly curved to margin; stems MP and

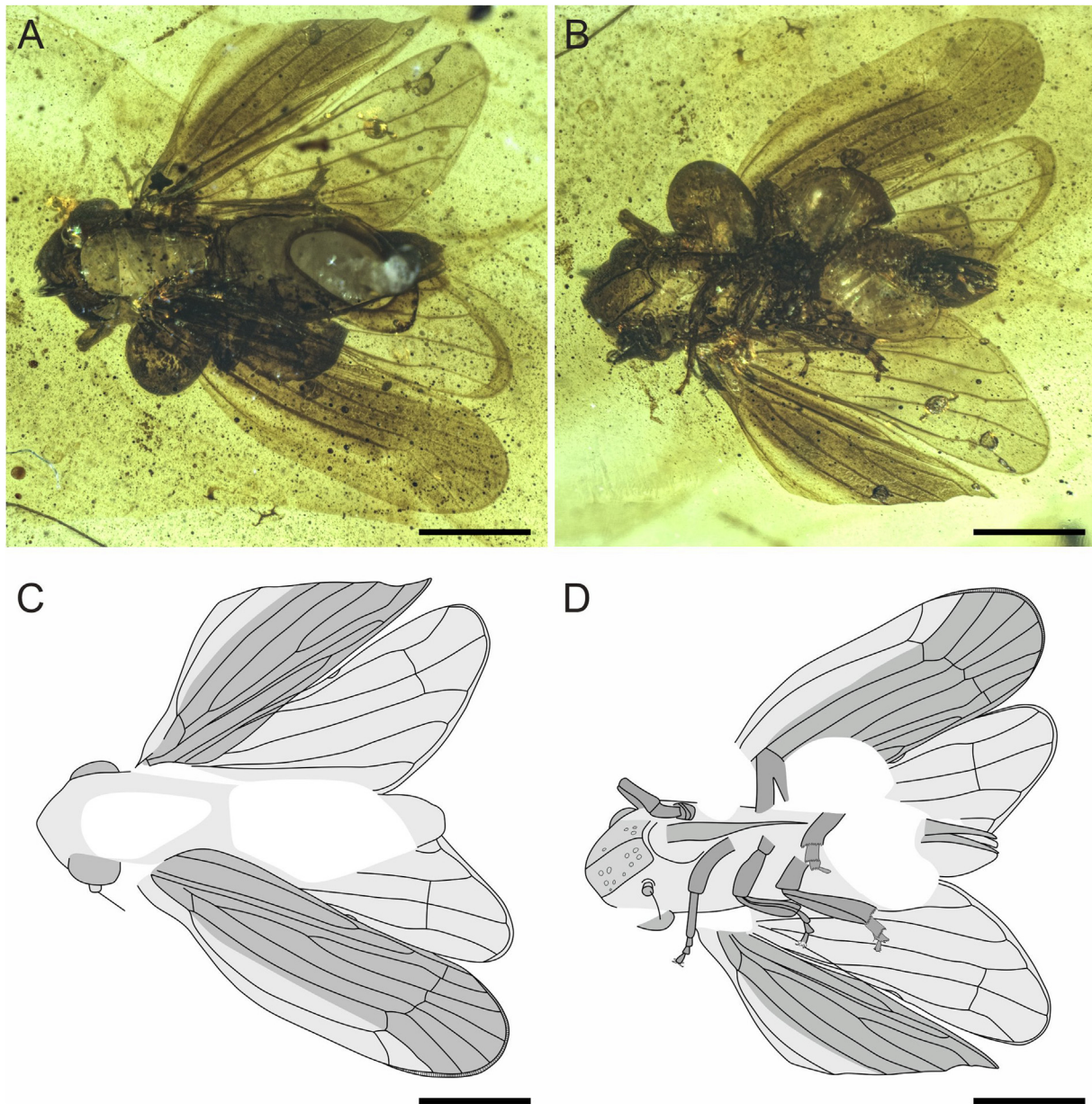


Fig. 1. Holotype of *Lanlakawa changdaensis* gen. et sp. nov. A, Photograph of dorsal view. B, Photograph of ventral view. C, Line drawing of dorsal view. D, Line drawing of ventral view. Scale bars = 1 mm.

CuA leaving basal cell with a short common stalk (about as long as basal cell), stem MP almost straight, subparallel to RP, forked at junction of veinlet *rp-mp* and stem MP_{3+4} , at about $3/4^{\text{th}}$ s of tegmen length, with 2 branches; branch MP_{1+2} almost straight, in line with stem MP, branch MP_{3+4} strongly bent at base mediad, until junction of MP_{3+4} and veinlet *mp-cua*, then almost straight; stem CuA straight, subparallel to claval margin, then forked at basal half of tegmen (obviously basad of claval veins junction), reaching margin with 2 terminals; branch CuA_1 slightly arched, branch CuA_2 almost straight, then arcuately curved at level of *icu* veinlet, to posteroapical angle, close to $CuP + Pcu + A_1$ junction to the margin point; CuP straight, then strongly arcuated distally, reaching $Pcu + A_1$ at about 0.7 of tegmen length; claval veins Pcu and A_1 fused slightly apical of half of tegmen length, in apical fourth of clavus length; common portion $Pcu + A_1$ distinctly shorter than free portion of Pcu ; fused

veins $CuP + Pcu + A_1$ subparallel and very close to tornus, reaching margin at posteroapical angle. Transverse veinlet *ir* slightly apical of the bifurcation of $ScP + RA$; veinlet *rp-mp* at the same level of the fork of stem MP; veinlet *mp-cua* little more apical than *rp-mp*; veinlet *icua* little more apical than *mp-cua*; veinlet *icu* between CuA_2 and $CuP + Pcu + A_1$ indistinctive, more basal than *icua*. Wing-coupling fore fold (WCFF) present, starting near the junction of A_1 and postclaval margin, subparallel to postclaval margin, fused to $Pcu + A_1$ at about 0.6 of tegmen length.

Hind wing (Fig. 3B, D) membranous, covered by very fine black granules, slightly wider than tegmen; wing-coupling lobe (WCL) about midlength; costal margin nearly straight before WCL, then slightly arched. All veins single, up to ambient vein; branch RP almost straight, then curved nearly to hind wing apex; stem MP near RP at base, then curved; stem CuA slightly sinuate; stem CuP

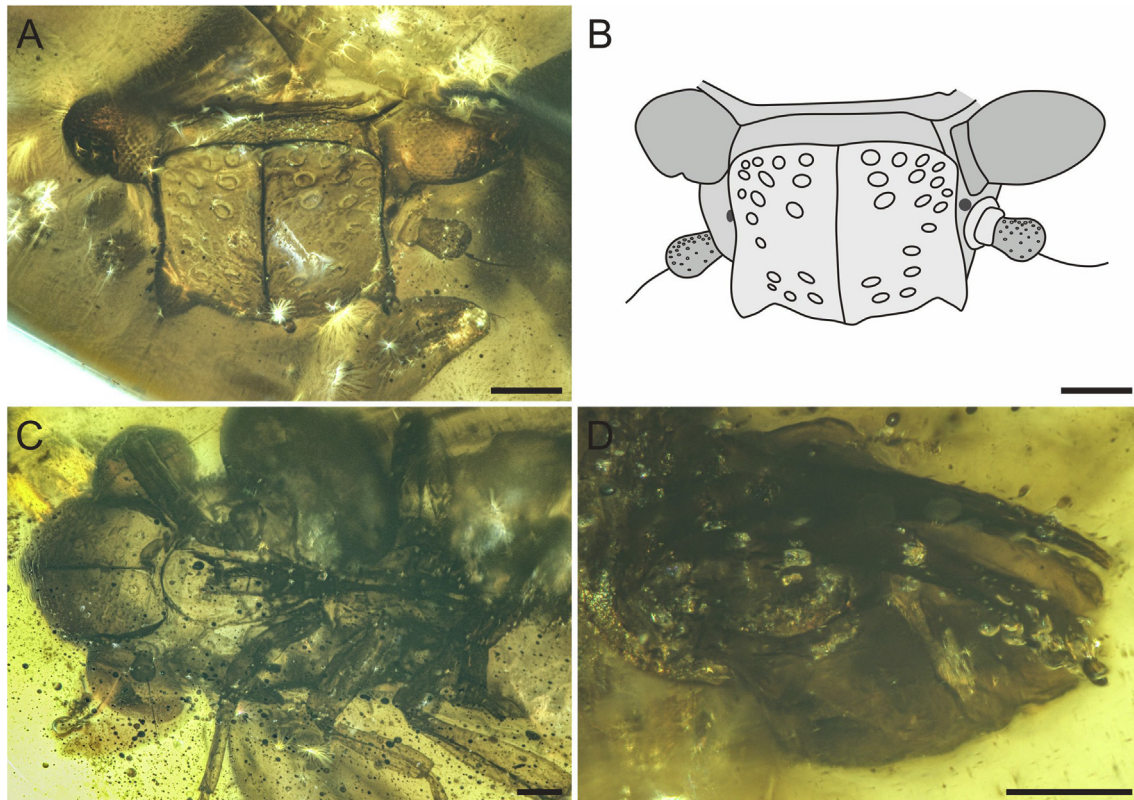


Fig. 2. Detailed photographs and line drawing of *Lanlakawa changdaensis* gen. et sp. nov. A, Head in frontal view. B, Line drawing of the head in frontal view. C, head and rostrum in ventral view. D, Ovipositor in ventral view. Scale bars = 0.2 mm.

slightly arched; stem Pcu nearly straight, close to CuP at base, then separated. Transverse veinlet *rp-mp* and *mp-cua* slightly sinuate, almost at the same level.

Proleg (Fig. 4A, B) 1.01 mm long, procoxa carinate; profore femur 0.43 mm long, carinate, curved, subcylindrical; protibia 0.41 mm long, margins carinate, covered with short setae, almost keeping the same width towards apex; length of fore tarsomeres: ≈ 0.12 mm, ≈ 0.08 mm, ≈ 0.10 mm, slightly widen towards apex; tarsal claws and arolium developed: tarsal claws narrow, arolium triangularly wide, with rounded apical margin. Mesoleg (Fig. 4A, C) 1.61 mm long, mesofemur 0.47 mm long, carinate, rectangular in cross section; mesotibia 0.58 mm long, margins carinate, covered with short setae, flattened and widened towards apex; length of mesotarsomeres: I 0.15 mm, II 0.11 mm, III 0.10 mm, widen towards apex, covered with short setae; tarsal claws and arolium developed: tarsal claws narrow, arolium semicircular, with rounded apical margin. Metaleg (Fig. 4A, D) slender, 1.84 mm long, with uniserial tibial and tarsal apical pectens; metafemur 0.66 mm long, carinate, rectangular in cross section, metatibia 0.87 mm long, carinate, with lateral sawtooth, covered with short setae, widened towards apex, with 13 apical setigerous teeth; metabasitarsomere 0.18 mm long, with 10 apical setigerous teeth, slightly widened towards apex; metamid tarsomere 0.12 mm long, with 5 apical setigerous teeth, slightly widened towards apex; metaapical tarsomere 0.09 mm long; tarsal claws and arolium developed: tarsal claws narrow, arolium semicircular, with rounded apical margin. Metatibio-tarsal formula 13(13): 10(10): 5(5).

Abdomen not clearly visible, only parts of ovipositor visible, ovipositor ensiform, of piercing-cutting type, curved dorsad, probably addressed to pygofer; gonapophyses VIII visible, gonoplacls merely shorter than gonapophyses VIII (Fig. 2D).

4. Discussion

Lanlakawa changdaensis gen. et sp. nov. can be referred to the family Perforissidae mainly based on the unique characters: the presence of sensory pits in adult, tegmina narrow with four main stems and little distal branching and apical pectens of hind tibia setigerous. The newly established genus *Lanlakawa* belongs to the subfamily Cixitettiginae based on that uniserial apical pectens on the metatibia, metabasitarsomere and metamid tarsomere with uniserial apical pectens. This new genus is separated from the other genera of Cixitettiginae by the combination of characters: tegmen widens beyond basal cell, costal margin slightly sinuate subbasally, gibbous slightly proximad of midlength, ScP + RA and RP leaving basal cell at same point (terminal of basal cell). Costal margin is widely angulate at base, slightly convex above the metepisternal carination, then delicately arcuate in *Aafrita* Szwedo et Azar, 2013; in *Aonikenkissus* Petrulevičius, Varela, Iglesias and Poiré, 2014 costal margin is convex but slightly concave at the basal half, gibbous about midlength; in *Cixitettix* Shcherbakov, 2007b tegmen is conspicuously widened beyond basal cell up to $2/3^{\text{rds}}$ of tegmen length, costal area not so narrow; in *Foveopsis* Shcherbakov, 2007b costal margin is gibbous slightly proximad of midlength; in *Iberofoveopsis* Peñalver et Szwedo, 2008 costal margin of tegmen is widened at base, gibbous in basal portion; in *Tsaganema* Shcherbakov, 2007b tegmen is not much widened beyond basal cell, costal area very narrow distally (Shcherbakov, 2007b; Peñalver and Szwedo, 2010; Szwedo et al., 2013; Petrulevičius et al., 2014; Zhang et al., 2017). Branches of ScP + RA and RP leaving basal cell at same point (terminal of basal cell) is unique autapomorphy of the new genus. In the other Cixitettiginae genera a short common stalk is present (the genera: *Aafrita*, *Foveopsis*, *Iberofoveopsis* and

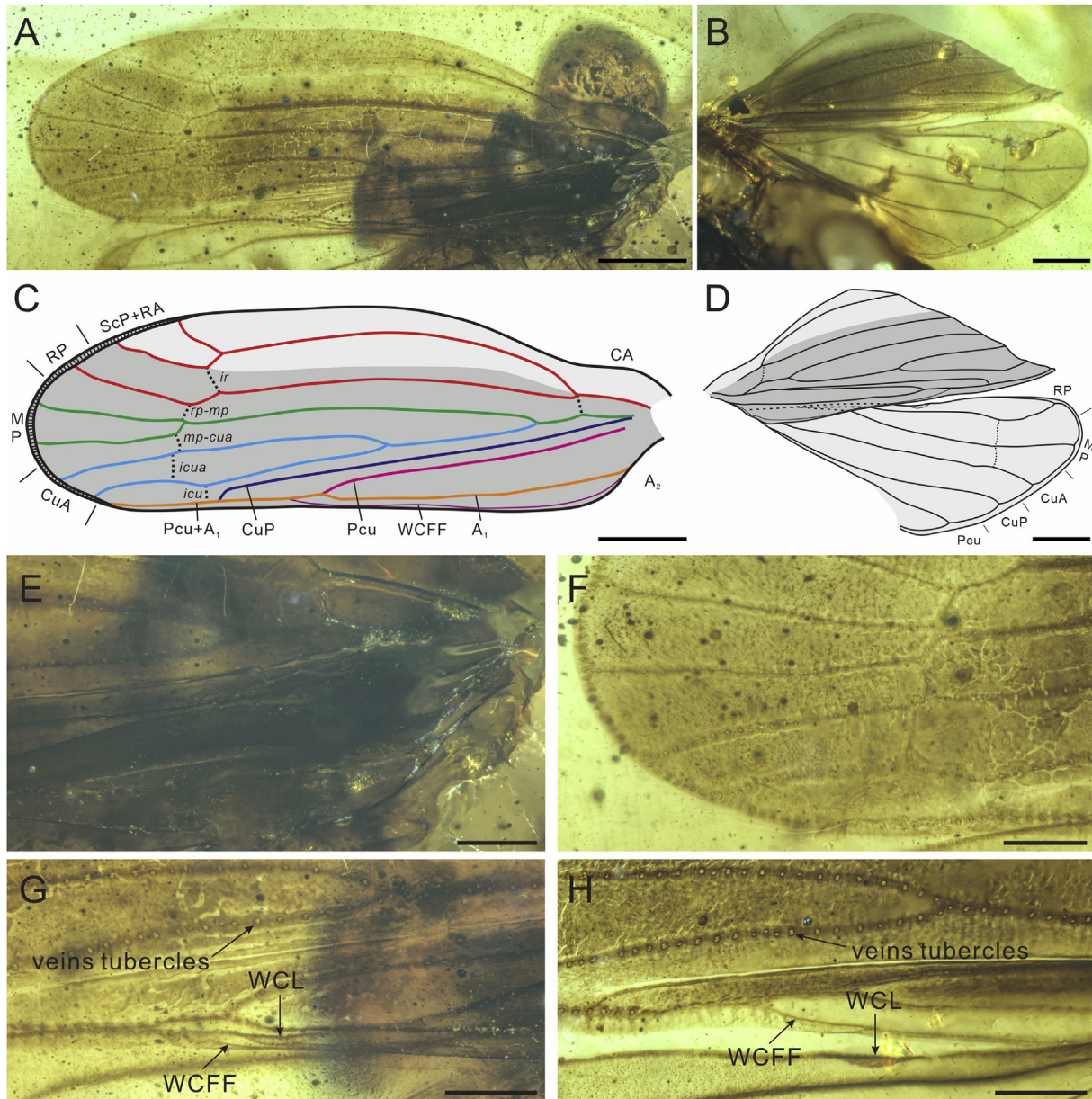


Fig. 3. Detailed photographs and line drawing of tegmen and hind wing of *Lanlakawa changdaensis* gen. et sp. nov. A, Left tegmen in dorsal view. B, Right tegmen and hind wing in dorsal view. C, Line drawing of left tegmen in dorsal view. D, Line drawing of right tegmen and hind wing in dorsal view. E, Detailed photographs of basal part of left tegmen in dorsal view. F, Detailed photographs of distal part of left tegmen in dorsal view. G, Wing-coupling apparatus of left tegmen and hind wing in dorsal view, coupled. H, Wing-coupling apparatus of right tegmen and hind wing in ventral view, uncoupled. Scale bars for A-D = 0.5 mm, E-H = 0.2 mm. Abbreviation: WCL, wing-coupling lobe; WCFF, wing-coupling fore fold.

Tsaganema) (Shcherbakov, 2007b; Peñalver and Szwed, 2010; Szwed et al., 2013; Zhang et al., 2017); from separate points of basal cell in *Aonikenkissus* (Petrulevičius et al., 2014) and long common stem of ScP + R is present in *Cixitettix* (Shcherbakov, 2007b). Only a single terminal of RP is present in *Aonikenkissus*, *Cixitettix*, *Foveopsis*, *Iberofoveopsis* (Shcherbakov, 2007b; Peñalver and Szwed, 2010; Petrulevičius et al., 2014). In *Tsaganema* RP is forked (but note variability in the latter – Shcherbakov, 2007b), and in *Aafrita* RP ends with 3 terminals (Szwed et al., 2013). Stem MP forked at level of nodal line is present in the new genus *Lanlakawa* gen. nov., but also in *Foveopsis* and *Iberofoveopsis* (Shcherbakov, 2007b; Peñalver and Szwed, 2010; Zhang et al., 2017); in the other genera of Cixitettiginae if MP is forked, then on membrane, apicad of nodal line (Shcherbakov, 2007b; Szwed et al., 2013; Petrulevičius et al., 2014).

Length of common stalk of MP and CuA also differs - it is about as long as basal cell in the new genus *Lanlakawa* gen. nov., and in *Aafrita* (Szwed et al., 2013), but longer than basal cell in *Cixitettix* and *Tsaganema* (Shcherbakov, 2007b) and slightly shorter in *Iberofoveopsis* (Peñalver and Szwed, 2010). Early bifurcation of stem CuA, distinctly basad of claval veins Pcu and A₁ junction, beside of the above described genus *Lanlakawa* gen. nov. is to be observed in the genera *Aafrita*, *Aonikenkissus*, *Foveopsis* and *Iberofoveopsis* (Shcherbakov, 2007b; Peñalver and Szwed, 2010; Petrulevičius et al., 2014). One of the characters of family Perforissidae is open clavus, with vein CuP weakened terminally and not reaching margin. Another feature of this family is close association of claval margin (vein A₂) with fused claval veins Pcu + A₁, and shifting of tornus (postclaval margin) anteriorad. In the newly described genus *Lanlakawa* gen. nov. tornus is very long, and the fusion of claval

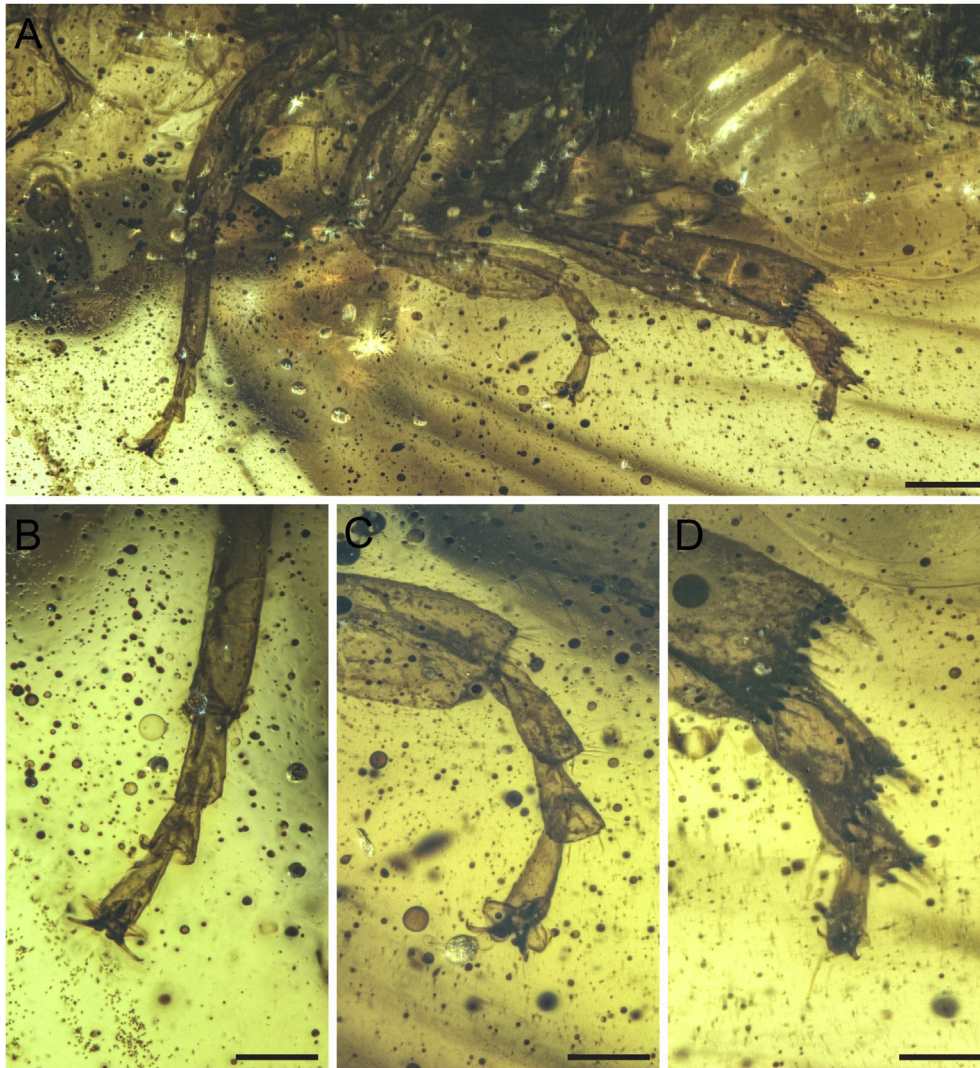


Fig. 4. Detailed photographs of legs of *Lanlakawa changdaensis* gen. et sp. nov. A, Photograph of legs in ventral view. B, Proleg. C, Mesoleg. D, Metaleg. Scale bars for A = 0.2 mm, B-D = 0.1 mm.

veins $Pcu + A_1$, and A_2 , and even fusion with CuP is to be observed, and the joined veins are very close to the tornus, with distinct appendix. The new genus is also distinctive presenting autapomorphic feature of metatibia, metabasitarsomere and metamid tarsomere widened apically. In *Cixitettix* metatibia and metatarsomers are less widened apically. Contrary to *Aafrita*, and similarly as in *Foveopsis*, *Cixitettix* and *Iberofoveopsis* the apical margins of metatibia and first two metatarsomers are not deeply incised. However, *Lanlakawa* gen. nov. clearly differs in number of apical teeth forming tibial pecten, composed of more than 10 teeth, while in the other genera (viz. *Aafrita*, *Cixitettix*, *Foveopsis* and *Iberofoveopsis*), this number is less than 10.

The retention of sensory pits is one of the significant characters in adult Perforissidae. Given that the Perforissidae (both adults and nymphs) were speculated to live on low herbaceous proangiosperms and/or angiosperms, and/or cheirolepidiacean gymnosperms (Shcherbakov, 2007b), this paedomorphic character may result from the transformation of the proangiosperms into angiosperms - angiospermization and habitat shifting of perforissid's host plants (Ponomarenko, 1998; Szwedo et al., 2013). The role of sensory pits as hygrometers was postulated by Šulc (1928), but it is still not supported by experimental evidence (Szwedo et al.,

2013; Zhang et al., 2017). Their other postulated function as exteroceptors or proprioceptors was already rejected, but their real function remains enigmatic (Bräunig et al., 2012), so we are still facing the apparent lack of knowledge concerning these sense organs and the understanding of the function of the sensory pits (Szwedo et al., 2013). In addition, according to Zhang et al. (2017), in adult Perforissidae, the abundance and distribution of paedomorphic sensory pits is variable, to some extent, so this character could not be considered as taxonomically very relevant.

Within the Hemiptera, the arrangement of the coupling parts in the wing-coupling apparatus are very variable and the structure of the coupling apparatus supplies characteristics of taxonomic value (d'Urso and Ippolito, 1994; d'Urso, 2002). Wing-coupling apparatus has been discovered in many genera in Perforissidae (*Aafrita*, *Cixitettix*, *Foveopsis* and *Perforissus*) (Shcherbakov, 2007b; Szwedo et al., 2013; Zhang et al., 2017), i.e. tegmen with a longitudinal wing-coupling fore fold (WCFF), hind wing with a short lobe (the wing coupling lobe - WCL) (Fig. 3G, H). The coupled tegmen and hind wings can operate together as a single aerofoil, hind wing gaining most anterior support from tegmen, in effect, forming an additional deformable area, and increasing flight versatility (Wootton, 1992; Zhang et al., 2017). Given that Perforissidae had

been widespread along both southern and northern shores of the Peri-Tethys Sea in a relatively short time (125 Ma to 85 Ma) (Szwedo et al., 2013), Zhang et al. (2017) presumed a higher migration ability may contribute to broad geographical distribution of Perforissidae in such a short period, like some delphacids (Sogawa, 2015), its broad geographical distribution may also associate with the moderately versatile flight capability and helpful atmospheric flow.

5. Conclusion

Lanlakawa changdaensis gen. et sp. nov. from the mid-Cretaceous Kachin amber is the ninth genus of extinct family Perforissidae and the sixth genus of subfamily Cixitettiginae. The new genus mainly differs from the five previously described genera in tegmen venation and the number of teeth in tibial pectens. The new genus enhances the state of knowledge of taxonomic diversity and morphological disparity of Perforissidae.

CRedit authorship contribution statement

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

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