Paradoxical derbid-like planthopper (Homoptera: Fulgoroidea) from Cretaceous Burmese amber

Парадоксальный, похожий на дерbid фулгороид (Homoptera: Fulgoroidea) из мелового бирманского янтаря

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ABSTRACT. Inoderbe rapunzel gen. et sp.n. from mid-Cretaceous Burmese amber, representing a new planthopper family Inoderbidae fam.n., shows modifications of the head and wings parallel to those in the higher Derbidae, combined with venation features of the primitive Jurassic family Fulgoridiidae, antennae enlarged as in some Delphacidae, and luxuriant wax plumege reminiscent of some Fulgoridae.

РЕЗЮМЕ. Inoderbe rapunzel gen. et sp.n. из среднемелового бирманского янтаря, представляет новое семейство фулгороидов Inoderbidae fam.n., демонстрирует преобразования головы и крыльев, параллельные таковым высших Derbidae, в сочетании с признаками жилкования примитивного юрского семейства Fulgoridiidae, усики, увеличенными как у некоторых Delphacidae, и пышным восковым плюмажем напоминающим некоторых Fulgoridae.

Mid-Cretaceous Burmese amber, formed about 100 Myr ago on an island in the tropical ocean between Gondwana and Laurasia [Westerweel et al., 2019], contains a rich insect fauna [Ross, 2021]. Among speciose Burmite Fulgoroidea, there are four endemic families — Dorytocidae, Yetkhatidae, Jubisentidae, Katlasidae [Emeljanov, Shcherbakov, 2018; Song et al., 2019, 2021; Luo et al., 2020; Shcherbakov, 2020], three widespread Cretaceous families — Perforissidae, Mimarachidae, Neazoniidae [Shcherbakov, 2007; Fu, Huang, 2021; Olmi et al., 2021], three extant families — Cixiidae, Achilidae, Derbidae [Shcherbakov, 2000; Szwedo, 2004; Emeljanov, Shcherbakov, 2020], and a few genera unassigned to the family [Luo et al., 2021]. A new find in Burmese amber, a unique planthopper showing a peculiar mixture of primitive and derived characters, is described below as a new family. The type specimen is deposited at Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera and z-stacked with Helicon Focus 7.0.

Superfamily Fulgoroidea Latreille, 1807
Family Inoderbidae Shcherbakov et Emeljanov, fam.n.

TYPE GENUS. Inoderbe Shcherbakov et Emeljanov, gen.n.

DIAGNOSIS. Rather small planthoppers with membranous wings not folded over abdomen in repose, held laterally, and possibly rolling longitudinally. Tegmina and hindwings narrowed to base, hindwings small. Body and appendages covered with filamentous wax, dorsum with numerous wax plates (in females only?) producing copious wax strands, especially long on posterior abdomen. Tegmina: Precostal area wide, crossed by veinlets, not continued with apical cell series. Basal cell much elongated. Stigmal cell with submarginal pterostigma. CuA bifurcating close to basal cell, with 3 main branches, and terminations as numerous as those of R and M combined. Few crossveins in one gradate series. Clavus with scutellar angle subdued and shifted distally. Hindwings much smaller than tegmina, with small anal lobe; costal margin proximally with series of hamuli. Head compressed laterally, coryphe and metope with foliaceous lateral carinae, metope with small horn at midline; eyepeus almost foliaceous, bicarinate; high preantennal carina with short subantennal branch. Antennae with scape and pedicel much elongate, compressed. Rostrum reaching beyond hind coxae.

How to cite this article: Shcherbakov D.E., Emeljanov A.F. 2021. Paradoxical derbid-like planthopper (Homoptera: Fulgoroidea) from Cretaceous Burmese amber // Russian Entomol. J. Vol.30. No.2. P.135–139. doi: 10.15298/rusentj.30.2.03
Inoderbe Shcherbakov et Emeljanov, gen.n.

TYPE SPECIES. *I. rapunzel* Shcherbakov et Emeljanov, sp.n.

DIAGNOSIS. As for family.

COMPOSITION. Type species.

ETYMOLOGY. From Russian *ушо*, different, other, alien) and *Derbe*; gender feminine.

**Inoderbe rapunzel** Shcherbakov et Emeljanov, sp.n.

Figs 1–14.

MATERIAL. Holotype female PIN 5608/204 (head apex and fore knee polished away, right antenna missing) — Burmese amber, Hukawng Valley, Kachin State, Myanmar; mid-Cretaceous (Albian–Cenomanian).

DESCRIPTION. Tegmen 6.5 mm long, 2.4 mm wide, elongate (2.7:1); narrow proximally, widest at nodus, acutely rounded at apex (at M terminations); anterior margin straight between base and nodus. Precostal area moderately wide, wider than costal area, with 5 irregularly spaced, slightly oblique veinlets; C joining dSc at nodus; vein running along anterior margin separated from it by narrow marginal membrane. Concave base of Sc (bSc) visible close to R+M base. Basal cell long and narrow, 1/5 tegmen length. Stigmal cell with lanceolate pterostigma along dSc and RA, not reaching outer and distal edges of the cell. R+M forked before arculus; R bifurcated at 0.3 tegmen length, fork narrow; RP fork and crossvein *ir* distal (in one tegmen RP 3-branched, with small extra fork). M bifurcated just beyond nodal level, 3-branched, pectinate backwards. CuA bifurcated just beyond arculus, CuA1 with distal fork, CuA2 forked at 1/3 tegmen length, pectinate forwards, with 4 terminations. 4–5 crossveins (*ir*, *r, m, m-cu, 1–2 icua*) in oblique gradeate series. CuP arched forwards. Claval veins united distally; common claval vein extremely short, entering commissural margin near acute claval apex; narrow marginal membrane before and just beyond claval apex. Marginal vein with dense erect hairs on both sides of tegmen, other main veins with sparse hairs. Membrane slightly infuscate, with pale fuscous pterostigma and small spots on veins and their terminations. Hindwing hyaline, 3.8 mm long, 1.6 mm wide, x1.7 shorter than tegmen. Costal margin with about dozen long crooked hamuli proximally, sinuate near midpoint, with long coupling lobe bearing row of spinules; R against the lobe in hindwing and part of commissural margin in tegmen with similar spinules. R forked near coupling lobe; RA short; RP simple, reaching wing apex. M with distal fork. CuA forked at 0.3 wing length. Two crossveins (*r-m and more proximal m-cu*). Medial fold running close to CuA–CuA1. CuP, Pcu and 1A simple; claval fold running from Pcu towards CuP. Anal area small, wing base narrow. Body 5.8 mm long (as preserved), slender, thorax and posterior abdomen 1.2 mm wide. Head narrow, eyes projecting (left eye partly preserved); coryphe (only posterior corner preserved) depressed, with lateral margins high and nearly straight, foliaceous lateral carinae, narrowed before clypeus; clypeus nearly foliaceous, projecting trapezoidal in profile, with two high, undulating, close-set submedian carinae. Genae bearing high preantennal carina with short subantennal branch. Scape long, flattened, curved; pedicel long, reaching tegmen base at rest, in distal 2/5 widened and covered with minute rounded sensory organs; base of flagellum small. Rostrum about 2.3 mm long, directed obliquely ventrally, with last segment about 1/4 of its length. Pronotum long, tectiform, carinate along midline, with broadly rounded side lobes covered with wax hair. Mesoscutum rounded pentagonal, flat, ecarinate, with pair of L-shaped wax areas (each with stem following course of lateral discal area, and wide transverse arm) and deep depressions at sides of posterior margin not forming scutellar grooves. Mesoscutum with pair of similar smaller wax areas. Metascutum diamond-shaped. Legs long, slender. Femora and outer sides of tibiae and 1st hind tarsomeres with long and very long erect hairs (much longer than leg diameter); inner side of fore and mid tibiae and 1st hind tarsomeres with short oblique setae; fore and mid tibiae and 1st and 2nd tarsomeres with ventroapical pectens of stout setae. Fore and mid tarsi long, 2nd tarsomeres longer than 1st, 3rd slightly longer than 1st plus 2nd. Hind tibia 2.0 mm long, without lateral spines, tibia and first two tarsomeres strongly swollen-tailed at apices, 1st tarsomere longer than 2nd plus 3rd, tibia with 3–3 broad asetigerous teeth, 1st tarsomere with 8, 2nd with 9 teeth, mostly with dark acutellae, 1(2) outermost teeth at each side asetigerous. Claws long, proximally stout with 2 pairs of pectinate backwards.

Figs 1–12. Inoderbe rapunzel gen. et sp.n., Burmite, Cretaceous, holotype: 1 — habitus, laterodorsal; 2 — habitus, lateroventral; 3 — head, anterolateral (arrow, preantennal carina); 4 — forebody, lateral; 5 — thorax and posterior abdomen, laterodorsal; 6 — left antenna, wings are not so small. Apical cell series, but in the latter family the basal cell is not enlarged, and when the carina near the antenna is developed, it is subantenal), not preantenal. Similar to the Jurassic family Fulgoridiidae in the early forked CuA with three main branches in the tegmen, and to the Early Jurassic genus *Eofulgoridium* Martynov, 1937 of this family in the wide precostal area crossed by veinlets and not continued with the apical cell series, but in the latter family the basal cell is not elongated, the submarginal pterostigma is absent, and hindwings are not so small.
strong setae, apically crooked; arolium broad. Abdomen long, slender, widest about 1/4 its length; anterior tergites short, raised, inverted V-shaped, separated by membranous spaces allowing to lift up posterior abdomen with wax tufts. Last pregenital tergite with small subtriangular side lobes. Ovipositor short, with two apposed pairs of subulate inner valvae and one dorsal, forceps-like pair of somewhat longer, acute outer valvae. Anal tube long, narrow basally, with crescent-shaped lateral lobes distally. Nearly all body parts, including scape and proximal pedicel, tegulae, wings, and legs up to tarsi, sparsely or densely covered with milky whitish wax filaments of various lengths. Distinct wax plates on mesoscutum and mesopostnotum (most of wax apparently removed from thorax) and abdominal tergites, those on middle tergites forming rows of 8 or 10 small rounded plates. Wax strands on posterior abdomen up to 3.6 mm long, slightly curly, white to golden reddish, forming somewhat tripartite plumage. Body dark brown, extremities nearly black.

ETYMOLOGY. *Rapunzel*, fairytale maiden with very long golden hair, imprisoned in a tower; noun in apposition.

The new planthopper bears superficial resemblance to some higher groups of the extant family Derbidae. The earliest, very primitive derbids still similar to Achilidae were recently described from Burmese amber [Emeljanov, Schcherbakov, 2020], whereas the higher tribes of Derbidae were recently described from Burmese amber [Emeljanov, Wilson, 1985; Lucchi, Mazzoni, 2004; Emeljanov, 2009]. The head of the new planthopper is derbid-like – compressed laterally, with foliaceous lateral carinae of the coryphe and metope, almost foliaceous clypeus with two high submedian carinae, antennae with both scape and pedicel much elongated, and the high preantennal carina with a low subantennal branch. However, in known Derbidae the scape is never enlarged, and when the carina or lobe near the antenna is developed, it is subantennal, not preantennal. Hypertrophy of the pedicel, and development of subantennal lobes and high lateral, posterior, or inferior carinae on the pronotum (sometimes forming a kind of funnel around the pedicel) in higher derbids presumably improve sensory abilities of their antennae [Emeljanov, 1996]. The new genus is also dissimilar to Derbidae in other basic characters (see below).

The antennae of the fossil are hypertrophied in a way similar to some primitive Delphacidae (Ugopinae, Asiracinae, Vizcayini), i.e. both scape and pedicel are elongated (in Derbidae only the pedicel). However, the new genus lacks any diagnostic characters of Delphacidae.

The tegmina of the new fossil show the CuA forked proximally with three main branches and as many terminations as on R and M, similar to the Jurassic family Fulgorididae, and also the wide precostal area crossed by veinlets and not continued into the apical cell series, like in the Early Jurassic genus of this family, *Eofulgoridium* Martynov, 1937. In the extant planthopper groups, the CuA is not so richly branched compared to R plus M, and the precostal area, if wide and cross-veined, is continued into the apical cell series. However, in Fulgorididae the basal cell is not elongated, the submarginal pterostigma is absent, and hindwings are not so small. *Inoderbe gen.n.* is apparently the first planthopper with a wide cross-veined precostal area described from the Cretaceous.

The rich waxy plumage of the new genus somewhat resembles those of large planthoppers, especially Fulgoridae [O’Brien, 2002]. The wax coating of Homoptera probably protects them from rain, UV radiation and predators and prevents contamination with honeydew. Females are more likely to produce large quantities of wax than males, often smearing wax over egg deposition sites, and in adult Fulgoroidea wax plates are developed only in females [O’Brien, Wilson, 1985; Lucchi, Mazzoni, 2004; Emeljanov, 2009]. Some plants, invertebrates and frogs preserved in Burmese amber are indicative of the presence of humid tropical forests [Xing et al., 2018; Rosa, Melo, 2021]. The derbid-like wing proportions and resting position and rich wax garment of the new genus can be considered anti-wetting adaptations. The same is true of the

**Discussion**

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longitudinal wing rolling, postulated to be a wing-strengthening device for adaptation to life in rain forests [O’Brien, 1982].

The new genus showing a previously unknown combination of characters is separated into a new family, which appears to be descended from Fulgoroidae. It is one more family of the primitive group related to fulgor-ridiids, or pre-cixioid group [Shcherbakov, 2007], which also includes Perforisididae, Jubi- sietidae, Mimarach- nidae, Dorytocidae, Neazoniidae, with deeply forked and/or richly branched CuA in the tegmen, and often setigerous hind tibial pectens.

Several characters of Inoderidae foreshadow traits that are fully developed in Derbidae. Inoderids, which were later replaced by true derbids, can be seen as an example of inadaptive group (the term of Vladimir Kovalevsky [1873–1874]).

Acknowledgements. We are grateful to Alexey Bashkuev for bringing this fossil to our attention, and to Roman Rakitov (both PIN) for valuable comments. The study is performed in the framework of the Russian State Research project no. AAAA-A19-119020690101-6.

Competing interests. The authors declare no competing interests.

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