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A new *Lapicixius* planthopper species (Fulgoromorpha: Lalacidae) from the Lower Cretaceous Yixian Formation of northeastern China

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Abstract

Lapicixius yixianensis **sp. nov.**, the second species of this genus, is described and illustrated on the basis of an almost complete specimen from the Lower Cretaceous Yixian Formation of Liaoning Province, China. This new representative of the extinct hemipteran family Lalacidae increases the taxonomic diversity of the group during the Cretaceous. The affinities of the new fossil with described lalacid planthoppers and the validity of Lalacidae are discussed.

Key words: Insecta, Hemiptera, Fulgoroidea, cixiid-planthopper group, fossil record, Cretaceous

Introduction

Lalacidae Hamilton, 1990 is an extinct planthopper family recorded from the Cretaceous of China and Brazil, currently encompassing 20 species attributed to 11 genera (Hamilton 1990; Ren *et al.* 1998; Szwedo *et al.* 2004; Bucher *et al.* 2024). Eight of these genera were assigned to three subfamilies: Ancoralinae Hamilton, 1990; Protodelphacinae Hamilton, 1990, and Lalacinae Hamilton, 1990. Three genera, *Yanducixius* Ren, Lu & Ji, 1995, *Lapicixius* Ren, Yin & Dou, 1998, and *Cretocixius* Zhang, 2002, were originally attributed to Cixiidae and later tentatively transferred to Lalacidae, but remain unattributed within the subfamilial classification of Lalacidae (Szwedo *et al.* 2004). Lalacidae were recently placed within the Delphacoidea Leach, 1815 with Cixiidae Spinola, 1839 and Delphacidae Leach, 1815 (Bourgoin & Szwedo 2023), but the original diagnosis of Hamilton (1990) for the family is not sufficient to discriminate Lalacidae from other cixiid-groups, which advocates for a broader revision of extant and extinct cixiid lineages.

The temporal duration of the family was short, as it went extinct during the Angiosperm Terrestrial Revolution, coinciding with the extinction of seven other planthopper families, marking a crucial turnover for Fulgoromorpha Evans, 1946 (Boderau *et al.* 2025a). Therefore, the better understanding of planthopper diversification requires further study of Cretaceous fossils. While the mid-Cretaceous is well-documented for the family with the Kachin amber (Chen 2022), the Early Cretaceous records are scarcer. Major insights into the Early Cretaceous evolution of insects are provided by the Yixian Formation of the Jehol Biota (Zhang *et al.* 2010). While heteropteran and cicadomorph insects are well described from the Yixian Formation, planthoppers are represented only by Lalacidae with the genus *Lapicixius*.

Herein, we report a second species attributed to the genus *Lapicixius*, *Lapicixius yixianensis* **sp. nov.**, from the Yixian Formation of Huangbanjigou, Liaoning Province, China. The affinities of *L. yixianensis* with the other lalacid species, as well as the systematics of the family, are discussed.

Material and methods

The studied specimen (NIGP209638), preserved as part and counterpart, was collected from the yellowish tuff of the Lower Cretaceous Yixian Formation at Huangbanjigou, Shangyuan Township, Beipiao City, Liaoning Province, northeastern China. The specimen was prepared using a sharp blade and photographed using a Zeiss Discovery V20 microscope and a Keyence VHX-6000 digital microscope. The line drawing was drafted with CorelDRAW Graphics Suite 2024. The type specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

The systematic framework follows Szwedo (2018), and wing venation terminology follows Nel *et al.* (2012) and Bourgoin *et al.* (2015), as adapted by Schubnel *et al.* (2019) for the postcubitus vein. Venation abbreviations are as follows: C costa; ScP subcostal posterior; RA₁ first branch of the radius anterior; RA₂ second branch of the radius anterior; RP radius posterior; M media; CuA₁ first branch of cubitus anterior; CuA₂ second branch of cubitus anterior; CuP cubitus posterior; PCu postcubitus; A₁ first anal vein. Crossveins are written in lowercase italics, e.g. *cua-cup* is the crossvein between CuA and CuP.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1946

Superfamily Delphacoidea Leach, 1815

Family Lalacidae Hamilton, 1990

Genus *Lapicixius* Ren, Yin & Dou, 1998

Type species. *Lapicixius decorus* Ren, Yin & Dou, 1998

***Lapicixius yixianensis* sp. nov.**

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(Fig. 1)

Type material. Holotype, NIGP209638, complete specimen preserved as part and counterpart; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Etymology. The specific epithet is derived from the Yixian Formation, from which the type specimen was collected.

Diagnosis. Differences from the type species as follows: vertex with a small elevation on its median carina; tegmen bearing dark-coloured patches over entire surface; three *rp-m* crossveins present, with the first one distal to the first forking of M; *icua* basad to the forking of CuA₁; and six *cup-pcu* crossveins present.

Type locality and horizon. Huangbanjigou, Shangyuan Township, Beipiao City, Liaoning Province, China; Yixian Formation; Lower Cretaceous.

Description. Adult. Macropterous. Female. Body length about 9.0 mm. Head narrower than pronotum; eyes large; vertex broad with a small elevation on its median carina; frons slightly broader than longer; postclypeus slightly longer than frons; rostrum long, reaching base of metacoxae; antennae poorly preserved. Pronotum with angulate margins, narrow but wider than mesoscutellum; mesoscutellum developed and triangular; metanotum small and triangular. Hind legs partially preserved, with hind tibia long and narrow; tarsus with basitarsomere about three times length of second tarsomere, basal and second tarsomeres armed with a row of 18–19 apical teeth. Tegmen about 7.6 mm long, 2.2 mm in maximum width across clavus apex, exceeding abdominal apex; pterostigma well-developed; ScP+R long, forking into ScP+RA and RP opposite point of fusion between PCu with A₁, slightly after first-level forking of CuA; RA with at least three terminals; RP stem long, about 0.75 length of ScP+RA stem, pectinate with five terminals; *ir* crossvein preserved between last terminal of RA and a point slightly before forking of RP, *ir* as long as first *rp-m*; three *rp-m* crossveins, first one apicad to first forking of M, other two very close to each other; M stem long, forking well distad level base of ScP+RA and CuA fork, nearly at level of clavus apex; M with two main branches forking into at least six terminals; three *im* crossveins preserved, subequal in length; CuA with first anterior branch CuA₁ slightly curved and longer than CuA₂, both with two terminals; *icua* short and inclined between CuA₁ and CuA_{2a}; PCu free portion slightly sinuous, fused with A₁ in apical third of clavus; PCu+A₁ short and reaching anal margin at mid-length of tegmen; six *cup-pcu* crossveins, with two anterior to fusion between PCu and A₁; tegmen irregularly covered by numerous brown patches of variable lengths and widths. Abdomen with nine preserved segments, ovipositor short, about 1.1 mm long; with lateral margins curved.

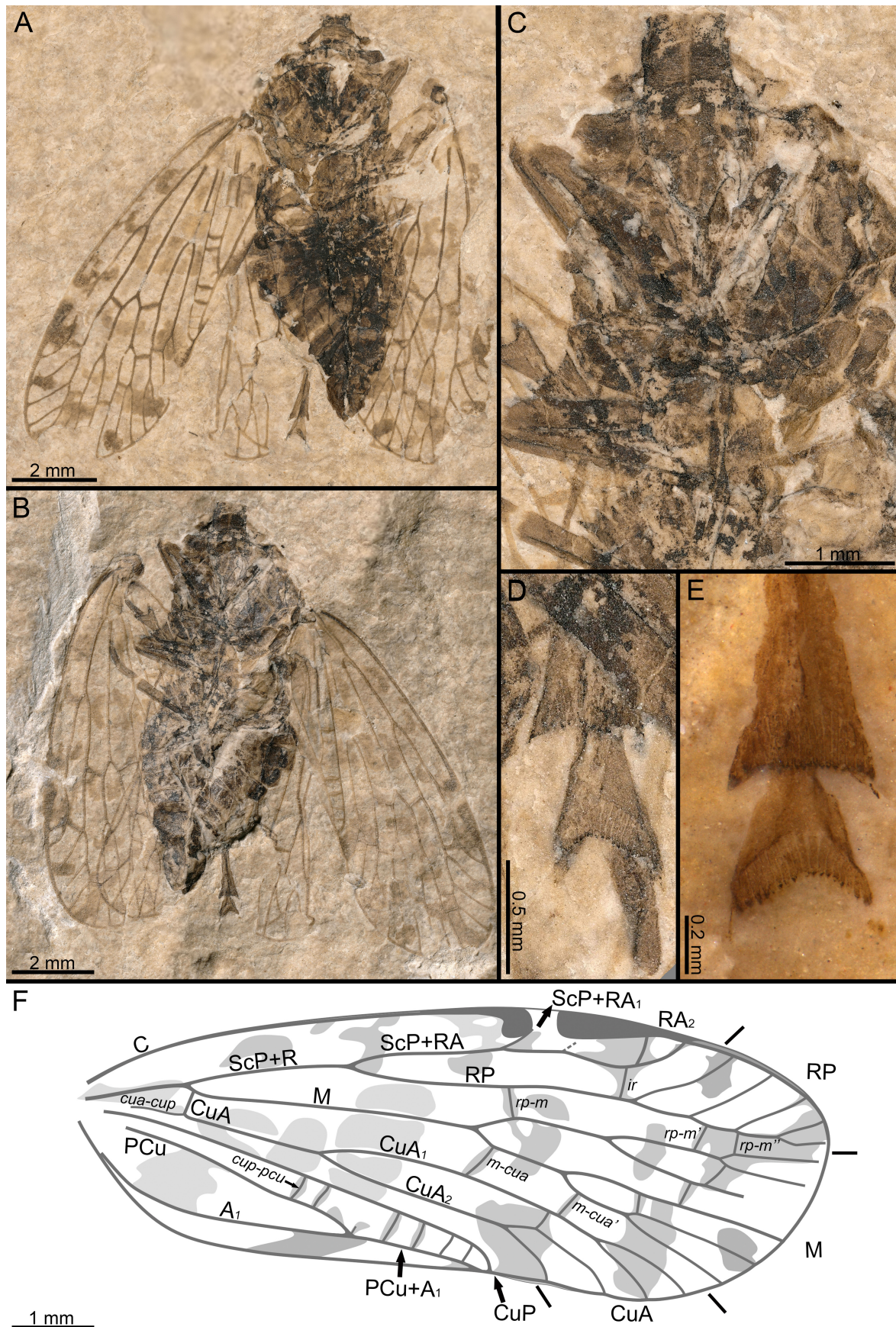


Figure 1. *Lopicixius yixianensis* sp. nov., holotype NIGP209638 (Fulgoromorpha: Lalacidae). **A**, General habitus, part. **B**, General habitus, counterpart. **C**, Head and thorax details, counterpart. **D**, **E**, Hind tarsi details. **F**, Tegmen venation reconstruction. **E**, was photographed moistened with 70% ethanol.

Discussion

The new fossil is attributable to the Fulgoromorpha based on its tegmen with very short *cua-cup*, small cells occurring mostly in the apical part of the tegmen, numerous crossveins in the distal part of the tegmen, and a large media sector (Shcherbakov 1984; Bucher *et al.* 2024). It fits into the superfamily ‘Fulgoroidea Latreille, 1807’ (Fulgoromorpha in Bourgoïn & Szwedo 2023) based on its ambient vein being transversely wrinkled, A_1 passing into PCu with PCu bent at the point of entry of A_1 (Shcherbakov 1981).

Based on the identification key of the extant fulgoromorphan families of Shcherbakov (1981) and the following combination of characters, the specimen would fall into the Cixiidae (Delphacoidea after Bourgoïn & Szwedo 2023): fully winged; clavus open; PCu+ A_1 passing into the anal margin at considerable distance from the clavus apex; precostal field not narrow; all supplementary crossveins forming part of the outer gradate crossveins row; R and CuA branching far before nodal crossveins, these being at the level of the clavus apex (cell between CuA₁ and CuA₂ very long); costal field developed from the wing base, not very broad; nodal row of crossveins undeveloped, all supplementary crossveins gathered in apical row; basal cell developed; *cup-pcu* located basally; clavus shorter; wing dilating at the level of the clavus apex and not constricted immediately behind it; pterostigma present and formed by dilation of the marginal vein, with a distinct border of its own; nodal *r-m* not distal to nodal *m-cu* and transverse *cup-pcu* developed.

Furthermore, Bourgoïn & Szwedo (2023) also proposed the following diagnostic features for the Delphacoidea, which are shared with our new fossil: no distinct costal area; ScP separating from RA distally; common stem ScP+R rather long; RA and RP usually respectively with less than three and five terminals; M with more than two main branches, usually four or more; median cell larger than cubital cell; CuA forking first at the same level or after RP and PCu+ A_1 node levels and only once before the ‘nodal line’ level; lateral and median carinae on clypeus usually present; first metatarsomere elongate; second metatarsomere with a row of apical teeth; and female genitalia of ‘orthopteroid’ type with ‘ensiform’ ovipositor.

Delphacoidea encompass Cixiidae, Delphacidae, and Lalacidae. Hamilton (1990) proposed diagnostic features for Lalacidae shared with the fossil: head short with intermediate carina; ambient vein narrow; appendix broad and wrinkled with striations; pterostigma developed and formed by thickening of the costal margin; appendix narrow on hind wings; long *r-m* crossveins; hind leg with pectens bearing movable setae; ovipositor short, strongly curved, sword-shaped with rounded tip.

Among Lalacidae, the fossil can be discriminated from Protodelphacinae species based on its short stigmal area; longitudinal veins with numerous branches with apical crossveins not aligned.

The fossil differs from the genus *Ancorale* Hamilton, 1990 based on its less convex longitudinal veins, the much longer M-stem and the significantly longer body size of our new fossil (more than 6.0 mm). Furthermore, our fossil differs from the other Ancoralinae genus, *Kinnarocixius* Hamilton, 1990, by the following combination of characters: its RP with five terminals; three *rp-m* crossveins; M_1 and M_2 not separated by a small *im*, with a *rp-m* crossvein reaching M_1 at the same position; M with six terminals; CuA forking into CuA₁ and CuA₂, which themselves forking again before reaching the anal margin of the wing.

Five genera have been assigned to the Lalacinae. Our fossil differs from *Lalax* Hamilton, 1990 based on the presence of four terminals of RP, the lack of a small crossvein between the two first terminals of RP, the presence of crossvein between RA₂ and RP; it has the same pattern of forking of M but the subapical cell between $M_{1,2}$ and $M_{3,5}$ is much larger in *Lalax*. RP is five-branched in *Patulopes* Hamilton, 1990, the M-stem is much smaller in this genus, and M has only three terminals and CuA₁ and CuA₂ are forked at the same position, unlike our new fossil. The new fossil strongly differs from *Carpopodus* Hamilton, 1990, based on the pectinate CuA₁ and the pattern of M with M_3 and $M_{4,5}$ not forked in the genus. The new fossil resembles *Psestocixius* Hamilton, 1990 and *Vulcanetoia* Allsopp, 2024 in the pattern of CuA forking, but they strongly differ from the new fossil in having a much longer ScP+R stem; a well-separated CuA₁ and CuA₂ forking before reaching the apex of the forewing, the presence of three *r-m* crossveins and M with six terminals. Thus, the fossil differs from *Psestocixius* that presents a typical pattern of apical cubital cells, aligned and subparallel to each other, and by $M_{3,5}$ with two terminals, vs. three in our new fossil. Lastly, *Vulcanetoia* has four cubital veins meeting anal margin of tegmen nearly vertically.

Three genera of Lalacidae are not placed within any Lalacidae subfamily, *Cretocixius* resembles *Psestocixius* and *Vulcanetoia* in the pattern of CuA forking; it strongly differs from the new fossil in having ScP+R stem much longer; a well-separated CuA₁ and CuA₂ forking before reaching the apex of the forewing, the presence of three *r-m* crossveins and M with six terminals. The new fossil differs from *Yanducixius* based on its RP pectinate with only five terminals; $M_{3,5}$ not pectinate without any *im* crossveins (in *Yanducixius yihii* Ren, Lu & Guo, 1995). The venation of the new

fossil resembles that of *Lapicixius decorus* Ren, Yin & Dou, 1998, with RP pectinate with more than four terminals; the pattern of forking of median vein; CuA forked into CuA₁ and CuA₂, each with two terminals; and the numerous *cup-pcu* crossveins (more than one) which is reported only in *Lapicixius*. The fossil exhibits only small differences with *Lapicixius decorus* such as the wing colour patterning; three *rp-m* crossveins; the first *rp-m* crossvein more distal than the first-level of forking of M; six *cup-pcu* crossveins and the shape of the median carina with a small elevation (Ren *et al.* 1998). These features are sufficient to erect a new species of *Lapicixius*.

Lalacidae systematics remains unclear. The original diagnosis from Hamilton (1990) is insufficient to discriminate it from Delphacidae and Cixiidae. Regarding wing venation, Lalacidae tend to have more branches of RP, M, and CuA and longer crossveins between radial and medial veins. Furthermore, the multi-forking of CuA is rather a lalacid than a cixiid character, but it is also present, for instance, in the recently described cixiid from Lower Cretaceous Jinju Formation, *Jinjucixius fui* Boderau, Nam, Jouault & Nel, 2025 (Boderau *et al.* 2025b). The venation complexity of the longitudinal veins appears not to be a reliable character for discriminating Lalacidae from Cixiidae. The hindlegs with pectens bearing movable setae and the short ovipositor being strongly curved and sword-shaped with rounded tip, appear to be more reliable, as they are present only in Lalacidae (Hamilton, 1990). However, while new delimitations of cixiid groups have been proposed by Bourgoïn & Szwedó (2022, 2023), phylogenetic analyses are required to assess the validity of these groups and provide clear synapomorphies of the Lalacidae and other cixiid lineages. Fossil evidence of new early cixiid planthoppers during the Cretaceous and possibly since the Jurassic (Deng *et al.* 2025) will be crucial to untangle the morphological divergence of these groups.

Conclusion

We documented a new species of *Lapicixius* from the Yixian Formation from a new locality. This discovery suggests that the planthoppers' diversity might be higher than suspected from the Yixian Formation and supports more intensive investigations to better clarify the diversification of Fulgoromorpha during the early Cretaceous, a linchpin of their evolutionary history.

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