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First record of Palaeontinidae (Hemiptera: Cicadomorpha) from the Jiufotang Formation illustrates entomofaunal continuity of the Jehol Biota

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Abstract

The first occurrence of the extinct cicadomorphan family Palaeontinidae from the Jiufotang Formation of China is reported based on a specimen assigned to *Ilerdocossus* cf. *fengningensis.* The genus *Ilerdocossus* Gomez Pallerola, 1984 is well known from the underlying Yixian Formation of northern China (Hebei, Liaoning provinces, and Inner Mongolia), as well as the Caliza con Caraceas Formation of Lerida, Spain and the Lower Weald Clay (Surrey, England), UK. The new record represents the stratigraphically youngest occurrence of the family in the Jehol Biota and extends the temporal range of *Ilerdocossus* into the Aptian (121–113 million years ago).

Key words: Aptian, Lower Cretaceous, Palaeontinoidea, Prosbolomorpha, *Ilerdocossus* cf. *fengningensis*

Introduction

Palaeontinidae Handlirsch 1906 is an extinct Mesozoic family of Cicadomorpha that is closely related to Dunstaniidae, Tillyard 1916 and Mesogereonidae Tillyard, 1921 (Xu *et al*. 2024). The palaeontinids were mostly large sized insects with stocky bodies and large, often intricately colored wings. They are similar in general appearance to large hairy moths and were initially mistaken as members of Lepidoptera upon their discovery (Handlirsch 1906). The oldest palaeontinids are known from the Triassic (Carnian) with the group flourishing primarily during the Jurassic up to the Early Cretaceous, then declining and disappearing from the fossil record by the Late Cretaceous (Menon *et al*. 2005; Xu *et al*. 2024; Boderau *et al*. 2025). These insects were widely distributed across both hemispheres, with records known from Europe, Central and Eastern Asia, Australia, South Africa, and Brazil (Riek 1976; Shcherbakov & Popov 2002; Menon *et al*. 2005; Nam *et al*. 2017; Szwedo 2018; Chen *et al*. 2019; Li *et al*. 2019; Fu *et al*. 2020).

Northeastern China presents a particularly diverse assemblage of Palaeontinidae from the Lower Cretaceous with 12 described species divided between 4 genera representing about a third of known global diversity. Of these, 7 species are attributed to the genus *Ilerdocossus* (Gomez Pallerola, 1984). This genus is known from a total of 11 described species occurring from the Hauterivian to the early Aptian stages of the Early Cretaceous which are spread over a wide geographic area across Laurasia, with occurrences recorded from China, England, and Spain (Table 1).

In the present contribution, we present the youngest record of Palaeontinidae from the Lower Cretaceous of northeastern China and the first record from the Jiufotang Formation, thereby extending the presence of the genus *Ilerdocossus* (Gomez Pallerola, 1984) beyond the earliest Aptian stage of the Lower Cretaceous.

Geological setting

The fossil palaeontinid is preserved as a limonitic impression in dark grey shale, and it was collected from the lower section of the Jiufotang Formation at Laoyemiao Town, Liaoning Province, China.

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The Jiufotang Formation was first recognized as a distinct geological stratum by Endo (1934), who dubbed it the 'Jiufotang Series'. In 1960, the Formation was typified and officially named based on an exposure near the Jiufotang Village in Kazuo County, situated in Liaoning Province in northeastern China with the stratotype consisting of siltstone and mudstone, intercalated by finely laminated limestones (Zhang 2024; Wang *et al*. 2013). The age of the Jiufotang Formation has been estimated at about 121 Ma to 113 Ma covering the entirety of the Aptian to the earliest Albian stage, forming the upper part of the well-known Jehol geological group which represents part of a wider depositional environment continuous across China, South Korea and Japan (Sha *et al.* 2012; Sun *et al*. 2025). The Jiufotang Formation lies unconformably on the underlying Yixian Formation and has conformable or disconformable contact with the overlying Shahai or Fuxin formations. This Formation is distributed across the Liaoning Province, as well as parts of the neighboring Hebei Province and the Inner Mongolia Autonomous Region.

The Jiufotang Formation yielded a rich terrestrial and lacustrine palaeobiota in an exceptional state of preservation, typical of the Jehol Group and the correlated reginal formations (Sha *et al*. 2012; Rosse Guillevic *et al.* 2023; Lee *et al.* 2024). The fossilized flora and fauna include vertebrates such as fish, dinosaurs, pterosaurs, and mammals, as well as plants and various arthropods. The insect fauna of these strata comprises 47 described species belonging to 9 orders, of which 13 are hemipterans (Zhang *et al*. 2010; Lü *et al*. 2025).

Material and methods

The studied specimen (NIGP209713) was prepared using a sharp tool with the help of a stereo microscope. The specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS), Nanjing, China.

Photographs were obtained using a CANON 5D DSLR camera with a Canon 100 mm microlens. The images were then stitched together using Helicon Focus 8 software for increased depth of field and the final figures were prepared using Adobe Photoshop CS6. Drawing of venation body outline was made using CorelDRAW Graphics Suite 2020 on the basis of the photographs and corrected via direct observations under a binocular Olympus SZX7 microscope.

Systematic framework of Palaeontinidae in this paper follows Szwedo *et al.* (2018) and Xu *et al.* 2024. Wing venation terminology and interpreation for Palaeontinidae follows the interprétations by Nel *et al.* (2012), updated by Schubnel *et al.* (2019) for the PCu vein.

Abbreviations used in the text indlude: Sc—subcostal, R—radius, M—media, CuA—anterior cubitus, CuP—posterior cubitus, discal cell—the cell bounded between M and CuA and closed by the m-cua cross vein.

Table 1. Overview of described species of *Ilerdocossus*.

Species	Formation, Age	Locality	Reference
I. villaltai	Caliza con Caraceas Formation, Lower Cretaceous	Lerida, Spain	Gomez-Pallerola, 1984
I. pulcherrima	Caliza con Caraceas Formation, Lower Cretaceous	Lerida, Spain	Whalley & Jarzembowski 1985
I. hui	Yixian Formation, Upper Barremian-lower Aptian	Liaoning, China	Ren, Yin & Dou 1998
I. beipiaoensis	Yixian Formation, Upper Barremian lower Aptian	Liaoning, China	Ren, Yin & Dou 1998
I. exiguus	Yixian Formation, Upper Barremian-lower Aptian	Liaoning, China	Ren, Yin & Dou 1998
I. fengningensis	Yixian Formation, Upper Barremian-lower Aptian	Pingquan, Hebei, China	Ren, Yin & Dou 1998
I. pingquanensis	Yixian Formation, Upper Barremian-lower Aptian	Pingquan, Hebei, China	Ren, Yin & Dou 1998
I. ningchengensis	Yixian Formation, Upper Barremian-lower Aptian	Inner Mongolia, China	Wang & Zhang 2007
I. dissidens	Yixian Formation, Upper Barremian-lower Aptian	Inner Mongolia, China	Li, Chen & Wang, 2019
I. prowsei	Lower Weald Clay, Upper Hauterivian	Surrey, England, UK	Li *et al.* 2019
I. mikewebsteri	Lower Weald Clay, Upper Hauterivian	Surrey, England, UK	Li *et al.* 2019

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Infraorder Prosbolomorpha Popov, 1980
Superfamily Palaeontinoidea Handlirsch, 1906
Suborder Cicadomorpha Evans, 1946
Family Palaeontinidae Handlirsch, 1906
Genus *Ilerdocossus* Gomez Pallerola, 1984
Type species *Ilerdocossus villaltai*

***Ilerdocossus* cf. *fengningensis* Ren, Yin & Dou, 1998**
(Fig. 1)

Material. NIGP209713, deposited at the Nanjing Institute of Geology and Palaeontology, CAS.

Locality and horizon. Lamadong, Jianchang County, Liaoning Province, China; Jiufotang Formation; Aptian, Lower Cretaceous.

Remarks. The presently described specimen is assigned to the genus *Ilerdocossus* based on the following combination of characters: faint remnants of longitudinal carinae present on the mesonotum; triangular forewing of large size; nodal indentation distinct; narrow costal area; an unbranched vein Sc; a discal cell about a quarter of wing length; antenodal discal region trapezoid and postnodaldiscal region reduced; CuA forked basad of the nodal indentation; CuA_1 and CuA_2 long; a reduced clavus, about a third of wing length; a straight CuP; a small hindwing with vein M_1 fused with RA for an interval (Li *et al.* 2019). The branching order of RA, RP and M veins is obscure in the specimen. Despite the taxonomic value of this character in the diagnosis of *Ilerdocossus*, the remaining venational features are sufficient to unequivocally assign the specimen to this genus.

The new specimen is most similar to *I. fengningensis* with the following shared characters distinguishing it from all other species in this genus: forewing large (43 mm); M_{1+2} forking at a point distal to the level of the nodal indentation; M_{3+4} forking at a point basal to the level of the nodal indentation; CuA_2 curved posteriad. The new specimen (43 mm) differs from *I. hui* Ren, Yin & Dou, 1998 (35 mm) and *I. exiguus* Ren, Yin & Dou, 1998 (19 mm) mainly in the size of forewings. Venational characters are nearly identical, with M_{1+2} forking a little further away from the nodal indentation in *I. hui* and the discal cell slightly narrower in *I. exiguus*. The specimen further differs from *I. ningchengensis* Wang & Zhang, 2007 (29 mm) and *I. beipiaoensis* Ren, Yin & Dou, 1998 (25 mm) by the size of forewings as well as the position of forking points in M_{1+2} and M_{3+4} in relation to the nodal indentation. M_{1+2} forks apicad of the nodal indentation in the specimen and basad in *I. ningchengensis*. M_{3+4} forks basad of nodal indentation in the specimen but at the same level in *I. beipiaoensis*. *I. prowsei* Li *et al*., 2019, *I. dissidens* Li, Chen & Wang, 2019, and *I. pulcherrima* Whalley & Jarzembowski, 1985 can be distinguished by the relatively short postnodal discal region. *I. villaltai* Gomez-Pallerola, 1984 can be distinguished via the M_{1+2} fork positioned anteriad of the nodal indentation and stronger curvature at the base of M_1.

Overall, *Ilerdocossus* spp. exhibit a strong morphological similarity, with their diagnosis heavily reliant on the basal venation of the forewings and supplemented by colour pattern. Because of the fragmentation of the forewing base, lack of color pattern preservation, and the difference in age from the taxa present in the Yixian Formation, the new specimen is only tentatively assigned to *I. fengningensis.*

Description. Adult male. Wings preserved in open position are incomplete, particularly at the base. Left hind wing almost entirely absent. Body robust, 33.5 mm long and 20.77 mm wide, length width ratio 33.5/20.77. Head small, 5.5 mm wide. Labium narrow and 11mm in length, reaching posterior margin of thorax. Mesonotum large and rounded, covering most of the thorax and a bit of the abdomen base. Legs absent. Abdomen about as long as thorax, subtriangular in shape. Apex ending with prominent rounded pygophore.

Forewing large, about 43mm long and 19mm wide. Length/width ratio about 43/19. Costal margin slightly curved anteriad. Nodal indentation distinct, with at 17.9/43 of wing length from base. Nodal line traceable as crease across RA, RP, then parallel near base of M_{1+2} to cross through fork of M into discal cell while curving basad; then continues to cross apex of CuA towards CuP. Veins Sc obscure, stem R+M nearly straight, cross vein r+m-cua straight and with unclear relation to fork of stem CuA. RA slightly curved anteriad. RP connected to M1 crossvein r-m_1 as point distal to nodal indentation. Stem M forking into M_{1+2} and M_{3+4} at the nodal line. M_{1+2} forking at point distal to nodal indentation, at 19.5/43 of wing length from base. M_1 more prominently curved anteriad, and straightening apicad. M_2 slightly curved anteriad. M_{3+4} forking at 13.7/43 of wing length from base. M_3 slightly curved anteriad, and M_4 nearly

straight. Crossvein m_4-cua long, oblique and slightly curved apicad, attaching near base of M_4 and at fork stem CuA. CuA forking at point basal to nodal indentation, at 11.1/43 of wing length from base. CuA_1 and CuA_2 curving slightly anteriad. Discal cell about 11 mm long, and 4.5 mm wide at nodal line, about a quarter of wing length. Antenodal discal region trapezoid in shape, and subequal to postnodal discal region in length. Clavus narrow, A forks near base. PCu obscure, and A1 slightly curved posteriad.

Hindwing, about 21 mm long and 15 mm wide. Length/width ratio about 1.4. Costal area obscure. M_1 and RP fused for a short interval at about half of wing length from base. M with four terminals. Clavus obscure.

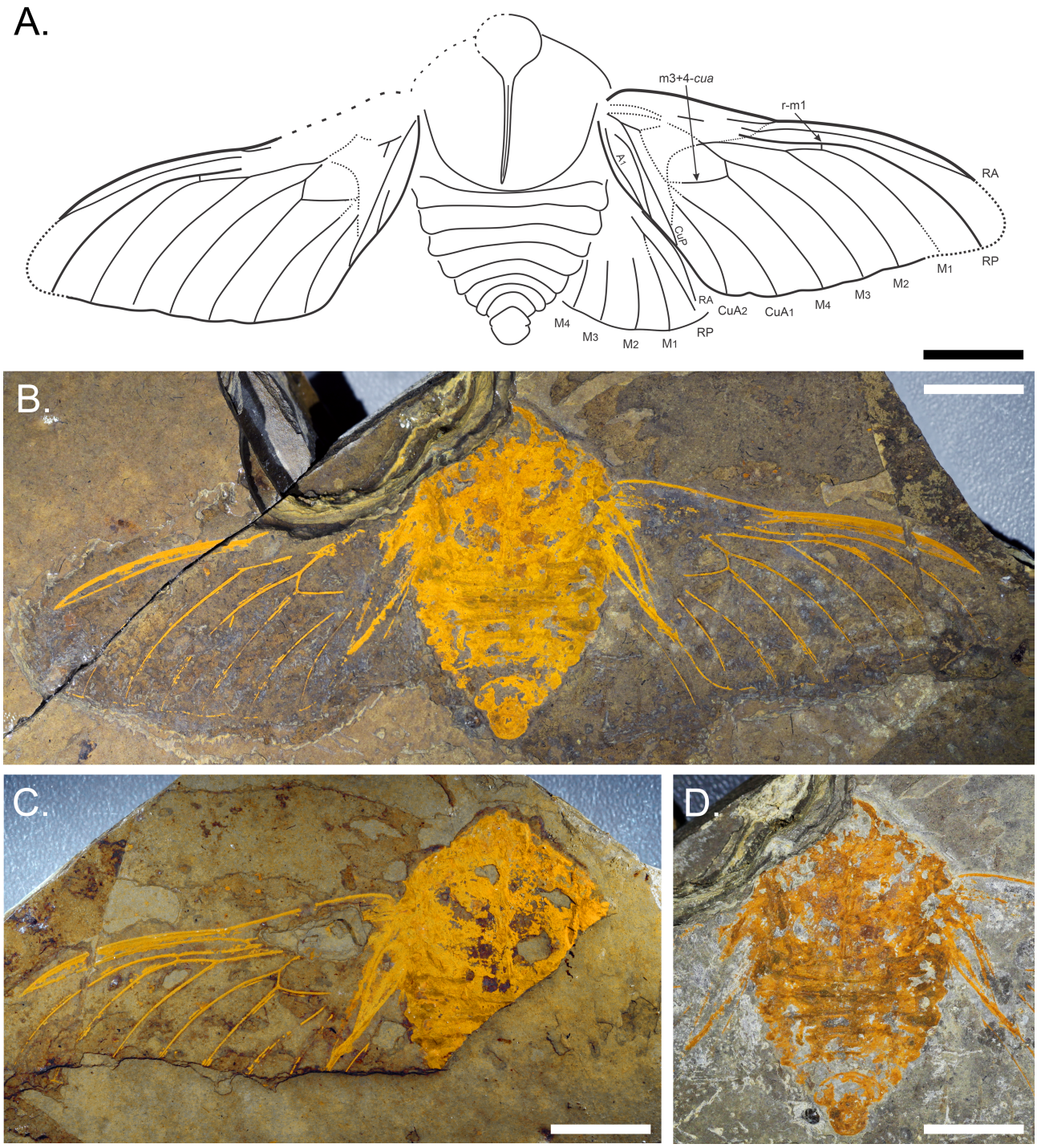

Figure 1. *Ilerdocossus* cf. *fengningensis*, Jiufotang Formation of northeastern China. **A,** Line drawing. **B,** General habitus imaged under alcohol, part (NIGP209713a). **C,** General habitus, part (NIGP209713b). **D,** Enlarged view of body, imaged dry. Scale bar: 10 mm. Entire lines indicate structure preserved as ferrous compression, the fine dotted lines indicate poor ferrous coverage with traceable impressions, and dashed lines represent suggested reconstruction of missing areas.

Discussion

The new fossil securely extends the known range of Palaeontinidae in China into the Jiufotang Formation, thus pushing the regional record of this group beyond the earliest Aptian.

The cause of apparent decline and extinction of Palaeontinidae in the Aptian–Albian interval is unknown and may have been driven by various factors including predation pressure or environmental change. The new fossil fills in a temporal gap in the presence of Palaeontinidae during the late phase of Jehol Entomofauna, illustrating the persistence of taxa similar to those found in the underlying Yixian Formation into the Aptian.

Recently a comprehensive phylogeny of Palaeontinidae was constructed by Xu *et al.* 2024 based on wing venation characters. Their analysis resolved the genus *Ilerdocossus* as a paraphyletic grouping lacking sufficient clear synapomorphies. We maintain the assignment of the new specimen to *Ilerdocossus* cf. *fengningensis* due to the close match in venation and presence of body characters such as the longitudinal carinae on the mesonotum. A revision of the genus *Ilerdocossus* is beyond the scope of the current study and would necessitate the inclusion of well-preserved whole specimens for taxa assigned based on wing venation alone.

Despite the rich vertebrate assemblages, and extensive collection, the number of publications on the late phase of the Jehol entomofaunas (Jiufotang Formation) and the overlying Fuxin group entomofaunas (Fuxin and Shahai formations) is relatively low. In addition to the apparent decline in insect diversity, the lack of publications is also a significant factor contributing to the apparent lack of Palaeontinidae in the younger strata of the Jehol group. Recently, Zhang *et al*. (2024, 2025) described five new species of *Stellularis* (Procercopidae) from the Jiufotang Formation of Liaoning Province, China, illustrating the cicadomorphan diversity still needs further exploration. It is suggested that the insufficient sampling of the Aptian and Albian strata of the region may have contributed to the apparent lack of Palaeontinidae rather than solely reflecting a biological signal decline.

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