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Investigation of *Cretodorus* (Hemiptera: Fulgoromorpha: Mimarachnidae) based on new adult and nymph fossils from mid-Cretaceous Myanmar amber

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Abstract

Here we report a new species, *Cretodorus lijuanae* **sp. nov.**, of extinct Mimarachnidae from mid-Cretaceous amber of northern Myanmar. *C. lijuanae* **sp. nov.** was described based on one adult and three nymphal fossils. The new adult specimen exhibits the diagnostic features of *Cretodorus* and possesses a unique number and arrangement of sensory pits in the pronotum: nine sensory pits on one side, with five sensory pits between median and pronotal carinae and four sensory pits between lateral carina and margin, which is consistent in the nymphs. We also conduct morphometric analyses of forewings of all known species of *Cretodorus*, demonstrating that morphometrics are effectively discriminative for identifying *Cretodorus* fossils featuring few longitudinal veins and minimal differences in venation. Additionally, we report the nymphal fossils of Mimarachnidae for the first time. Three nymphal fossils, preserved in the same piece of amber alongside the adult specimen, exhibit the same nodule pattern on the thoracic notum in dorsal view, suggesting a feature linking adult

and nymph of Mimarachnidae. These new specimens show morphological characteristics of the different developmental stages of *C. lijuanae* **sp. nov.**, increasing the diversity of the Mimarachnidae in mid-Cretaceous amber from Myanmar. The preservation of three nymphs of the same age with an adult in the same piece of amber likely indicates aggregation behaviour in Mimarachnidae.

Keywords: planthopper, Burmese amber, fossil, morphometrics, Insecta

Introduction

Mimarachnidae, an extinct family of the Hemiptera, currently placed within eucixioidian lineage of Fulgoromorpha (Bourgoin & Szwedo, 2022, 2023), was first established by Shcherbakov (2007) based on forewing fossils, initially including two genera and two species,

along with some undescribed specimens. Currently, this family comprises 15 described genera and 24 species, in addition to some undescribed specimens or newly discovered material (Liu *et al.*, 2023; Fabrikant *et al.*, 2024). In Mimarachnidae, the primary distinctive features include simplified longitudinal veins interconnected by veinlets, forming irregular grid-like patterns, and the presence of dual median longitudinal carinas on both the pronotum and mesonotum. Additional characteristics observed in some genera within the family include the forward-protruding head, the extremely long face and rostrum, sensory pits, wing camouflage, and eye spot linked with putative mimicry. Genus-level identification within Mimarachnidae primarily involves analysing the arrangement and branching of the main longitudinal veins, complemented by the examination of additional body morphological features (Jiang *et al.*, 2018; Brysz & Szewo, 2019; Zhang *et al.*, 2021; Bucher *et al.*, 2024). Due to the simplified structure of wing venation, quantitative analysis of minor differences between longitudinal veins may significantly enhance genus-level identification as previously demonstrated for the Mimarachnidae has been conducted (Jiang *et al.*, 2023). However, given the very subtle interspecific variations within the same genus and the variability of fossil preservation conditions, further verification of this method's effectiveness across the genera of this family is necessary in pursuing the description of new specimens.

Additionally, all recorded fossils from Mimarachnidae are adults, and no nymphal fossils have been reported so far. Research on the nymphs of Fulgoromorpha has progressed significantly over the past three decades

(Yang & Yeh, 1994; Emeljanov, 2000; Zenner *et al.*, 2005; Stöckmann *et al.*, 2013). The study of extinct fulgoromorphan nymphs remains largely open, with only a few fossil records of nymphs having been identified in the Perforissidae, Neazoniidae, Dictyopharinae, Dorytocidae, Mimarachnidae, and one species *incertae sedis* (as shown in Table 1). The earliest known record of a fulgoromorphan nymph dates to the Late Triassic of a specimen from the Ipswich Basin, Queensland, Australia (Jell, 1993). Due to the relative scarcity of nymphal fossils and the complexities involved in morphologically matching nymphs with their adult counterparts, directly associating separately preserved adult and nymph fossils from paleontological finds is inherently challenging. Increasing evidence underscores that juvenile forms can provide crucial insights into evolutionary processes (*e.g.*, Hörnig *et al.*, 2022; Mengel *et al.*, 2023; Haug *et al.*, 2024; Jiang *et al.*, 2024). Consequently, comprehensive research into the relationships between adult and nymph fossils is instrumental in documenting evolutionary morphological sequences across various life stages and in identifying patterns of morphological correspondence among different developmental stages within a species.

In this study, we report a new species of *Cretodorus*, featuring a comparative analysis of three fossil nymphal planthopper and one adult specimens, all fossils preserved in the same piece of amber. Additionally, we conducted a forewing geometric morphometric analysis to distinguish the newly discovered adult specimen from previously identified species of *Cretodorus*. This analysis reinforces the efficacy of morphometric methods to quantitatively discriminating simplified venations under ideal conditions

TABLE 1. The nymphal fossil records of Fulgoromorpha.

Family	Species	Age (Ma)	Geological Time	Locality	Reference
<i>incertae sedis</i>	<i>Knezouria unicus</i> Jell, 1993	237–227	Late Triassic Carnian	Ipswich Basin, Queensland, Australia	Jell, 1993
Neazoniidae	<i>Neazonia tripleta</i> Szewo, 2007a	ca. 135	Early Cretaceous	Lebanese amber	Szewo, 2007a
Neazoniidae	<i>Neazonia immatura</i> Szewo, 2007a	ca. 135	Early Cretaceous	Lebanese amber	Szewo, 2007a
Neazoniidae	<i>Akmazeina santonorum</i> Szewo, 2007b	ca. 100	Early Cretaceous	French amber	Szewo, 2007b
Perforissidae	<i>Perforissus muiri</i> Shcherbakov, 2007	98.79 ± 0.62	mid-Cretaceous	Kachin amber	Shcherbakov, 2007
Perforissidae	<i>Cretargus emeljanovi</i> Shcherbakov, 2007	98.79 ± 0.62	mid-Cretaceous	Kachin amber	Shcherbakov, 2007
Dorytocidae	<i>Dorytocus ornithorhynchus</i> Emeljanov & Shcherbakov, 2018	98.79 ± 0.62	mid-Cretaceous	Kachin amber	Emeljanov & Shcherbakov, 2018
<i>incertae sedis</i>	<i>Spinonymphia shcherbakovi</i> Luo, Wang & Jarzembowski, 2021	98.79 ± 0.62	mid-Cretaceous	Kachin amber	Luo <i>et al.</i> , 2021
Mimarachnidae	<i>Cretodorus lijuanae</i> sp. nov.	98.79 ± 0.62	mid-Cretaceous	Kachin amber	This study
Dictyopharinae	<i>Alicodoxa rasnitsyni</i> Emeljanov & Shcherbakov, 2011	56–34	Eocene	Rovno and Baltic ambers	Emeljanov & Shcherbakov, 2011
Dictyopharinae	<i>Bathymyza longirostris</i> Emeljanov & Shcherbakov, 2020	25.3–23.8	Eocene	Bitterfeld amber	Emeljanov & Shcherbakov, 2020

and establish a corresponding range of forewing venation metrics for *Cretodorus*, based on specific characters.

Material and methods

The amber piece with syninclusions was collected from the Angbamo site, Tanai Township, Myitkyina District, Kachin Province of northern Myanmar. It was cut into four sections, each containing either one adult or one nymph. Each of these four sections of amber was numbered accordingly. NM-T3546 is the number of the amber piece containing the adult fossil, while NM-T3547, NM-T3548, and NM-T3549 are the numbers of the three pieces of amber containing nymphs. The specimens described herein are permanently deposited at National Museum, Prague, Czech Republic.

The maximum age of amber is 98.8 ± 0.6 million years, according to U-Pb dating of zircons from the volcanoclastic matrix (Shi *et al.*, 2012). Biostratigraphy suggests that the amber-bearing bed corresponds to an age between late Albian to early Cenomanian (Cruickshank & Ko, 2003). The amber piece was collected between 2013–2016, well before the Myanmar army closed the Kachin amber mines in November 2017. The fossil was acquired in full compliance with the laws of Myanmar. All authors declare that the specimen reported in this study is not involved in armed conflict and ethnic strife in Myanmar.

Reflected light micrographs were acquired using a Zeiss AXIO ZoomV16 stereo microscope system. Each image is digitally superimposed from approximately 40–60 images taken in separate focal planes, and combined using Helicon Focus 7 software. Data acquisition and data analysis for morphometrics used TpsDig232, OriginPro 2020 and PAST3.15. In this paper, hierarchical clustering analysis was used, and the UPGMA algorithm and Euclidean Distance were as the methods of the similarity measure.

Wing venation terminology follows Nel *et al.* (2012), Bourgoïn *et al.* (2015), and Schubnel *et al.* (2019), proposed for the Acercaria and the Fulgoromorpha. Venation abbreviations are as follows: CA costa anterior; CP costa posterior; PC praecosta; RA radius anterior; RP radius posterior; MP media posterior; CuA cubitus anterior, CuP cubitus posterior; PCu postcubitus and A_1 first anal vein.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1946

Eucixioidian lineage sec. Bourgoïn & Szwedó, 2022

Family Mimarachnidae Shcherbakov, 2007

Genus *Cretodorus* Fu & Huang, 2020

Type species. *Cretodorus granulatus* Fu & Huang, 2020; by original designation.

Other species. *Cretodorus angustus* Fu & Huang, 2020, *Cretodorus rostellatus* Zhang, Yao & Pang, 2021, *Cretodorus multifoventatus*, Liu, Luo & Song, 2023.

Cretodorus lijuanae Liu & Jiang sp. nov.

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(Figs 1–5, 6A)

Material. Types, *Cretodorus lijuanae* sp. nov., including an adult and three nymphs; holotype imago, NM-T3546 (Fig. 1); paratype nymphs, NM-T3547 (Fig. 4A), NM-T3548 (Fig. 4B), NM-T3549 (Fig. 4C); amber piece with holotype and paratypes deposited in National Museum, Prague, Czech Republic.

Etymology. The specific name is dedicated to Dr Juan Li, who tragically passed away during a scientific expedition on the Tibetan Plateau in 2023. This memorialization is intended to pay tribute to Dr Juan Li as an outstanding scientist, her contributions, and passion for the geological sciences.

Diagnosis. Forewing about 12 mm in length; ScP+R unbranched; CuA single in hind wing. Pronotum with nine sensory pits on one half in adult and nymphs; five sensory pits between median and lateral carinae, arranged in two columns: three in inner column, two in outer column; four sensory pits between lateral carina and margin: two in a column close to lateral carina; third upper pit rightward between first two; fourth lower pit diagonally opposite third, in lower outer corner.

Locality and horizon. Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

Description. Adult (Figs 1, 2A, 3). Head in main part not preserved, faint outline impression on amber matrix, no discernible details.

Pronotum: length about 3.54 mm, width about 1.16 mm. Mesonotum: length about 2.33 mm, width about 2.88 mm. Both pronotum and mesonotum with a pair of median and lateral longitudinal carinas. Pronotal carinas closer at middle, arcing outward at ends. Mesonotal carinas relatively parallel. Pronotal lateral carinas nearly straight and parallel. Mesonotal lateral carinas almost straight, opening diagonally before second pit, arcing at pits, beginning to contract inward. Pronotum with nine sensory pits on right half. Five sensory pits between median and lateral carinas, arranged in two columns—three pits in one, two in the other. Upper pit of outer column positioned



FIGURE 1. *Cretodorus lijuanae* sp. nov., adult, holotype NM-T3546, photograph. **A**, Dorsal view, taken under transmission light from the bottom. **B**, Dorsal view, taken under reflected light.

between first and second pits of inner column. Second pit of outer column aligned with third pit of inner column. Pattern symmetrically preserved on left half of pronotum. Right half shows four sensory pits between lateral carina and margin. Two pits form inner column close to lateral carina; third pit rightward between first two; fourth pit diagonally opposite third, in lower right corner, nearly aligned with second pit. Mesonotum preserves three sensory pits each half. Right half pits between median and lateral carinas, near inner lower corner of lateral carina. Pits in triangular layout, one pit rightward between two aligned vertically. Left half shows symmetrical pattern. Scutellum present, surface with transverse wrinkles.

Forewing: membranous about 11.04 mm in length, about 2.90 mm in width. Longitudinal veins simplified; irregular veinlets meshwork between main veins; with brown irregular patches pattern. Costal area narrow, elongated. Stem PC + CP nearly parallel to costal margin at about 0.76 of wing length. ScP + R divided from MP at about 0.56 mm from the forewing base. RP divided from ScP + RA at about 1.9 mm from the forewing base. ScP+RA nearly straight and curved towards the costal margin of the wing at about 9.06 mm for the base of the forewing. RA and MP straight nearly parallel to

each other. CuA straight and forked at the first half of the forewing; first branch of CuA straight and second branch slightly sinuate. CuP almost straight. PCu vein fused with A1 before mid-length of forewing; fused vein PCu+A1 slightly straight and fused after with A2 about 6.5 mm of forewing base and reaching margin at about 0.63 of wing length. Narrow marginal membrane present.

Hind wing: membranous, about 10.50 mm in length, anal area indistinct. Costal margin straight, then arched at about 4.56 of wing length, apical margin rounded. ScP+R and MP nearly straight and not forked. CuA slightly arched at base, then straight and forked at about 0.68 of wing length into CuA₁ and CuA₂. CuP slightly sinuate. PCu basal part unpreserved, apex of vein sinuate. Irregular network of veinlets between longitudinal veins.

Leg and abdomen are not preserved.

Nymph (Figs 4, 5). Total length of body 2.65 mm (no. NM-T3547), 2.44 mm (no. NM-T3548), 2.76 mm (no. NM-T3549); width 1.35 mm, 1.32 mm, 1.35 mm. Shape ovoid, flattened. Head: Vertex subtriangular, about 0.30 in length, 0.23 in width, with well-developed lateral carinae and median groove, and with finely transversely striated. Lateral margins almost straight, originating anterior to compound eye, slightly elevated, extending to

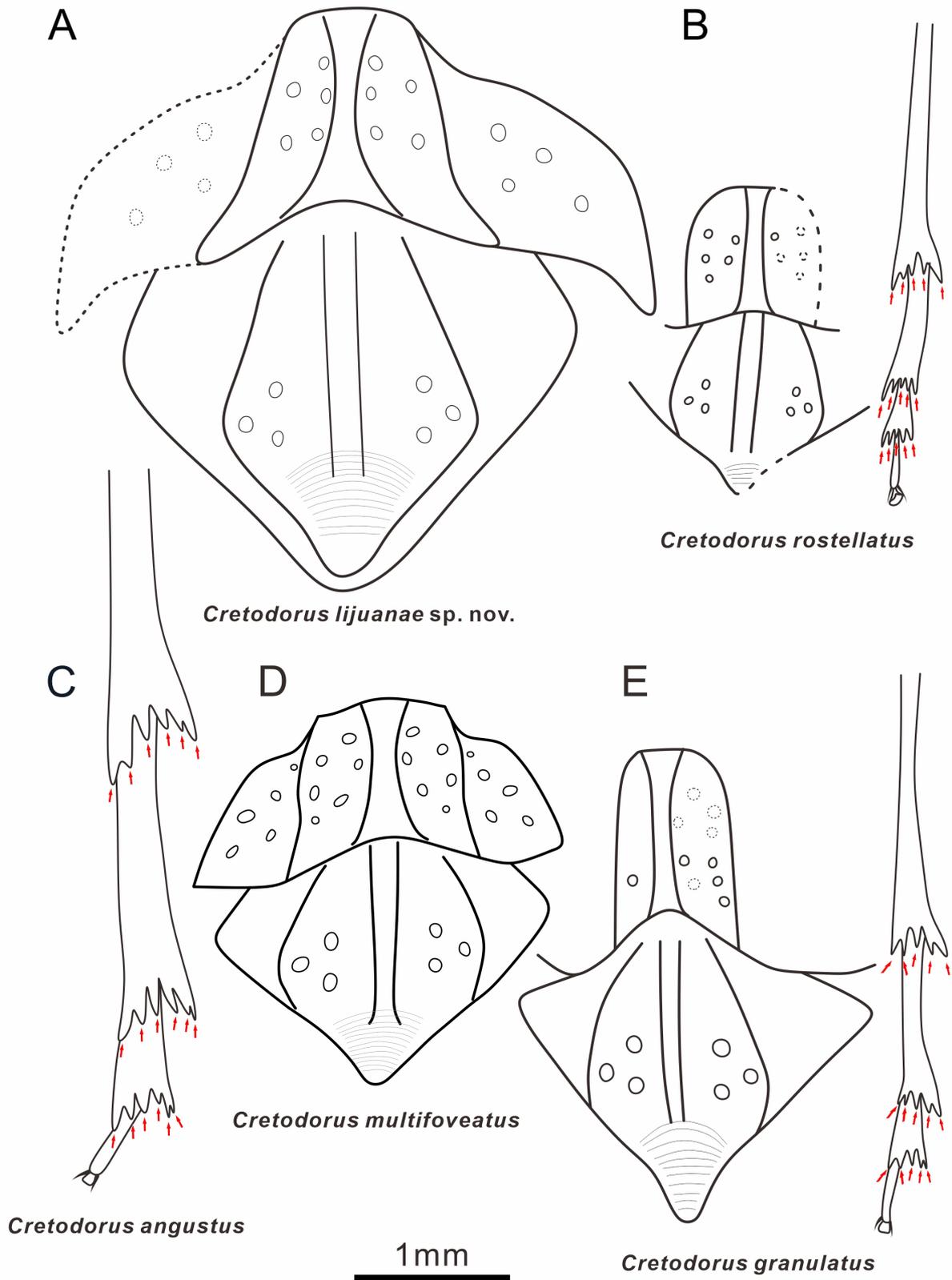


FIGURE 2. Line drawing of thorax in dorsal view and leg structures of *Cretodorus* species. **A**, *C. lijuanae*, showing number and arrangement of sensory pits on pronotum and mesonotum in dorsal view. **B**, *C. rostellatus*, showing number and arrangement of sensory pits in pronotum and mesonotum in dorsal view and apex spines of leg. **C**, *C. angustus*, showing number and arrangement of apex spines of leg. **D**, *C. multifoveatus*, showing number and arrangement of sensory pits on pronotum and mesonotum in dorsal view. **E**, *C. granulatus*, showing number and arrangement of sensory pits on pronotum and mesonotum in dorsal view and apex spines of leg.

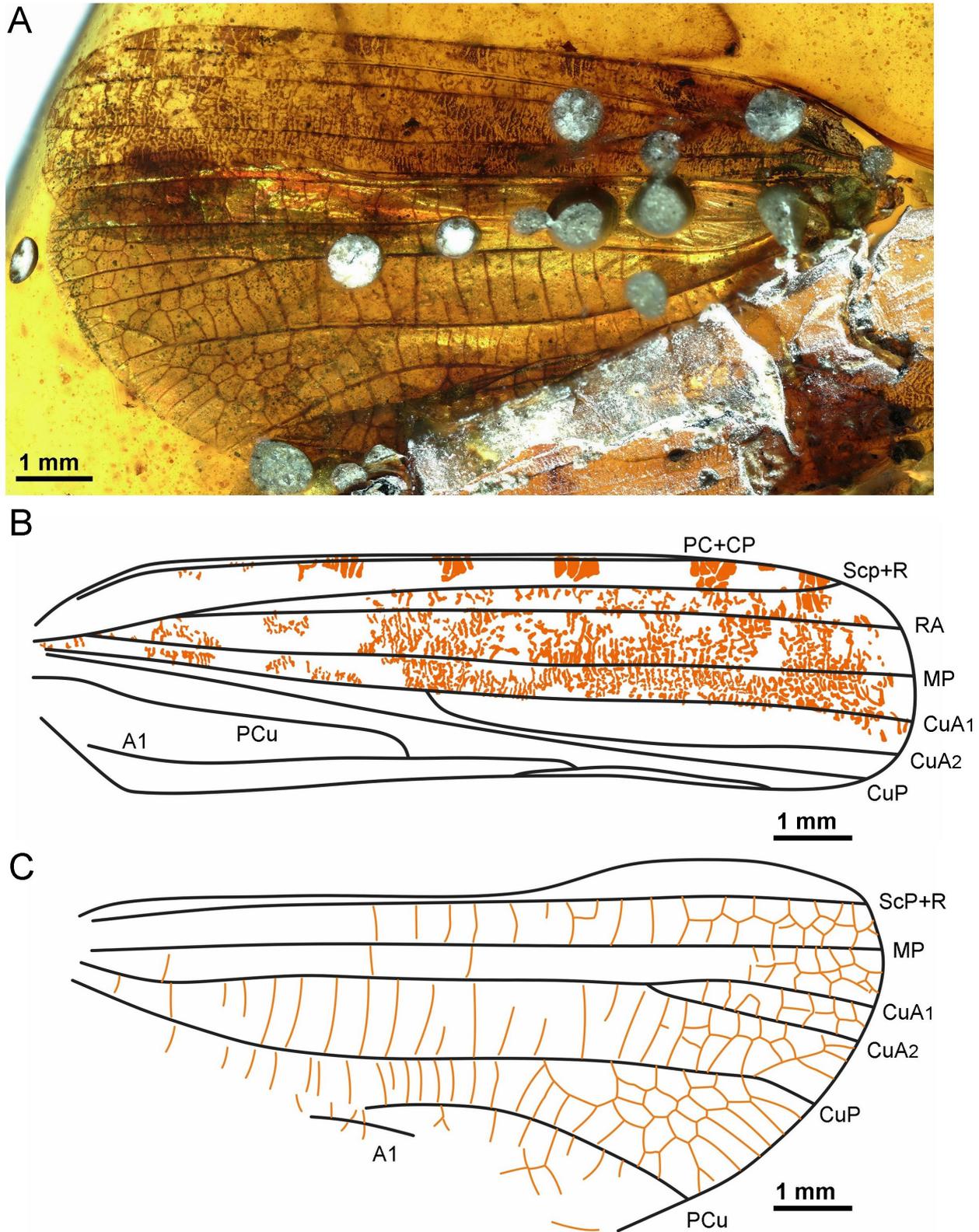


FIGURE 3. Wings of *Cretodorus lijuaenae* sp. nov., holotype NM-T3546. **A**, Photograph, from dorsal view. **B**, Drawing, left forewing. **C**, Drawing, left hind wing.

level of frontoclypeal suture. They converge at a point, forming a straighter inner carina from the vertex to near the clypeus. Posterior margin slightly indented directly

behind the centre of the compound eyes; disc of vertex concave and split into left and right sides by a central, longitudinal ecdysial line. Frons sub-rectangular, about

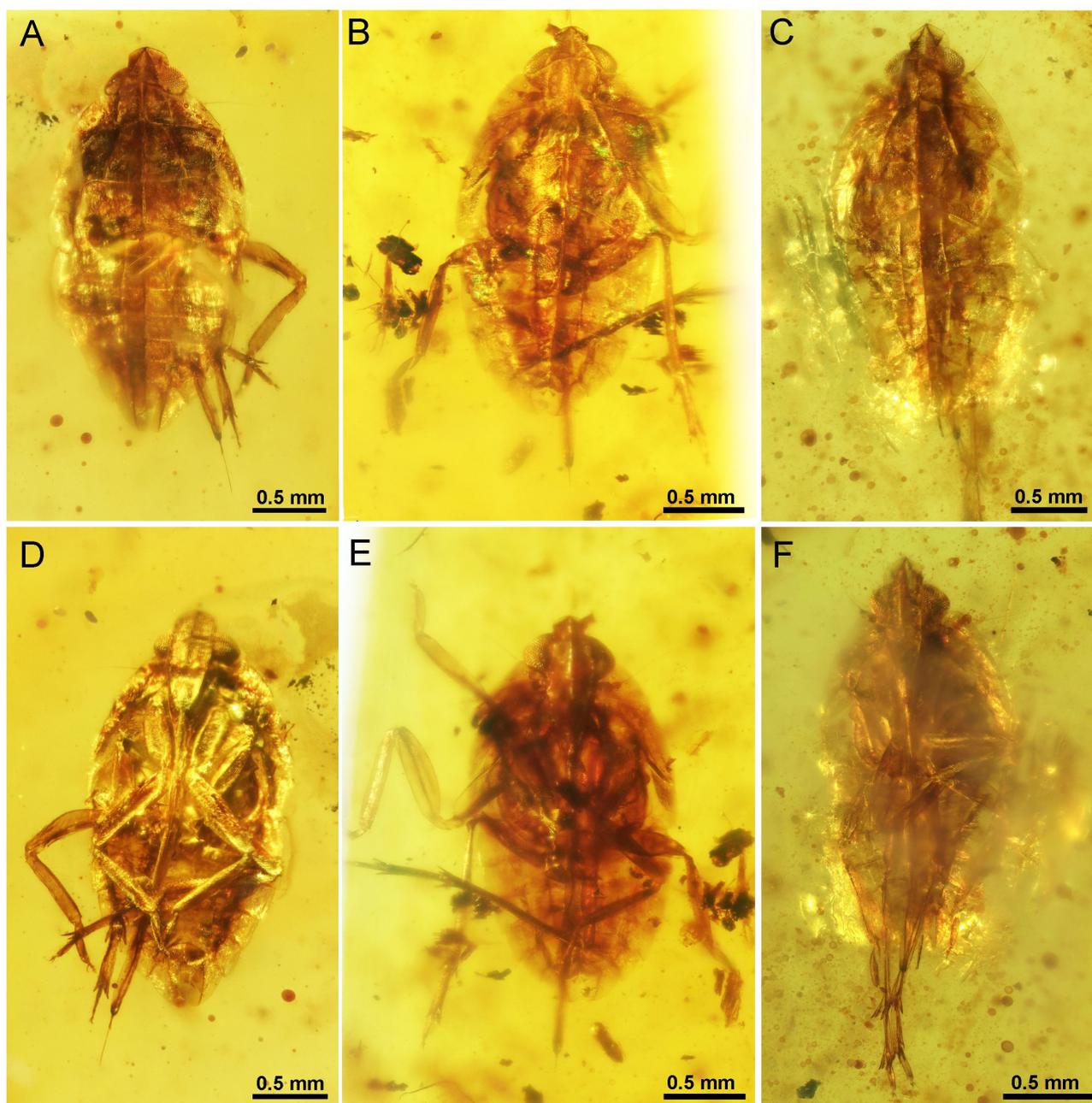


FIGURE 4. *C. lijuanae* sp. nov., nymphs, photograph. **A**, NM-T3547, dorsal view. **B**, NM-T3548, dorsal view. **C**, NM-T3549, ventral view. **D**, NM-T3547, ventral view. **E**, NM-T3548, ventral view. **F**, NM-T3549, ventral view.

1.48 times as long as wide. Clypeus narrowing distally, about 0.49 mm in length. Rostrum three-segmented, with tip of rostrum exceeding apex of abdomen, about 2.23 mm long. Three antennomeres; about 0.59 mm in length; scape cylindrical; pedicel subcylindrical; flagellomere bulbous basally, narrower than pedicel; arista elongate, bristle-like extension distally.

Thorax: Thoracic nota divided by longitudinal middorsal line into three pairs of plates. Pronotum sub-rectangular, distinctly wider than head including compound eyes; about 1.07 mm in length, about 0.27 mm in width; anterior margin following posterior margin of

head, lateral anterior angles slightly protruding anteriorly, lateral margins distinctly diverging posteriorly, lateral margins distinctly diverging posteriorly, posterior margin excavate. Pronotum with nine sensory pits on right half. Five sensory pits between median and lateral carinas, arranged in two columns—three pits in one, two in other. Upper pit of outer column positioned between first and second pits of inner column. Second pit of outer column aligned with third pit of inner column. Pattern symmetrically preserved on left half of pronotum. Right half showing four sensory pits between lateral carina and margin. Two pits forming inner column; third

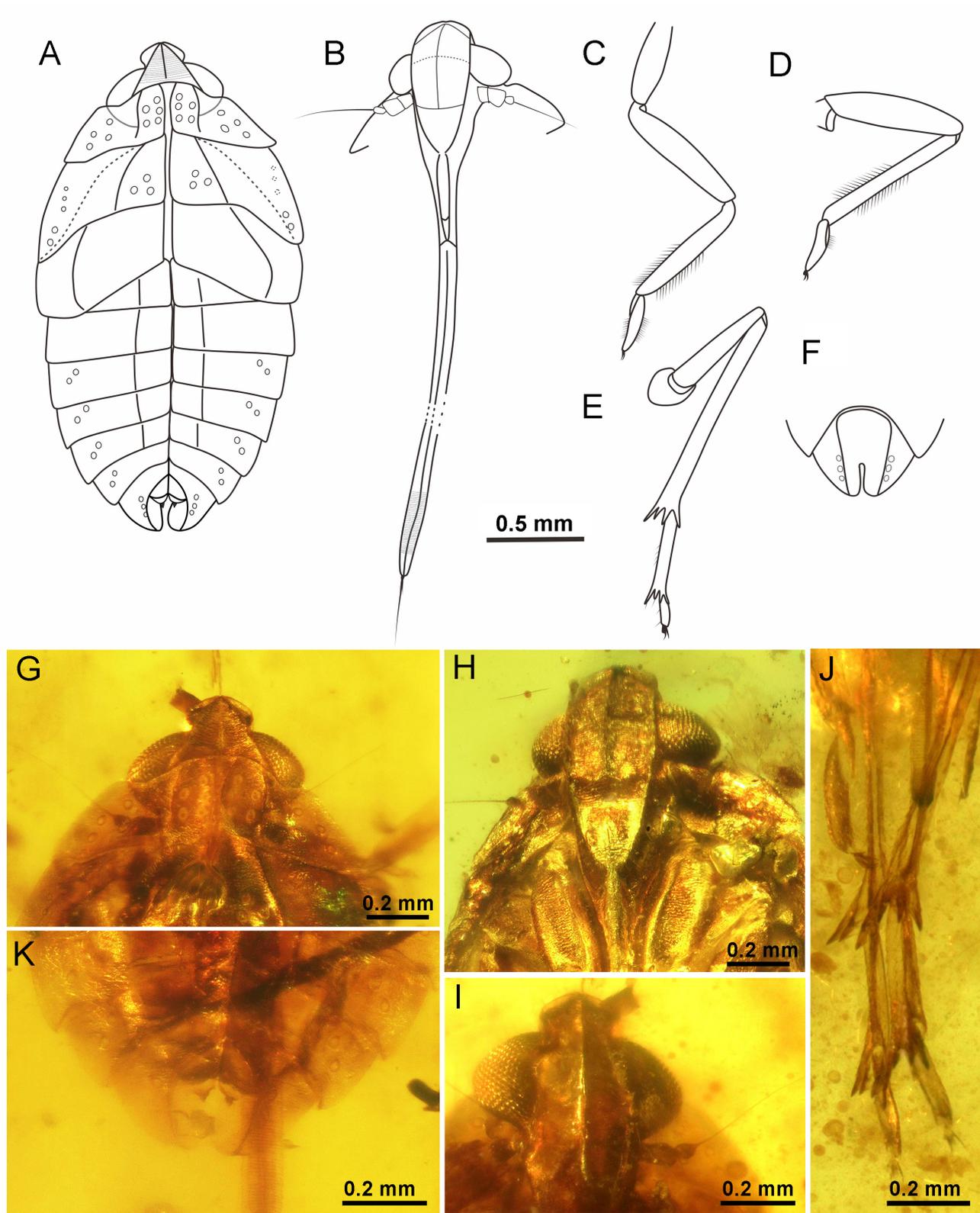


FIGURE 5. Line drawing schematic diagram of nymphal structures and detailed light microscope photos of nymphs of *C. lijuae* sp. nov. **A–G**, Line drawing. **A**, Dorsal view. **B**, Head. **C**, Left fore leg. **D**, Left mid leg. **E**, Left hind leg. **F**, lobes of pygofer in ventral view. **G–K**, Photographs. **G**, Head and pronotum in dorsal view, NM-T3548. **H**, Face, NM-T3547. **I**, Face, NM-T3548. **J**, Hind legs, NM-T3549. **K**, Last three abdominal segments and terminalia in dorsal view, NM-T3548.

pit rightward between first two; fourth pit diagonally opposite third, in lower right corner, nearly aligned with second pit. Mesonotum about 1.37 mm long with wing pads, about 0.45 mm wide. Mesonotum preserves three

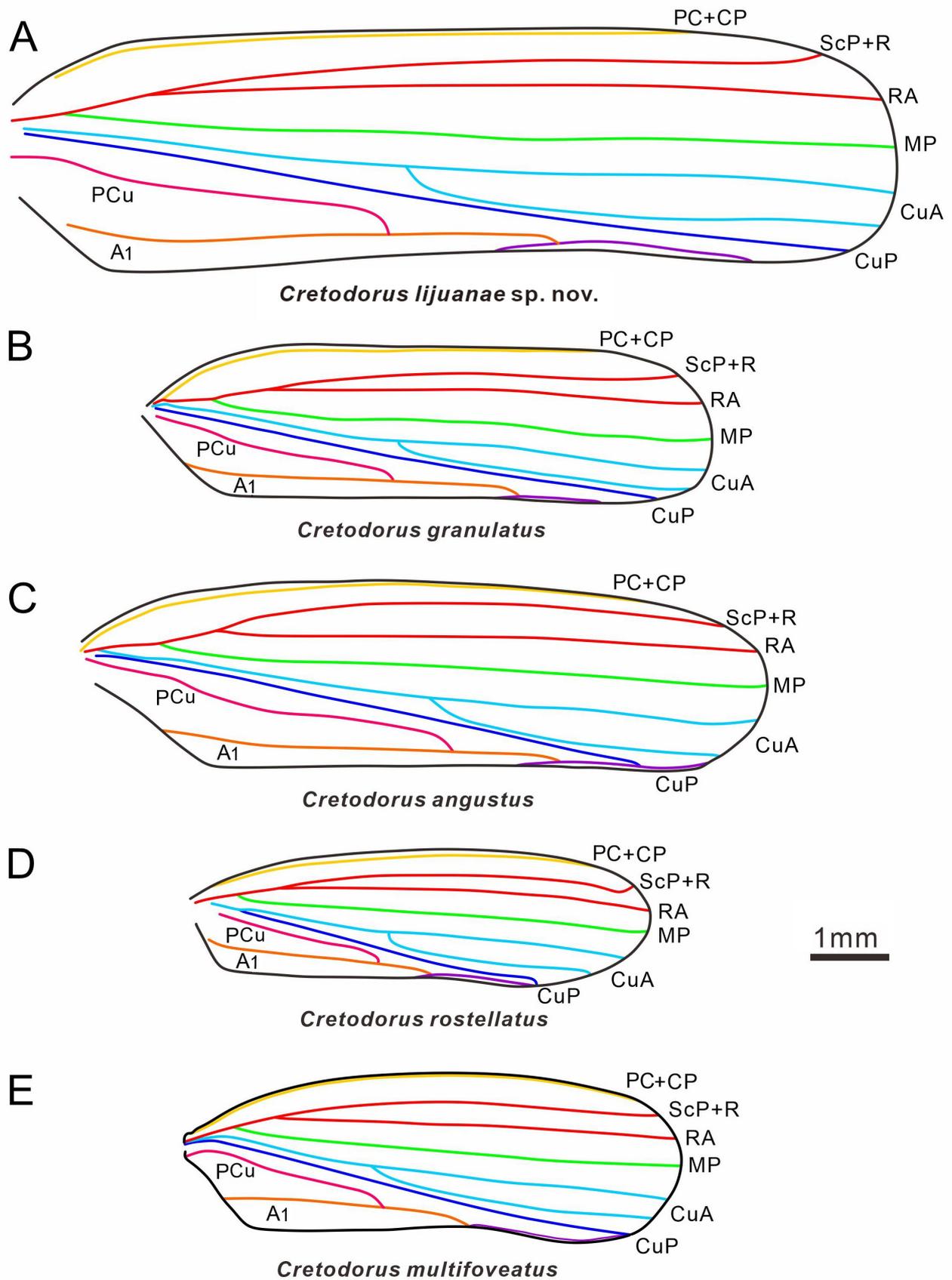


FIGURE 6. Line drawings of forewings of *Cretodorus*. **A**, *Cretodorus lijuanae* sp. nov. **B**, *C. granulatus* Fu & Huang, 2020. **C**, *C. angustus* Fu & Huang, 2020. **D**, *C. rostellatus* Zhang, Yao & Pang, 2021. **E**, *C. multifoveatus* Liu, Luo & Song, 2023.

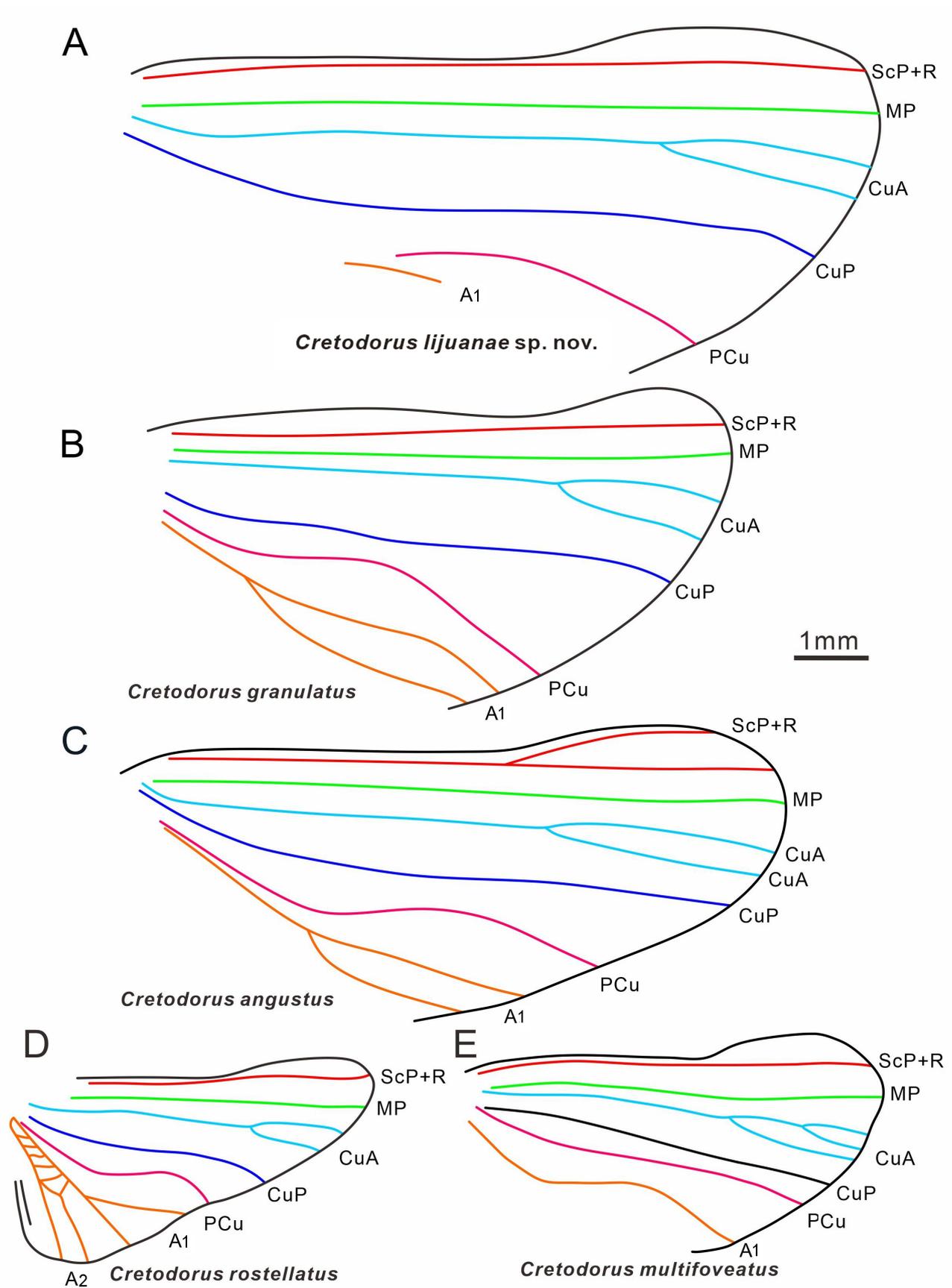


FIGURE 7. Line drawings of hind wings of *Cretodoros*. **A.** *C. lijuanae* sp. nov. **B.** *C. granulatus* Fu & Huang, 2020. **C.** *C. angustus* Fu & Huang, 2020. **D.** *C. rostellatus* Zhang, Yao & Pang, 2021. **E.** *C. multifoveatus* Liu, Luo & Song, 2023.

sensory pits each half. Right half pits between median and lateral carinas, near inner lower corner of lateral carina. Pits in triangular layout, one pit rightward between two aligned vertically. Left half shows symmetrical pattern. Prothoracic and mesothoracic coxae elongate, slender and ridged. Prothoracic coxa about 0.46 mm long. Prothoracic femur slightly longer about 0.68 mm long. Prothoracic tibia about 0.62 mm long; sub-quadrangular in cross section, with rows of setae; first tarsomere long; claws relatively large; arolium spatulate. Mesothoracic leg with femur 0.51 mm long, shorter than mesothoracic tibia 0.58 mm long; mesothoracic tibia sub-quadrangular in cross section, slightly flattened with rows of long setae; mesothoracic tarsus 0.27 mm long; first tarsomere long; tarsal claws distinct; arolium spatulate. Metathoracic femur 0.57 mm long; metathoracic tibia 0.84 mm long, with apical row of four teeth, covered with long setae; first tarsomere long.

Abdomen: nine-segmented; flattened dorsoventrally, widest across segments 4 and 5. Tergites 1 and 2 reduced; tergites 3–8 each with two pits displaced on either side at laterally in dorsal view. Abdomen with pygofer about 1.45 mm long and 1.36 wide in dorsal view. Pygofer (segment IX) triangular, 0.35 mm long along mid-line, 0.48 mm wide at base, with distinct narrow median incision ventrally, sensory pits on lateral lobes of pygofer blurred in preservation, posterior margins of pygofer lobes excavate, anal “combs” lobe-like. NM-T3547 and NM-T3548 are female with one pair of subacute processes extending caudally from juncture of sternites 8 and 9. NM-T3549 unknown.

Remarks. The adult specimen of the new species is significantly larger than other known species in this genus. The number and arrangement of sensory pits on the pronotum are different from those of other known species and are relatively consistent in the nymphs and adult; for other comparisons, see Table 2. The non-winged body parts of the adult specimen are missing, leaving only impressions in the resin fossil. The body is internally mineralized, and the wings are covered by bivalve borings with mineral precipitations. Mineralized inclusions in mid-Cretaceous amber from Myanmar are documented in Jiang *et al.* (2022).

Discussion

The new adult fossil shares with Mimarachnidae the simplified venation, tegmen with narrow costal area and open clavus, features also shared with Perforissidae Shcherbakov, 2007. The specimen can be assigned in Mimarachnidae based on the following characters: double carination of pronotum and mesonotum, tegmina with

narrow costal area, simplified longitudinal venation and abundant irregular network of veinlets (Shcherbakov, 2007). The currently recognized genera of Mimarachnidae include *Saltissus*, *Mimarachne*, *Nipponoridium*, *Mimamontsecia*, *Chalicoridulum*, *Burmissus*, *Dachibangus*, *Xiaochibangus*, *Jaculistilus*, *Mimaplax*, *Ayaimatum*, *Cretodoros*, *Mimaerypterus*, *Multistria*, and *Tenebricosus* (Jiang *et al.*, 2023: Table 1; Liu *et al.*, 2023). The new fossil has the diagnostic features of *Cretodoros*, *viz.* moderately elongated head, pronotum with lateral carinae nearly parallel, pronotum and mesonotum with many large, rounded sensory pits, longitudinal veins of tegmen straight, nearly parallel to each other, ScP+RA, RP and MP simple, and distal fusion of PCu with anal veins (Fu & Huang, 2020). Four species belonging to this genus had been previously recorded. Because of the simplified forewing venation in the Mimarachnidae, few differences can be detected, justifying a quantitative approach to detect subtle structural differences.

Benefiting from the well-preserved wings of the *Cretodoros* specimens from the mid-Cretaceous Kachin amber, we conducted a geometric morphometric analysis of the forewing contours and wing vein topology (Figs 6, 8). A total of 15 landmarks were selected on the specimens to capture the morphology of the wing veins and contours, with definitions for each landmark provided in Table 3. We performed four tests: using 15 landmarks without considering body size, using 15 landmarks while considering body size, using landmarks 1 and 7–15 to represent contour morphology without considering body size, and using landmarks 1–11 to represent wing vein features without considering body size. The results are presented in Fig. 8 and Tables 4 and 5. PCA and cluster analysis results indicate that the body size is the most distinguishing feature of the new species compared to other known species (Fig. 8A–F). When body size is not considered, the primary distinguishing features of the forewings of these species include the position of the CuA vein fork, the fusion point of the PCu and A₁ veins, the intersection of the PCu+A₁ with narrow marginal membrane edge, as well as the relative distances and terminal positions between other longitudinal veins (Fig. 8A–C, G–L). Additionally, we present line drawings of previously preserved hind wings for comparison (Fig. 7). The new species, *C. lijuanae* **sp. nov.**, is primarily distinguished from other *Cretodoros* species with preserved hind wings by its larger size. Specifically, the bifurcation of the CuA vein differentiates it from *C. multifoveatus*; the unbranched ScP+R vein distinguishes it from *C. angustus*; and the PCu ridge located in the mid-posterior part of the wing, along with the smaller distance between CuA bifurcations compared to the distance between the ScP+R and MP terminals, distinguishes it from *C. granulatus*. Further examination of hind wings

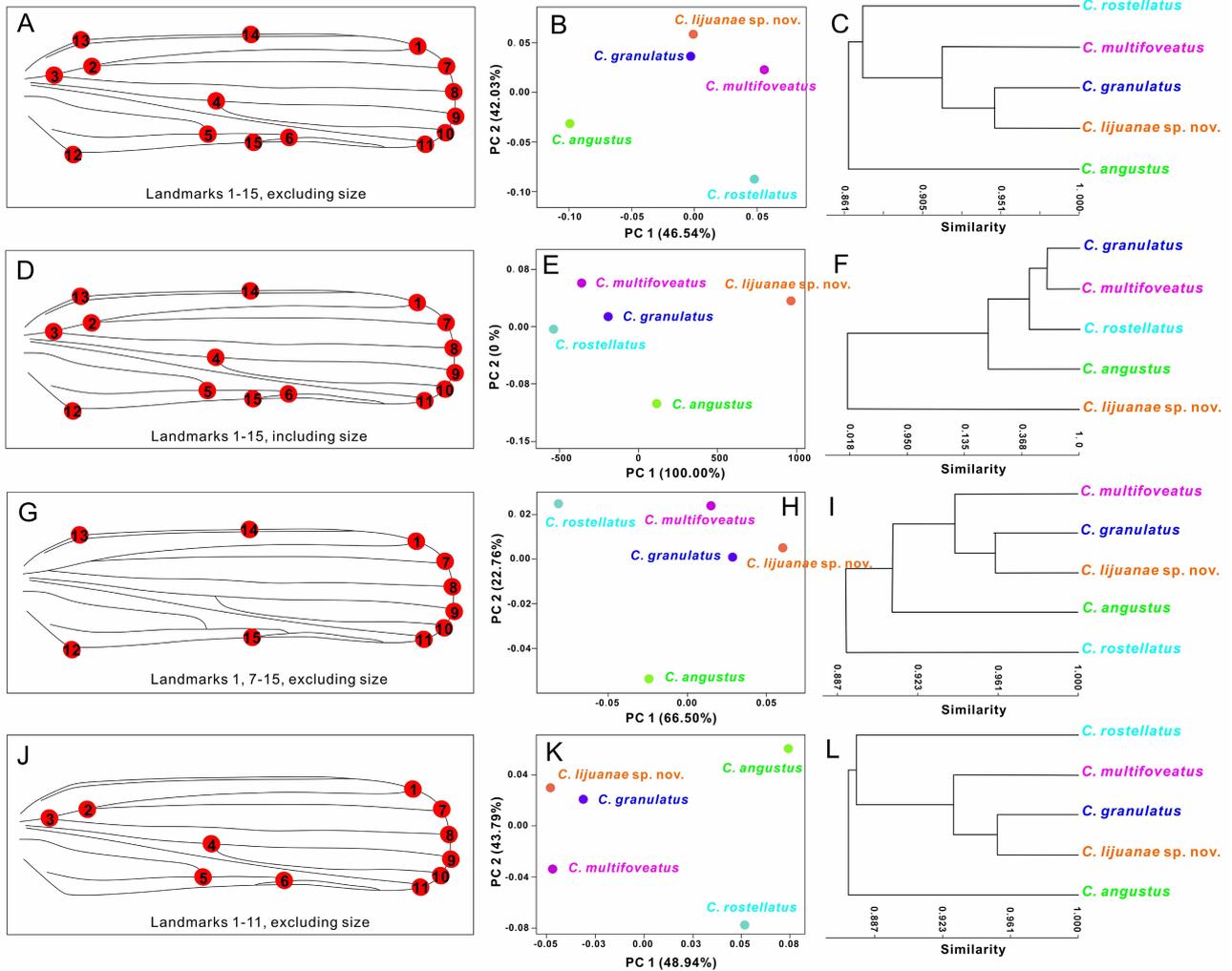


FIGURE 8. Geometric morphometrics analysis of forewings of species in *Cretodorus*. **A**, Landmarks of modelling of forewing, showing 15 landmarks associated with vein difference of forewings of five *Cretodorus* species. **B**, Result of principal component analysis based on model **A**, showing principal components 1 and 2. **C**, Result of cluster analysis based on model **A**. **D**, Landmarks of modelling of forewing, showing 15 landmarks associated with vein difference of forewings of five *Cretodorus* species. **E**, Result of principal component analysis based on model **D**, showing principal components 1 and 2. **F**, Result of cluster analysis based on model **D**. **G**, Landmarks of modelling of forewing, showing 10 landmarks associated with wing outline difference of forewings of five *Cretodorus* species. **H**, Result of principal component analysis based on model **G**, showing principal components 1 and 2. **I**, Result of cluster analysis based on model **G**. **J**, Landmarks of modelling of forewing, showing 11 landmarks associated with vein difference of forewings of five *Cretodorus* species. **K**, Result of principal component analysis based on model **J**, showing principal components 1 and 2. **L**, Result of cluster analysis based on model **J**.

is needed to obtain additional characteristics for potential morphometric analysis, which will allow for a more quantitative assessment of morphological features and their role in species identification.

When using the forewing as a basis for classification, it is crucial to also compare other body characteristics. Since the head, legs, and abdomen of *C. lijuanae sp. nov.* are not preserved, the number and arrangement of sensory pits seem to be important diagnostic features for *C. lijuanae*. Figure 3 summarizes the current number and arrangement of sensory pits for known species of *Cretodorus*. In

Cretodorus, species have three distinct sensory pits on the mesonotum, arranged in a triangular layout. The number and arrangement of sensory pits on the pronotum serve as interspecific diagnostic features. *C. lijuanae sp. nov.* and *C. rostellatus* each present five sensory pits on the half part of the pronotum between the median and lateral carinae, arranged in two columns. In *C. lijuanae sp. nov.*, there are three pits in the inner column closer to the median carina and two in the outer column. Conversely, *C. rostellatus* has two pits in the inner column and three in the outer column. *C. multifoveatus* presents six sensory pits. The

number of sensory pits in *C. granulatus* is recognized from Fu & Huang (2020, Fig. 4A), showing more than five pits in the half part of the pronotum. The number of sensory pits on one half of the pronotum between the lateral carina and the margin is four in *C. lijuanae* **sp. nov.** and five in *C. multifoventus*. Additionally, the number of spines on the legs, reproductive structures, and other body characteristics are used as diagnostic features among species of *Cretodorus*. For a detailed comparison of body characteristics, see Table 2.

In addition, this study allowed to describe three preserved nymphs along with adults in the same piece of amber, with no other identified Hemiptera or other insect fossils observed in this amber. Therefore, these three nymphal specimens appear to most probably belong to *C. lijuanae* **sp. nov.** The pattern of the sensory pits on the thoracic notum in the dorsal view of the nymphs is consistent with that of the adults, greatly facilitating their association (Fig. 2A, 9A). The structure of the sensory pits appears to be an important distinguishing feature linking the adults and nymphs. Sensory pits are regularly distributed on the frontal head area, all thoracic plates, wing buds, and most abdominal segments. Each pit generally contains with a sensory hair. Fossils usually only

preserve traces of the sensory pits. The size, location, and orientation of the pits show almost bilateral symmetry, and their number can change with each molt (*e.g.*, Wilson & Tsai, 1982; Sforza *et al.*, 1999; Bräunig *et al.*, 2012; Ortega-Gómez *et al.*, 2022). Our comparisons between nymphs and the adult indicate that the distinctly identifiable larger sensory pits in *Cretodorus* have a relatively stable distribution and arrangement on the dorsal thoracic plates of both adult and nymphs. In this study, we report the nymph of Mimarachnidae for the first time. Previously, nymphal fossil records within Fulgoromorpha have been found in Perforissidae, Neazoniidae, Dictyopharinae, Dorytocidae, and two species of uncertain placement (as shown in Table 1), including nine genera: *Knezouria*, *Neazonia*, *Akmazeina*, *Perforissus*, *Cretargus*, *Alicodoxa*, *Dorytocus*, *Bathymyza*, and *Spinonympha*. The number and arrangement of their sensory pits on the dorsal thoracic notum and abdominal tergites in dorsal view are shown in Figs 9 and 10. Some distinct features can quickly identify them.

The sensory pits in *Cretargus* are relatively evenly distributed as single units. The mesonotum has three distinct sensory pits on each half, arranged in a triangular layout, and there are two sensory pits on each half of

TABLE 2. The differential diagnosis of each species of *Cretodorus*. The line drawings of main features can be seen in Figs. 2, 6, and 7.

Features/Name	<i>Cretodorus granulatus</i> Fu & Huang, 2020	<i>Cretodorus angustus</i> Fu & Huang, 2020	<i>Cretodorus rostellatus</i> Zhang, Yao & Pang, 2021	<i>Cretodorus multifoventus</i> Liu, Luo & Song, 2023	<i>Cretodorus lijuanae</i> sp. nov.
Frons sensory pits	not present	unknown	unknown	at least three pits irregularly arranged on each half	at least two pits irregularly arranged on each half
Rostrum	beyond tip of tegmina	unknown	beyond hind coxae	unknown	unknown
Pronotum median carinae	straight and parallel	unknown	straight and parallel	slightly sinuate	slightly sinuate
Pronotum sensory pits	present but number unknown	not present	present but number unknown	with eleven symmetrical distribution on each half	with nine symmetrical distribution on each half
Mesonotum median carinae	slightly diverging anteriad	diverging anteriad	parallel	slightly converging anteriad	parallel
Mesonotum sensory pits (each half)	three arranged in triangle between the median and lateral carinae	not present	three arranged in triangle between the median and lateral carinae	three arranged in triangle between the median and lateral carinae	three arranged in triangle between the median and lateral carinae
Forewing length to width ratio	about 3:4–3:5	3:8	about 3:4	about 3:2	about 3:9
Forewing length	7.97 mm	10.45 mm	6.18 mm	6.94 mm	12.63 mm
Hind wing ScP + R	single	two terminals	single	single	single
Hind wing CuA	two terminals	two terminals	two terminals	three terminals	two terminals
Metatibio-metatarsal formula	5:5:5	6:6:6	5:5:5	unknown	unknown
Anal tube	apex oval	unknown	apex concave	apex protruded	unknown

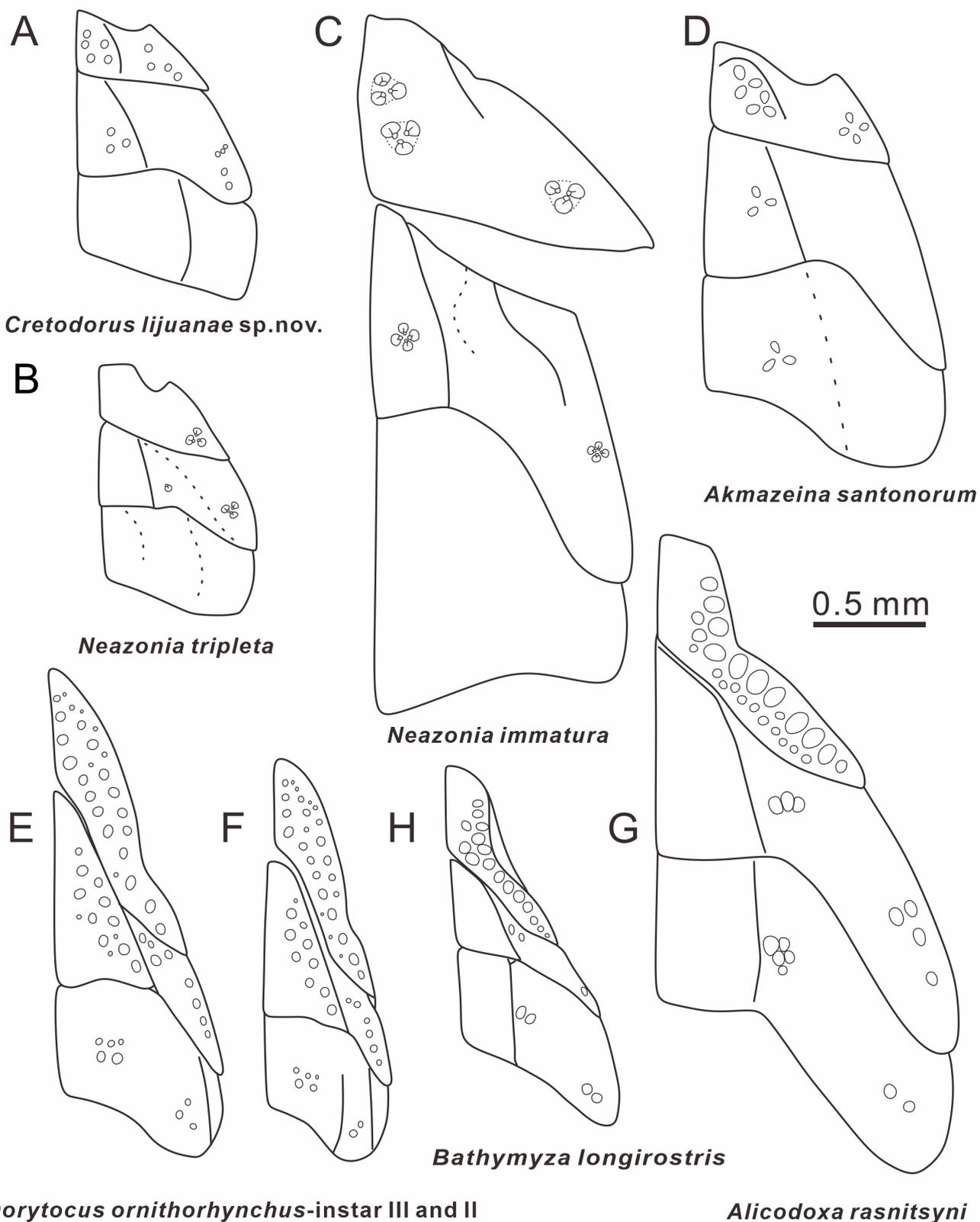


FIGURE 9. Comparisons of arrangement patterns of sensory pits in thoracic notum of nymphal fossils. **A**, *C. lijuanae* sp. nov. **B**, *Neazonia tripleta* Szwedo, 2007a. **C**, *N. immatura* Szwedo, 2007a. **D**, *Akmazeina santonorum*, Szwedo, 2007b. **E–F**, *Dorytocus ornithorhynchus* Emeljanov & Shcherbakov, 2018. **G**, *Alicodoxa rasnitsyni*, Emeljanov & Shcherbakov, 2011. **H**, *Bathymyza longirostris*, Emeljanov & Shcherbakov, 2020.

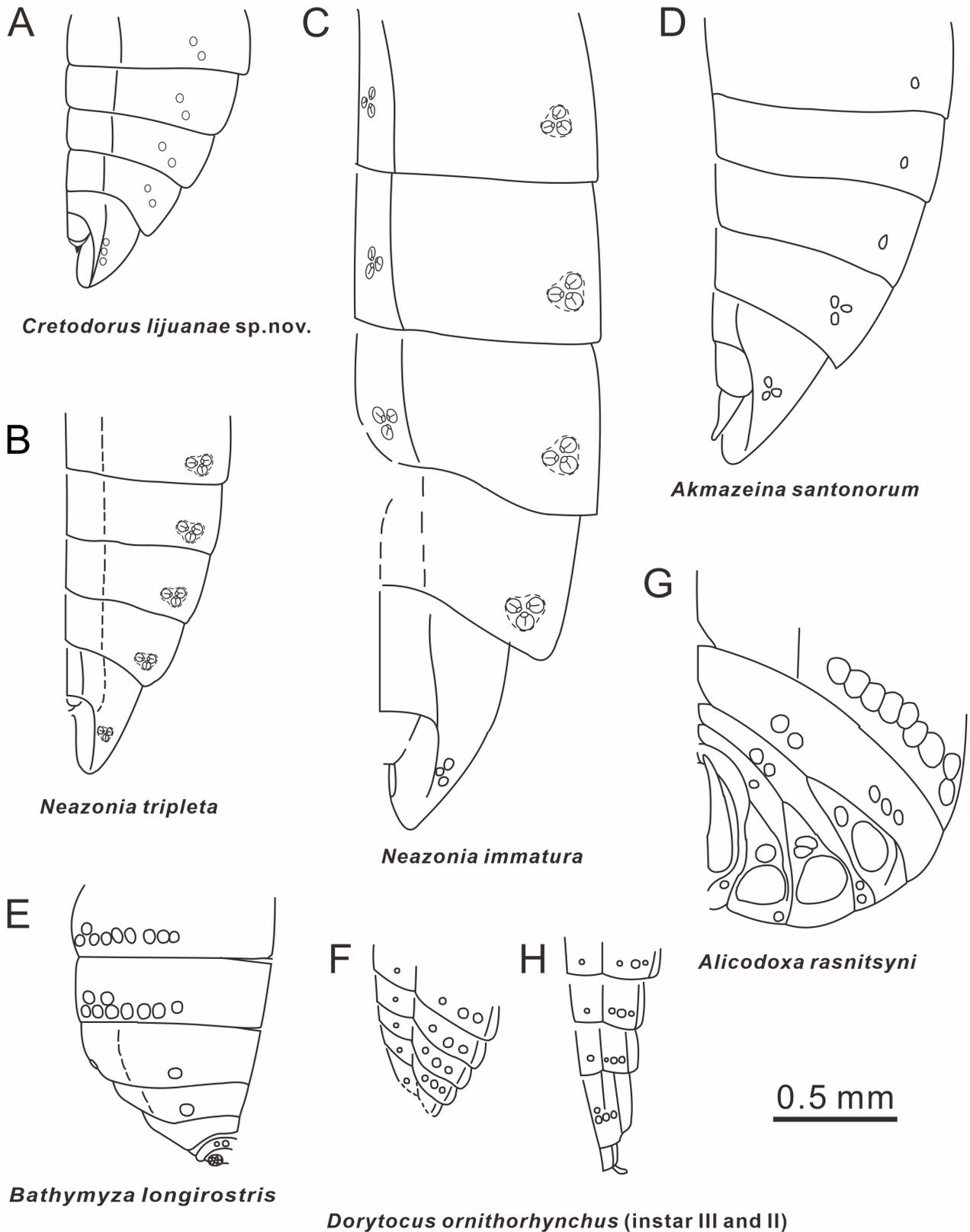


FIGURE 10. Comparisons of arrangement patterns of sensory pits on half part of abdominal tergites of nymphal fossils. **A**, *C. lijuanae* sp. nov. **B**, *Neazonia tripleta* Szwedo, 2007a. **C**, *N. immatura* Szwedo, 2007a. **D**, *Akmazeina santonorum*, Szwedo, 2007b. **E**, *Bathymyza longirostris*, Emeljanov & Shcherbakov, 2020. **F–H**, *Dorytocus ornithorhynchus* Emeljanov & Shcherbakov, 2018. **G**, *Alicodoxa rasnitsyni*, Emeljanov & Shcherbakov, 2011.

TABLE 3. The description of landmarks in Figure 6.

Number	Position	Number	Position
1	ScP+RA vein intersection with margin	9	CuA ₁ intersection with margin
2	RP vein separation from ScP+R vein	10	CuA ₂ intersection with margin
3	M vein separation from ScP+R+M vein	11	CuP intersection with margin
4	CuA vein separation	12	corner of anal area margin
5	PCu vein intersection with A ₁ vein	13	oblique vertical intersection of no. 2 with wing margin
6	PCu+A ₁ intersection with narrow marginal membrane edge	14	middle of upper margin
7	RP intersection with margin	15	middle of lower margin
8	M intersection with margin		

TABLE 4. Eigenvalues and contributions of the first two or three principal components of landmarks.

Source	Principal Component Number	Eigenvalue	Percentage of Variance (%)	Cumulative (%)
Figure 5B	1.000	0.004	46.534	46.534
	2.000	0.003	42.030	88.564
	3.000	0.001	8.330	96.894
Figure 5E	1.000	350191.000	100.000	100.000
	2.000	0.004	0.000	100.000
Figure 5H	1.000	0.003	66.491	66.491
	2.000	0.001	22.760	89.251
	3.000	0.000	9.003	98.254
Figure 5K	1.000	0.003	48.934	48.934
	2.000	0.003	43.788	92.722
	3.000	0.000	5.083	97.805

the abdominal tergites. The sensory pits in *Neazonia* are arranged in a rosette-like pattern, with two quadruplets of sensory pits in the upper portion of the frons and two triplets of sensory pits in the lower portion of the frons. The sensory pits in *Akmazeina* feature with two quadruplets of sensory pits in the upper portion of the frons, and with a single pair of triplets of or a single sensory pit in abdominal tergites. The sensory pits in *Alicodoxa*, *Bathymyza*, *Dorytocus* (instars II, III) form long rows of sensory pits in notum. *Alicodoxa* has sensory pits in rows or groups of no fewer than six; *Bathymyza* has a single pair of triplets of or a single sensory pit in abdominal tergites; and *Dorytocus* has three or four sensory pits in abdominal tergites.

The simultaneous preservation of nymphs and adults is extremely rare, especially in rock-preserved fossils. Resin fossil offers a unique opportunity to preserve both developmental stages together. Increasing research emphasizes that nymphs can provide critical evolutionary insights into morphology and ecological behaviours (e.g., Hörnig *et al.*, 2022; Mengel *et al.*, 2023; Haug *et al.*, 2024; Jiang *et al.*, 2024). Importantly, the co-preservation of nymphs and adult may not be coincidental but rather indicative of aggregation (gregarious) behaviour in mymarachnids, which increases the likelihood of multiple nymphs and adult being captured simultaneously.

Aggregation behaviours are widely observed in Fulgoromorpha (e.g., Wilson & Tsai, 1984; Krstić *et al.*, 2016; Kron, 2020) where conspecifics congregate within confined environmental spaces to enhance their interactions. Aggregation behaviour, while prevalent in both social and non-social extant insects, are infrequently highlighted in insect fossil studies (e.g., Hörnig *et al.*, 2022). This behaviour significantly impact reproduction and survival, affecting both population dynamics and evolutionary patterns (e.g., Waters, 1959; Bengtsson, 2008). Continued examination of more specimens preserved in amber may yield deeper understanding of the communal evolutionary trends of insects. In our specimens, the nymphs preserve distinct reproductive structures, while the adult lacks preserved abdominal structures. Given the high diversity of mymarachnids preserved in Kachin amber, it is anticipated that future discoveries will include additional specimens that could enhance our understanding of the morphological connections between adults and nymphs. The mid-Cretaceous amber from Myanmar has preserved numerous nymphs of other groups (e.g., Hörnig *et al.*, 2022; Haug *et al.*, 2024; Jiang *et al.*, 2024). Our specimens also indicate that nymphs are not uncommon in mid-Cretaceous amber of northern Myanmar. Therefore, it is promising to find more nymph specimens in the future, establish morphological evolutionary sequences between

TABLE 5. Eigenvector matrix of principal components 1, 2 and 3 of forewings with landmarks of five *Cretodorus* species.

Number	Figure 5B			Figure 5E			Figure 5H			Figure 5K					
	PC 1	PC 2	PC 3	Number/type	PC 1	PC 2	PC 3	Number	PC 1	PC 2	PC 3	Number	PC 1 (48.934%)	PC 2 (43.788%)	PC 3 (5.0834%)
X1	0.198	-0.336	-0.115	X1	0.000	0.007	0.338	X1	-0.377	0.338	0.138	X1	0.182	-0.373	-0.177
Y1	0.089	-0.045	-0.020	Y1	0.000	0.055	0.166	Y1	-0.057	0.166	0.019	Y1	-0.010	-0.110	-0.072
X2	0.175	-0.069	0.026	X2	0.000	0.119	-	X2	-	-	-	X2	-0.035	-0.205	0.005
Y2	-0.037	0.040	-0.163	Y2	0.000	-0.015	-	Y2	-	-	-	Y2	-0.015	0.055	-0.179
X3	0.207	-0.051	-0.033	X3	0.000	0.155	-	X3	-	-	-	X3	-0.068	-0.227	-0.072
Y3	-0.060	0.056	-0.140	Y3	0.000	-0.027	-	Y3	-	-	-	Y3	-0.017	0.086	-0.163
X4	-0.339	-0.169	0.518	X4	0.000	-0.369	-	X4	-	-	-	X4	0.333	0.240	0.700
Y4	-0.017	0.050	-0.034	Y4	0.000	0.010	-	Y4	-	-	-	Y4	-0.034	0.043	-0.005
X5	-0.485	-0.230	-0.093	X5	0.000	-0.534	-	X5	-	-	-	X5	0.460	0.339	-0.064
Y5	0.014	0.051	0.050	Y5	0.000	0.038	-	Y5	-	-	-	Y5	-0.051	0.015	0.072
X6	-0.548	0.197	-0.158	X6	0.000	-0.391	-	X6	-	-	-	X6	0.122	0.633	-0.423
Y6	-0.037	0.017	0.219	Y6	0.000	-0.020	-	Y6	-	-	-	Y6	0.006	0.047	0.294
X7	0.090	-0.245	0.049	X7	0.000	-0.039	0.153	X7	-0.265	0.153	-0.060	X7	0.163	-0.219	0.081
Y7	0.043	-0.071	-0.099	Y7	0.000	0.000	0.066	Y7	-0.083	0.066	0.113	Y7	0.038	-0.081	-0.152
X8	0.051	-0.188	0.045	X8	0.000	-0.047	0.083	X8	-0.203	0.083	-0.073	X8	0.135	-0.150	0.050
Y8	0.052	-0.088	-0.085	Y8	0.000	0.002	0.082	Y8	-0.098	0.082	0.126	Y8	0.048	-0.099	-0.083
X9	-0.036	0.033	0.032	X9	0.000	-0.016	-0.062	X9	0.036	-0.062	-0.068	X9	-0.009	0.053	0.003
Y9	-0.017	-0.057	0.026	Y9	0.000	-0.042	-0.037	Y9	-0.059	-0.037	-0.042	Y9	0.059	-0.014	0.042
X10	0.003	0.289	0.063	X10	0.000	0.144	0.039	X10	0.309	0.039	-0.034	X10	-0.251	0.154	0.085
Y10	0.050	0.012	0.096	Y10	0.000	0.051	0.105	Y10	0.013	0.105	-0.095	Y10	-0.036	-0.041	0.141
X11	0.166	0.718	0.071	X11	0.000	0.496	0.393	X11	0.759	0.393	0.101	X11	-0.709	0.229	0.157
Y11	-0.001	0.022	0.178	Y11	0.000	0.012	0.018	Y11	0.027	0.018	-0.235	Y11	-0.018	0.015	0.205
X12	-0.119	0.104	-0.538	X12	0.000	-0.059	-0.271	X12	0.109	-0.271	0.711	X12	-	-	-
Y12	-0.067	0.038	0.217	Y12	0.000	-0.037	-0.301	Y12	0.050	-0.103	-0.301	Y12	-	-	-
X13	0.229	-0.065	0.039	X13	0.000	0.167	0.438	X13	-0.088	0.438	-0.020	X13	-	-	-
Y13	-0.109	0.052	-0.050	Y13	0.000	-0.072	-0.206	Y13	0.058	-0.206	0.002	Y13	-	-	-
X14	0.182	0.030	0.123	X14	0.000	0.178	0.361	X14	0.028	0.361	-0.046	X14	-	-	-
Y14	0.088	-0.116	-0.359	Y14	0.000	0.014	0.123	Y14	-0.141	0.123	0.460	Y14	-	-	-
X15	0.224	-0.016	-0.030	X15	0.000	0.189	0.424	X15	-0.031	0.424	0.130	X15	-	-	-
Y15	0.009	0.038	0.165	Y15	0.000	0.029	0.035	Y15	0.046	0.035	-0.185	Y15	-	-	-
-	-	-	-	Size	1.000	0.000	-	-	-	-	-	-	-	-	-

adults and nymphs, and evaluate aggregation behaviours throughout their lifecycle to provide deeper insights into their ecological and evolutionary history.

Conclusion

In this study, we describe a new species, *Cretodorus lijuanae* **sp. nov.**, from the family Mimarachnidae, identified through both adult and nymphal fossils. Morphological and morphometric analyses of the adult body and wing vein structures support the classification of the specimen as a new species within the genus *Cretodorus*. Analysis of nymphal specimens found alongside adults in the same amber piece supports the identification of three nymphs of *C. lijuanae* **sp. nov.**, marking the first report of nymphal fossils belongs to the Mimarachnidae. Morphometric evaluations of the simplified wing veins within the genus emphasize the efficacy of this method for quantitatively assessing the characteristics of fossilized wing veins and should be applied to more complex wing venation patterns that can provided also more potential landmarks and accurate estimations of the forewing shape. We present a morphological framework for the forewings of the genus *Cretodorus* and compare the morphological characteristics between conspecific adult and nymphs. This establishes a preliminary reference framework for future identifications of *Cretodorus* adult and nymphs. These new fossils contribute to the diversity recorded in the Mesozoic fossil record of the Mimarachnidae and provide direct evidence of nymphal aggregation behaviour. This study underscores the necessity of continuing to search for syninclusions embedding adults and nymphs to enhance the description of extinct fossil taxa and to reveal more about their evolutionary and ecological dynamics.

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