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A new species and the first description of the female of *Fiaponeura* Lu *et al.* (Neuroptera: Psychopsoidea) from Cretaceous Kachin amber

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Lacewings (Insecta: Neuroptera) are a remarkable group of insects displaying astonishing diversity during the Jurassic and Cretaceous. Neuroptera is an order of holometabolous insects, which, together with Megaloptera and Raphidioptera, comprise the superorder Neuropterida (Engel *et al*., 2018). The morphologically diverse larvae of Neuroptera are known for their specialized sucking mouthparts for fluid feeding, as well as for their distinct life histories, such as trap builders (antlions), freshwater parasites (spongillaflies), and termite predators (beaded lacewings) (Oswald & Machado, 2018). The adults are usually predators, with some exceptions, and exhibit greatly reticulated wings, with variable sizes, shapes and coloration patterns. The order comprises *ca*. 6,000 extant species in 15 families, and the fossil record impressively adds 15 and 1,078 extinct families and species, respectively (Winterton *et al*., 2018; Oswald, 2024). During the past decades, extinct lacewings with long proboscides have been discovered in fossil records and placed in the superfamily Psychopsoidea. Investigating the role of these insects in pollination and examining the comparative morphological structure of mouthparts is paramount to our understanding of lacewing diversity, evolution, and function (Lu *et al*., 2016).

Species in Psychopsoidea have broad wings and abundantly branched venation. These lacewings contribute to a diverse palaeofauna, which include families such as Aetheogrammatidae, Kalligrammatidae, Osmylopsychopidae, and the enigmatic genus *Fiaponeura* Lu *et al*., 2016. *Fiaponeura* currently contains a single species, *F. penghiani* Lu *et al*., 2016, which was described based on the female holotype; subsequently, Liu *et al*. (2018) associated a male specimen to this species. The genus exhibits traits associated with the families Aetheogrammatidae and Kalligrammatidae, including the haustellate mouthparts and more than two oblique radial branches (ORBs) originating from radial anterior (RA) vein in the forewing. However, in contrast to members of these two families, the forewing of *Fiaponeura* has nygmata, trichosors, sparse crossvenation, and the posterior branch of MP lacks many distal pectinate branches (Lu *et al*., 2016). Due to this odd combination of characters, it has been challenging to establish the systematic position of *Fiaponeura*. Upon its description, the genus was placed in Psychopsoidea, as family *incertae sedis* (Lu *et al*., 2016). This position was later confirmed by the phylogenetic hypothesis proposed by Liu *et al*. (2018), who recovered the genus as the sister group to the clade containing Aetheogrammatidae + Kalligrammatidae, maintaining the placement of the genus *Fiaponeura* as *incertae sedis* to family.

Herein, despite the challenging placement of *Fiaponeura*, we describe a new species in the genus from Cretaceous Kachin amber. This description brings new insights into the phylogenetic position of this enigmatic genus and provides significant information about the previously unknown female genital structures.

Material and methods. The specimen was collected in Kachin state (26°0′0″N, 97°30′0″E), located in northern Myanmar. The Kachin Burmese amber is dated to about 98.8 Ma, suggesting a formation age in the Cenomanian period of the Late Cretaceous. The specimen is deposited in the American Museum of Natural History (AMNH), New York, USA, and it was collected and donated to the museum by Mr. Keith Luzzi. The donation is recorded in 2016. It was examined using a Wild Heerbrugg M7 stereomicroscope during a visit to the AMNH in May 2023. Surfaces of the amber inclusion are trimmed, ground, and polished on each side. Photographs were taken at multiple focal points and stacked using the following equipment: Canon EOS 40D Macro Photo and a Zeiss AXIO Zoom V16 stereomicroscope equipped with an attached camera.

Terminology for the wing venation follows Breitkreuz *et al*. (2017) and for the genitalia follows Aspöck and Aspöck (2008). Abbreviations used are as follows: 1A, 2A, first and second anal veins; Cu, cubital vein; CuA, cubitus anterior; CuP,

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cubitus posterior; M, medial vein; MA, media anterior; MP, media posterior; RA, radial anterior; RP, radial posterior.

Order Neuroptera Linnaeus, 1758
Superfamily Psychopsoidea Handlirsch, 1906
Family *Incertae sedis*
Genus *Fiaponeura* Lu *et al*., 2016
Species *Fiaponeura maculipennis* **sp. nov.**

Type material. Holotype female from Myanmar: Kachin Cretaceous (AMNH Bu-KL-20-30), without additional verbatim data on label. The amber inclusion displays an almost complete lacewing adult, missing half of the head and the mouthparts. It also possesses syninclusions of parts of one Diptera, one Psocodea and several small Coleoptera and Hymenoptera. The amber is polished in the form of an irregular rectangle, and it is clear and transparent.

Etymology. The specific name '*maculae*' means 'spots', and '*pennis'* means 'wing' in Latin. When combined, the two words form 'maculipennis', or spotted wings. The species name is in reference to the large brown dots on the wings.

Diagnosis. *Fiaponeura maculipennis* **sp. nov.** differs from *F. penghiani* based on forewing venation and the presence of tibial spurs. The forewing of the new species has large brown dots, as opposed to the transverse bands of *F. penghiani*. It has four ORBs while *F. penghiani* has five or six. Finally, *F. maculipennis* **sp. nov.** lacks the tibial spurs present in *F. penghiani*.

Description. Length: body 8 mm, forewing 11 mm, hind wing 10 mm. Head damaged, only half of the dorsal part remains, eyes large, ocelli absent, antennae filiform, hairy and longer than head and thorax combined. Thorax also damaged, but pronotum seems elongated. Forewing: broad with the apical region rounded; membrane mostly hyaline with dark rounded marks, three large marks at the costal area, posterior margin, and central area; and a few smaller marks at the apex. Basal nygma and trichosors present. Costal area narrowed at the base but greatly broadened medially; subcostal veinlets long, curved, and dichotomously branching apically. Subcostal space with basal half dark, and with a total of seven crossveins. Four ORBs, first one bifurcating medially; second ORB forking near the margin; third ORB dichotomously branching basally, and both branches dichotomously forking medially in the right wing; third ORB of the left wing apparently branching near wing margin; fourth ORB with four major branches. Area between RA and the fourth ORB with five crossveins. M vein forking into MA and MP basally; MA forking medially, as well as its anterior branch, while posterior branch only forks near the wing margin. MP forking basal to MA fork, with its anterior branch forking medially. MP posterior branch of the right wing only forking near the wing margin, while it forks medially in the left wing. Cu vein forking into CuA and CuP basally, with five crossveins between them in the right wing, it is unclear in the left wing; CuA with four major branches distally; CuP dichotomously branching medially. 1A deeply forked, 2A with a small fork distally. Hind wing: shorter and narrower; with more dark marks specially at the distal portion. Venation similar to forewing except by the MA fused to RP at the base; presence of the sigmoid vein, 1r-m, stem of MA; RP with six to seven branches, MP deeply dichotomously forked, and each of its branches forking medially; CuP simple or dichotomously branched and 1A simple. Legs slender and hairy; femur almost half the size of the tibia; tibia much longer than other segments; tibial spurs absent; tarsi with five segments, the basal one approximately with the same length as the other four combined; pretarsus with two curved claws and an arolium. Abdomen elongated. Female terminalia: sternite 7 broad; tergite 8 mostly membranous with a narrow sclerotized band posteriorly; ectoprocts hairy and narrowing apically, nearly fusiform, callus cerci present; tergite 9 ventrad to ectoproct, slightly smaller than gonocoxite 9; gonocoxite 9 ovoid.

Remarks. Even though the head is damaged, preventing the examination of the mouthparts, the new species described here clearly belongs to *Fiaponeura* based on the elongate pronotum, the shape and marks of the wings, the broad costal space, the distal fusion of Sc and RA, the forewing with more than two ORBs, and the long and haired antennae and legs. However, *F. maculipennis* **sp. nov.** can be easily distinguished from *F. penghiani* based on the overall marking patterns on the wings, the lower number of ORBs, and by the absence of the tibial spurs, as mentioned in the diagnosis section above.

Discussion. The familial affiliation of *Fiaponeura* has not yet been clarified since the original description of the genus. The placement of this genus in Psychopsoidea by Liu *et al*. (2018) is supported primarily by the characters of wing shape and venation, including the broad wing and profusely pectinated veins. However, these characters do not represent strong evidence of evolutionary affinity because they may be present in other lacewing superfamilies outside of Psychopsoidea, for example, Osmyloidea or Hemerobioidea. Moreover, the close relationship of *Fiaponeura* with Kalligrammatidae is supported by only two mouthpart characters (*i.e*., the type of mouthpart and the shape of the terminal segment of the maxillary palp), while the long mouthparts forming a proboscis are also present in Paradoxosisyrinae, which is tentatively placed in the extant family Sisyridae (Lu *et al*., 2016; Lu & Liu, 2021). Therefore, we still lack the crucial evidence to unequivocally resolve the phylogenetic placement of *Fiaponeura*.

The description of the female genitalia of *Fiaponeura maculipennis* **sp. nov.** provides novel data for reevaluating the familial placement of this genus. Compared to the kalligrammatid species *Oregramma illecebrosa* Yang, Wang, Labandeira, Shih & Ren (Yang *et al*., 2014), the female genitalia of *Fiaponeura* have a relatively shorter ovipositor. However, when compared to species of Cretanallachiinae, *Cretanallachius magnificus* Huang *et al*. (Chang *et al*., 2018) for example, the ovipositor is of similar size to that of the new species. Notably, tergum 9 in *F. maculipennis* **sp. nov.** is simple and not expanded posteriad into a pair of valves, which largely cover the gonocoxites 9 as in the species of Cretanallachiinae (Liu *et al*., 2018). Moreover, the gonostyli 9 are also absent in *Fiaponeura*. Thus, the female genitalia of *Fiaponeura* consist

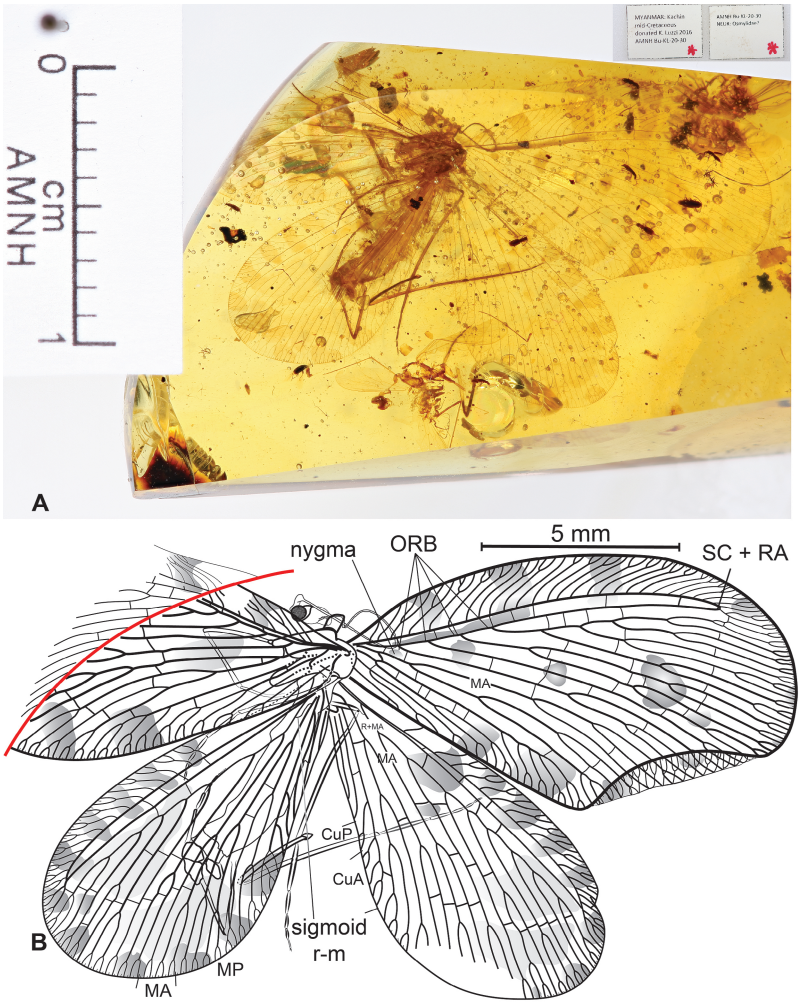

FIGURE 1. *Fiaponeura maculipennis* **sp. nov.**, female holotype. **A**, Habitus photo, with label, laterodorsal view. **B**, Illustration of the habitus, detailing the wings. Abbreviations: ORB, Oblique radial branch; SC + RA, Fusion of subcostal and radial anterior veins.

of a unique combination of plesiomorphic (*i.e.*, short ovipositor and simple tergum 9) and apomorphic character (*i.e.*, absence of gonostyli 9). Therefore, based on characters of female genitalia, we can unambiguously conclude that *Fiaponeura* at least does not belong to Cretanallachiinae or Oregrammatinae.

This genus may represent an independent family distinguished from all known families of Psychopsoidea or even of Neuroptera. Nevertheless, we could not exclude the possibility of the kalligrammatid affiliation of *Fiaponeura* as the female genitalia may greatly vary among subfamilies in a same family. A similar case is found in Mantispidae, in which the subfamily Symphrasinae has an elongated ovipositor, but the other subfamilies have short valvate female gonocoxites 9 (Aspöck & Aspöck, 2008); for an alternative classification see (Ardila-Camacho *et al.*, 2021). Moreover, the general configuration of the male genitalia of *Fiaponeura* appears to be similar to that of Cretanallachiinae (Liu *et al.*, 2018). Unfortunately, the male genitalic characters of the other subfamilies of Kalligrammatidae and other extinct families of Psychopsoidea are unknown. When described, those male genitalic characters will likely provide additional important evidence to decipher the familial placement of *Fiaponeura*.

Fiaponeura maculipennis **sp. nov.**, a new species with still uncertain familial affiliation, is described from Cretaceous Kachin formation, in Myanmar. The well-preserved holotype of the new species allowed for detailed examination of the female genitalic structures, revealing a plesiomorphic ovipositor and tergum, and the apomorphic absence of the gonostyli 9. Based on current knowledge and modest available morphological evidence, the placement of *Fiaponeura* within Neuropterida still remains elusive. However, based on female genitalic characters, we conclude that the genus does not belong in the subfamilies Cretanallachiinae or Oregrammatinae (Kalligrammatidae).

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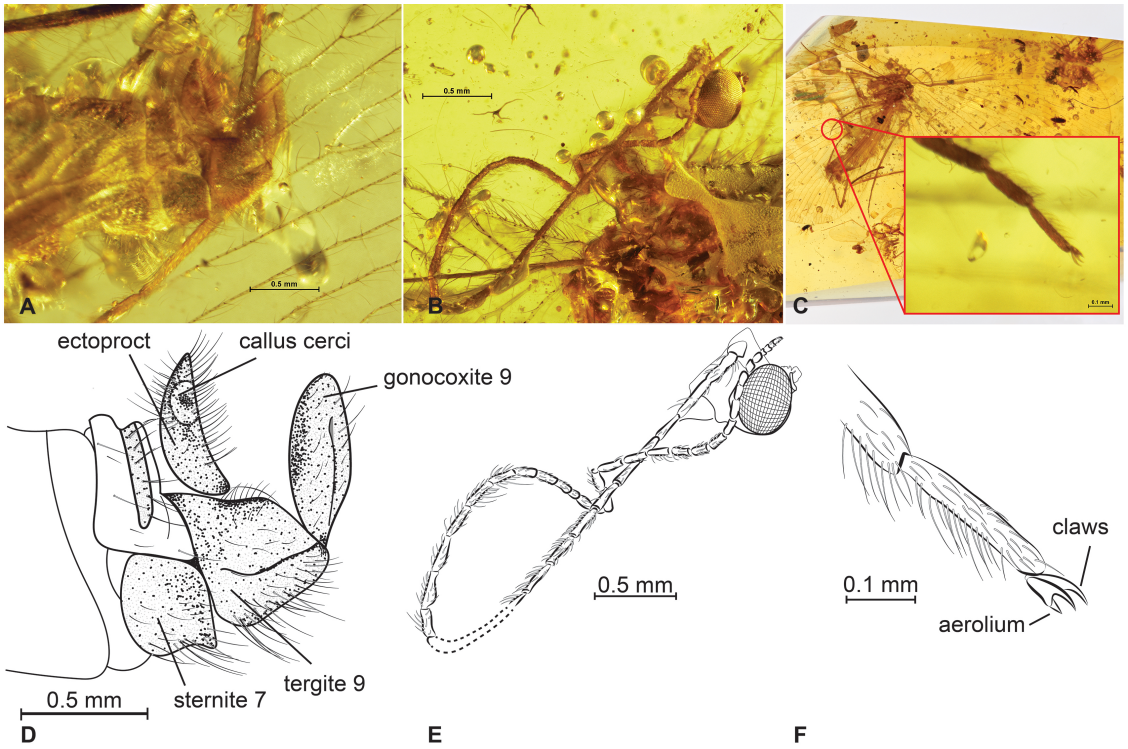

FIGURE 2. *Fiaponeura maculipennis* **sp. nov.**, female holotype. **A**–**C**, Photo. **D**–**F**, Illustration. **A**, **D**, Genitalia. **B**, **E**, Head with antennae. **C**, **F**, Habitus, highlighting the tarsomere with claws and the aerolium. Photos **A**–**C** by Agnieszka Pierwola.

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