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Immature planthoppers had longer mouthparts 100 million years ago as exemplified by quantitative morphology

Hemiptera, Fulgoromorpha

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Quantitative morphology is a powerful tool to assess fossil biodiversity, circumventing many difficulties of taxonomic approaches. The method is especially useful when dealing with fossil immature insects, which are often difficult (to impossible) to determine taxonomically. Based on 45 fossil and 258 extant specimens of Fulgoromorpha (Insecta, Hemiptera), we performed a shape analysis of their heads and mouthparts. Our results show a greater morphological diversity in extant forms, with varied relative head widths and lengths, and beak lengths. The results also show a lost morphology, only found in the fossil specimens, which had a very narrow head with extremely long beak. This shift in shapes could be linked to a distinct lifestyle during the Cretaceous followed by the rise of flowering plants, which are currently the main hosts of these insects. These findings add up to an increasing number of Mesozoic insects described with unusually elongate body parts.

Resumo: Morfologia quantitativa é uma poderosa ferramenta para avaliar a biodiversidade fóssil, contornando as dificuldades dos métodos taxonômicos tradicionais. O método é especialmente útil no estudo de insetos imaturos, devido à frequente dificuldade na identificação taxonômica desses organismos. A partir de 45 espécimes fósseis de Fulgoromorpha (Insecta, Hemiptera) e 258 viventes, realizamos uma análise da forma de suas cabeças e aparelho bucal. Os resultados obtidos mostram uma maior diversidade morfológica nas formas atuais, com maior variação na largura e comprimento da cabeça e comprimento do rostro. Os resultados também indicam um tipo de morfologia que foi perdido, apenas encontrado nos espécimes fósseis, com uma cabeça muito estreita e um rostro extremamente longo. Esta mudança de forma pode estar relacionada com uma mudança nos hábitos de vida durante o Cretáceo, coincidindo com a radiação das angiospermas que são atualmente as principais hospedeiras desses insetos. Nossos resultados se somam a um número crescente de descrições de insetos do Mesozóico com partes do corpo notavelmente alongadas.

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Introduction

It is well known that we are currently undergoing a human-driven decline of the diversity of Insecta, with many studies documenting the loss of species, habitats, and ecosystem functions (Hallmann et al. 2017, Sánchez-Bayo & Wyckhuys 2019, Wagner et al. 2021). This ongoing extinction is recognised based on multiple available methods. Yet, we are much more limited when it comes to measuring the diversity in the past ages. Estimating the palaeo-diversity is particularly useful to understand the history (and the future) of the planet (Ceballos et al. 2015, Haug et al. 2021a) and the context in which the extant organisms evolved, either increasing or decreasing their diversity over time.

When approaching changes in biodiversity over time we face a challenge, as biodiversity is often estimated by measuring species richness (Maclaurin & Sterelny 2008, Borkent et al. 2018, Nel et al. 2018). Yet, identifying fossil species is often challenging, given the variable preservation condition of fossilized animals (Badano et al. 2018), the limitations of taxonomy to deal with early representatives of a lineage (Donoghue 2005, Donoghue & Purnell 2009) and the general problem of species concepts lacking well-delineated time aspects (Haug & Haug 2017). An alternative to counting species is to analyse the morphological diversity, not related to species richness but disparity (Nel et al. 2018). By quantifying and comparing the shape of the body, or of specific structures in fossilized animals, it is possible to work around the taxonomic limitation and estimate the functional diversity, since the form and the function of morphological structures are intimately interconnected (Nel et al. 2018, Herrera-Flórez et al. 2020, Haug et al. 2021a, 2023a, b, Baranov et al. 2022, Amaral et al. 2023). For representatives of the group Insecta, mouthparts and associated structures provide a useful mean for assessing morphological diversity (Haug et al. 2022a, b) and by this, ecological diversity, as they are directly related to the habits of an organism and its ecological interactions.

For instance, the dimensions and shape of the components forming a piercing apparatus can indicate if a given individual feeds on hemolymph, blood, nectar, or sap, and what are some of the characteristics of the hosts upon which it feeds (Lee & Craig 1983, Krenn 2019, Khramov et al. 2020). Since niche differentiation and specialization are drivers of speciation (Via et al. 2000, Rundle & Nosil 2005), it is expected that the variation of morphology, also influenced by neutral evolution, should as well reflect taxonomic diversity to some degree.

Hemiptera is an ingroup of Pterygota, the group of "flying insects" (although many do not fly, at least during major parts of their lives). Hemipterans are easily recognizable by their distinctive piercing and sucking mouthparts (Shcherbakov & Popov 2002) forming a functional beak (see Material and Methods section for terminological issues on the use of "beak"). The first hemipterans appeared and radiated during the late Palaeozoic, and underwent a loss of diversity during the Permian-Triassic mass extinction, with a new major radiation by the mid-Triassic and another in the Cretaceous (Shcherbakov 2002, Shcherbakov & Popov 2002, Szwedo 2008, Chen 2022, Bourgoin & Szwedo 2022, 2023, Bucher et al. 2023). One of the oldest branches in Hemiptera, originated in the late Paleozoic, is that of Fulgoromorpha, with its representatives commonly called planthoppers. They are distinguished from other hemipterans by several characters: 1) small antennae (with specialized sensory structures), usually situated functionally below the compound eyes; 2) a bristle-like distal region of the antennae; 3) the proximal leg elements of the hindlegs (metacoxae) are not jointed off from the sternal sclerites of the thorax; 4) the presence of sensory pits along the body (specially on immatures); and 5) the lack of a row of strong setae on the hindleg tibia (O'Brien & Wilson 1985, Shcherbakov & Popov 2002, Wilson 2005). The history of Fulgoromorpha is intimately associated with that of land plants, on which they spend most of their lives, where they breed and feed on plant fluids (Shcherbakov 2000). Their specialized mouthparts form a tipped tube, with elongated piercing mandibles and maxillae (together termed as stylets), ensheathed by an articulated labium (Shcherbakov & Popov 2002). Although common in the fossil record (especially in amber deposits), and ecologically important, immatures of Fulgoromorpha have been, so far, little studied (Szwedo et al. 2004, Szwedo 2009), possibly due to the difficulties of dealing with immatures in a taxonomic frame.

Here we compare (mostly) immature planthoppers in the past and today with quantitative morphology. We do this by analysing the morphology of the mouthparts of planthoppers from Kachin amber, Myanmar, and those of extant specimens in a quantitative frame. We aim to estimate and compare the diversity of fulgoromorphans in the Cretaceous with the one of present times. Similar approaches applied to other ingroups of Pterygota have demonstrated that they can circumvent challenges of taxonomic uncertainty and can pick up signal that cannot be recognised by taxonomic methods (summed up in Haug et al. 2023a). Therefore, this study concentrates on these quantitative aspects instead of taxonomic issues, such as formally naming or classifying specimens.

Material and methods

Material examined

The dataset includes fossil and extant fulgoromorphan specimens which could be examined in ventral view and provided access to the general shape of the head and the mouthparts. In total, 45 fossil and 258 extant specimens were analysed. Only specimens that allowed a good ventral view on the mouthparts and had a complete beak were used.

Four of the fossil specimens were retrieved from the literature (Szwedo 2009, Emeljanov & Shcherbakov 2018, Jiang et al. 2019; see Electronic Supplement 1). The remaining ones were directly examined from inclusions of Cretaceous Myanmar amber deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany. Each amber piece received the repository code PED followed by a unique number. All these specimens come from Kachin amber, Myanmar, and are about 100 million years old (Cretaceous). Specimens were legally purchased on the trading platform ebay.com from the trader burmite-miner.

More than 100 specimens were directly examined, only the ones in appropriate orientation were further considered. Of the extant specimens, 221 were retrieved from the website bugguide.net (Electronic Supplement 1) and 37 from the literature (Wang & Liang 2011, Meng & Wang 2012, Rahman et al. 2012, Constant 2015, Constant & Pham 2019, Lv et al. 2021; see Electronic Supplement 1).

Identification and terminology

The directly studied amber specimens were identified as representatives of Fulgoromorpha, based on publications of various sources (O'Brien & Wilson 1985, Yang & Yeh 1994, Shcherbakov & Popov 2002, Wilson 2005, Zenner et al. 2005, Stöckmann et al. 2013). Specimens from other sources were previously identified to variable levels (Electronic Supplement 1).

Terms were based on general insect terminology (as in Snodgrass 1935) but are amended by neutral terms well established for Euarthropoda. The mouthparts of fulgoromorphans (hemipterans in general) form a distinct functional structure. This structure has often been addressed as "proboscis" or more often "rostrum". Unfortunately, this term has implications that are in fact not fulfilled by the compound mouthparts in fulgoromorphans. "Rostrum", in representatives of Vertebrata, many lineages of Insecta, and many other crustaceans refers to an anterior structure that is forward-projecting; the term rostal is equivalent to anterior in these cases. In fulgoromorphans, the mouthparts are neither anterior-, nor forward-projecting. We will therefore use the alternative term "beak" which is commonly used in hemipterans (e.g., Labandeira 1997, 2019, Labandeira & Eble 2000, Grimaldi & Engel 2005, Cirino & Miller 2017, Allen et al. 2021).

The beak of hemipterans is a compound piercing-sucking structure formed by the mouthparts: labrum, mandibles, maxillae, and labium (Krenn 2019, Wang et al. 2019, 2020, Zhai et al. 2023). The stylets, which are the sclerotized parts inserted in the plant tissues, are composed by the mandibles and maxillae. In the fossils these are often visible as they relax in the dead animal.

The length of each specimen was measured from the top of the head to the posterior end of the trunk. Some of the specimens might represent exuviae, and some are partly incomplete. Length is a rather reliable measure for exuviae, while width becomes more affected by the moulting process.

Image acquisition and processing

Amber inclusions were documented on a VHX-6000 digital microscope, following the procedures by Haug & Haug (2019). Images were post-processed in Adobe Photoshop CS2. Colour-markings indicate visible joints and should allow the reader to understand our interpretation of structures used for further analysis. Colours were chosen to maximise the contrast. Similar colours do not always indicate correspondence of structures (especially concerning the leg elements).

Outlines of head and beak were redrawn in Inkscape 1.2. Only half of the head and beak (right or left half) was outlined, straightened, and then mirrored (Haug et al. 2021a).

Shape analysis

The shape analysis employs the principles of Elliptic Fourier transformation to translate the outlines (see point above) into a series of numbers that could be further analysed with multivariate statistic (in this case, Principal Component Analysis or PCA). The shape analysis with a final data set of 303 specimens including 45 fossils from the Cretaceous and 258 extant specimens was performed using the software package SHAPE (Iwata & Ukai 2002). Similar analyses were performed in earlier studies (see e.g., Haug et al. 2020a, 2021a, 2023a, Baranov et al. 2022 for more details).

The fossil subsample includes immatures of various instars. These immatures were available in larger quantities (several hundreds were inspected, the ones in proper orientation were chosen for documentation), while adults in the right orientation appeared much rarer and were not considered. Lumping the instars together was done purposefully in order to consider the entire range of morphologies of immatures.

For the extant side, the full range was considered, including adults. This approach was chosen to explore if certain aspects of heterochronic shifts could be observed.

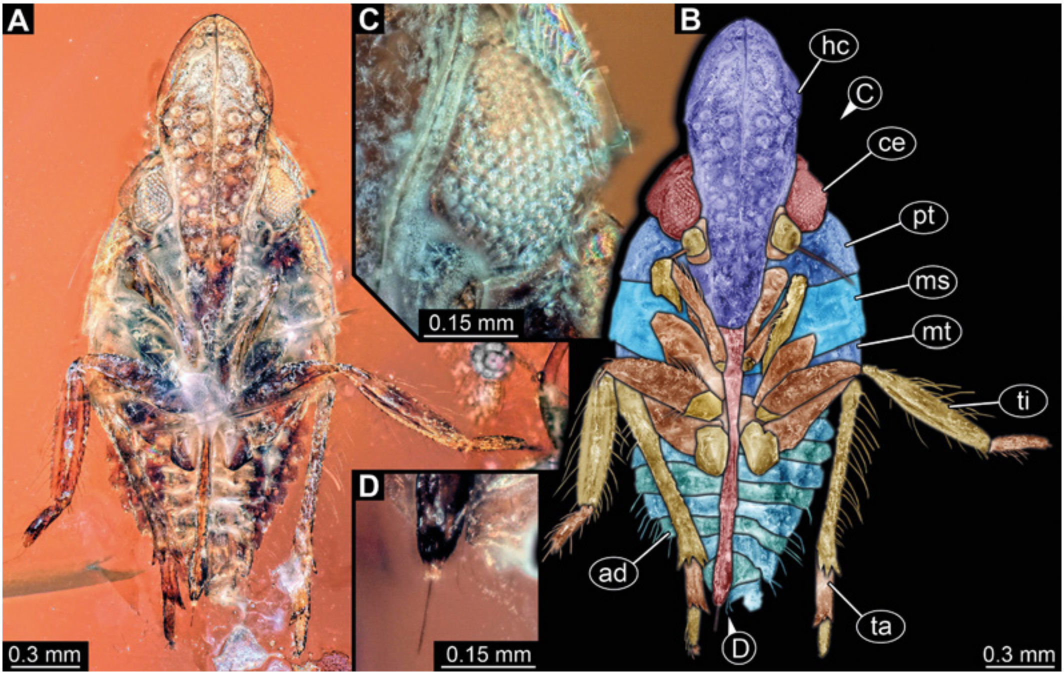

Fig. 1. Fulgoromorphan preserved in Cretaceous Kachin amber, Myanmar, specimen 0267, PED 0959. **A.** Overview in ventral view. **B.** Colour-marked version of A. **C.** Close-up on compound eye. **D.** Close-up on stylet. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

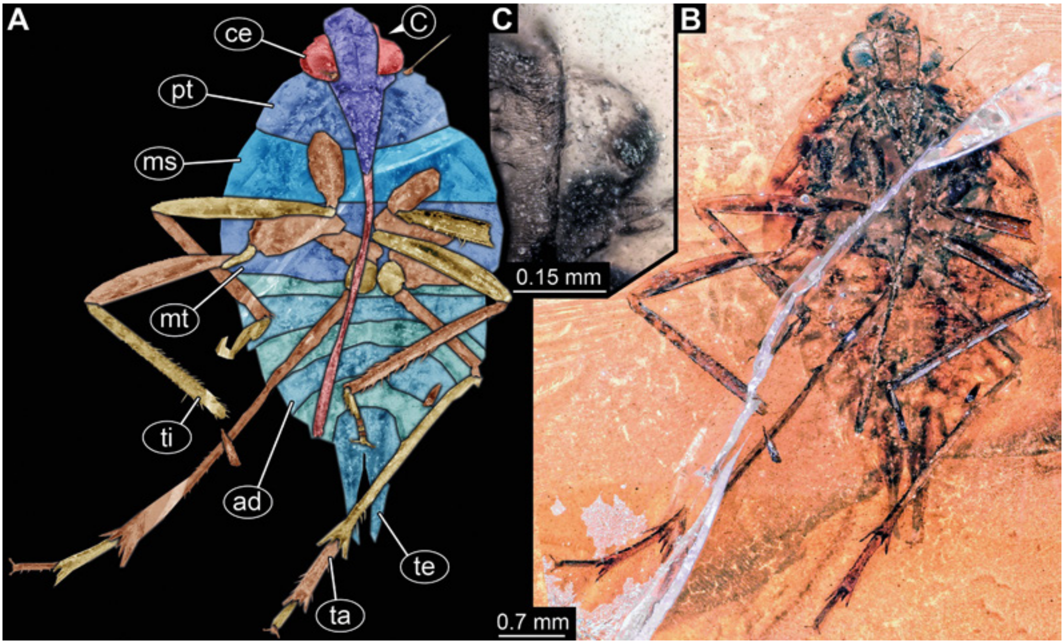

Fig. 2. Fulgoromorphan preserved in Cretaceous Kachin amber, Myanmar, specimen 0266, PED 0958. **A.** Colour-marked version of B. **B.** Overview in ventral view. **C.** Close-up on compound eye. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; te, trunk end; ti, tibia.

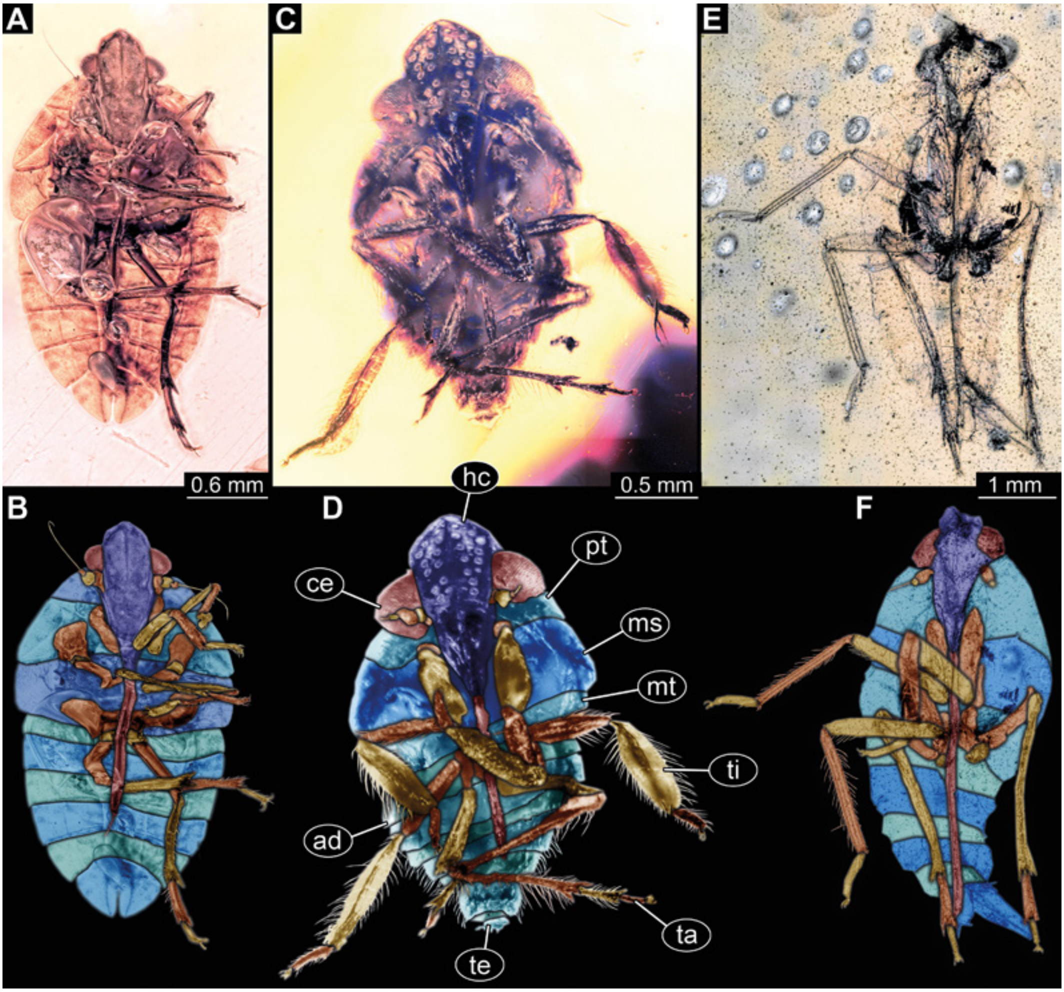

Fig. 3. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar. **A, B.** Specimen 0265, PED 0888. **C, D.** Specimen 0270, PED 1120. **E, F.** Specimen 0263, PED 0288. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; te, trunk end; ti, tibia.

Results

Brief description of the inclusions

1. Specimen 0267 (PED 0959): Almost completely preserved (Fig. 1A–C). Small cloudy areas at the specimen prevent a better view of the transition from clypeus to beak. The pedicels (second element of antenna) are relatively enlarged. The beak extends to the tip of the abdomen. The stylets inside the labium extend even further (Fig. 1D). Parts of the tibiae and tarsi of the forelegs are missing. The length of the specimen is about 1.80 mm.
2. Specimen 0266 (PED 0958): Almost completely preserved (Fig. 2). A crack in the amber runs across the specimen (Fig. 2B) covering a small part of the thorax segments and legs, and may have caused a separation of the leg elements. The tibia and part of the femur of the right foreleg are absent. The tarsus of the right foreleg is present but not connected to the other parts of the leg. The tarsus of the left midleg and the tibia of the left hindleg are also separated. The length of the specimen is about 4.75 mm.

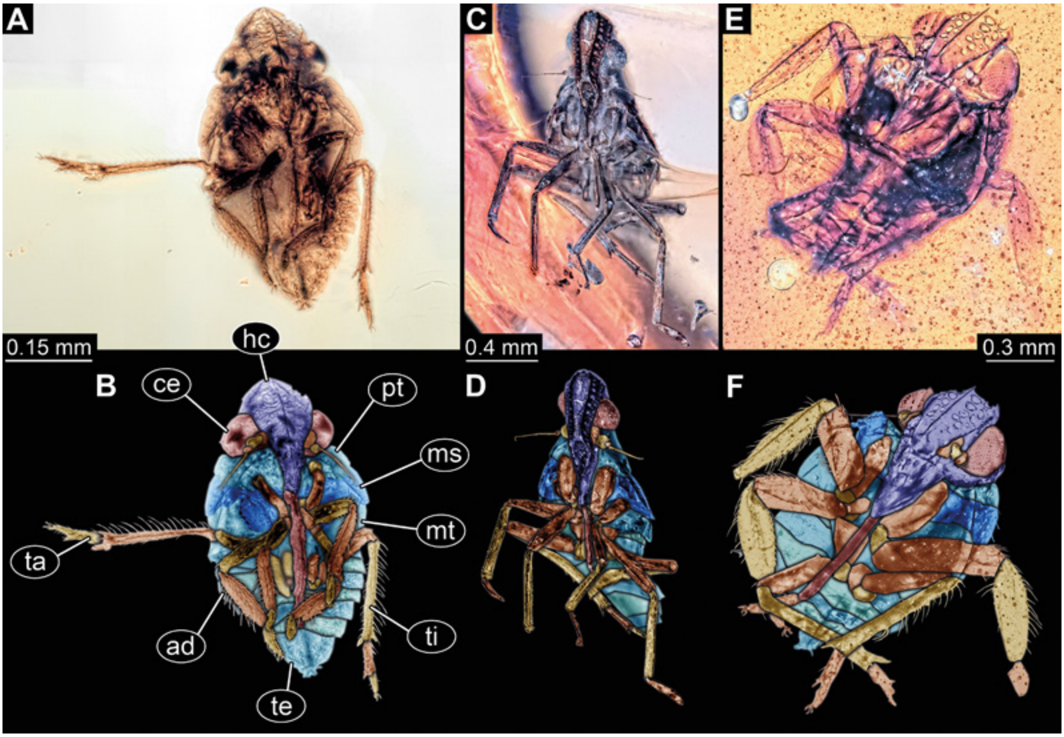

Fig. 4. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0287, PED 1983. **C. D.** Specimen 0286, PED 1982. **E, F.** Specimen 0279, PED 1719. **A, C, E.** Overview in ventral view. **B, D, F**. Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; te, trunk end; ti, tibia.

3. Specimen 0265 (PED 0888): Completely preserved (Fig. 3A, B). The view is partly disturbed by bubbles inside the amber partially blocking the view on the beak and right side of the specimen as well as on parts of the hindleg. The stylets extend beyond the labium. The left tibia of the midleg as well as one of the air bubbles partially block the view of the labrum and labium. The length of the specimen is about 2.90 mm.
4. Specimen 0270 (PED 1120): Blurred, but fully preserved (Fig. 3C, D). The view of the beak is blurred at the middle. The right foreleg partially blocks the view of the labium as well as tibia of the right hindleg. The fore- and midleg tibiae have a foliaceous or leave-like structure. The length of the specimen is about 2.34 mm.
5. Specimen 0263 (PED 0288): Bubbles and debris hamper the view of the specimen. The thorax and abdomen are mostly decomposed and transparent (Fig. 3E, F), possibly due to the specimen representing an exuvia. The antenna on the right side is missing. The beak is partially decomposed but the stylets are present and extend almost to the tip of the abdomen. The right hindleg is missing. The length of the specimen is about 6.0 mm.
6. Specimen 0287 (PED 1983): Fully preserved (Fig. 4A, B). The labium is partially decomposed and damaged, but the beak is largely preserved. The view of the thorax and abdomen is partially blurred by foggy regions in the amber. The length of the specimen is about 0.5 mm.
7. Specimen 0286 (PED 1982): Largely well preserved (Fig. 4C, D). The view of the metathorax is mostly blurred, caused by distortions of the amber and a backwards bending of the abdomen. The view on the abdomen is blurred as well. The view on the beak is partially blurred by a crack in the amber. The left foreleg tarsus is missing. The view on the hind coxa is blurred by a crack in the amber. Due to the backwards bending of the abdomen, the total length of the specimen could not be measured.

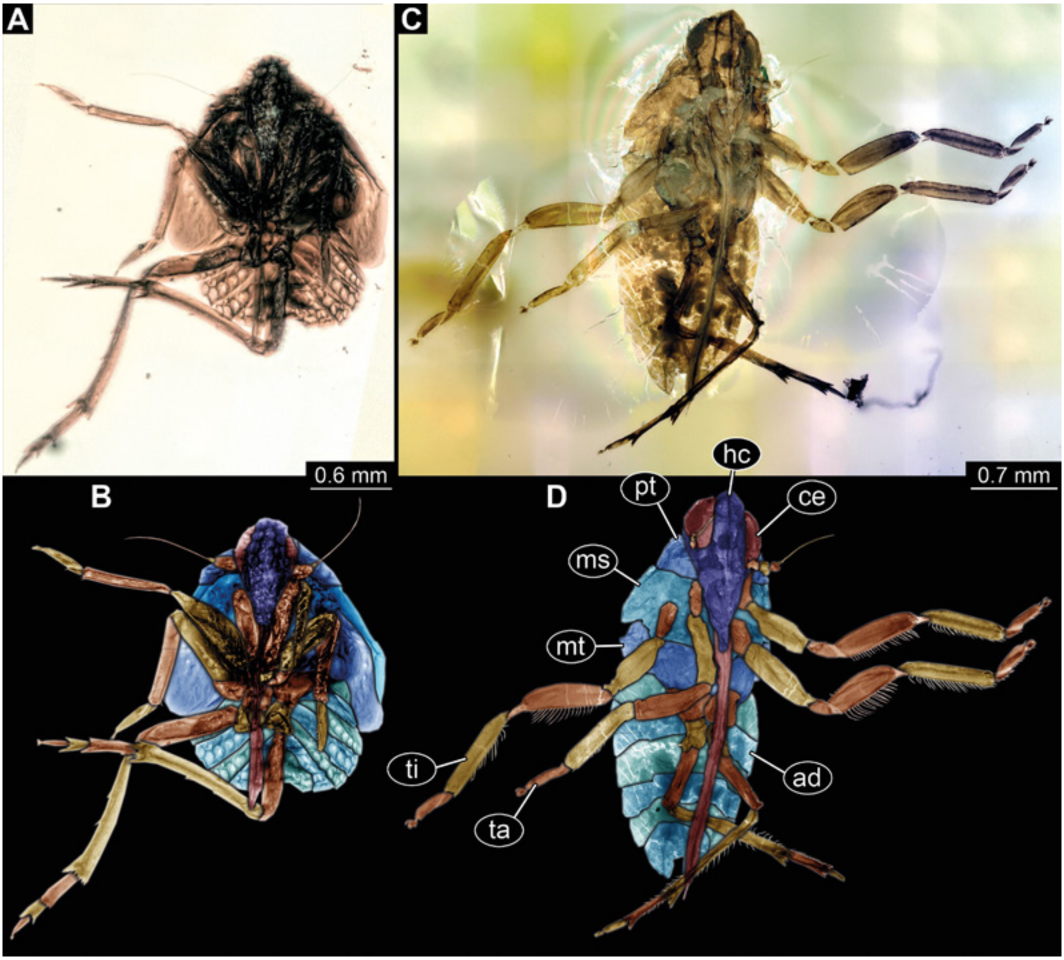

Fig. 5. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0275, PED 1284. **C, D.** Specimen 0268, PED 1006. **A, C.** Overview in ventral view. **B, D.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

8. Specimen 0279 (PED 1719): Largely well preserved (Fig. 4E, F). The overall view on the specimen is hampered by air bubbles, debris, and particles in the amber. The head capsule is damaged. The prothorax is ripped on the left side. The meso- and metathorax are partially ripped as well. The view on the beak is blurred. The stylets extend beyond the labium. The left foreleg tarsus is missing, as well as the entire right midleg. The length of the specimen is about 1.44 mm.

9. Specimen 0275 (PED 1284): Fully preserved, but darkened at head capsule and thorax (Fig. 5A, B). Compound eyes appear damaged. The head capsule and the thorax are partially not accessible due to dark areas. The beak extends beyond the abdomen. The abdomen is compressed and has numerous pores. The distal portions of the tibiae of fore- and midlegs have a spine-like extension (spur). The length of the specimen is about 1.98 mm.

10. Specimen 0268 (PED 1006): Fully preserved (Fig. 5C, D). The view on the thorax is foggy and the abdomen is partially torn. The beak is well-preserved and extends beyond the abdomen. The stylets also extend beyond the labium. Fore- and midlegs are almost separated at each joint and widespread. The amber is almost clear, but there are cracks around the specimen. The length of the specimen is about 3.97 mm.

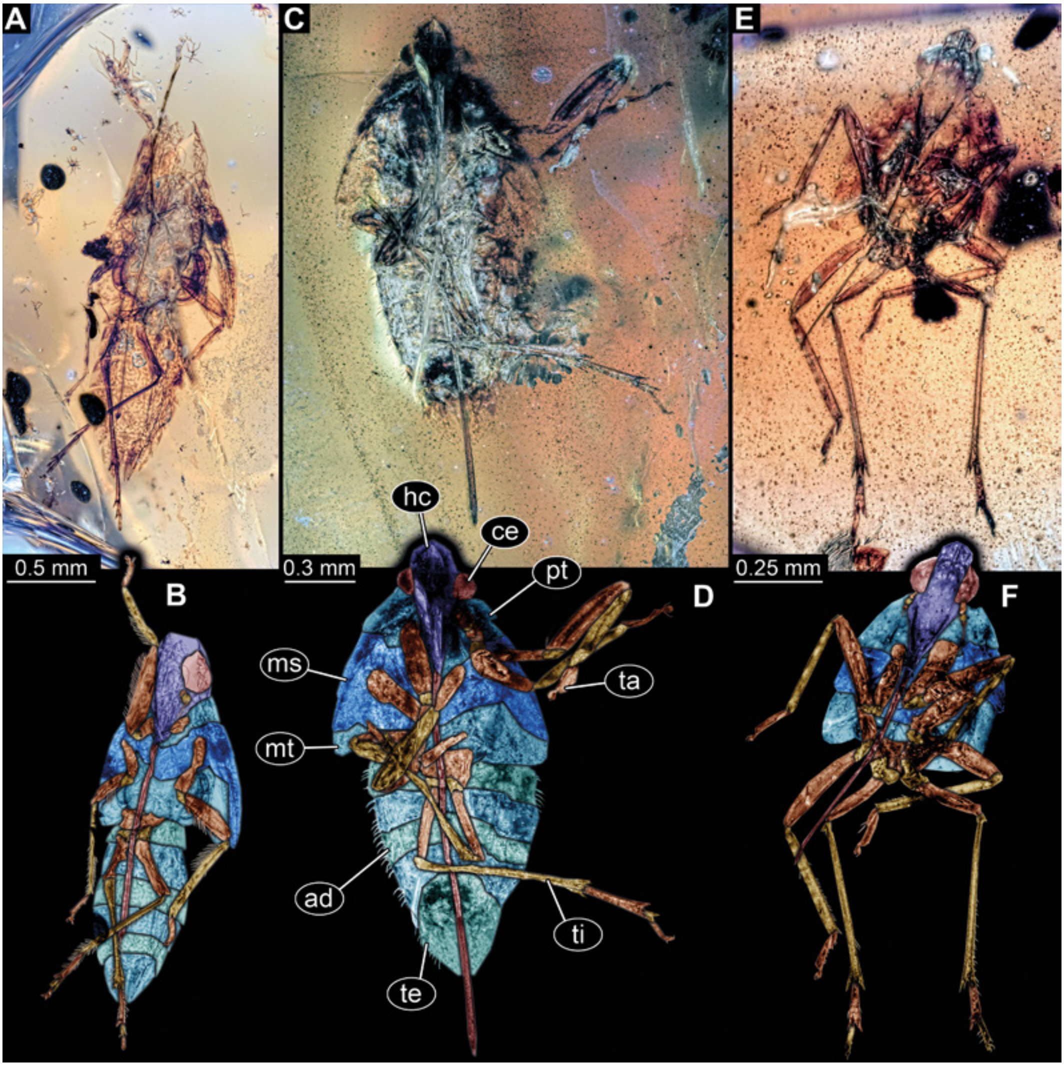

Fig. 6. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0288, PED 1988. **C, D.** Specimen 0280, PED 1897. **E, F.** Specimen 0269, PED 1011. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; te, trunk end; ti, tibia.

11. Specimen 0288 (PED 1988): Almost completely preserved (Fig. 6A, B), but possibly representing an exuvia. A crack inside the amber as well as particles, debris, and air bubbles restrict the view on parts of the specimen. The head capsule is damaged and ripped open, and the thorax is partially decomposed. Part of the thorax is blurred, caused by bubbles. The beak is well preserved and accessible. The prothoracic leg on the right side is missing. The length of the specimen is about 2.01 mm.
12. Specimen 0280 (PED 1897): Almost completely preserved (Fig. 6C, D). The view on the specimen is considerably hampered by cracks, bubbles, and small parts of debris inside the amber. The beak extends far beyond the abdomen. The length of the specimen is about 1.80 mm.
13. Specimen 0269 (PED 1011): The view on the specimen is partially hampered by bubbles and debris (Fig. 6E, F). The head capsule, as well as the beak, are well preserved. The abdomen is

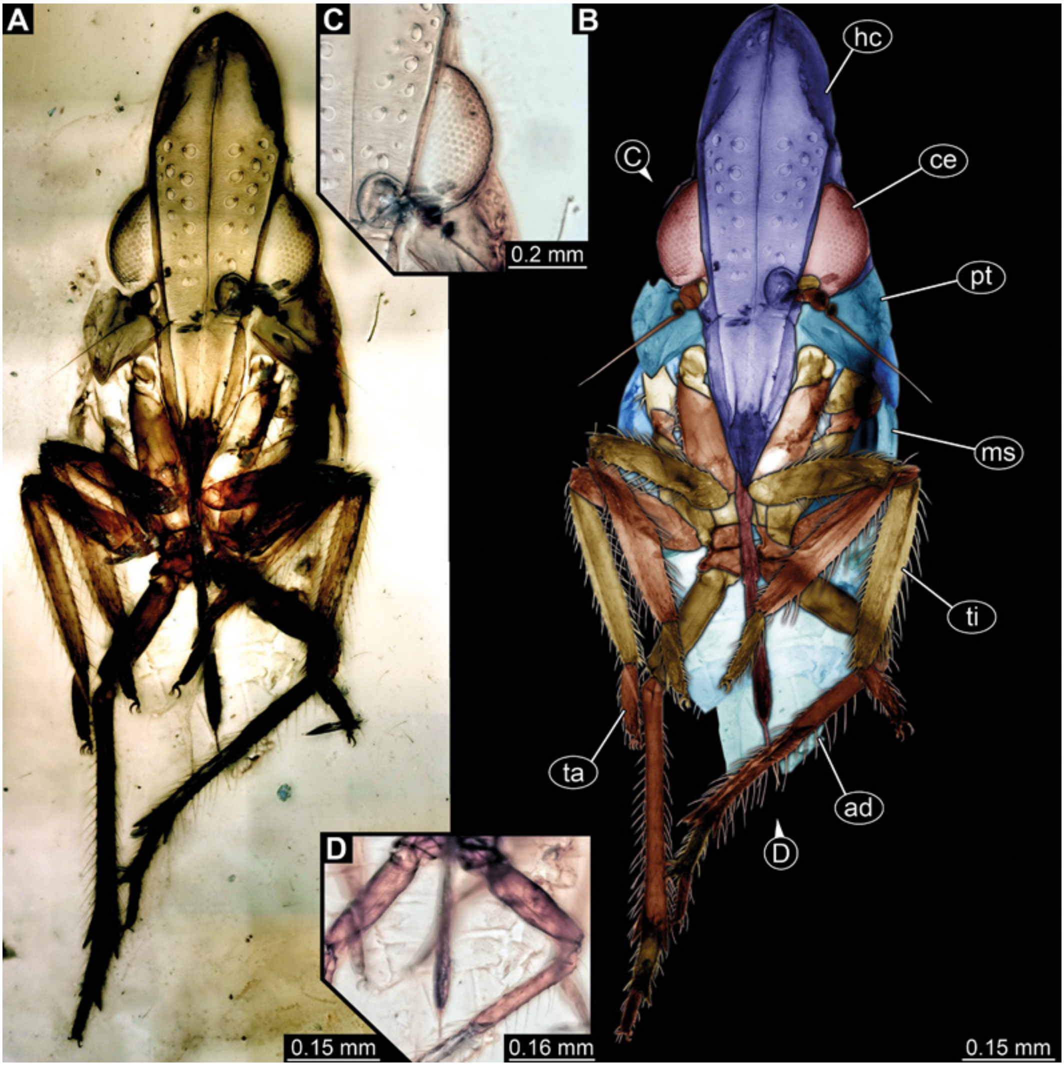

Fig. 7. Fulgoromorphan preserved in Cretaceous Kachin amber, Myanmar, specimen 0276, PED 1516. **A.** Overview in ventral view. **B.** Colour-marked version of A. **C.** Close-up on compound eye. **D.** Close-up on stylet. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

missing, possibly due to the specimen representing an exuvia. The labium is very slim, extending far beyond the thorax. The right foreleg tarsus cannot be seen because of interfering particles. The length of the specimen could not be measured due to the missing abdomen. The length of the specimen without the abdomen is about 0.66 mm.

14. Specimen 0276 (PED 1516): Almost completely preserved (Fig. 7). The abdomen is mostly transparent. The head capsule is longer than wide, clypeus ornate with pustules, well preserved. Stylets extend beyond the labium (Fig. 7D). Left side of the prothorax seems ripped off. The length of the specimen is about 1.21 mm.
15. Specimen 0285 (PED 1950): Strongly decomposed (Fig. 8A, B), possibly an exuvia. The compound eyes seem damaged and the body appears shrunken. Head capsule about as long as thorax and abdomen, with beak elongating far beyond the abdomen. Particles of debris partially hamper

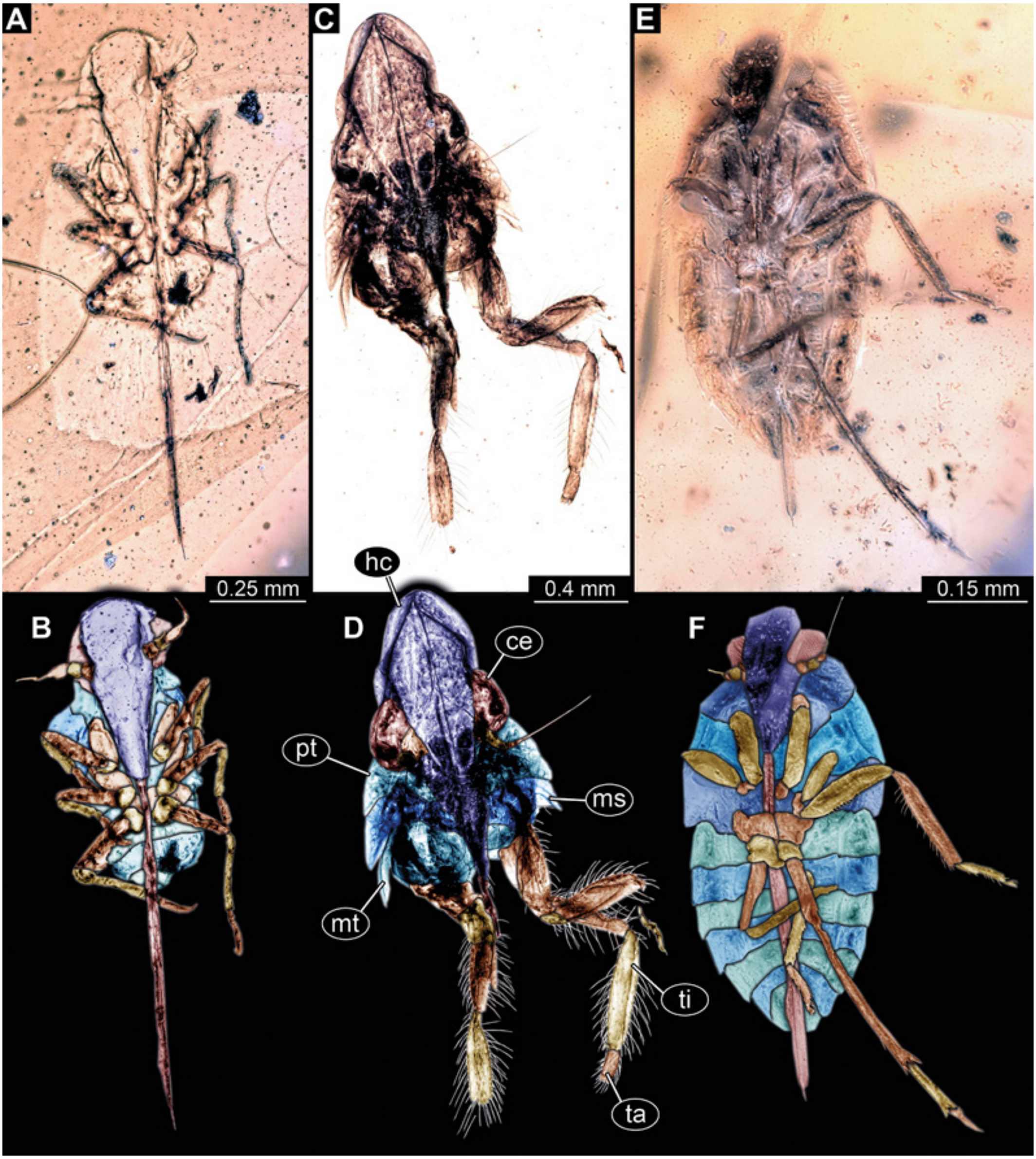

Fig. 8. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0285, PED 1950. **C, D.** Specimen 0298, PED 2218. **E, F.** Specimen 0264, PED 0298. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

the view on the specimen. The specimen may be in an early immature stage. The length of the specimen is about 0.83 mm.

16. Specimen 0298 (PED 2218): Missing the metathorax with legs and abdomen (Fig. 8C, D), possibly due to the specimen representing an exuvia. The beak seems damaged, but the length is measurable. The left midleg is missing, as well as all tarsi or parts of them for each present leg. The specimen is covered in small cracks. The total length could not be measured because of the missing abdomen and metathorax. Length without missing parts is about 1.23 mm.

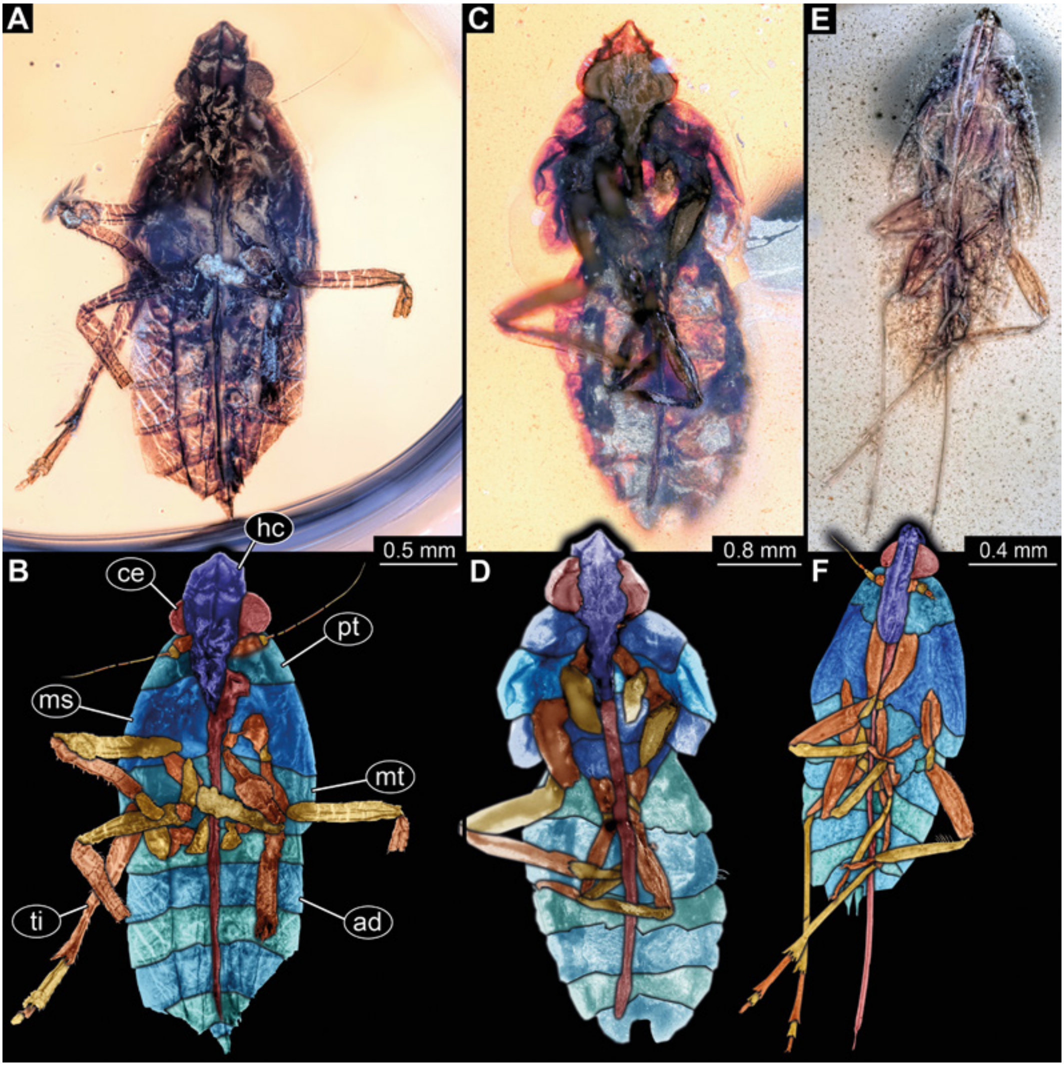

Fig. 9. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0271, PED 1134. **C, D.** Specimen 0272, PED 1150. **E, F.** Specimen 0274, PED 1219. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ti, tibia.

17. Specimen 0264 (PED 0298): Almost completely preserved (Fig. 8E, F). Parts of the specimen are blurred by the amber. The specimen is almost transparent and covered by cracks at the head and around the thorax. The beak elongates beyond the abdomen, and the stylets can be seen extending beyond the labium. The tibia and tarsus of the left foreleg and the femur of the right foreleg are missing as well as the left midleg. The length of the specimen is about 0.66 mm.
18. Specimen 0271 (PED 1134): Almost completely preserved (Fig. 9A, B). View on the specimen is interfered with foggy areas and locked-in air. The body and legs of the specimen are covered by cracks. The beak is well accessible. Parts of the tibia and tarsus of the right foreleg and of the left midleg are missing, as well as parts of the tibia and tarsus of the right hindleg. The length of the specimen is about 2.98 mm.

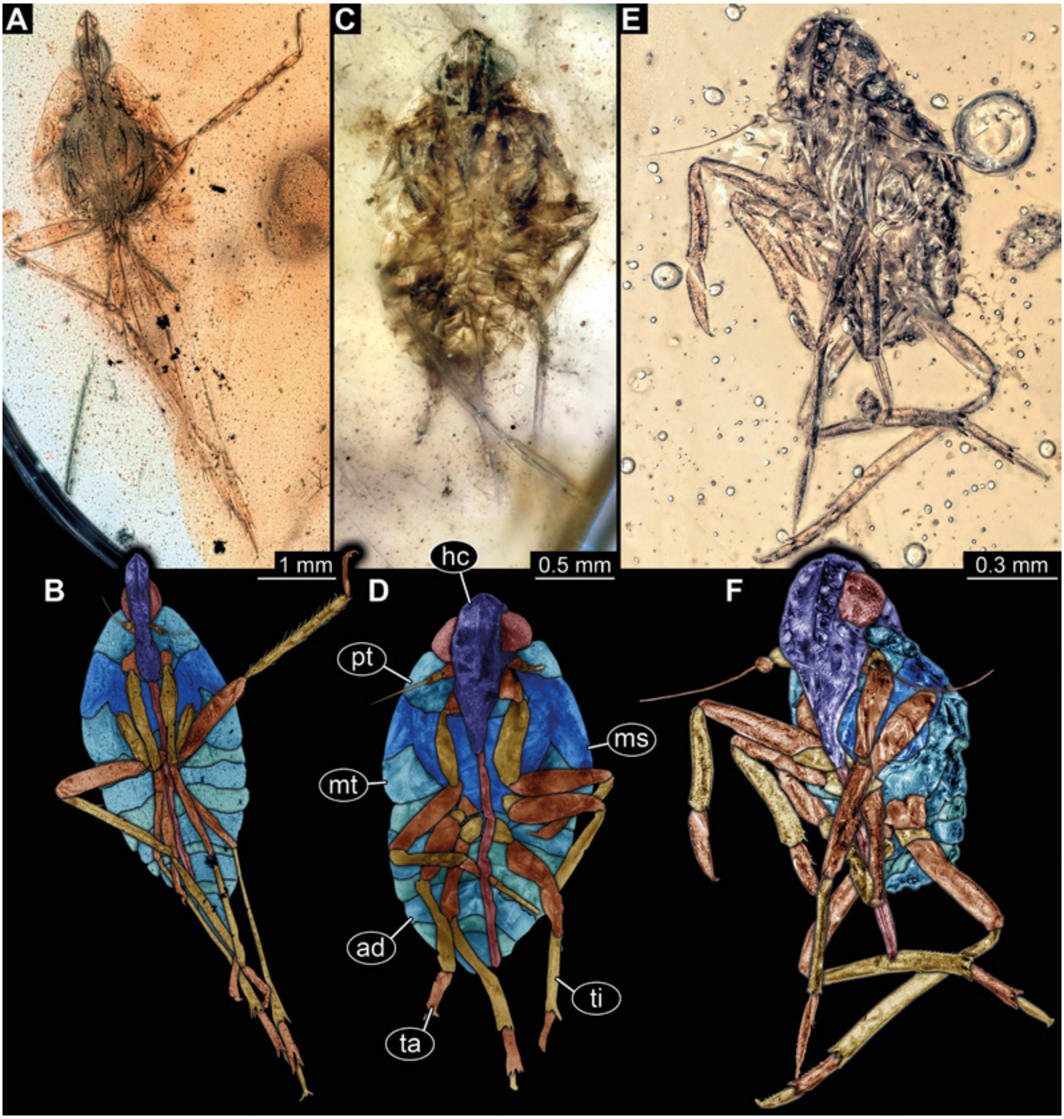

Fig. 10. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0283, PED 1936. **C, D.** Specimen 0282, PED 1925. **E, F.** Specimen 0281, PED 1921. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

19. Specimen 0272 (PED 1150): Partially decomposed and blurry (Fig. 9C, D). The head capsule and clypeus are partially damaged. The shape of the body is almost wasp-like. Parts of the beak covered behind the legs. The anterior pair of legs is missing from the femora to the tarsi, as well as the entire right midleg. The left hindleg is almost completely decomposed. The length of the specimen is about 4.73 mm.
20. Specimen 0274 (PED 1219): Completely preserved (Fig. 9E, F). The view of the specimen is hampered by bubbles and debris. The head capsule and the clypeus are relatively narrow. A small part of the head capsule seems to be broken off. The beak is elongated considerably beyond the abdomen, but partially covered by the legs. The stylets extend beyond the labium. The length of the specimen is about 1.76 mm.

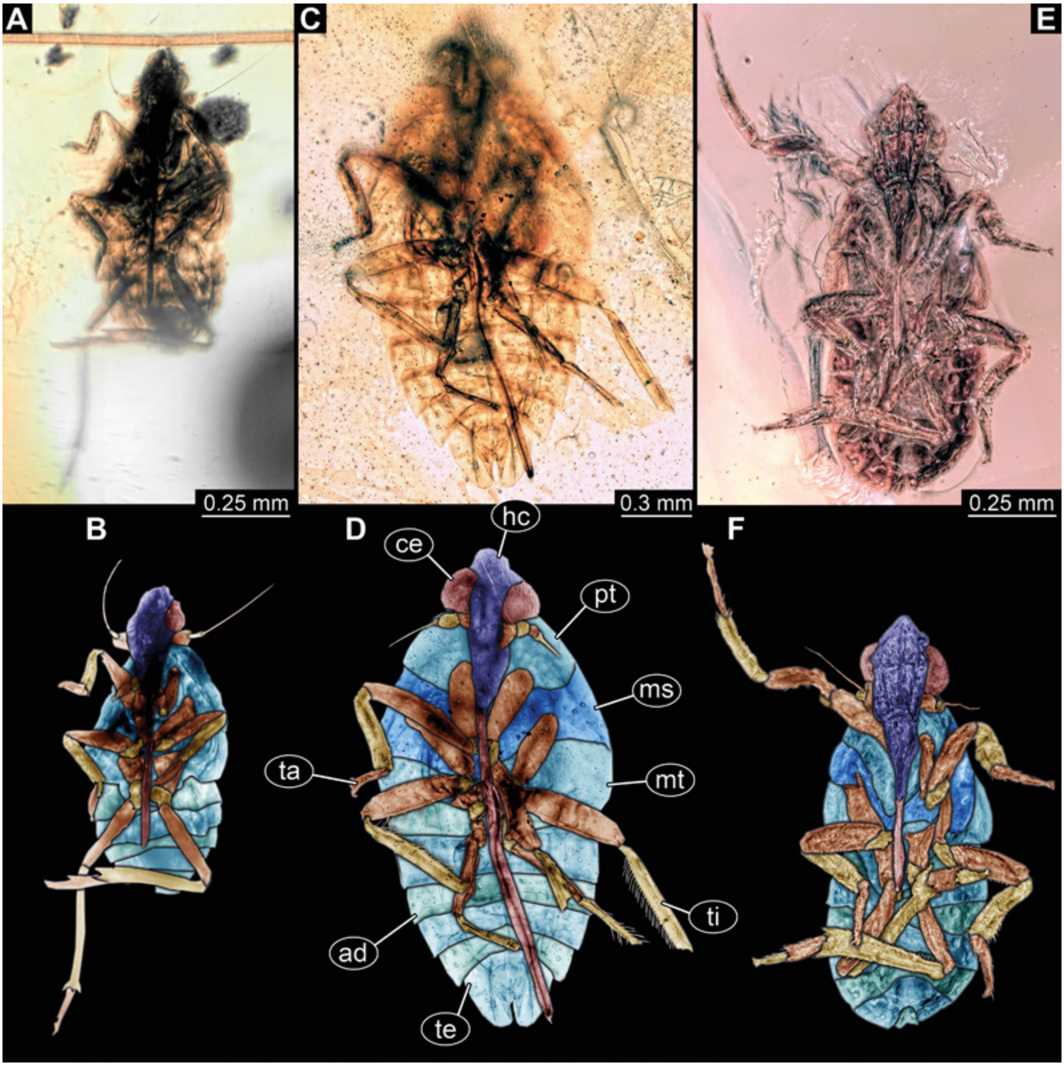

Fig. 11. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0284, PED 1942. **C, D.** Specimen 0277, PED 1545. **E, F.** Specimen 0278, PED 1613. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; te, trunk end; ti, tibia.

21. Specimen 0283 (PED 1936): Well preserved (Fig. 10A, B). The view is hampered by many particles of debris. The head capsule and the clypeus are slim. The clypeus gets broader closer to the labrum. The beak is strongly decomposed, but the stylets are well preserved. Parts of the abdomen are blurred as well as parts of the thorax and legs. The legs are long and slender. The length of the specimen is about 4.4 mm.
22. Specimen 0282 (PED 1925): Largely well preserved (Fig. 10C, D). The view on the specimen is hampered by debris, bubbles and a crack at the lower half of the specimen. The beak is blurred, and the stylets are partially decomposed. The leg elements are difficult to examine, as they appear transparent. The tarsi and tibia of the hindlegs are almost completely blurred. The length of the specimen is about 2.3 mm.

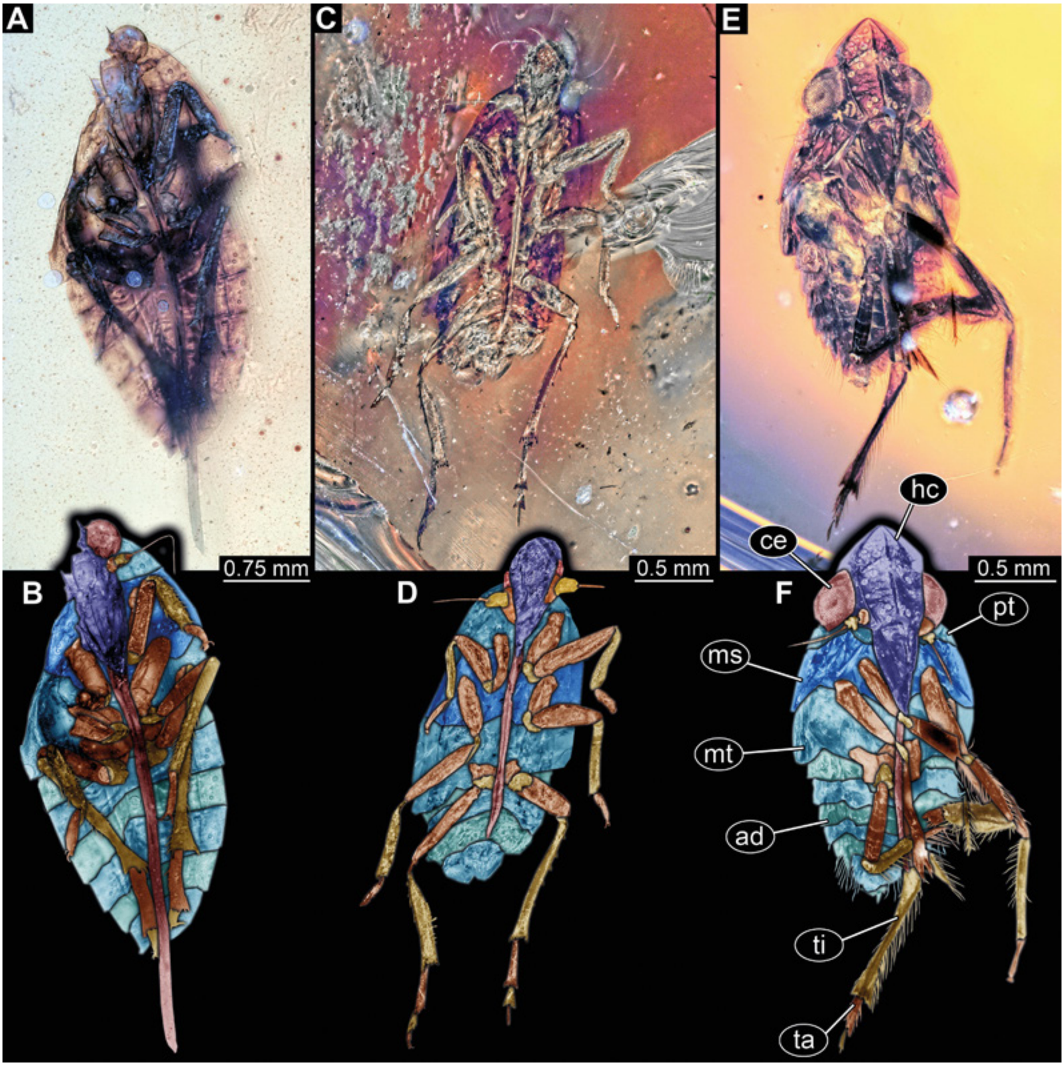

Fig. 12. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0302, PED 2230. **C, D.** Specimen 0273, PED 1205. **E, F.** Specimen 0299, PED 2224. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

23. Specimen 0281 (PED 1921): Completely preserved (Fig. 10E, F). The view on the specimen is hampered by many bubbles. A small crack over the clypeus blurs the view. The specimen seems overall transparent. The beak is partially covered by the legs. The length of the specimen is about 1.13 mm.
24. Specimen 0284 (PED 1942): Completely preserved (Fig. 11A, B). Part of the head and thorax of the specimen are darkened. Due to the position of the specimen, its ventral half is difficult to access. The first half of the beak is difficult to examine due to the darkened areas. The stylets extend beyond the labium. The length of the specimen is about 0.86 mm.
25. Specimen 0277 (PED 1545): Almost completely preserved (Fig. 11C, D). The view of the upper half of the specimen is blurred due to a rough surface of the amber. The view on the specimen is also hampered by debris and bubbles. Part of

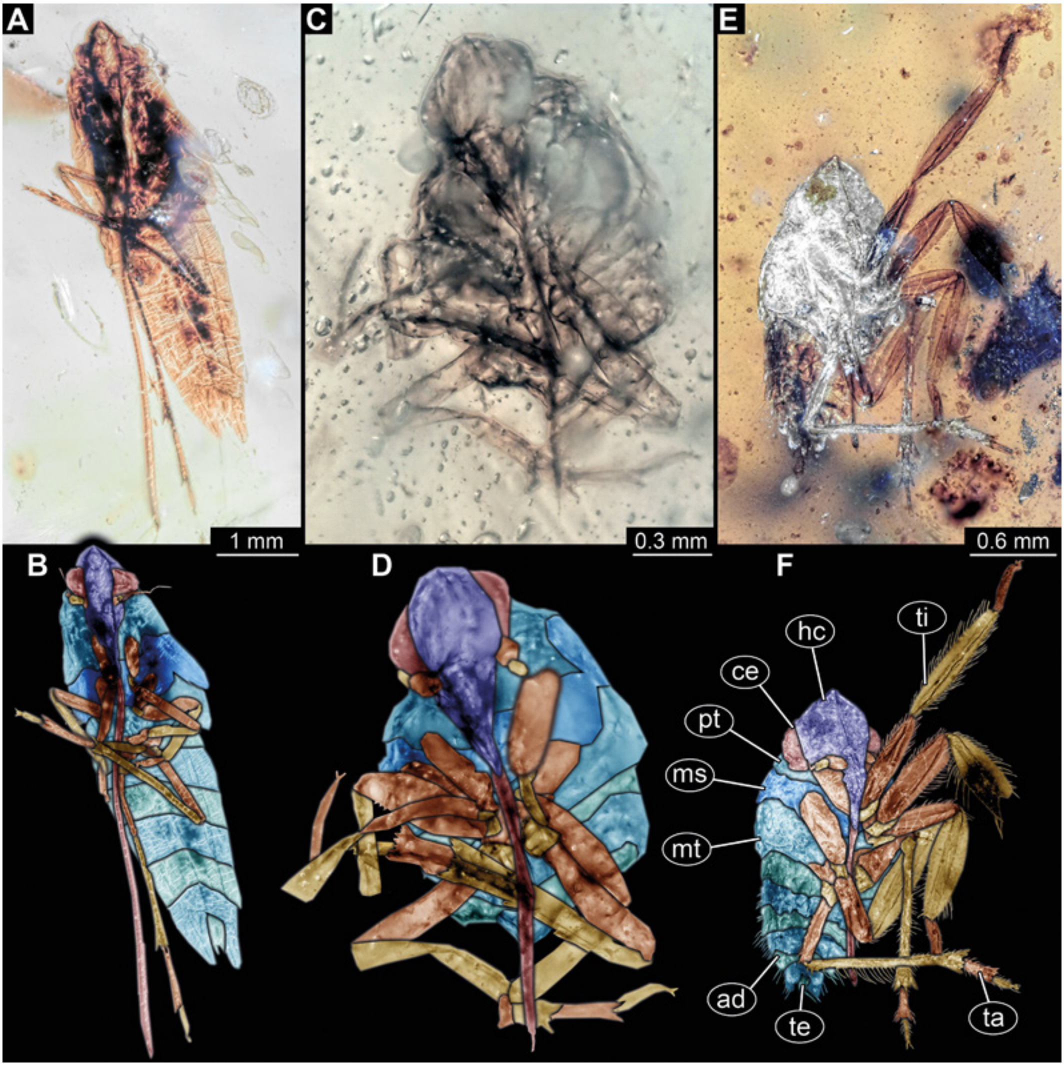

Fig. 13. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B**. Specimen 0301, PED 2228. **C, D.** Specimen 0297, PED 2217. **E, F.** Specimen 0303, PED 2232. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; te, trunk end; ti, tibia.

the tibia and tarsus are missing on the right foreleg and both on mid- and hindlegs. The length of the specimen is about 2.02 mm.

26. Specimen 0278 (PED 1613): Completely preserved (Fig. 11E, F). The view on the specimen is hampered by several cracks around and across it. Clypeus and beak are well preserved. The total length of the specimen is 1.24 mm.
27. Specimen 0302 (PED 2230): Almost completely preserved (Fig. 12A, B). Half of the head capsule, and the left compound eye and antenna are missing. The view on the bottom half of the specimen is blurry, because of the very rough surfaces on the amber. Bubbles and debris prevent a clear view of the specimen as well. The beak extends significantly beyond the abdomen. The prothorax also seems distorted. Part of the femur, the tibia and the tarsus are missing from the fore- and midlegs on the left side. The length of the specimen is about 3.67 mm.

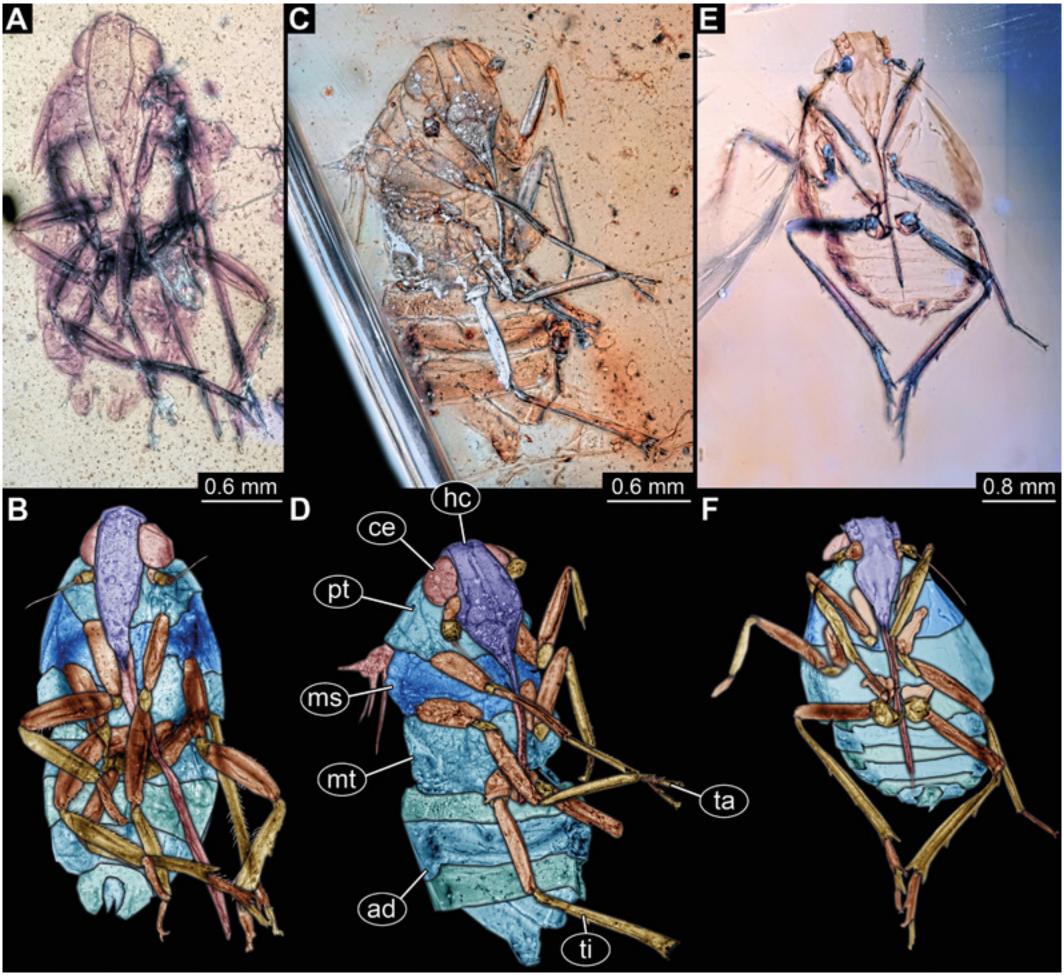

Fig. 14. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0300, PED 2227. **C, D.** Specimen 0295, PED 2197. **E, F.** Specimen 0293, PED 2154. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

28. Specimen 0273 (PED 1205): Well preserved (Fig. 12C, D). The view on the specimen is hampered by a big crack on the left side of the specimen and by bubbles, debris, and cracks. The body and legs are almost transparent. The compound eyes seem damaged. The length of the specimen is about 2.15 mm.

29. Specimen 0299 (PED 2224): Almost completely preserved (Fig. 12E, F). The view on the specimen is almost clear, with only some bubbles interfering. The beak is partially covered by the legs. The stylets extend beyond the labium. Parts of the left foreleg are missing, the tarsi are missing completely, as well as the tarsus of the left midleg. The length of the specimen is about 2.14 mm.

30. Specimen 0301 (PED 2228): Completely preserved (Fig. 13A, B). The view on the specimen is very good. The specimen is slim, but covered by small cracks. The right compound eye seems damaged. The beak is long and almost fully visible. The length of the specimen is about 5.16 mm.

31. Specimen 0297 (PED 2217): Largely well preserved (Fig. 13C, D). The view is hampered by bubbles. The tibiae of the forelegs and left midleg seem folded. The beak extends beyond the

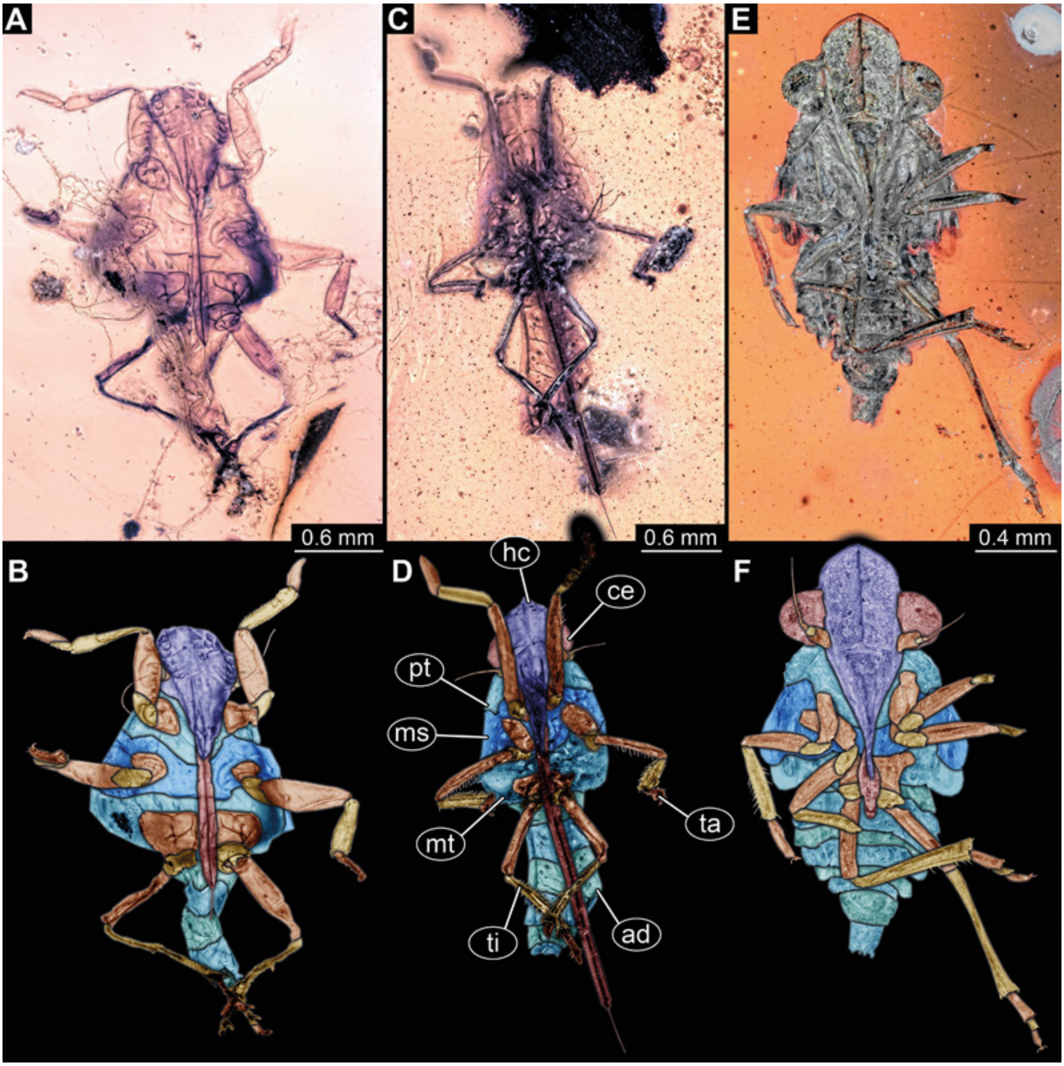

Fig. 15. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0292, PED 2151. **C, D.** Specimen 0296, PED 2199. **E, F.** Specimen 0290, PED 2083. **A, C, E.** Overview in ventral view. **B, D, F.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

abdomen. The stylets extend beyond the labium, bearing spines at the shaft. The length of the specimen is about 1.44 mm.

32. Specimen 0303 (PED 2232): Almost completely preserved (Fig. 13E, F). The view on the specimen is slightly hampered by pieces of debris. The head capsule and thorax are surrounded by a large bubble partly concealing the specimen. Part of the tibia and tarsus are missing on the left fore- and midleg. The length of the specimen is about 2.25 mm.

33. Specimen 0300 (PED 2227): Largely well preserved (Fig. 14A, B). The view of the specimen is slightly hampered by debris and bubbles. Part of the thorax appears decomposed, as well as parts of the abdomen. The length of the specimen is about 2.95 mm.

34. Specimen 0295 (PED 2197): Slightly transparent (Fig. 14C, D). The view of the specimen is hampered by debris. The mesothorax seems to have remains of wings attached, which could mean

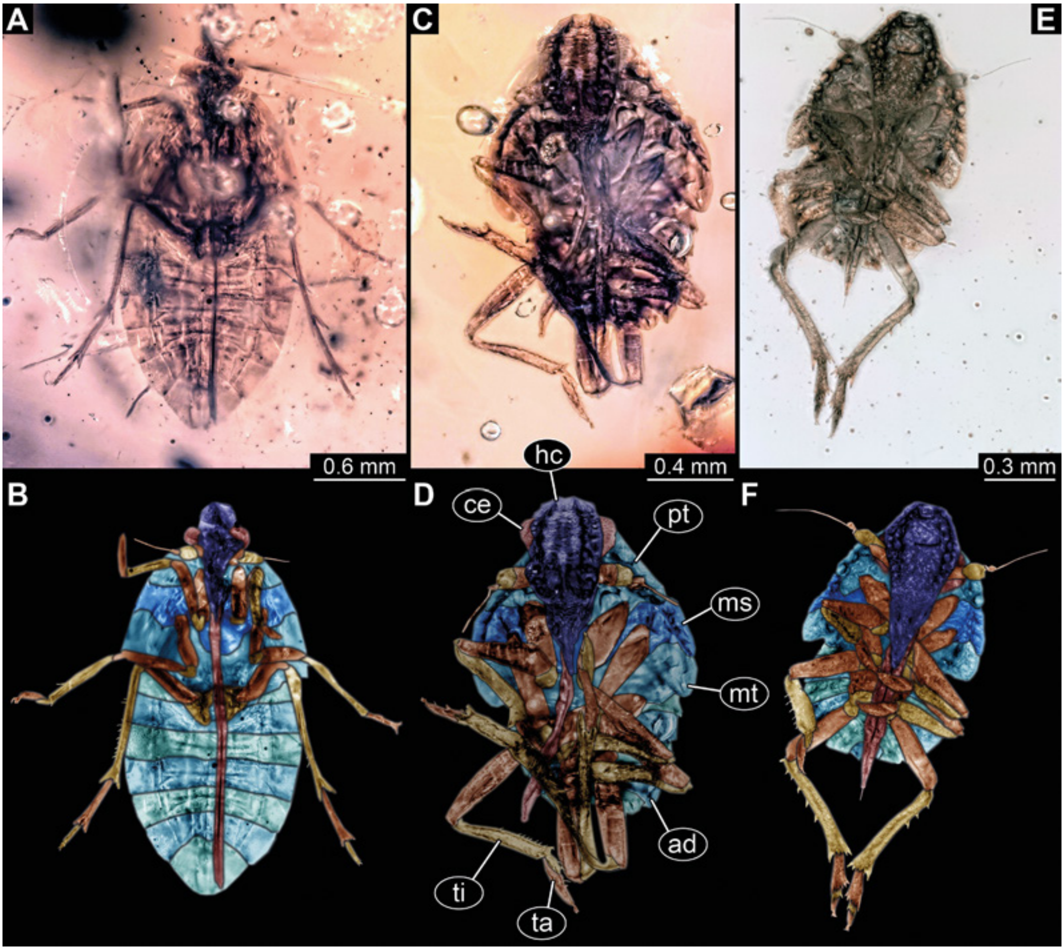

Fig. 16. Fulgoromorphans preserved in Cretaceous Kachin amber, Myanmar, continued. **A, B.** Specimen 0294, PED 2167. **C, D.** Specimen 0289, PED 2043. **E, F.** Specimen 0291, PED 2123. **A, C, E.** Overview in ventral view. **B, D, E.** Colour-marked versions of the above. Abbreviations: ad, abdomen; ce, compound eye; hc, head capsule; ms, mesothorax; mt, metathorax; pt, prothorax; ta, tarsus; ti, tibia.

that this specimen is an adult; yet the region is difficult to access and it cannot be further corroborated whether this is indeed a wing of the specimen. Parts of the tibia and tarsus of the right foreleg are missing. The left hindleg tibia and the right hindlegs are also missing. The length of the specimen is about 3.8 mm.

35. Specimen 0293 (PED 2154): Largely well preserved (Fig. 14E, F). Thorax and abdomen are almost completely decomposed. The right compound eye is missing. The stylets extend from the labium. A crack in the amber blurs the right midleg. The length of the specimen is about 3.14 mm.

36. Specimen 0292 (PED 2151): Completely preserved, but wrinkled, possibly due to the specimen representing an exuvia (Fig. 15A, B). The head and the compound eyes are partially covered by the forelegs. The beak is completely preserved. The stylets extend beyond the labium. The abdomen is damaged. The view of the specimen is partially hampered by debris. The left and right hindlegs tibiae and tarsi are damaged. The length of the specimen is about 2.49 mm.

37. Specimen 0296 (PED 2199): Completely preserved, but wrinkled possibly due to the specimen representing an exuvia (Fig. 15C, D). The compound eyes and the head, as well as the antennae

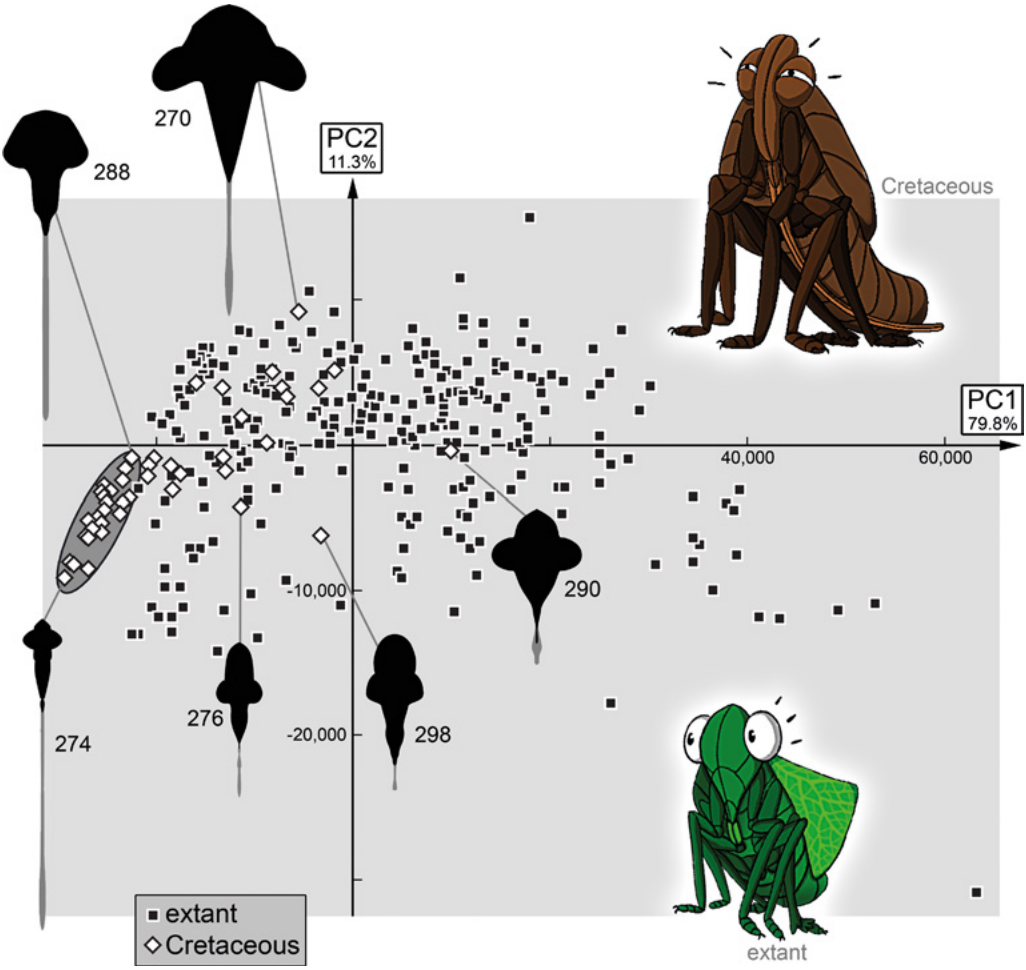

Fig. 17. Scatterplot of PC2 vs. PC1 of the shape analysis of the head (incl. beak). Note the distinct group of Cretaceous specimens far left. The two cartoons represent the "typical" Cretaceous morphology, i. e. that of the long-beaked morphotype and the average modern morphotype.

are partially covered by the forelegs. Part of the right hind tarsus is missing. The abdomen is slender, but slightly damaged. The beak is fully preserved, extending a little beyond the abdomen. The stylets extend long beyond the labium. The right foreleg is partly covered by a large piece of debris; the left foreleg is blurred. Part of the right hind tarsus is missing. The length of the specimen is about 2.70 mm.

38. Specimen 0290 (PED 2083): Well preserved (Fig. 15E, F). The view of the specimen is clear. The beak is short and the stylets are not visible. The fore- and midleg tibiae and tarsi are missing, as well as the left midleg tarsus. The length of the specimen is about 2.01 mm.
39. Specimen 0294 (PED 2167): Almost completely preserved (Fig. 16A, B). The view is hampered by debris and bubbles, as well as a crack going through the head capsule. The beak extends to the end of the abdomen, the stylets do not extend beyond the labium. The view of the prothoracic legs is blurred. The femora and tibiae of the fore- and midlegs are slim. The length of the specimen is about 2.48 mm.
40. Specimen 0289 (PED 2043): Well preserved (Fig. 16C, D). The view of the thorax is blurred, but the rest of the specimen is almost clear, only hampered by some air bubbles. Parts of the labrum and labium are blurred. The tibiae of fore- and midlegs have a spur on the distal ends.

The hindlegs are bent in. The length of the specimen is about 1.48 mm.

41. Specimen 0291 (PED 2123): Well preserved (Fig. 16E, F). The view on the specimen is almost clear. The beak is partially covered by the fore- and midlegs. The labium elongates beyond the abdomen with the stylets extending beyond the labium. The length of the specimen is about 3.47 mm.

Shape analysis

The first analysis of the head and beak resulted in four effective principal components which together explain 95.7 % of the overall variation (detailed output files in the Electronic Supplement 2). The stylets extending beyond the labium shown by many specimens were excluded from the analysis, as the stylets are retractable structures.

PC1 explains 79.8 % of the overall variation in morphology. It describes the length and width of the head with the beak included. The positive values describe a broad head with a short beak while the negative values describe a narrow head with a long beak (Fig. 17).

PC2 explains 11.3 % of the overall variation. It describes the shape of the head process. The positive values describe a flattened forehead while the negative values describe a long and pointed forehead (Fig. 17).

PC3 explains 2.9 % of the overall variation. It describes the shape of the forehead and the width of clypeus. Positive values describe a flat forehead with a broad clypeus and negative values describe a pointed head with a thinner clypeus.

PC4 explains 1.7 % of the overall variation. It describes the definition of the eyes and shape of clypeus. Positive values describing a more block-like shape of the clypeus with more flattened compound eyes, and negative values describing a rectangular clypeus with more defined compound eyes.

Discussion

Identity of the specimens

The specimens reported here can easily be recognised as representatives of the group Fulgoromorpha, as many of them show the characterising features (antenna morphology, sensory pits etc.) already on a first sight. Other aspects such as the non-separation of the hindleg coxae can be seen on closer inspection. Yet, further-reaching interpretations remain difficult, as most, if not all, specimens reported here are immatures. Only one has possible remains of wings, but the wing region is difficult to assess, and it cannot be further supported whether this is indeed a wing of the specimen. It would not be surprising that the specimens with well-accessible mouthparts are immatures. Immatures are smaller than adults and are therefore more likely to be fully embedded without parts sticking out of the amber. Moreover, it has been reported from other amber deposits that the majority of fulgoromorphans (and cicadomorphans) are immatures (Weitschat & Wichard 2002, p. 128).

Yet, as already pointed out, immatures are more challenging to deal with within a taxonomic frame. Most characters that are generally used to further narrow down the taxonomic identity of fulgoromorphans (as in most pterygotans) are adult characters, such as wings and genitalia. Recognising new species based on immatures can complicate the overall taxonomy also for adults, and especially younger immature stages (instars) can be very challenging to identify to possibly already known species. We will therefore here not focus on a taxonomic frame of the specimens, but on the quantitative morphology (following Haug et al. 2023a, b); we will still provide a coarse sorting into morphotypes to streamline the discussion.

Long-beaked morphotype

A distinct cluster of specimens can be recognised when plotting PC2 versus PC1 (Fig. 17) on the far left side. The heads of these specimens are all rather elongate, and the beak is prominently drawn out, in many cases being longer than the trunk end. Specimens in this cluster have varying sizes (Fig. 18), indicating that this long beak is not only present in later immature stages (instars) and that the morphology does not significantly change throughout the immature phase. It seems unlikely that all specimens of this morphotype represent a single species. There are some specimens in which the functional anterior tip of the head (vertex) forms a continuous line with the eyes (e. g., specimen 0288, Fig. 6A, B), while in others the vertex is slightly projecting (e. g., specimen 0274, Fig. 9E, F). These differences could well represent characters of different species.

Overall, many of the specimens of this cluster exhibit several similarities with immatures of the group Neazoniidae, an extinct ingroup of Fulgoromorpha known from older, Lebanese amber (Szwedo 2007) and from French amber (Szwedo 2009), but they also resemble representatives of the group Mimarachnidae in certain aspects. Neazoniidae is known only from immatures, while Mimarachnidae is mostly known from adults (exception in Emeljanov & Sherbakov 2018). The relationship between the two groups is, given the current state of knowledge, challenging to further evaluate. They may be closely related, or one may even be an ingroup of the other. Given the similarities, it seems likely that some fossils reported here are also representatives of the one and/or the other of the two groups, more likely of Mimarachnidae.

The majority of the specimens reported here, more than half of them, fall into the cluster of the long-beaked morphotype. It seems that this morphotype was rather abundant in the Kachin amber forest, while the others were much rarer.

Other morphotypes

All other specimens reported here do not form tight clusters and are more challenging to group into distinct morphotypes. Specimen 0270 (Fig. 3C, D) occupies an extreme position among the new fossils (uppermost) and should be understood as a morphotype of its own (morphotype 2); its beak is still moderately long, but the head is very wide. Specimen 0290 (Fig. 15E, F) also occupies an extreme position (rightmost); its beak is rather short, and the head is moderately wide, representing a third distinct morphotype (morphotype 3).

All other specimens are (roughly) distributed between the long-beaked cluster and the two extreme specimens. Specimens 0298 (Fig. 8C, D) and 0276 (Fig. 7) are separated slightly from the rest towards the lower middle (0298 more so). They both share a rather short beak, a not very wide head, but a pronounced vertex, and may represent another distinct morphotype (morphotype 4). The remaining specimens could be understood as a (rather polymorphic) morphotype 5, but are in fact likely representing several species. As pointed out, all specimens that are not of the long-beaked type seem much rarer, therefore, recognising more discrete morphotypes would require an increase of the sample size.

Shape analysis

Plotting PC2 against PC1 (Fig. 17) shows that extant specimens occupy a significantly larger area of the morphospace. They are scattered along the PC1 axis, with both positive and negative values, hence presenting a diverse morphology of head and mouthparts, ranging from broad heads with short beaks to narrow heads with long beaks. The fossil specimens are concentrated on a smaller area on the negative side of the PC1 axis (only one specimen with a positive value), which indicates, on average, narrow heads with long beaks. In fact, the absolute lowest values come from the long-beaked morphotype cluster. The cluster has little overlap with the extant specimens. On the PC2 axis, which relates to the shape of the head process, extant specimens are also more spread than the fossil ones, ranging from short and flattened to elongate and slender head shapes. The fossil specimens are closer to 0, with intermediate shapes.

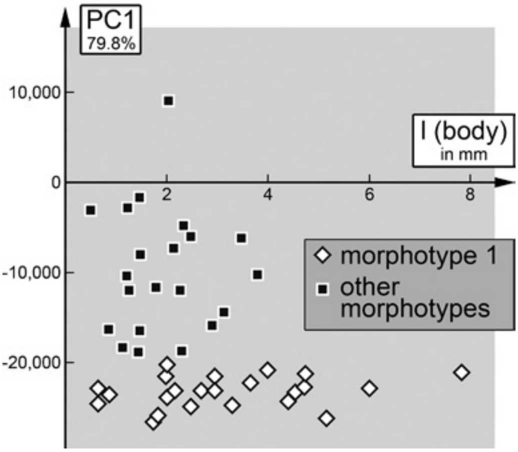

Fig. 18. Scatterplot of PC1 vs. total body length for the Cretaceous specimens. Note how the long-beaked morphotype specimens do not scatter along the PC1 axis, but along the size axis.

These results show a significantly higher morphological diversity of head and mouthparts of the extant specimens than the fossil specimens analysed. Yet, there are some considerations to make. The first one is regarding the sample sizes. The sample of the extant fauna is much larger than the fossil one, which might have its diversity underrepresented. Part of this issue is due to the preservation conditions of the amber and the difficulty to examine the relevant structures. Additionally, extant specimens are much more readily available, especially those retrieved from databases. Also, as the fossils represent (mostly) immatures, it cannot be excluded that fossil adults would still expand the occupied area of the fossils. Finally, we have sampled data from the extant fauna basically worldwide, while all of the new fossils (and most of the Cretaceous forms in total) come from a single locality.

Nevertheless, there is an area of the plot with negative values of both PC1 and PC2 where only fossil specimens form a cluster (long-beaked morphotype). This pattern indicates that a certain specialized morphology adapted to a specific life habit is not present in the extant fauna.

Cretaceous and extant diversity

Specimens with the beak extending posteriorly beyond the abdomen were found in the Cretaceous ambers, but not in the extant fauna examined. This is consistent with the fact that the very elongate heads occur only in the Cretaceous but are not present in the modern fauna.

This apparent shift in morphology could be explained by a shift in the feeding habits of the animals. Since the diet of representatives of Fulgoromorpha is essentially plant fluids, a change in the flora (and plant morphology) and niche occupation over time could have led to such a morphological modification. Even though the present study is based on a limited sample of amber fossils from Myanmar, this observation is supported by many other studies describing similar morphologies from other Mesozoic fossils (Shcherbakov & Popov 2002, Szwedo 2007, Shcherbakov 2017, Emeljanov & Shcherbakov 2018, Luo et al. 2021a). It has been suggested that the "long-snouted" planthoppers were probably feeding on phloem of tree trunks and thick branches of the pre-angiosperm flora, including the amber-producing trees. This assumption is supported by the long beak (to access the plant vascular system under the thick bark) and the narrow clypeus (which bears the dilator muscle, used to pump in fluids, in this case less necessary given the turgor pressure of the phloem transport; Emel'yanov 1987, Shcherbakov & Popov 2002).

The rise of magnoliopsidan plants ("angiosperms"), which coincided with the radiation of other sap-feeding insects, must have influenced a shift in the feeding habits of planthoppers (Shcherbakov 2002). The reasons might have been the competition with those newly diversifying groups, the suppression of the old flora by the emerging flowering plants, or access to new ecological functions created by the diverse morphology of magnoliopsidan plants. In fact, over 90 % of the extant fulgoromorphan species feed on magnoliopsidan plants (mostly grasses and other grass-like plants, but also many others), and only about 7 % feed on non-magnoliopsidans ("pteridophytes", "gymnosperms"; Wilson et al. 1994). Still, the situation seems much more complex, with different factors providing multifold selective pressures, such as abiotic factors like climate change (Luo et al. 2022, p. 463), but also due to radiation of new ecologically important players such as parasitoid and eusocial "flying insects" as well as mammals (Lloyd et al. 2008, Meredith et al. 2011, Jiang et al. 2018, Bao et al. 2019, Genise et al. 2020, Luo et al. 2021b, Pohl et al. 2021).

The data set used here is skewed, and it remains to be seen whether the morphological diversity of the Cretaceous fulgoromorphans is indeed smaller than that of the extant ones. Yet, it would be clearly plausible that it expanded after the Cretaceous in concert with magnoliopsidan flowering plants.

The Cretaceous: a time for elongated animals?

As pointed out, the long-beaked morphotype seems to have no counterpart in the modern fauna. Also for other groups of "flying insects", representatives with elongated structures not seen in the modern fauna have been recognised, including snakeflies (Haug et al. 2020b, Haug et al. 2022c), lacewings (Liu et al. 2018, Haug et al. 2019a, Haug et al. 2021b) or earwigs (Haug et al. 2023b).

It has been suggested that the Cretaceous was a time when also more "experimental" morphologies occurred (e. g., Haug et al. 2019b, Khramov et al. 2019, Poinar 2022), i. e. that the range of variation was higher due to initial burst of diversification. In the other groups, it indeed appears that modern-type morphologies were also already present and that the overall range was higher in the Cretaceous (recently summed up in Haug et al. 2023a). Yet, for fulgoromorphans this seems to have been different, as long beaks on slender heads were present and later disappeared, yet short beaks on very wide heads seem to have not yet been present, but only evolved later. Hence although Fulgoromorpha also seems to be an old group (as has been suggested also for snakeflies and the others), the pattern over time does not necessarily indicate an overall loss, but a distinct shift, possibly including a diversification after the Cretaceous.

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