

# EARLY CRETACEOUS ENIGMATIC INSECT GROUP SHOWING UNIQUE WING VENATIONS AND ANTENNAL SENSILLA

by HONGRU YANG<sup>1</sup>, CHUNGKUN SHIH<sup>1,2</sup>, ALEXANDR P. RASNITSYN<sup>3,4</sup>,  
DONG REN<sup>1</sup>\*  and TAIPING GAO<sup>1</sup>\* 

<sup>1</sup>College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China; rendong@mail.cnu.edu.cn, tpgao@cnu.edu.cn,

<sup>2</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

<sup>3</sup>A. A. Borissiak Palaeontological Institute, Russian Academy of Sciences, 117647 Moscow, Russia

<sup>4</sup>Natural History Museum, Cromwell Road, London SW7 5BD, UK

\*Corresponding authors

Typescript received 23 October 2020; accepted in revised form 5 July 2021

**Abstract:** A new extinct insect group, *Magicivena* gen. nov. in Magicivenidae fam. nov., with *M. sticta* sp. nov. (type species), *M. elegans* sp. nov., *M. antennalis* sp. nov. and *M. sp.*, is reported as Insecta *incertae ordinis* based on four specimens from the Lower Cretaceous Yixian Formation of north-eastern China. Magicivenidae are characterized by special antennal structures, such as each flagellomere having two lateral transverse rows of setiferous pits, and forewing venations such as a very short subcostal anterior (Sc), the radial posterior (RS) apparently lost, a weak cubital posterior (CuP), and a single cross-vein crossing the CuP and joining the cubital anterior (CuA) to the first anal vein, all of which differ from those of any other fossil or extant insect taxa documented hitherto. According to the characters forewing with multibranched CuA, hind wing with several long anal veins, and segmented cerci,

Magicivenidae should belong to Polyneoptera. The light constitution of a good flier, similar structure of the pterostigma in the hind wing, and transverse furrow on the pronotum all suggest the parallel evolution of Magicivenidae and a dictyopterid family, Alienopteridae. However, the advanced bimotory and loss of an identifiable RS make the possible affinity of Magicivenidae with Alienopteridae problematic, as the latter possess utmost posteromotory and a distinct RS. The antennae of Magicivenidae with their sophisticated sensory apparatus suggest that the four known specimens of *Magicivena* described here are all males; females are still to be discovered. This new finding enriches the known diversity of Cretaceous insect groups.

**Key words:** *Magicivena*, Magicivenidae, flagellomere, flight, Yixian Formation, Alienopteridae.

DIVERSE insect fossil records have shown a spectacular variety in the morphological characters, sizes and shapes of insects, suggesting a wide range of habits and behaviours (Wootton & Kukalová-Peck 2000; Rasnitsyn & Quicke 2002; Grimaldi & Engel 2005). Although the internal relationships of extant insect orders have been confirmed by many phylogenetic studies based on morphological characters and/or DNA sequence data (Beutel *et al.* 2011; Misof *et al.* 2014; Wipfler *et al.* 2018), many extinct fossil groups of insects are difficult to classify.

Rasnitsyn & Quicke (2002) designated many extinct insect groups as *incertae sedis*, from descriptions based on compression fossils. Staniczek *et al.* (2011) erected a new insect order, Coxopteroptera within Palaeoptera, from the Lower Cretaceous Crato Formation of Brazil. Recently, many unique groups of insects have been reported from well-preserved insects in Myanmar amber. For example, Huang *et al.* (2016) erected a new order of

Permopsocida (formerly a suborder of Psocoptera; see Tillyard 1926) to elucidate major radiation and evolution of suction feeding in hemimetabolous insects. The phylogenomic analysis of Yoshizawa & Lienhard (2016) also confirmed the monophyly of Permopsocida. Mey *et al.* (2017) erected the insect Order Tarachoptera in the Superorder Amphiesmenoptera and suggested its independent origin and evolution from an amphiesmenopteran ancestor, which was not the ancestor of the Trichoptera–Lepidoptera clade. Gao *et al.* (2019) reported a new insect taxon (order *incertae sedis*) feeding on dinosaur feathers. Alienopteridae, erected based on both male and female insects from the Lower Cretaceous Crato Formation of Brazil, middle Cretaceous Myanmar amber, and the Eocene Green River Formation of the USA, exhibit a seemingly weird combination of characters, such as shortened forewings combined with fully developed, operational hind wings (Bai *et al.* 2016, 2018; Kočárek 2019;

Wipfler *et al.* 2019). Vršanský *et al.* (2018) ascribed the Family Alienopteridae to the Superfamily Umenocoleoidea within Dictyoptera. These interesting fossil insects have provided us with a window of opportunity to study and understand the ontogeny and evolution of insects over a hundred million years.

Diverse insect taxa and associated interactions on the rhythms of insect evolution have been reported based on numerous scientifically important fossil insects from the Middle Jurassic to the Early Cretaceous (c. 164 – 125 Ma) in Hebei, Liaoning and Inner Mongolia in China (Ren *et al.* 2019; Yang *et al.* 2021). To date, with the exception of Zoraptera and Mantodea, most orders of insects have been documented from north-eastern China. The new fossil described herein from the Jehol Biota, Lower Cretaceous Yixian Formation in north-eastern China represents a new addition to the broad diversity (Gao *et al.* 2021).

## MATERIAL AND METHOD

### *Specimen imaging and terminology*

The type specimens described herein are housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator). All specimens were examined, and all photographs taken, with a Nikon SMZ 25 microscope with an attached Nikon DS-Ri2 digital camera system and a Nikon ECLIPSE Ni microscope with an attached Nikon DS-Ri2 digital camera system. Line drawings were prepared by using Adobe Illustrator CC and Adobe Photoshop CC graphics software.

*Wing venation abbreviations.* 1A, first anal vein; 2A, second anal vein; 3A, third anal vein; A, anal; C, costa; Cu, cubitus; CuA, cubital anterior; CuP, cubital posterior; M, media; MA, medial anterior; MP, medial posterior; R, radius; R<sub>1</sub>, radial anterior; RS, radial posterior (= radial sector); Sc, subcostal anterior.

## SYSTEMATIC PALAEONTOLOGY

by Hongru Yang, Alexandr Rasnitsyn and Dong Ren.

Class INSECTA Linnaeus, 1758  
Order INCERTAE SEDIS  
Family MAGICIVENIDAE nov.

*LSID.* urn:lsid:zoobank.org:act:4F02EC4F-314A-4100-9579-828A53970903

*Type genus.* *Magicivena* gen. nov.

*Diagnosis.* Head transversely expanded, orthognathous; compound eyes large, ocelli present; antenna long, moniliform, scape longer than pedicel, each flagellomere with two lateral conspicuous transverse rows of setiferous pits at mid-length. Cervical sclerites present. Prothorax narrower than mesothorax and metathorax; pronotum with a transverse furrow, without paranota. Flight apparatus bimotorous, with no distinct prevailing of either mesothorax and forewings or metathorax and hind wings. Wings not elytrized, each one with pterostigma. Venation oligomerous, with few cross-veins and branches of longitudinal veins. Sc very short, ending in C or with an apical fork; R lacks identifiable RS, with pterostigmata present in both wings between R apical branchlets; M free and connecting to CuA with M<sub>5</sub> or fused with CuA basally; CuA pectinate backward, with dark spot among basal four branches in forewing, with few branches in hind wing; CuP lone, curved and weak, crossing cu-a cross-vein in forewing (unknown in hind wing); forewing anal area very small, with 1A and 2A short, interconnected apically with oblique cross-vein, at least four long veins present in wide anal area of hind wing. Legs cursory, slender, with hind pair distinctly longer than others; coxae large; femora wider than tibiae, with no spines or spurs visible; tarsi five-segmented, short; claws small; arolia and euplantulae unknown. Abdomen elongate, about as wide as thorax, with no paranota; cerci moderately short, with more than five free segments; genitalia unknown.

*Genera included.* Type only.

### Genus MAGICIVENA nov.

*LSID.* urn:lsid:zoobank.org:act:A1A30A43-054F-4736-B607-1D72B4971F7A

*Derivation of name.* The generic name is a combination of the Latin *magicus*, meaning fantastic, and *vena*, meaning vein. The gender is feminine.

*Type species.* *Magicivena sticta* sp. nov.

*Species included.* *Magicivena sticta* sp. nov., *M. elegans* sp. nov., *M. antennalis* sp. nov., *Magicivena* sp.

*Diagnosis.* As for family.

### *Magicivena sticta* sp. nov.

Figs. 1, 2

*LSID.* urn:lsid:zoobank.org:act:33E6C581-6B4A-451A-AC1E-FD741BCBDD1E

*Derivation of name.* The epithet is from the Latin word *stictus*, meaning speckle.

*Holotype.* CNU-LB2013101p/c, part and counterpart.

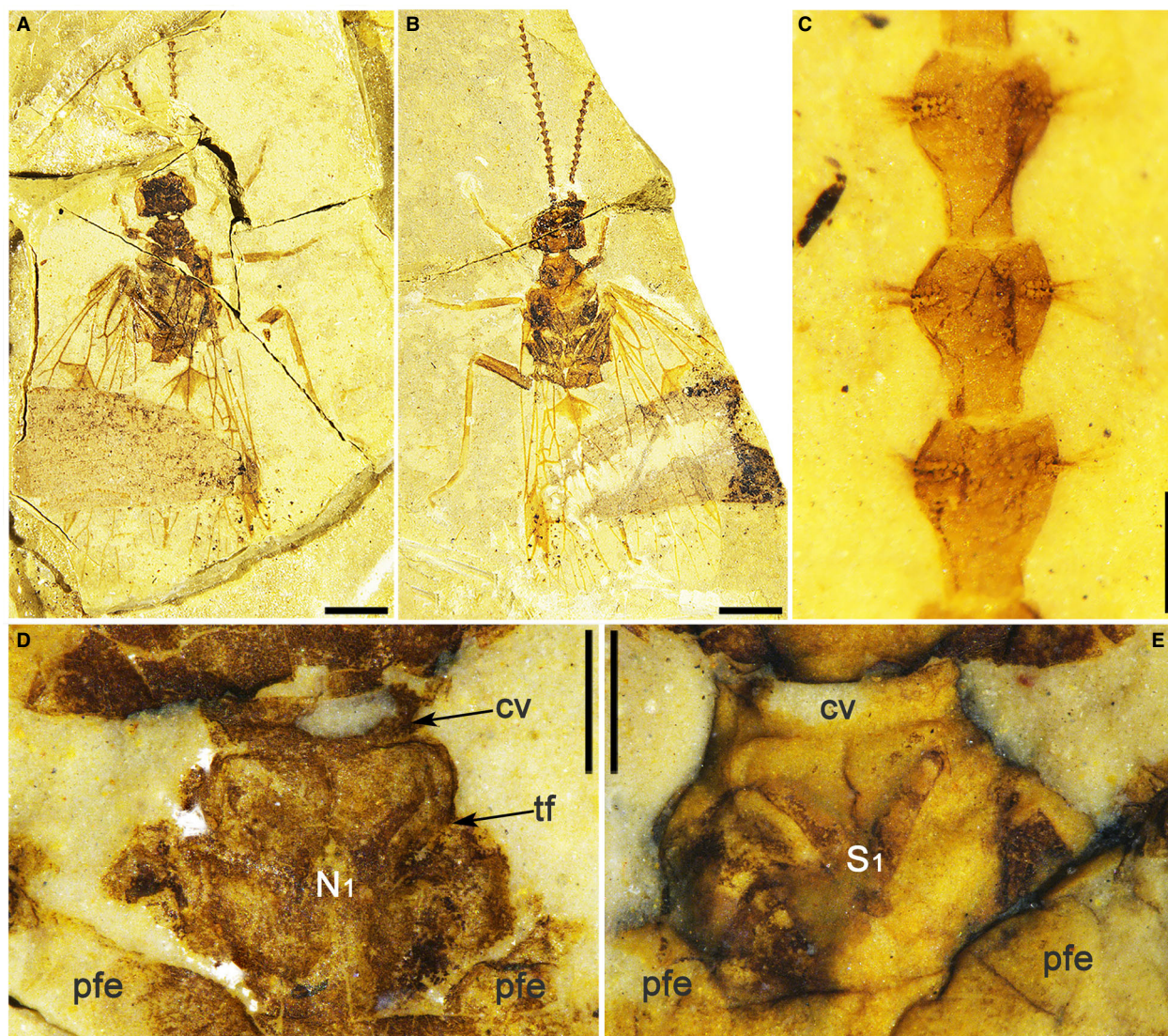


**FIG. 1.** Photographs of *Magicivena sticta* gen. et sp. nov.; holotype, CNU-LB2013101. A, habitus, part as preserved. B, habitus, counterpart as preserved. C, flagellomeres of antenna. D, pronotum, showing the transverse furrow. E, prosternum. *Abbreviations:* cv, cervical sclerite; N<sub>1</sub>, pronotum; pfe, profemur; S<sub>1</sub>, prosternum; tf, transverse furrow of pronotum. Scale bars represent: 2 mm (A, B); 0.2 mm (C); 0.5 mm (D, E).

*Type locality & horizon.* Yixian Formation, Lower Cretaceous, Huangbanjigou Village, Beipiao City, Liaoning Province, China.

*Diagnosis.* Forewing M with five apical branches, between M and CuA with a strong sub-basal cross-vein. Hind wing with three cross-veins between R and M. Antennal setae shorter than flagellomere width.

*Description.* As preserved, dorsal view (Fig. 1A) slightly darker than ventral view (Fig. 1B). Head slightly wider than long in dorsal view; orthognathous; compound eyes moderately convex, 0.3 times head length; one ocellus visible. Antenna moniliform, longer than head + thorax; scape longer and wider than pedicel,

cylindrical; flagellomeres cylindrical in proximal and spherical in terminal; setiferous pits and sensory setae present on both sides of every spherical flagellomere; at least 20 setiferous pits; sensory setae shorter than flagellomere width and only present in the middle of setiferous pits (Fig. 1C). Dorsal cervical sclerites present. Prothorax shorter than mesothorax and metathorax, divided transversely, anterior part narrower but longer than posterior (Fig. 1D); prosternum rectangular (Fig. 1E); mesothorax similar to metathorax. Coxae distinct, large; femora thicker than tibiae; tibiae slightly widening distally; tarsi five-segmented; euplantulae and arolia not visible due to poor preservation; claws small. Abdominal segments I and II short, other segments unpreserved.

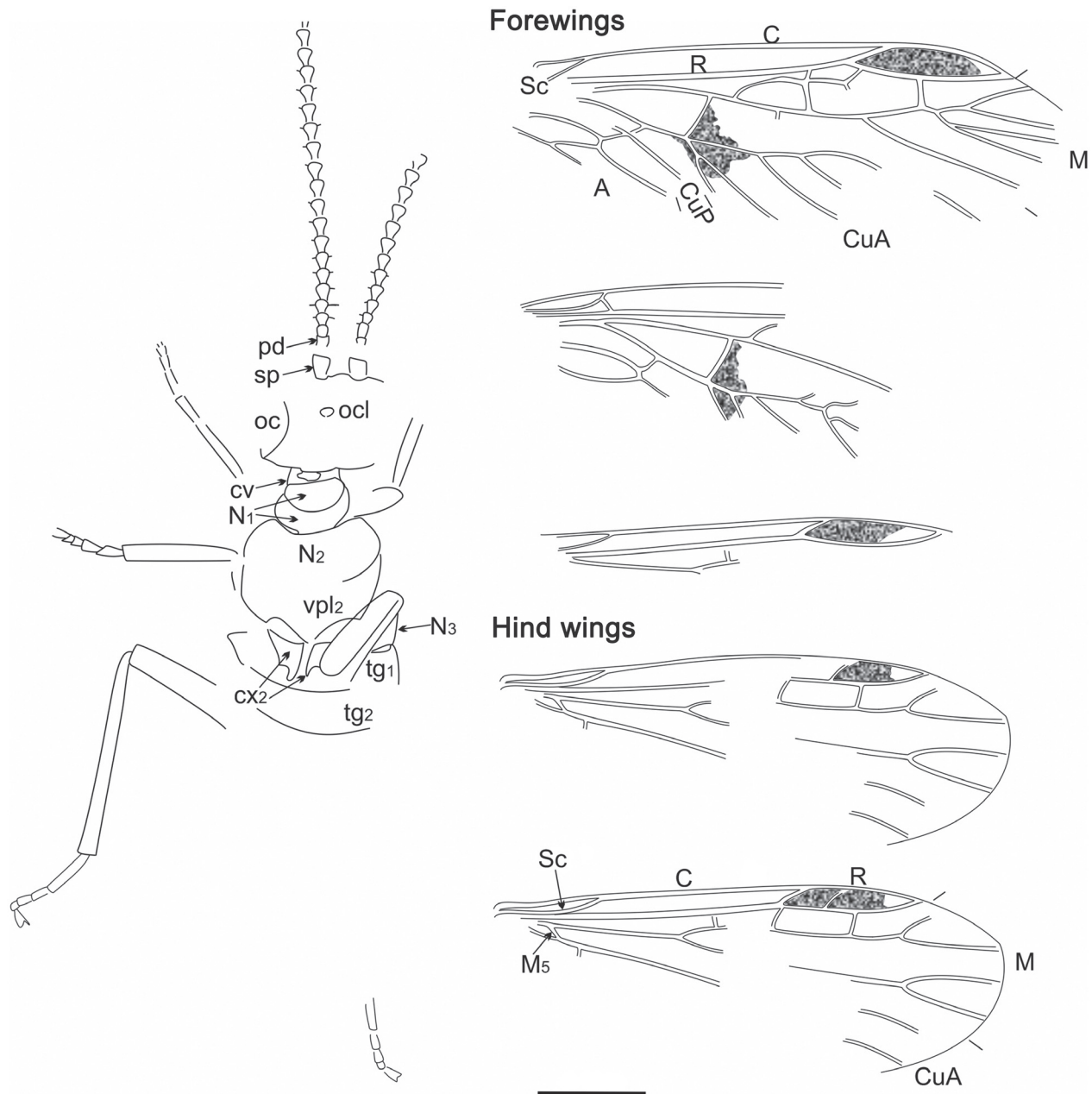


**FIG. 2.** Line drawings of *Magicivena sticta* gen. et sp. nov.; holotype, CNU-LB2013101. *Abbreviations:* A, anal; C, costa; cv, cervical sclerite; cx<sub>2</sub>, coxa; M, media; N<sub>1</sub>, pronotum; N<sub>2</sub>, mesonotum; N<sub>3</sub>, metanotum; oc, compound eye; ocl, ocellus; pd, pedicel; R, radius; Sc, subcostal anterior; sp, scape; tg<sub>1, 2</sub>, tergum of abdominal segment I, II; vpl<sub>2</sub>, ventral mesopleuron. Scale bar represents 2 mm.

Forewing Sc very short with two short apical branches ending in C and R; R with three short apical branches enclosing pterostigma; M with five apical branches, with several irregular cross-veins toward R before pterostigma in right wing but apparently not in left one and not in other congeners (perhaps individual aberration of no diagnostic value); at least one strong sub-basal m-cu cross-vein coinciding with basal posterior branch of CuA and possibly another m-cu cross-vein more distally; M + CuA about as long as Sc; CuA with at least seven branches forming a backward comb, with two basal branches with short common

base coinciding with basal m-cu cross-vein, with cross-vein and basal CuA branch forming basal boundary of a dark spot; CuP single, incomplete preserved; 1A with short free apex and with cu-a cross-vein meeting CuA halfway between apex of M + CuA and basal CuA branch, shortly before oblique cross-vein 1a-2a that aligned with 2A, free end of 1A and 2A present. Hind wing slightly shorter than forewing; Sc short, simple, ending at C; R with three apical branches enclosing pterostigma like in forewing; M basally with M<sub>5</sub> meeting CuA, branching before mid-length, each branch with short apical forks; CuA with at least

two branches and one posterior sub-basal stub of cross-vein or branchlet; CuP and anal area not preserved (Fig. 2).

**Measurements.** Body 13.41 mm (as preserved, excluding antennae); head width 1.95 mm, length 1.58 mm; antenna 6.48 mm (as preserved); flagellomere 0.31 mm; prothorax 0.94 mm; mesothorax 1.67 mm; metathorax 1.95 mm; forewing 10.71 mm; hind wing 9.69 mm; forefemur 1.47 mm; middle femur 2.39 mm; hind femur 2.89 mm; middle tibia 2.16 mm; hind tibia 3.96 mm; tarsi 1.59 mm.

*Magicivena elegans* sp. nov.

Fig. 3

LSID. urn:lsid:zoobank.org:act:B6DDA816-812E-4455-92E9-857F77892853

**Derivation of name.** The epithet is from the Latin word *elegans*, meaning elegant.

**Holotype.** CNU-LB2013102.

**Type locality & horizon.** Yixian Formation, Lower Cretaceous, Huangbanjigou Village, Beipiao City, Liaoning Province, China.

**Diagnosis.** Forewing M with two simple branches only, with two strong cross-veins between R and M, and one strong sub-basal cross-vein between M and CuA.

**Description.** Only head, prothorax and partial mesothorax preserved (Fig. 3A–C). Head wider than long in dorsal view; compound eyes convex; ocelli unclear. Antenna moniliform; scape and pedicel cylindrical; seven flagellomeres preserved; two lip-shaped setiferous pits occupy a quarter of both sides of every flagellomere, at least 20 setiferous pits arranged in two rows on every lip-shaped setiferous pit; sensory setae inconspicuous (Fig. 3D). Dorsal cervical sclerite present. Pronotum with a deep transverse furrow, anterior part narrower than posterior part, shorter and thinner than mesothorax; mesothorax large and

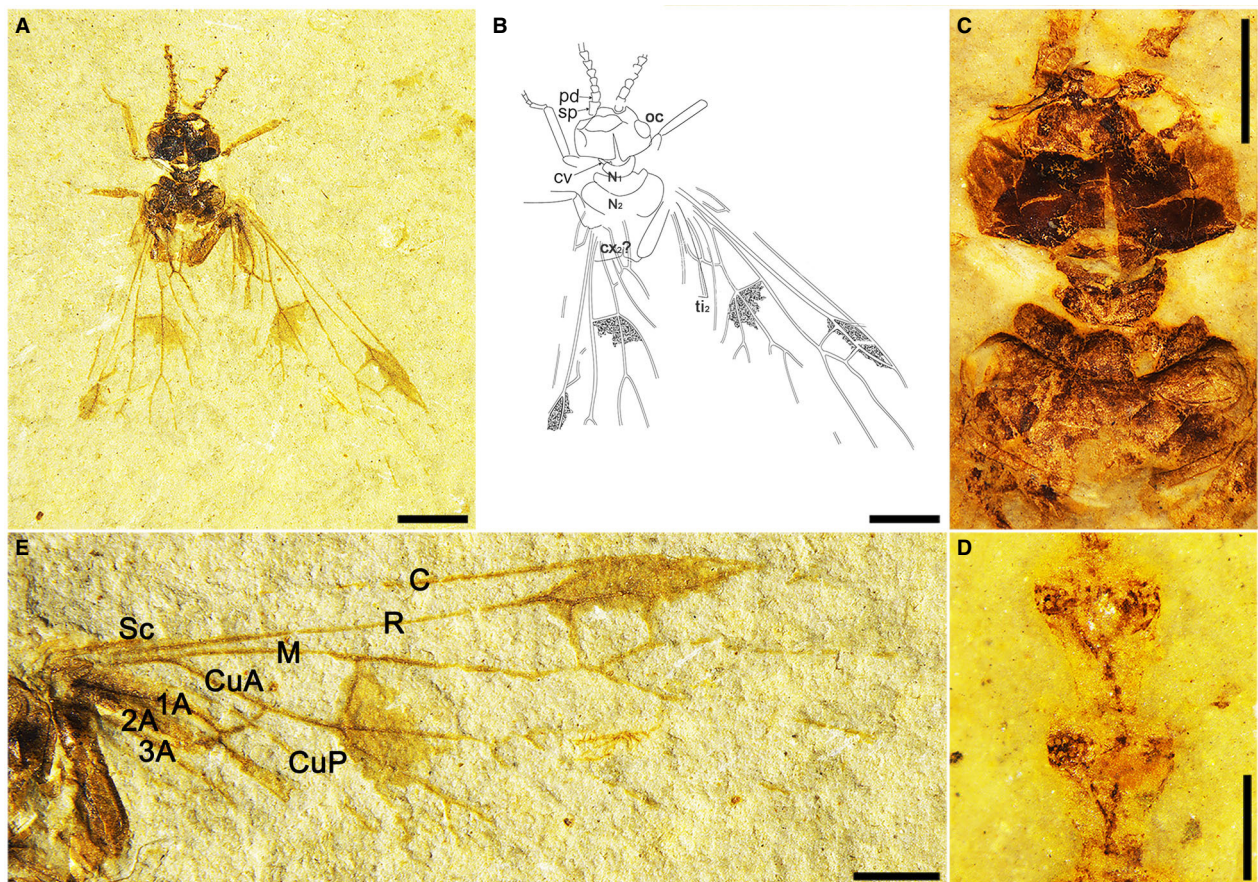


**FIG. 3.** Photographs of *Magicivena elegans* sp. nov.; holotype, CNU-LB2013102. A, habitus. B, line drawing of habitus. C, head and thorax. D, flagellomeres of antenna. E, forewing. **Abbreviations:** 1A, 2A, 3A, first, second, third anal veins; C, costa; CuA, cubital anterior; CuP, cubital posterior; cv, cervical sclerite; cx<sub>2</sub>, coxa; M, media; N<sub>1</sub>, pronotum; N<sub>2</sub>, mesonotum; R, radius; Sc, subcostal anterior; oc, compound eye; pd, pedicel; sp, scape; ti<sub>2</sub>, tibia. Scale bars represent: 2 mm (A, B); 1 mm (C, E); 0.2 mm (D).

oval. Femora thicker than tibiae; tibiae elongate, middle ones particularly so; tarsi incompletely preserved.

Forewing with Sc short, meeting at least C (incompletely preserved); R with three short apical branches and pterostigma in between; M with apical fork starting slightly distal of pterostigma base, with two r-m cross-veins before and after M fork and with a sub-basal m-cu cross-vein; CuA similar to that of *M. sticta* (including similar dark spot) except that its basal branch twice branching in one of wings and apparently simple in another; CuP weak but distinct, crossing cu-a cross-vein; 1A and 2A similar to that of *M. sticta* except free end of 1A longer and free end of 2A lost, instead a free 3A present (Fig. 3E).

**Measurements.** Body 13.18 mm (as preserved, excluding antennae); head width 2.23 mm, length 1.58 mm; antenna 2.35 mm (as preserved); flagellomere 0.26 mm; prothorax 0.69 mm; mesothorax 1.01 mm; forewing 10.39 mm; middle femur 2.31 mm; foretibia 1.61 mm; foretarsi 1.06 mm (as preserved).

**Remarks.** *Magicivena elegans* is differentiated from *M. sticta* in having forewing with a two-branched M (not with numerous branches) and free 3A vein, and in having legs longer (mid tibia

distinctly longer than mesonotum wide). In both species, venation varies between right and left wings; this makes the inclusion of body characters in their diagnoses important.

*Magicivena antennalis* sp. nov.

Fig. 4

**LSID.** urn:lsid:zoobank.org:act:A2FF2FCD-BEAE-4B9E-BC9C-57BA70AEC787

**Derivation of name.** The epithet is from ‘antenna’, alluding its long antennal vestiture.

**Holotype.** CNU-LB2013103.

**Type locality & horizon.** Yixian Formation, Lower Cretaceous, Huangbanjigou Village, Beipiao City, Liaoning Province, China.

**Diagnosis.** Forewing with simple M (possibly except short apical branches); no distinct r-m cross-vein; no distinct sub-basal m-cu cross-vein nor respective dark spot. Antennal setae not

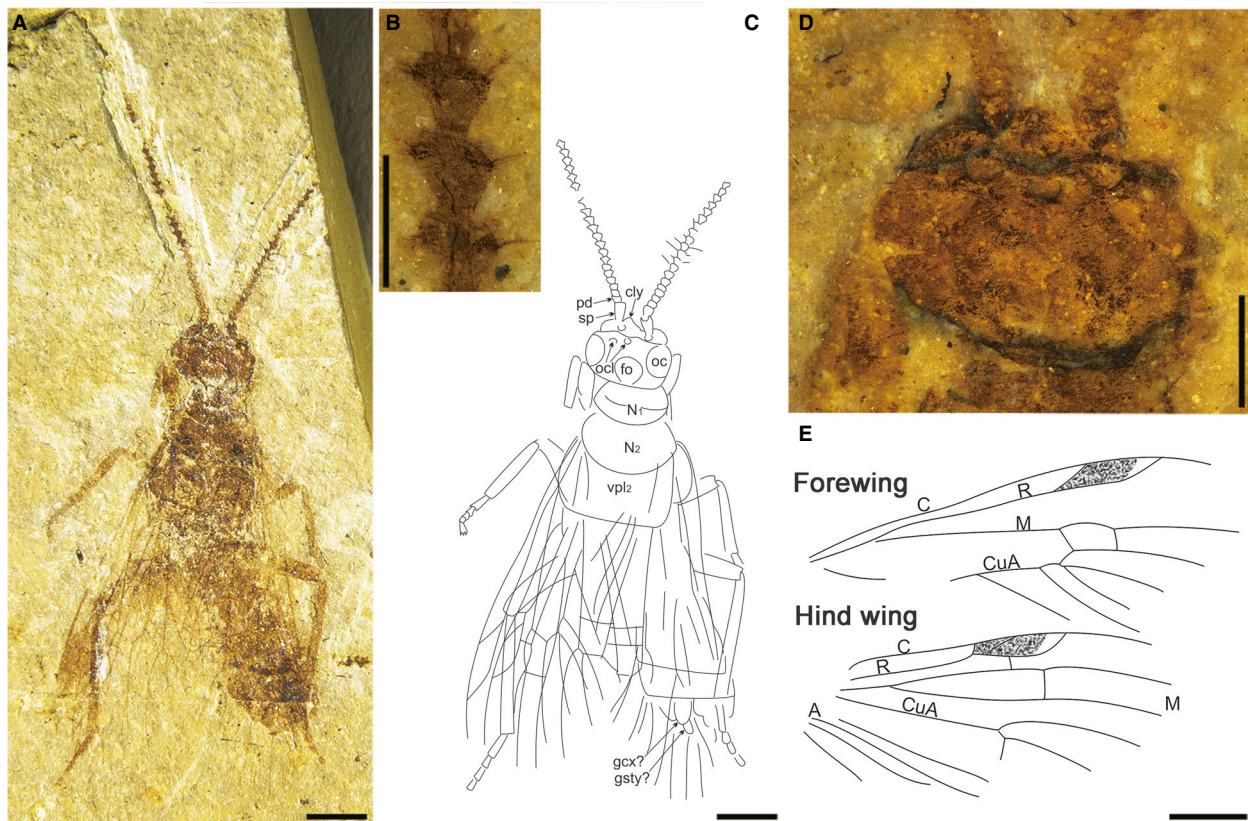


**FIG. 4.** Photographs of *Magicivena antennalis* sp. nov.; holotype, CNU-LB2013103. A, habitus. B, flagellomeres of antenna. C, line drawing of habitus. D, head. E, line drawings of forewing and hind wing. **Abbreviations:** C, costa; cly, clypeus; CuA, cubital anterior; fo, foramen occipitale; gcx, gonocoxa; gsty, gonostylus; M, media; N<sub>1</sub>, pronotum; N<sub>2</sub>, mesonotum; oc, compound eye; ocl, ocellus; pd, pedicel; R, radius; sp, scape; vpl<sub>2</sub>, ventral mesopleuron. Scale bars represent: 2 mm (A, C, E); 0.5 mm (B); 1 mm (D).

shorter than flagellomere width. Legs short (mid tibia shorter than mesonotum wide).

**Description.** Head orthognathous, slightly wider than long; compound eyes 0.3 times of head length; three ocelli present; clypeus and foramen occipital visible (Fig. 4D). Antenna moniliform, far longer than head + thorax; setiferous pits and setae present on both sides of every flagellomere, sensory setae equal to or longer than flagellomere (possibly about twice as long as flagellomere width) (Fig. 4B); scape and pedicel without setiferous pits and setae. Prothorax smaller than mesothorax and metathorax, pronotum with a weak transverse furrow. Fore and mid legs short (mid tibia shorter than mesonotum wide), hind legs longer than fore and mid legs; femora slender, slightly thicker than tibiae, tibiae hardly widening distally; tarsi five-segmented; euplantulae and arolia not visible due to poor preservation; claws visible. Abdomen long and slightly narrower than thorax, segmentation unclear (Fig. 4A, C).

Forewing with Sc not preserved; R with three short apical branches and pterostigma in between; M simple (possibly except short apical branches); two distinct m-cu cross-veins under pterostigma, no distinct r-m cross-vein; no distinct sub-basal m-cu cross-vein nor respective dark spot. CuA with five simple posterior branches visible, CuP and anal veins not preserved. Hind wing with similar R and pterostigma; M with a very long simple fork, with r-m cross-vein at pterostigma mid-length and m<sub>1</sub>-m<sub>2</sub> cross-vein slightly more distal. CuA with simple fork under pterostigma mid-length and with posterior cross-vein near fork base; CuP not visible; four long parallel anal veins present (Fig. 4E).

**Measurements.** Body 17.26 mm (excluding antennae); head width 2.91 mm, length 2.17 mm; antenna 9.86 mm (as preserved); flagellomere 0.29 mm; prothorax 1.08 mm; mesothorax 1.54 mm; metathorax 1.96 mm; forewing 11.5 mm; hind femur 3.90 mm; middle tibia 2.62 mm; hind tibia 4.35 mm; abdomen 9.20 mm.

**Remarks.** *Magicivena antennalis* is differentiated from both *M. sticta* and *M. elegans* in having long antennal setae (up to twice as long as antennal flagellomere width) and forewing with M simple and with no sub-basal m-cu cross-vein and respective dark spot.

#### *Magicivena* sp.

##### Figure. 5

**Material.** CNU-NL2013104p/c, part and counterpart.

**Locality and horizon.** Yixian Formation, Lower Cretaceous, Liutiaogou Village, Ningcheng Country, Inner Mongolia, China.

**Description.** Body somewhat distorted, with most details unclear, wing venation incompletely preserved. Antenna moniliform, slightly shorter than body, apparently 28-segmented, with setiferous pits and setae present on both sides of every flagellomere, with setae about twice as long as flagellomere width (Fig. 5D). Prothorax apparently shorter but not distinctly

narrower than mesothorax and metathorax. Femora shorter and thicker than tibiae, tarsi not preserved. Abdomen moderately elongate; cerci short, conical, with 5–6 closely placed segments, no genitalia visible (Fig. 5C). Wing venation as preserved apparently similar to that of *M. sticta*, and, to a lesser extent, *M. elegans*: forewing with one r-m (at pterostigma base), sub-basal m-cu and respective dark spot present, M with at least three branches and anal veins apparently as in *M. sticta* (Fig. 5A, B).

**Measurements.** Body 13.71 mm (excluding antennae); head width 1.94 mm, length 1.59 mm; antenna 8.15 mm (as preserved); flagellomere 0.33 mm; prothorax 0.81 mm; mesothorax 1.12 mm; metathorax 1.26 mm; forewing 10.2 mm; abdomen 7.95 mm; cercus 0.87 mm.

**Remarks.** *Magicivena* sp. combines characters diagnostic of *M. sticta* (available details of wing venation) and *M. antennalis* (antennae with long setae and wide pronotum) and hence cannot be attributed to any of species described above. However, incomplete preservation prevents description of the specimen as a new species.

## DISCUSSION

Although the taxonomy and classification system of extant Neoptera have been established rather well now, it is difficult to assign *Magicivenidae* to any extant or fossil taxa due to their distinctively different venational, antennal and body structures. There are several potentially decisive characters to identify the taxonomic position of *Magicivenidae*. First, a combination of characters (e.g. forewing with CuA multibranched, hind wing with at least four long anal veins and by inference wide anal area, and multi-segmented cerci) suggests an assignment of *Magicivenidae* to Polyneoptera. In contrast, all fore and hind wings with pterostigmata occur in various insect orders but are not characteristic of Polyneoptera. This holds true also of antenna with sophisticated sensoria and specifically arranged long setae. Additionally, wings that have lost RS are, to our knowledge, characteristic of no higher taxa of Pterygota. Yet in the balance of all evidence available, we prefer to refer *Magicivenidae* to the Infra-class Gryllones (Polyneoptera) until better evidence is found.

Within Polyneoptera, affinity of *Magicivena* to Orthopteroidea is unlikely because of the presence of segmented cerci (which are entire in Orthopteroidea). A choice between blattoid and perloid polyneopterans is difficult because diagnostic characters of either group are not visible in available *magicivenid* fossils, and there is no known reliable similarity to any subordinate taxa of either blattoid or perloid polyneopterans in *Magicivenidae* (Aristov 2014, 2015). On the other hand, the blattoid hypothesis is attractive because one of its group, the family

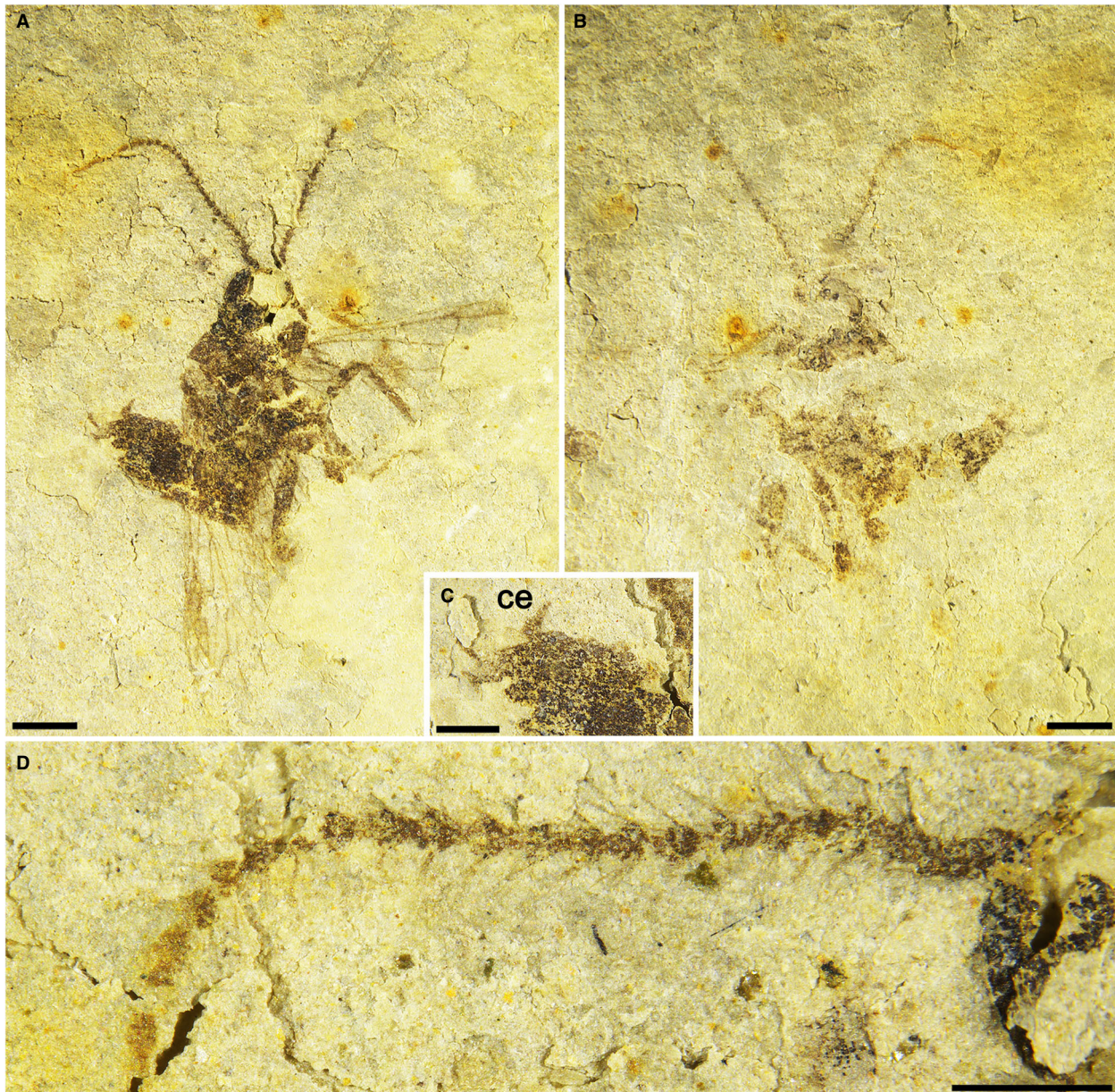


**FIG. 5.** Photographs of *Magicivena* sp.; CNU-NL2013104. A, habitus, part as preserved. B, habitus, counterpart as preserved. C, cerci (ce). D, antenna. Scale bars represent: 2 mm (A, B); 1 mm (C, D).

Alienopteridae (Bai *et al.* 2016, 2018; Vršanský *et al.* 2018), is nearly as deviant from the bulk of Blattodea as *Magicivena* is from other insects. There are some features of *Magicivena* that are parallel to those of Alienopteridae, such as: the light constitution of a good flier; superficially similar (hind) wing venation including similar pterostigma; and a transversely grooved pronotum in *Magicivena* and many Alienopteridae. Differences are unquestionably significant between these two groups, including particularly a pronounced posteromotor and rudimentary forewings that contrast strongly with the

bimotory arrangement of *Magicivenidae*, as well as the absence of a distinct RS in *Magicivena*.

The antennae of *Magicivena* need additional consideration. The antenna is one of the most important insect sensory organs, playing an important role in sexual selection, food selection, feeding, mating, etc. (Cardé & Minks 1997; Tegoni *et al.* 2004; Xiao *et al.* 2009). Occasionally sensilla have been recognized in the fossil record, such as those on well-preserved antennae in amber (Labandeira 2014; Du *et al.* 2020) and few compression fossils (e.g. Rasnitsyn & Quicke 2002, fig. 346;



**FIG. 6.** Reconstruction of *Magicivena sticta*. Artwork by Dr Chen Wang.

Gao *et al.* 2016). All Magicivenidae flagellomeres have two conspicuous lateral transverse rows of setiferous pits at mid-length, the sensilla chaetica, which are located in the upper and most prominent part, and are similar to the capitate flagellomeres of gall midges (Diptera) (Fedotova & Perkovsky 2009, 2019). The sensilla chaetica are mechanoreceptors and may protect the finer underlying structure on the antennae or perceive differences in substrate texture, movement and wind direction (Crook & Mordue 1999; Wang *et al.* 2016). An antenna with sophisticated sensory apparatus is often a male character, and this might be the case for all four known specimens of Magicivenidae. Females have not yet been identified. We would usually rely primarily on the characteristic wing venation rather than body structures. However, wingless or reluctant-flyer females sometimes correlate with hypersensoric male antennae, making identification more difficult in this case.

## CONCLUSION

The new family Magicivenidae (Order *incertae sedis*) is mainly found in the Upper Cretaceous of north-eastern China and has a unique combination of antennal structures and wing venations which are different from those of

any other fossil or extant insect taxa documented hitherto (Fig. 6). However, Magicivenidae are here assigned to Polyneoptera and might have closer relationship with Alienopteridae. Furthermore, wing venations and antennal structures suggest that Magicivenidae were good at flight and probably had antennae with unique sensing and perceptual functions. The exact taxonomic position and life habits of Magicivenidae require further study based on more fossil specimens.

**Acknowledgements.** We are grateful to Dr Chen Wang (Capital Medical University) for the reconstruction picture. We thank Dr Yongjie Wang for providing helpful comments and discussions. We appreciate Qiong Wu, Zhipeng Zhao, Yanjie Zhang, Xiao Zhang, Ye Han and Sheng Li (Capital Normal University) for their helpful advice. DR was supported by grants from the National Natural Science Foundation of China (No. 31730087, 41688103 and 32020103006). The work of APR was partially supported by the Presidium of the Russian Academy of Sciences Program 'Origin of the Biosphere and Evolution of Geobiological Systems'. The authors declare that they have no competing interests. Three anonymous referees commented on an earlier draft of this manuscript.

**Author contributions.** T.P. Gao and D. Ren conceived and designed the experiments; H.R. Yang, C.K. Shih, A.P. Rasnitsyn, D. Ren and T.P. Gao performed the analysis and experiments; H.R. Yang and A.P. Rasnitsyn prepared photographs and line drawings. All authors wrote, read and approved the final manuscript.

## DATA ARCHIVING STATEMENT

This published work, and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/references/7F3476DD-D92E-4934-A4EB-788C0618793A>

**Editor.** Conrad Labandeira

## REFERENCES

- ARISTOV, D. S. 2014. Classification of the order Cnemidolestida (Insecta: Perlidea) with description of new taxa. *Far Eastern Entomologist*, **277**, 1–46.
- 2015. Classification of the order Eoblattida (Insecta: Blattellidae) with description of new taxa. *Far Eastern Entomologist*, **301**, 1–56.
- BAI, M., BEUTEL, R. G., KLASS, K. D., ZHANG, W. W., YANG, X. K. and WIPFLER, B. 2016. †Alienoptera — a new insect order in the roach–mantodean twilight zone. *Gondwana Research*, **39**, 317–326.
- — ZHANG, W. W., WANG, S., HÖRNIG, M., GRÖHN, C., YAN, E., YANG, X. K. and WIPFLER, B. 2018. A new Cretaceous insect with a unique cephalothoracic scissor device. *Current Biology*, **28**, 1–6.

- BEUTEL, R. G., FRIEDRICH, F., HÖRNSCHEMEYER, T., POHL, H., HÜNEFELD, F., BECKMANN, F., MEIER, R., MISOF, B., WHITING, M. F. and VILHELMSEN, L. 2011. Morphological and molecular evidence converge upon a robust phylogeny of the megadiverse Holometabola. *Cladistics*, **27**, 341–355.
- CARDÉ, R. T. and MINKS, A. K. 1997. *Insect pheromone research: new directions*. Chapman & Hall.
- CROOK, D. J. and MORDUE, A. J. 1999. Olfactory responses and sensilla morphology of the blackcurrant leaf midge *Dasineura tetensi*. *Entomologia Experimentalis et Applicata*, **91**, 37–50.
- DU, B.-J., CHEN, R., TAO, W.-T., SHI, H.-L., BU, W.-J., LIU, Y., MA, S., NI, M.-Y., KONG, F.-L., XIAO, J.-H. and HUANG, D.-W. 2020. A Cretaceous bug with exaggerated antennae might be a double-edged sword in evolution. *iScience*, **24**, 101932.
- FEDOTOVA, Z. A. and PERKOVSKY, E. E. 2009. New gall midges of the tribe Leptosynini (Diptera, Cecidomyiidae) from the Late Eocene ambers and the classification of the supertribe Heteropezidi. *Paleontological Journal*, **43**, 1101–1179.
- . 2019. First findings of gall midges (Diptera, Cecidomyioidea, Cecidomyiidae) of the Tribes Karshomyiini (Mexican amber) and Bremiini (Dominican amber). *Paleontological Journal*, **53**, 1060–1073.
- GAO, T.-P., SHIH, C.-K., LABANDEIRA, C. C., SANTIAGO-BLAY, J. A., YAO, Y.-Z. and REN, D. 2016. Convergent evolution of ramified antennae in insect lineages from the Early Cretaceous of Northeastern China. *Proceedings of the Royal Society B*, **283**, 20161448.
- , YIN, X.-C., SHIH, C.-K., RASNITSYN, A. P., XU, X., CHEN, S., WANG, C. and REN, D. 2019. New insects feeding on dinosaur feathers in mid-Cretaceous amber. *Nature Communications*, **10**, 5424.
- , SHIH, C.-K. and REN, D. 2021. Behaviors and interactions of insects in mid-Mesozoic ecosystems of northeastern China. *Annual Review of Entomology*, **66**, 337–354.
- GRIMALDI, D. and ENGEL, M. S. 2005. *Evolution of the insects*. Cambridge University Press.
- HUANG, D.-Y., BECHLY, G., NEL, P., ENGEL, M. S., PROKOP, J., AZAR, D., CAI, C.-Y., VAN DE KAMP, T., STANICZEK, A. H., GARROUSTE, R., KROGMANN, L., DOS SANTOS ROLO, T., BAUMBACH, T., OHLHOF, R., SHMAKOV, A. S., BOURGOIN, T. and NEL, A. 2016. New fossil insect order Permopsocida elucidates major radiation and evolution of suction feeding in hemimetabolous insects (Hexapoda: Acercaria). *Scientific Reports*, **6**, 1–9.
- KOČÁREK, P. 2019. *Alienopterella stigmatica* gen. et sp. nov.: the second known species and specimen of Alienoptera extends knowledge about this Cretaceous order (Insecta: Polyneoptera). *Journal of Systematic Palaeontology*, **17**, 491–500.
- LABANDEIRA, C. C. 2014. Amber. 163–217. In LAFLAMME, M., SCHIFFBAUER, J. D. and DARROCH, S. A. F. (eds). *Reading and writing of the fossil record: Preservation pathways to exceptional fossilization*. The Paleontological Society Papers, **20**.
- LINNAEUS, C. 1758. *Systema naturae*. Tenth edition, vol. 1. Laurentius Salvius, Holmiae, 824 pp. <https://doi.org/10.5962/bhl.title.542>
- MEY, W., WICHARD, W., MUELLER, P. and WANG, B. 2017. The blueprint of the Amphiesmenoptera – Tarachoptera, a new order of insects from Burmese amber (Insecta, Amphiesmenoptera). *Fossil Record*, **20**, 129–145.
- MISOF, B., LIU, S.-L., MEUSEMANN, K., PETERS, R. S., DONATH, A., MAYER, C., FRANDSEN, P. B., WARE, J., FLOURI, T., BEUTEL, R. G., NIEHUIS, O., PETERSEN, M., IZQUIERDO-CARRASCO, F., WAPPLER, T., RUST, J., ABERER, A. J., ASPÖCK, U., ASPÖCK, H., BARTEL, D., BLANKE, A., BERGER, S., BÖHM, A., BUCKLEY, T. R., CALCOTT, B., CHEN, J.-Q., FRIEDRICH, F., FUKUI, M., FUJITA, M., GREVE, C., GROBE, P., GU, S.-C., HUANG, Y., JERMIIN, L. S., KAWAHARA, A. Y., KROGMANN, L., KUBIAK, M., LANFEAR, R., LETSCH, H., LI, Y.-Y., LI, Z.-Y., LI, J.-G., LU, H.-R., MACHIDA, R., MASHIMO, Y., KAPLI, P., McKENNA, D. D., MENG, G.-M., NAKAGAKI, Y., NAVARRETE-HEREDIA, J. L., OTT, M., OU, Y.-X., PASS, G., PODSIADLOWSKI, L., POHL, H., VON REUMONT, B. M., SCHÜTTE, K., SEKIYA, K., SHIMIZU, S., SLIPINSKI, A., STAMATAKIS, A., SONG, W.-H., SU, X., SZUCSICH, N. U., TAN, M.-H., TAN, X.-M., TANG, M., TANG, J.-B., TIMELTHALER, G., TOMIZUKA, S., TRAUTWEIN, M., TONG, X.-L., UCHIFUNE, T., WALZL, M. G., WIEGMANN, B. M., WILBRANDT, J., WIPFLER, B., WONG, T. K. F., WU, Q., WU, G.-X., XIE, Y.-L., YANG, S.-Z., YANG, Q., YEATES, D. K., YOSHIZAWA, K., ZHANG, Q., ZHANG, R., ZHANG, W.-W., ZHANG, Y.-H., ZHAO, J., ZHOU, C.-G., ZHOU, L.-L., ZIESMANN, T., ZOU, S.-J., LI, Y.-G., XU, X., ZHANG, Y., YANG, H.-M., WANG, J., WANG, J., KJER, K. M. and ZHOU, X. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.
- RASNITSYN, A. P. and QUICKE, D. L. J. 2002. *History of insects*. Kluwer.
- REN, D., SHIH, C. K., GAO, T. P., WANG, Y. J. and YAO, Y. Z. 2019. *Rhythms of insect evolution – evidence from the Jurassic and Cretaceous in Northern China*. Wiley Blackwell.
- STANICZEK, A., BECHLY, G. and GODUNKO, R. 2011. Coxopteroptera, a new fossil order of Palaeoptera (Arthropoda: Insecta), with comments on the phylogeny of the stem group of mayflies (Ephemeroptera). *Insect Systematics & Evolution*, **42**, 101–138.
- TEGONI, M., CAMPANACCI, V. and CAMBILLAU, C. 2004. Structural aspects of sexual attraction and chemical communication in insects. *Trends in Biochemical Sciences*, **29**, 257–264.
- TILLYARD, R. J. 1926. Kansas Permian insects, Part 8: The Order Copeognatha. *American Journal of Science, Series 5*, **11** (64), 315–349.
- VRŠANSKÝ, P., BECHLY, G., ZHANG, Q.-Q., JARZEMBOWSKI, E. A., MLYNSKÝ, T., ŠMÍDOVÁ,

- L., BARNA, P., KÚDELA, M., ARISTOV, D. S., BIGALK, S., KROGMANN, L., LI, L.-Q., ZHANG, Q., ZHANG, H.-C., ELLENBERGER, S., MÜLLER, P., GRÖHN, C., XIA, F.-Y., UEDA, K., Vd' AČNÝ, P., VALAŠKA, D., VRŠANSKÁ, L. and WANG, B. 2018. Batesian insect-insect mimicry-related explosive radiation of ancient alienopterid cockroaches. *Biologia*, **73**, 987–1006.
- WANG, Y., LI, D., LIU, Y., LI, X.-J., CHENG, W.-N. and ZHU-SALZMAN, K. 2016. Morphology, ultrastructure and possible functions of antennal sensilla of *Sitodiplosis mosellana* Géhin (Diptera: Cecidomyiidae). *Journal of Insect Science*, **16** (93), 1–12.
- WIPFLER, B., LETSCH, H., FRANDBSEN, P. B., KAPLI, P., MAYER, C. U., BARTEL, D., BUCKLEY, T. R., DONATH, A., EDGERLY, J., FUJITA, M., LIU, S., MACHIDA, R., MASHIMO, Y., MISOF, B., NIEHUIS, O., PETERS, R. S., PETERSEN, M., PODSIAD-LOWSKI, L., SCHÜTTE, K. A., SHIMIZU, S., UCHI-FUNE, T., WILBRANDT, J., YAN, E., ZHOU, X. and SIMON, S. 2018. Evolutionary history of Polyneoptera and its implications for our understanding of early winged insects. *Proceedings of the National Academy of Sciences*, **116**, 3024–3029.
- KOČÁREK, P., RICHTER, A., BOUDINOT, B., BAI, M. and BEUTEL, R. G. 2019. Structural features and life habits of †Alienoptera (Polyneoptera, Dictyoptera, Insecta). *Palaeoentomology*, **2**, 465–473.
- WOOTTON, R. J. and KUKALOVÁ-PECK, J. 2000. Flight adaptations in Palaeozoic Palaeoptera (Insecta). *Biological Reviews*, **75**, 129–167.
- XIAO, B., FANG, N., ZHANG, Y.-Y., XUAN, W. J. and JIANG, G.-F. 2009. Fine structures of the antennal sensilla from the eight species of Blattodea. *Acta Zootaxonomica Sinica*, **34**, 292–300.
- YANG, H.-R., SHI, C.-F., ENGEL, M. S., ZHAO, Z.-P., REN, D. and GAO, T.-P. 2021. Early specializations for mimicry and defense in a Jurassic stick insect. *National Science Review*, **8**, nwaa056.
- YOSHIZAWA, K. and LIENHARD, C. 2016. Bridging the gap between chewing and sucking in the hemipteroid insects: new insights from Cretaceous amber. *Zootaxa*, **4079**, 229–245.