Insect Systematics and Diversity, 8(4), 8; 2024, ixae016 https://doi.org/10.1093/isd/ixae016 Research



## Paleontology

## New Cretaceous snakeflies highlight the morphological disparity of Mesoraphidiidae and its response to the Cretaceous Terrestrial Revolution

Xiumei Lu<sup>1,2,\*,0</sup>, Thomas L. Stubbs<sup>3</sup>, De Zhuo<sup>4</sup>, Chunpeng Xu<sup>5</sup>, Philip C.J. Donoghue<sup>2,0</sup>, Xingyue Liu<sup>6,\*,0</sup>

<sup>1</sup>Institute of Ecological and Environmental Protection, Shanghai Academy of Agricultural Sciences, Shanghai, China, <sup>2</sup>Bristol Palaeobiology Group, School of Earth Sciences, University of Bristol, Bristol, UK, <sup>3</sup>Faculty of Science, Technology, Engineering & Mathematics, School of Life, Health & Chemical Sciences, The Open University, Milton Keynes, UK, <sup>4</sup>Beijing Xiachong Amber Museum, Beijing, China, <sup>5</sup>State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China, <sup>6</sup>Department of Entomology, China Agricultural University, Beijing, China <sup>\*</sup>Corresponding authors: Xiumei Lu, email: lxm2361892563@126.com; Xingyue Liu, email: xingyue\_liu@yahoo.com

#### Subject Editor: Rolf Beutel

Received on 20 March 2024; revised on 6 June 2024; accepted on 25 June 2024

Mesoraphidiidae is an extinct family of the order Raphidioptera with an evolutionary history that is largely unexplored. Here, we uncovered the evolutionary history of Mesoraphidiidae using phylogenetic comparative approaches, based on an updated morphological dataset, with an additional description of two new genera and species with distinct cephalic elongation, Dracoraphidia brachystigma gen. et sp. nov. and Teratocephala macrostigma gen. et sp. nov., from mid-Cretaceous Myanmar amber. Phylogenetic analysis shows their affinity to the subfamily Alloraphidiinae. Our results show that the radiation of species diversity and morphological disparity of Mesoraphidiidae dates back to the Lower Cretaceous and experienced a distinct peak approximately 130-118 million years ago (Ma). This timeframe aligns with the Cretaceous Terrestrial Revolution (KTR), a period from 125 to 80 Ma marked by the proliferation of flowering plants and their interactions with insects. The habitat preference of mesoraphidiid larvae to gymnosperm plants might have led to their extinction during the KTR, with the associated decline of gymnosperm diversity. Despite reduction in the occupation of morphospace by Mesoraphidiinae, there is surprising expansion of morphospace occupation by Alloraphidiinae in the Upper Cretaceous, possibly related to cephalic elongation, which may have enhanced pollen-feeding or predation ability, in response to extrinsic changes to biodiversity and ecosystems during the KTR. This study enriches our understanding of the macroevolution of snakeflies during the Mesozoic and provides new evidence for the impact of the KTR on insects.

Key words: Raphidioptera, macroevolution, diversity, disparity, Myanmar amber

## Introduction

Raphidioptera (snakeflies) are the holometabolous order with lowest modern species diversity, currently comprising about 250 extant species. However, Raphidioptera is one of the major components of the Late Jurassic and Early Cretaceous insect paleofauna, with a rich paleodiversity consisting of over 100 fossil species (Engel 2002, Jepson et al. 2008, Makarkin and Khramov 2015, Lyu et al. 2017a, 2017b, 2020, Lu et al. 2020). The most diverse group of Mesozoic Raphidioptera is the extinct family Mesoraphidiidae, which presently comprises 35 genera and 82 species sorted in two subfamilies, i.e., Alloraphidiinae and Mesoraphidiinae (Lyu et al. 2020, Oswald 2007, 2009).

Despite a rich species diversity, the monophyly and phylogeny of Mesoraphidiidae remains poorly resolved, reflecting an equally poorly developed taxonomy of the family. A recent study (Lyu et al. 2020) presented a systematic revision of Mesoraphidiidae based on Cretaceous fossils from the Yixian Formation of China. The phylogenetic analysis of Mesoraphidiidae in Lyu et al. (2020) assigned

Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com. Version of Record, first published online August 23, 2024 with fixed content and layout in compliance with Art. 8.1.3.2 ICZN. two synapomorphies for the family: the forewing MP vein with stem subequal to or longer than the length of first discoidal cell and the presence of two forewing discoidal cells. This study also recovered the monophyly of Alloraphidiinae and the mesoraphidiine tribe Nanoraphidiini. However, the monophyly of Mesoraphidiinae and the relationships among many mesoraphidiid genera were not resolved. As mentioned in Lyu et al. (2020), further resolution of the systematics and phylogeny of Mesoraphidiidae needs additional (especially genital) morphological characters because the wing characters alone are insufficient or even misleading in phylogenetic inference.

Snakeflies preserved in amber open a unique window for illuminating the phylogeny and evolution of this order by facilitating the acquisition of exquisitely preserved key morphological characters of the head, prothorax, legs, genitalia, as well as wings. So far, there have been 30 species attributed to Baissopteridae, Mesoraphidiidae, Inocelliidae, and Raphidiidae, recorded from the Cretaceous and Tertiary amber inclusions (Lu and Liu 2021). The palaeodiversity of snakeflies from the mid-Cretaceous of Myanmar is extraordinarily rich, currently represented by 4 genera and 6 species of Mesoraphidiidae, and 6 genera and 11 species of Baissopteridae (Engel 2002, Liu et al. 2016, Lu et al. 2020, Jouault et al. 2022, Makarkin 2023). Among these Myanmar amber snakeflies, a number of spectacular morphological traits, e.g., the strongly elongated antennae (Liu et al. 2016: fig. 3), the enlarged compound eyes (Liu et al. 2016: fig. 7, Lu et al. 2020: fig. 14), the strongly elongated head (Lu et al. 2020: fig. 13), the asymmetrical tarsomere 3 (Lu et al. 2020: fig. 1), and the presence of wing markings (Lu et al. 2020: figs. 1 and 2), have been documented, showing remarkable morphological diversity, which appears to be higher than that in the extant snakeflies. Moreover, Haug et al. (2020, 2022) reported many snakefly larvae from the mid-Cretaceous Myanmar amber and performed morphometric analysis showing the decline of the morphological diversity in the snakefly larvae since the mid-Cretaceous. However, there has been no quantitative analysis on the morphological diversity of adult snakeflies.

Here, we report two new species, each representing a new genus of Mesoraphidiidae, from the mid-Cretaceous amber of northern Myanmar, namely *Dracoraphidia brachystigma* gen. et sp. nov. and *Teratocephala macrostigma* gen. et sp. nov. Both new species share a remarkably elongated occiput, but have greatly different wing characters, especially the pterostigma. The male genitalia of *T. macrostigma* sp. nov. are well preserved and provide new data on the genital morphology of Mesozoic snakeflies. We performed a quantitative analysis to investigate the morphological disparity in Mesoraphidiidae based on a previously published dataset of discrete adult characters (Lyu et al. 2020). Our new findings and results shed light on the Mesozoic diversification of Raphidioptera.

### **Materials and Methods**

## Materials

The amber specimens described herein are from the Hukawng Valley, Tanai Township, Myitkyina District, Kachin State, Myanmar (see Kania et al. 2015: fig. 1) and they were acquired prior to 2017. The age of this deposit is dated to be ~99 million years (the earliest Cenomanian) by U-Pb dating of zircons from the volcaniclastic matrix of the amber (Shi et al. 2012).

The holotype of *D. brachystigma* sp. nov., and the holotype and a paratype of *T. macrostigma* sp. nov. are deposited in the Nanjing Institute of Geology and Paleontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The other three paratypes of *T. macrostigma* sp. nov. are deposited in the Xiachong Amber Museum (XAM), Beijing, China.

#### Taxonomy

Photographs and drawings were taken or made using a Leica M125C microscope system connecting with a Canon EOS 5D Mark IV camera system (Canon Inc., Japan). The figures were prepared with Adobe Photoshop CC 2019.

Abbreviations used for wing veins and cells are as follows: A, anal vein; C, costa; Cu, cubitus; CuA, cubitus anterior; MP, media posterior; R, radius; RA, radius anterior; RP, radius posterior; ScA, subcostal anterior; ScP, subcostal posterior; pt, pterostigma; *r*, radial cell; *dc*, discal cell; *m*, medial cell; *doi*, discoidal cell. The terminology of the genitalia generally follows that of H. Aspöck et al. (1991) and U. Aspöck and H. Aspöck (2008).

The published work and the taxonomic acts it contains have been registered with ZooBank: urn:lsid:zoobank. org:pub:5D0D621A-8349-4370-8DEF-0D833D3323E5.

#### Phylogeny

Aiming to recover the phylogenetic position of the two new mesoraphidiid genera, a phylogenetic analysis of Mesoraphidiidae was performed based on an updated morphological dataset from Lyu et al. (2020), with the two new genera added.

The present data comprises a total of 35 adult characters obtained from Lyu et al. (2020) with additional updates. Unknown characters were coded as "?", while inapplicable characters were coded as "-". The data matrix is provided in Supplementary File 1. All characters were treated as unordered and with equal weight.

We performed the maximum parsimony analysis of the dataset using NONA v.2.0 (Goloboff 1997). The analysis employed a heuristic research, retaining up to 10,000 maximum trees, with 100 replications. The search strategy utilized the multiple Tree Bisection and Reconnection [TBR] operation. Bootstrap values were calculated using 10,000 replicates and 100 search replicates. Character states were mapped on the strict consensus tree using WinClada v.1.00.08 (Nixon 2002), showing unambiguous changes.

#### **DivergenceTime Estimation**

Bayesian inference analysis was conducted using MrBayes v.3.2.7a (Ronquist et al. 2012) (Supplementary File 2). The consensus result obtained from NONA was utilized for topological constraints (Supplementary Files 3 and 4). Morphological character evolution was analyzed using Mkv model with gamma rate distribution (Lewis 2001, Ronquist et al. 2012, Simões et al. 2020).

The fossilized birth-death process was employed as a timetree prior to capture the dynamics of speciation (birth), extinction (death), fossil sampling, and sampling of extant taxa throughout the evolutionary history (Zhang et al. 2016, Zhang and Wang 2019). The branch length parameter was set to "clock: fossilization". Taxa sampling strategy was configured as random. The sampling proportion of extant taxa was set to 0. An exponential distribution prior with parameter 100 was applied to the speciation rate. The relative extinction rate and relative fossil sampling rate were assigned a beta distribution as the prior, with both parameters set to 1. The other parameters were left at default settings.

The age of each fossil species was assigned a uniform prior with lower and upper bounds from their respective stratigraphic range. The root age was determined using an offset exponential prior with a minimum 175 million years ago (Ma) and a mean 220 Ma. The minimum age of the offset exponential prior was set according to the lower bound of the stratigraphic range of the oldest fossil record.

The relaxed clock model was employed to characterize the variation of evolutionary rate of morphological features along branches within a phylogenetic tree. The Independent Gamma Rate (IGR) model was utilized for the base of clock rate (Ronquist et al. 2012). The prior on the variance of the gamma distribution from which the branch lengths are drawn in the IGR model was set to exponential (10).

The MCMC analysis consisted of searches run for 30 million generations with 2 runs, 4 chains of 3 heated and 1 cold. A burn-in phrase removed 25% of sampled trees. Sample frequency was 1,000, and effective sample size was larger than 200 (Supplementary File 5). A consensus time-calibrated phylogeny was derived from the sample of generated trees, based on the maximum a posteriori (MAP) tree, with a burn-in of 25%, and using the function "obtainDatedPosteriorTreesMrB" from the R package "paleotree v.3.4.5" (Bapst 2012). The "plotTree" function of the "phytools v.1.9-16" package was used to visualize the MAP tree (Revell 2012).

## Ancestral Character State Estimation

All macroevolutionary analyses were performed using RStudio v.4.2.2 (R Core Team 2013) (Supplementary File 6). The number of forewing doi serves as a crucial distinguishing character that exhibits variation across different mesoraphidiid genera. To shed light on the evolutionary timing of this distinctive feature within Mesoraphidiidae, ancestral character state estimation was undertaken. Initially, the character states of taxa are examined to ensure there are no absences. Subsequently, maximum likelihood reconstruction of ancestral states was carried out using the "ace" function from the "ape v.5.7-1" package (Paradis and Schliep 2019). The Equal Rates model was chosen for this analysis. The resulting character states of the number of forewing doi, encompassing both tips and nodes, were then visualized on the phylogenetic tree using the "tiplabels" and "nodelabels" functions from the "ape" package. The legends were added with "add.simmap.legend" functions of the "phytools" package. This process serves to illustrate the presence of different character states at various points in the evolutionary history of Mesoraphidiidae.

#### Lineages through Time

The number of mesoraphidiid lineages was determined using MAP tree, and the "ltt" function from the "phytools" package facilitated the calculation, and the "plot" function from the "graphics" package in R was used for visualization. Subsequently, it was combined with plot of ancestral character state estimation with "par" function in R. The geological timescale was added with Adobe Photoshop CC 2019.

# Phylomorphospace and Morphospace Occupation across Time

First, any zero-length branches in the MAP tree were replaced with 0.0001 million year lengths to stop zero-length branches from preventing downstream analyses. The MAP tree and original morphological character matrix were then used to calculate a pairwise Maximum Observable Rescaled Distances (MORD) matrix, incorporating ancestral nodes, and simultaneously generating an ordinated phylomorphospace based on principal coordinates analysis, all using the functions "ordinate\_cladistic\_matrix" and "plot\_morphospace" of the package "Claddis v.0.6.3" (Lloyd 2016) (Supplementary Files 6–8). The resulting phylomorphospace shows the locations of both terminal taxa and estimated ancestral taxa at node divergence points. The locations of subfamilies within the morphospace were denoted using convex hulls. Morphospace occupation through time was visualized with the "plot\_morphospace\_ stack" function from Claddis, by assigning taxa to broad time bins; "Middle Jurassic," "Early Cretaceous," and "Late Cretaceous."

#### Disparity through Time

To calculate disparity through time, we used both continuous time slices and discrete time bins. Under both approaches, we measure disparity from morphospace positions across all axes using 2 distinct metrics, namely the sum of variances (SOV) and the length of a minimum spanning tree (MST) through the morphospace. The sum of a MST captures the spread of points in morphospace but can be more susceptible to outliers (but less so than range and area based metrics). In contrast, the SOV method focuses on variance and dispersion and provides a more conservative measure of disparity. To calculate error margins around the disparity values, a bootstrapping and rarefaction procedure was applied for both metrics.

Disparity within discrete time bins is the traditional approach and was calculated for the broad bin of the Jurassic, Early Cretaceous, and Late Cretaceous. This method is exclusively based on the terminal taxa. The continuous time slices disparity approach incorporates both terminal taxa and ancestral node morphospace locations within the disparity calculations (Guillerme and Cooper 2018), by slicing through a tree and selecting either the terminal taxon or node based on which is closest to the geological timing of the slice. The time range of MAP tree was evenly divided into 10 time slices and the initial 3 time slices were then deleted as they only included a small number of node-based morphospace coordinates. The Claddis function "chrono.subsets" (Lloyd 2016) was utilized to partition the data into continuous chronological subsets. This step involved the proximity model that selects the ancestral node or the descendant node/tip with a probability relative to branch lengths. Consequently, disparity was calculated at 7 fixed time points through the evolutionary history of Mesoraphidiidae independent of any specific geological interval, and accounting for ancestral nodes within disparity calculations.

## Results

Systematic Paleontology Order Raphidioptera Navás, 1916 Suborder Raphidiomorpha Engel, 2002 Family Mesoraphidiidae Martynov, 1925 Genus *Dracoraphidia* Lu, Xu & Liu gen. nov. (Fig. 1) Type species.

Dracoraphidia brachystigma Lu, Xu & Liu sp. nov.

#### Diagnosis.

Body small (forewing length 6.9 mm). Head with distinctly prolonged occiput, nearly half length of head. Pronotum elongated, slightly longer than occiput. Legs slender. Forewing: costal space short, terminating into costal margin proximad midpoint of wing; subcostal space broadened distad; pterostigma short and broad, ca. 1/5 of wing length, proximally closed by 2scp-ra, distally closed by second veinlet of RA; inclined proximal RA veinlet present within pterostigma; RP and MA, respectively, bifurcated into 2 simple branches; MA with stem originating from anterior branch of MP; 2



Fig. 1. Dracoraphidia brachystigma gen. et sp. nov., holotype: NIGP205386, sex unknown. A) habitus, ventral view; B) head and prothorax, dorsal view; C) right wings; D) drawings of fore- and hind wings. Scale bar = 1.0 mm.

radial cells, 1 discal cell, 2 medial cells, 3 discoidal cells. Hind wing: venation similar to that of forewing; MA originating from R; 3 radial cells, 1 discal cell, 1 medial cell, 1 discoidal cell.

#### Etymology.

From the Greek "drac-" (meaning "dragon") and "Raphidia" (the type genus-group name of Raphidioptera), in reference to the dragon-like head of the new genus. Gender: Feminine. The name is registered with ZooBank LSID urn:lsid:zoobank. org:act:1E45E91D-517E-4901-A655-B51B3C93435A.

#### Remarks.

The new genus is assigned to Mesoraphidiidae by the long MP stem, the presence of 2 ra-rp crossveins, and the presence of 3 triangularly arranged discoidal cells in the forewing. It appears to be similar to *Stenoraphidia* Lyu et al., 2018 and *Teratocephala* gen. nov. by the presence of prolonged occiput. Besides, *Dracoraphidia* gen. nov. is more similar to *Stenoraphidia* by the presence of 2 ra-rp crossveins in the forewing and 2 ra-rp crossveins in the hind wing. However, *Dracoraphidia* gen. nov. can be distinguished from *Stenoraphidia* by the bifurcated RP + MA and the strongly broadened pterostigma proximally closed by the 2scp-ra crossvein. However, the RP + MA composed of multiple branches, and the pterostigma is narrow and proximally diffused in *Stenoraphidia*. *Dracoraphidia* gen. nov. can be distinguished from *Teratocephala* gen. nov. by the bifurcated RP + MA, the presence of 2 forewing ra-rp crossveins, the broad forewing pterostigma without posterior extension to the radial space, and the broad hindwing pterostigma proximally closed by the 2scp-ra crossvein. In *Teratocephala* gen. nov., the RP + MA composed of multiple branches, 3 ra-rp crossveins are present in the forewing, the forewing pterostigma is strongly broadened and extends to the radial space, proximally closed by the 2scp-ra crossvein, and the hindwing pterostigma is narrowly elongated, with a diffuse base.

## Dracoraphidia brachystigma Lu, Xu & Liu sp. nov.

## (Fig. 1)

#### Diagnosis.

Same as for the genus.

### Description.

Body length 8.9 mm; head length 1.7 mm; length of preserved part of antenna 1.5 mm; diameter of compound eye 0.7 mm; vertex length 0.5 mm; occiput length 1.0 mm; pronotum length 1.9 mm; meso- plus metathorax length 1.4 mm; forewing 6.9 mm long, 2.0 mm wide; hind wing 5.5 mm long, 2.0 mm wide; abdomen length 3.0 mm.

Body integument brown, with abdomen darker. Head ovoid, with short vertex and distinctly elongated occiput. Compound eyes large, globular; distance between compound eyes slightly wider than diameter of compound eye; ocelli absent. Antennae filiform, flagellum with ca. 15 segments preserved. Mouthparts slightly elongated, labial palps with 5 segments. Pronotum nearly as long as head (including occiput). Legs slender, without distinct inflation on tibiae; tarsomere 3 bilobed.

Wings transparent and without spots. Forewing costal space narrow, with 5 costal crossveins; ScP terminating into costal margin proximad midpoint of wing; subcostal space gradually broadened distad; RA distally with 3 simple veinlets, proximal one of them present within pterostigma; pterostigma uniformly colored, located at distal 1/4 of wing, short and broad, ca. 1.5 times as long as wide, gradually broadened distad, proximally closed by 2scp-ra, distally closed by second veinlet of RA; 2 radial crossveins present between RA and RP, r1 nearly as long as r2, r2 distinctly broadened distad, 2ra-rp posteriorly connecting with anterior branch of RP; RP bifurcated into 2 simple branches at proximal 3/5; 1 rp-ma crossvein present, forming 1 discal cell; MA with stem short, originating from anterior branch of MP, coalescent with RP stem for a short distance, MA with 2 simple branches, slightly shorter than that of RP; 2 ma-mp crossveins, and 2 medial cells present; MP deeply forked into 5 terminal branches, forming 3 triangularly arranged discoidal cells; CuA with 2 branches; CuP simple; A1 simple, A2 bifurcated.

Hind wing similar to forewing; costal space narrow, with 5 costal crossveins; RA distally with 3 simple veinlets, proximal one of them slightly sigmoid and present within pterostigma; 3 radial crossveins present, *r*1, *r*2, and *r*3 each longer than proximal neighboring one; 1 rp-ma crossvein, forming 1 discal cell; MA with stem sinuated, originating from R; 2 ma-mp crossveins; MP deeply forked, anterior branch with 3 branches, posterior branch with 2 branches; 1 discoidal cell present; 2 mp-cua crossveins, with 1mp-cua distinctly inclined; CuA distally bifurcated; CuP simple; A1 bifurcated.

Abdomen slender, uniform in width; genitalia not preserved.

#### Type material.

Holotype: NIGP205386, Amber piece preserved with a complete adult (sex unknown) of *D. brachystigma* sp. nov.

#### Etymology.

From the Greek "brachy-" (meaning "short") and the Greek "stigma" (meaning "marking"), in reference to the presence of short pterostigma in the new genus. Gender: Feminine.



Fig. 2. Teratocephala macrostigma gen. et sp. nov., holotype NIGP205387, male. A) habitus, lateral view; B) right wings; C) head and prothorax, lateral view. Scale bar = 1.0 mm.

The name is registered with ZooBank LSID urn:lsid:zoobank. org:act:C532CDCB-4BB9-4AEC-948B-9F2F36F26087.

#### Genus Teratocephala Lu, Zhuo, Xu & Liu gen. nov.

#### (Figs. 2-7)

Type species.

Teratocephala macrostigma Lu, Zhuo, Xu & Liu sp. nov.

### Diagnosis.

Body small (forewing length 6.5-10.1 mm). Head with distinctly prolonged vertex and occiput, and occiput and vertex subequal in length. Pronotum elongated, almost as long as vertex plus occiput. Legs slender, tarsomere 3 bilobed. Forewing: costal space short, terminating into costal margin proximad midpoint of wing; subcostal space almost uniformly broad, slightly narrower than costal space; pterostigma ovoid, ca. 1/4-1/5 of wing length; strongly broadened, posteriorly extended to radial space, proximally closed by 2scp-ra and 2ra-rp, distally closed by terminal branch of RP, 1-2 RA veinlets and 3ra-rp present within pterostigma. RP and MA multiply branched; MA with stem originating from anterior branch of MP; 3 radial cells, 1 discal cell, 1 medial cell, 3 discoidal cells. Hind wing: venation similar to that of forewing; subcostal space narrow; pterostigma elongated and narrow and distinctly broadened distad, proximally diffused, distally closed by anterior branch of RA, no veinlet present within pterostigma. MA originating from R; 3 radial cells, 1 discal cell, 1 medial cell, 1 discoidal cell.

#### Etymology.

From Greek "terato-" (meaning "monster") and "cephalus" (meaning "head"), in reference to the bizarre appearance of the head. Gender:

Feminine. The name is registered with ZooBank LSID urn:lsid:zoobank. org:act:C296FF89-1A71-4B1A-B705-1ED6CCEC9403.

#### Remarks.

The new genus shows unique forewing pterostigma, which is strongly broadened and extended into the radial space. This feature has never been found in all the other extinct and extant snakeflies. However, based on the strongly elongated occiput, the new genus appears to be closely related to *Stenoraphidia* and *Dracoraphidia* gen. nov. The morphological comparison is provided above in the Remarks of *Dracoraphidia* gen. nov.

*Teratocephala macrostigma* Lu, Zhuo, Xu & Liu sp. nov.

#### (Figs. 2–7)

**Diagnosis.** Same as for the genus.

#### Description.

Male (holotype and 2 paratypes). Body length 9.0-11.1 mm; head length 2.0-2.1 mm; antenna length 2.3-3.7 mm; diameter of compound eye 0.5-0.8 mm; vertex length 0.4-0.5 mm; occiput length 0.7-1.2 mm; pronotum length 1.5-2.4 mm; meso- plus metathorax length 1.0-2.4 mm; forewing 6.5-7.6 mm long, 2.0-2.3 mm wide; hind wing 5.9-7.2 mm long, 1.7-2.2 mm wide; abdomen length 3.0-3.8 mm.

Body integument brown. Head ovoid, with distinctly prolonged vertex and occiput. Compound eyes poorly preserved; ocelli absent. Antenna filiform, flagellum with 65 segments. Prothorax nearly as



Fig. 3. Teratocephala macrostigma gen. et sp. nov., holotype NIGP205387, male. A) right forewing; B) right hind wing. Scale bar = 1.0 mm.

long as head (including occiput). Legs slender, without distinctly inflation on tibiae; tarsomere 3 bilobed; pretarsal claws slender.

Wings transparent and without spots. Forewing costal space and subcostal space obscure; ScP terminating into costal margin proximad midpoint of wing; RA not visible; pterostigma located at proximal 1/4 of wing, strongly broadened, posteriorly extended to radial space, proximally closed by 2ra-rp, distally closed by terminal branch of RP; 3ra-rp crossvein present within pterostigma; 3 radial crossveins present between RA and RP, *r1* nearly as long as *r2*, *r2* slightly broadened distad, *r3* nearly half length of *r2*; RP pectinately



Fig. 4. Teratocephala macrostigma gen. et sp. nov., paratype NIGP205388, female. A) habitus, dorsal view; B) head, dorsal view; C) proximal parts of left wings; D) pterostigma of right forewing; E) right forewing; F) right midleg; G) genitalia, lateral view; H) drawing of genitalia, lateral view. Scale bar = 1.0 mm (A–E, G and H); 0.1 mm (F).



Fig. 5. Teratocephala macrostigma gen. et sp. nov., paratype NIGP205388, female. A) right forewing; B) left forewing; C) left hind wing; D) right hind wing. Scale bar = 1.0 mm.

branched into 4 branches at its midpoint, with proximal second one bifurcated at its midpoint; 1 rp-ma crossvein, forming 1 discal cell; MA with stem short, originating from anterior branch of MP, coalescent with RP for a short distance, distally with a trifurcate branch, almost as long as that of RP; 2 ma-mp crossveins, and 2 medial cells present; MP deeply forked, with 6 branches, forming 3 triangularly arranged discoidal cells; CuA and CuP separated near wing base, CuA with 2 branches, CuP simple; A1 simple, A2 bifurcated. Hind wing similar to forewing; costal space narrow, with at least 4 costal crossveins; 2 simple RA veinlets present; pterostigma uniformly colored, elongated, narrow and distinctly broadened distad, proximally diffused, distally closed by anterior branch of RA; no veinlet present within pterostigma; 3 radial crossveins present, *r1*, *r2*, and *r3* each longer and broader than proximal neighboring one; RP with 2 branches, with proximal second one marginally forked at distal 1/4; MA with stem sinuated, originating from R; 2 ma-mp

crossveins; MP deeply forked, anterior branch with 2 branches, posterior branch with 3 branches; a line of 2 discoidal cells present; 2 mp-cua crossveins, with 1mp-cua distinctly inclined; CuA and CuP simple; A1 bifurcated, A2 simple.

Abdomen slender, almost as long as head plus prothorax, uniform in width. Genitalia: tergum 9 strongly extending ventrad, seemingly fused with sternum 9; ectoprocts fused into a short sclerite, directed dorsad, distally with several stout spinous setae; a pair of gonocoxites 9 present, subtriangular, with obtuse apex slightly curved medially; a pair of hook-like sclerites (putative parameres or gonocoxites 10) present inside genital chamber; endophallus membranous, nearly cylindrical; a single horn-like sclerite (putative gonarcus or gonocoxites 11) present on posterodorsal portion of endophallus.

Female (2 paratypes). Body length (including ovipositor) 11.1– 14.1 mm; head length 2.6–3.5 mm; diameter of compound eye 0.3–0.4 mm; vertex length 0.4–0.7 mm; occiput length 0.9–1.2 mm; pronotum length 1.3–2.1 mm; meso- plus metathorax length Body integument brown, with abdomen darker. Head with strongly elongated occiput. Compound eyes large, globular; distance between compound eyes slightly wider than eye diameter; ocelli absent. Antenna incomplete, with ca. 15 flagellomeres preserved. Pretarsal claws slender, broadened proximally, each with a dentoid protuberance proximally.

Wing venation and pterostigma similar to that of male. Forewing costal space with 6 crossveins; RA veinlet simple; 3ra-rp crossvein present within pterostigma; RP pectinately branched into 5 branches, with proximal third one marginally forked; CuP simple; A1 simple, A2 bifurcated, connecting with A1 by a short crossvein. Hind wing with at least 4 or 5 crossveins; RP with at least 4 simple branches; at least 1 ma-mp crossvein; MP with at least 4 terminal branches; CuA bifurcated, CuP simple; A1 bifurcated, A2 simple.



Fig. 6. Teratocephala macrostigma gen. et sp. nov., paratype: BXAM-RAP-24001, male. A) habitus, ventral view; B) head and prothorax, dorsal view; C) left wings; D) genitalia, caudolateral view; E) drawings of genitalia, caudolateral view. Scale bar = 1.0 mm.

#### Type material.

Holotype: NIGP205387, Amber piece preserved with a nearly complete adult male of *T. macrostigma* sp. nov. Paratype: NIGP205388, Amber piece preserved with a nearly complete adult female of *T. macrostigma* sp. nov. Paratype: BXAM-RAP-24001: Amber piece preserved with a complete male of *T. macrostigma* sp. nov. Paratype: BXAM-RAP-24002: Amber piece preserved with a nearly complete male of *T. macrostigma* sp. nov. Paratype: BXAM-RAP-24003: Amber piece preserved with a nearly complete female of *T. macrostigma* sp. nov.

## Etymology.

From the Greek "macro-" (meaning "big") and "-stigma" (meaning "pterostigma"), in reference to the presence of broad pterostigma in the new species. The name is registered with ZooBank LSID urn:lsid: zoobank.org:act:650A25FC-3504-4B95-B792-0B62585DF5DB.

## **Phylogenetic Analysis**

The phylogenetic analysis using NONA yielded 8,016 most parsimonious trees (MPTs) (length = 119 steps, consistency index = 42, retention index = 61). The strict consensus tree of all MPTs is shown in Fig. 8. All genera of Mesoraphidiidae were found to form a monophylum supported by the following 4 synapomorphies: the presence of 2 forewing radial cell I distad separating point between RP and MA (char. 19:1), the stem of forewing M subequal to or longer than length of 1*doi* (char. 26:1), and the presence of 3 hindwing *doi* (char. 35:1). The topology concerning the relationships among the mesoraphidiid genera is generally similar to that in Lyu et al. (2020). *Dracoraphidia* gen. nov. and *Teratocephala* gen. nov. were

assigned within the monophyletic Alloraphidiinae, and clustered with *Stenoraphidia*, *Archeraphidia*, and *Alloraphidia*, supported by the forewing ScP terminating into C proximad the midpoint of wing (char. 9:2).

## **Divergence Time Estimation**

The MAP tree indicates that the clade of Mesoraphidiidae originated around the Middle Jurassic (Fig. 9). Nanoraphidiini and Alloraphidiinae originated during the Lower Cretaceous, which generally coordinates with the known fossil records. All lineages of Nanoraphidiini were present during the mid-Cretaceous, while Alloraphidiinae slightly predates Nanoraphidiini with all lineages present at the Lower Cretaceous.

## Ancestral State Reconstruction of Forewing doi

The number of forewing discoidal cells (*doi*) is an important diagnostic character of Mesoraphidiidae. Mesoraphidiinae and Alloraphidiinae species have 3 forewing *doi*, whereas most Nanoraphidiini species typically possess 2 forewing *doi*, with some exceptions having fewer. The ancestral state reconstruction (Fig. 9) indicates that the ancestral state of forewing *doi* in Mesoraphidiidae has a high probability of being 3, which is also the case in Mesoraphidiinae and Alloraphidiinae. Although the number of forewing *doi* varies in Nanoraphidiini, the ancestral state of the entire clade is probably the presence of 3 *doi*, but the ancestor of this clade except *Grimaldiraphidia* has only 2 *doi*.

## Lineages through Time

The lineages through time plot (Fig. 9) illustrate the changing diversity of Mesoraphidiidae over time. Mesoraphidiid diversity increased from the Late Jurassic, sharply peaking in the middle of the Barremian (130–125 Ma) during the Lower Cretaceous. Subsequently, there was a distinct decrease, leading to extinction in the Upper Cretaceous.

Fig. 7. Teratocephala macrostigma gen. et sp. nov., habitus. A) paratype BXAM-RAP-24002, male, dorsal view; B) paratype BXAM-RAP-24003, female, right lateral view. Scale bar = 1.0 mm.



Fig. 8. Strict consensus tree of Mesoraphidiidae. Topology represents the strict consensus tree yielded from NONA. Unambiguous state changes of the morphological characters at different levels are shown on the tree. Black circle represents the homologous state and white circle represents the homoplasious state. Bootstrap values are shown at relevant nodes.

#### Phylomorphospace and Morphospace across Time

The first two principal components, PC1 and PC2, collectively explain 29.0% of the total morphological variation, effectively distinguishing clades within the morphospace. PC1 contributes 19.72%, while PC2 contributes 9.32% to the overall variation (Fig.

**10A**, **B**). It is important to note that the percentage of variation on the axes appears to be relatively lower due to the application of the "Cailliez correction." Notably, the phylomorphospace confirms that Nanoraphidiini diverged notably from other subfamilies and separated from others on PC1. Mesoraphidiinae occupy the greatest area



Fig. 9. Ancestral state estimation of the number of forewing discoidal cells (*doi*) and lineages through time in Mesoraphidiidae based on the MAP tree. Circles depict character states for tips or nodes.

of morphospace across PC1 and PC2, and are located centrally (Fig. 10A). Overall, all subfamilies occupy mutually exclusive regions of morphospaces throughout their evolution, with minimal overlap observed between Alloraphidiinae and Mesoraphidiinae (Fig. 10A).

The morphospace through time plot (Fig. 10B) shows the change in morphospace occupation by Mesoraphidiinae, Nanoraphidiini, and Alloraphidiinae. Mesoraphidiidae originated in the Jurassic, occupying a small area of morphospace, increased markedly during the Lower Cretaceous to occupy an area multiple times its Jurassic peak, but then diminished by the Upper Cretaceous. Nanoraphidiini is presumed to have originated in the Jurassic with a single species, exhibiting an increase in morphospace occupation during the Lower Cretaceous (particularly along PC1), followed by a marginal decrease in the Upper Cretaceous. Alloraphidiinae first appeared in the Lower Cretaceous, with a slight increase in morphospace observed during the Upper Cretaceous. Mesoraphidiidae exhibits the highest level of disparity when compared to the other 2 groups. In comparison with Nanoraphidiini, the region morphospace occupied by Alloraphidiinae is closer to that of Mesoraphidiinae.

## Disparity through Time

The MST quantified disparity (Fig. 10C, E) results highlight a more dynamic trend for Mesoraphidiidae when compared to the SOV (Fig. 10D, F). The MST analysis based on both time bins and time

slices, including estimated ancestors, reveals that the disparity of Mesoraphidiidae was notably low during the Jurassic, followed by a sharp increase in the Lower Cretaceous and a distinct decrease in the mid-Cretaceous. Interestingly, the peak of disparity occurred during the Valanginian–Hauterivian, approximately 132 Ma (Fig. 10C, E). This pattern reflects the expansion of morphospace occupation, and also more closely tracks the diversity of the group (Fig. 9). On the other hand, the SOV suggests a different trend, with Mesoraphidiidae showing minimal changes in disparity through the Lower and Upper Cretaceous, with a generalized increase in disparity through time. High disparity in the final steps of the time series may reflect a reduced density of morphospace occupation, where variance remains high, as a smaller number of taxa are still spread widely in the morphospace.

## Discussion

# Morphological and Phylogenetic Implications from the New Genera

We described and assigned *D. brachystigma* and *T. macrostigma* from Myanmar amber to Alloraphidiinae, based on the presence of forewing with 2scp-r approximating RA1, the distance between 2scp-r and RA1 subequal to distance between RA1 and RA2 (11:0), the forewing pterostigma 1/7 to 1/5× forewing length (13:1), and the

PC2 (9.32% of total variance)

Within bin minumum-spanning tree length

Time-sliced minumum-spanning tree length



**Fig. 10.** Phylomorphospace, morphospace occupation through time, and disparity through time of Mesoraphidiidae. A, B) The axes represent morphological disparity, derived from observed dissimilarities among taxa projected by principal coordinates analysis. The shaded convex hull highlights the morphospace occupations within different Mesoraphidiidae subfamilies. Both pictures share the same group legend. A) Empirical phylomorphospace. The branching pattern corresponds to the MAP tree, with branching events denoting the locations of estimated ancestors. B) Morphospace occupation through time. The distribution of Mesoraphidiidae morphospace is depicted across 3 time intervals spanning the Jurassic to the Upper Cretaceous. C–F) "x" denotes the observed disparity value for each bin or time slice, whereas the box plots and line plus shaded regions show the mean disparity value from the rarefied and bootstrapped samples, with confidence intervals. C, D) Disparity through time based on discrete time bins. E, F) Disparity through time based on time slicing at 7 points through MAP tree, incorporating estimated ancestors within the disparity calculations.

forewing with stem of MA diverged from M distinctly distad initial branching point of MP (22:2). This mesoraphidiid subfamily currently comprises 7 genera and 14 species, most of which are recorded from the Lower Cretaceous of Eurasia (Lyu et al. 2018, 2020). Previously, only two species (both belonging to *Alloraphidia*, i.e., *A. dorfi* Carpenter, 1968 and *A. kyzylzharica* Makarkin and Khramov, 2015) are recorded from the Upper Cretaceous, but showing a potential broad distribution (one from Canada, and another one from Kazakhstan). The discovery of *Dracoraphidia* gen. nov. and *Teratocephala* gen. nov. enriches our knowledge on the species diversity of snakeflies during the Upper Cretaceous. They also inform on the morphological diversity of Upper Cretaceous Alloraphidiinae, documenting the cephalic elongation in Raphidioptera and a new morphotype of pterostigma (as shown in *Teratocephala* gen. nov.) among the diverse morphologies of this wing trait.

More importantly, the exquisitely preserved male genitalia of Teratocephala gen. nov. improves our understanding of the genital morphology of Mesoraphidiidae. Liu et al. (2016) and Makarkin (2023) described the male genitalia of several species of Nanoraphidiini from the mid-Cretaceous Myanmar amber. In these species, the male genitalia show some similar characters with that of Raphidiidae, such as the external gonocoxites 9 with some externally discernible sclerites (e.g., gonostylus 9 or some projections of gonocoxite 9), and the presence of fused gonapophyses 9 as a ventral sclerite (Liu et al. 2016). However, the male genitalia of Teratocephala gen. nov., as a representative of Alloraphidiinae, have a pair of broad shell-like gonocoxites 9, which lack additional external modification, but do not possess the fused gonapophyses 9. In this respect, it shows similarity with Inocelliidae and Baissopteridae (Lu et al. 2020). Nonetheless, the presence of a pair of hook-like sclerites (putative parameres or gonocoxites 10) inside genital chamber of Teratocephala gen. nov. is shared by some genera of Raphidiidae (Aspöck et al. 1991). Thus, the male genital morphology of Teratocephala gen. nov. suggests possible relationships of Alloraphidiinae with the other 3 families of Raphidiomorpha, showing an extremely complex nature of the phylogeny of Raphidioptera. As previously assumed (Makarkin and Archibald, 2014, Liu et al. 2016, Lu et al. 2020), both extant families of Raphidioptera may be derived survivors of the Mesozoic families. The interfamilial male genital similarities provide evidence for these relationships, but this needs to be tested with a large morphological dataset with a comprehensive sampling of extinct and extant snakeflies.

## Morphological Disparity and Macroevolution of Mesoraphidiidae

Our analyses (Figs. 9 and 10) reveal that both lineage diversity and morphological disparity of Mesoraphidiidae increased distinctly from the Jurassic, reaching its a peak at about 130–118 Ma, and decreasing sharply 118–94 Ma (as reflected in the reduction of morphospace occupation by Mesoraphidiinae from the Upper Cretaceous). Mesoraphidiinae, Alloraphidiinae, and Nanoraphidiini explored distinct regions of morphospace throughout their evolution, as reflected by their non-overlapping phylomorphospace occupation (Fig. 10A, B). The significant morphological differentiation among these 3 lineages indicates that they might have been adapted to different ecological niches, functional needs, or other evolutionary factors.

Notably, the decrease in morphospace occupation and decline in the MST-based disparity measure fit well with the timing of the Cretaceous Terrestrial Revolution (KTR) (Lloyd et al. 2008) in which angiosperms (flowering plants) and animals, especially pollinators and herbivores, including insects, reptiles, birds, and mammals during the mid- to Upper Cretaceous, all underwent diversification c. 125–80 Ma. This is inferred to have resulted in the turnover of terrestrial biodiversity surpassing marine biodiversity for the first time and made profound impact in the formation of modern biodiversity in which angiosperms and insects dominate the biodiversity of modern terrestrial ecosystems (Lloyd et al. 2008). At the same time, gymnosperms and ecologically associated animals underwent mass extinctions. Considering the arboreal habits of many snakeflies, with their preference to coniferous trees (Aspöck H. 2002, Aspöck U. and Aspöck H. 2009), these extinctions likely caused the decline of snakefly diversity during the Upper Cretaceous.

With the reduction of morphospace occupation by Mesoraphidiinae, it is surprising to note the morphospace expansion of Alloraphidiinae in the Upper Cretaceous. This morphospace expansion by Alloraphidiinae is probably associated with the strongly elongated vertex and occiput in the two Myanmar amber new genera. In fact, the evolutionary changes in the shape of head of Raphidioptera, sometimes together with prothorax, may be associated with the divergence of feeding preferences (Liu et al. 2014, Lyu et al. 2018). Extant snakefly adults are generally predacious, while some are known to visit flowers for pollenfeeding (Aspöck H. 2002). Moreover, the species of Raphidiidae, in which the elongation of head and prothorax is more developed than that in Inocelliidae, have been encountered more frequently on flowers than Inocelliidae (Aspöck H. 2002). Thus, elongation of the head and prothorax may reflect adaptation to pollen-feeding. Alternatively, such morphological specialization may have evolved for enlarging the striking range of the mandibles during hunting (Lyu et al. 2018). In any case, the cephalic modification in alloraphidiine snakeflies from the Myanmar amber is likely a product in morphological evolution responding to the dramatic environmental changes of the KTR. This evolutionary novelty was also gained in derived species of contemporary Baissopteridae (e.g., Rhynchobaissoptera from the Myanmar amber) (Lu et al. 2020), suggesting a convergent outcome of the KTR on the macroevolution of Upper Cretaceous snakeflies. In sum, the evolutionary history of Mesoraphidiidae probably aligned with the floral changes as well as the environmental changes during the KTR when the diversity and disparity of Mesoraphidiidae decreased.

## **Specimen Collection Statement**

The authors attest that all legal and regulatory requirements, including export and import collection permits, have been followed for the collection of specimens from source populations at any international, national, regional, or other geographic level for all relevant field specimens collected as part of this study.

## Acknowledgements

We appreciate the subject editor and two anonymous reviewers for their comments to improve the manuscript.

## Author Contributions

Xiumei Lu (Conceptualization [lead], Data curation [lead], Methodology[lead], Software [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead], Funding acquisition [lead]), Thomas L. Stubbs (Methodology [lead], Visualization [lead], Writing—original draft [equal]), De Zhuo (Resources [lead], Writing—original draft [supporting]), De Zhuo (Resources [lead], Writing—original draft [supporting]), Philip C.J. Donoghue (Conceptualization [equal], Methodology [equal], Project administration [equal], Writing—review & editing [equal], Funding acquisition [lead]), and Xingyue Liu (Conceptualization [lead], Data curation [lead], Writing—original draft [lead], Writing—review & editing [lead], Funding acquisition [lead])

#### **Supplementary Data**

Supplementary data are available at Insect Systematics and Diversity online.

### Funding

This research was supported by the Royal Society Newton International Fellowship (Royal Society K.C. Wong Education Foundation) (NIF R1 211688), the National Natural Science Foundation of China (Nos. 32370485, 31900348, 31672322), and a Leverhulme Trust Research Fellowship (RF-2022-167).

## **Data Availability**

We have included all data in both the article and its Supplementary Material available online. For further inquiries, please feel free to contact the corresponding authors via the provided email addresses.

## References

- Aspöck H. 2002. The biology of Raphidioptera: a review of present knowledge. Acta Zool. Acad. Sci. Hung. 48(Suppl. 2):35-50.
- Aspöck U, Aspööck H. 2008. Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). Syst. Entomol. 33(1):97-127.
- Aspöck U, Aspöck H. 2009. Raphidioptera (snakeflies). In: Resh VH, Cardé RT, editors. Encyclopedia of insects. 2nd ed. Chapter 217. Amsterdam: Academic Press; p. 864-866.
- Aspöck H, Aspööck U, Rausch H. 1991. Die Raphidiopteren der Erde. Eine monographische Darstellung der Systematik, Taxonomie, Biologie, Ökologie und Chorologie der rezenten Raphidiopteren der Erde, mit einer zusammenfassenden übersicht der fossilen Raphidiopteren (Insecta: Neuropteroidea). Vol. 2. West Germany: Goecke & Evers, Krefeld; p. 33-34, 50-54.
- Bapst DW. 2012. Paleotree: an R package for paleontological and phylogenetic analyses of evolution. Methods Ecol. Evol. 3(5):803-807. https://doi. org/10.1111/j.2041-210x.2012.00223.x
- Engel MS. 2002. The smallest snakefly (Raphidioptera: Mesoraphidiidae): a new species in Cretaceous amber from Myanmar, with a catalog of fossil snakeflies. Am. Mus. Novit. 3363:1-22. https://doi. org/10.1206/0003-0082(2002)363<0001:tssrma>2.0.co;2
- Goloboff PA. 1997. NONA version 2.0. New York: American Museum of Natural History.
- Guillerme T, Cooper N. 2018. Time for a rethink: time sub-sampling methods in disparity-through-time analyses. Palaeontology 61(4):481-493. https:// doi.org/10.1111/pala.12364
- Haug JT, Müller P, Haug C. 2020. A 100 million-year-old snake-fly larva with an unusually large antenna. Bull. Geosci. 95(2):167-177. https://doi. org/10.3140/bull.geosci.1757
- Haug JT, Engel MS, Mendes dos Santos P, et al. 2022. Declining morphological diversity in snakefly larvae during last 100 million years. PalZ 96(4):749-780. https://doi.org/10.1007/s12542-022-00609-7
- Jepson JE, Jarzembowski EA, Gallery BA. 2008. Two new species of snakefly (Insecta: Raphidioptera) from the lower Cretaceous of England and Spain with a review of other fossil raphidiopterans from the Jurassic/Cretaceous transition. Alavesia 2:193-201.
- Jouault C, Engel MS, Nel A. 2022. A new baissopterid snakefly (Raphidioptera: Baissopteridae) from mid-Cretaceous amber of northern Myanmar. Cretac. Res. 129:105028. https://doi.org/10.1016/j.cretres.2021.105028
- Kania I, Wang B, Szwedo J. 2015. Dicranoptycha Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Cenomanian Burmese amber. Cretac. Res. 52:522-530. https://doi.org/10.1016/j.cretres.2014.03.002
- Lewis PO. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Syst. Biol. 50(6):913-925. https://doi. org/10.1080/106351501753462876
- Liu XY, Ren D, Yang D. 2014. New transitional fossil snakeflies from China illuminate the early evolution of Raphidioptera. BMC Evol. Biol. 14(1):84. https://doi.org/10.1186/1471-2148-14-84
- Liu XY, Lu XM, Zhang WW. 2016. New genera and species of the minute snakeflies (Raphidioptera: Mesoraphidiidae: Nanoraphidiini) from the mid-Cretaceous of Myanmar. Zootaxa 4103(4):301-324.
- Lloyd GT. 2016. Estimating morphological diversity and tempo with discrete character-taxon matrices: implementation, challenges, progress, and

future directions. Biol. J. Linn. Soc. 118(1):131-151. https://doi.org/10.1111/ bij.12746

- Lloyd GT, Davis KE, Pisani D, et al. 2008. Dinosaurs and the Cretaceous Terrestrial Revolution. Proc. Biol. Sci. 275(1650):2483-2490. https://doi. org/10.1098/rspb.2008.0715
- Lu XM, Liu XY. 2021. The Neuropterida from the mid-Cretaceous of Myanmar: a spectacular palaeodiversity bridging the Mesozoic and present faunas. Cretac. Res. 121:104727. https://doi.org/10.1016/j.cretres.2020.104727
- Lu XM, Zhang WW, Wang B, et al. 2020. A new and diverse paleofauna of the extinct snakefly family Baissopteridae from the mid-Cretaceous of Myanmar (Raphidioptera). Org. Divers. Evol. 20(4):565-595. https://doi. org/10.1007/s13127-020-00455-y
- Lyu YN, Ren D, Liu XY. 2017a. Systematic revision of the fossil snakefly family Baissopteridae (Insecta: Raphidioptera) from the Lower Cretaceous of China, with description of a new genus and three new species. Cretac. Res. 80:13-26.
- Lyu YN, Ren D, Liu XY. 2017b. Systematic revision of the fossil snakefly family Mesoraphidiidae (Insecta: Raphidioptera) in the middle Jurassic of China, with description of a new genus and three new species. Cretac. Res. 41:1-10.
- Lyu YN, Ren D, Liu XY. 2018. A remarkable new genus of the snakefly family Mesoraphidiidae (Insecta: Raphidioptera) from the Lower Cretaceous of China, with description of a new species. Cretac. Res. 89:119-125.
- Lyu YN, Shen RR, Wang YJ, et al. 2020. The snakefly family Mesoraphidiidae (Insecta: Raphidioptera) from the Lower Cretaceous Yixian Formation, China: systematic revision and phylogenetic implications. J. Syst. Paleontol. 18(21):1743-1768.
- Makarkin VN. 2023. A new species of Mesoraphidiidae (Raphidioptera) from mid-Cretaceous Kachin amber, with a discussion on anal veins in Raphidiomorpha. Cretac. Res. 146:105484.
- Makarkin VN, Archibald SB. 2014. A revision of the late Eocene snakeflies (Raphidioptera) of the Florissant Formation, Colorado, with special reference to the wing venation of the Raphidiomorpha. Zootaxa 31(3784):401-444. https://doi.org/10.11646/zootaxa.3784.4.4
- Makarkin VN, Khramov AV. 2015. A new fossil species of snakeflies (Raphidioptera: Mesoraphidiidae) from the Late Cretaceous of Kazakhstan, with notes on Turonian Neuropterida. Cretac. Res. 52:407-415. https://doi.org/10.1016/j.cretres.2014.02.010
- Martynov AV. 1925. To the knowledge of fossil insects from Jurassic beds in Turkestan. 1. Raphidioptera. Izv. Akad. Nauk. SSSR. 19(6):235-246.
- Navás L. 1916. Notas sobre el orden de los Rafidiópteros (Ins.). Mem. R. Acad. Cienc. Artes. Barc. 12(3):507-513.
- Nixon KC. 2002. WinClada; ver. 1.00.08. Ithaca (NY): Published by the author.
- Oswald JD. Neuropterida Species of the World. Lacewing Digital Library, Research Publication No. 1. http://lacewing.tamu.edu/SpeciesCatalog/ Main. Last accessed [Sep 1, 2023].
- Oswald JD.Bibliography of the Neuropterida. Lacewing Digital Library, Research Publication No. 2. http://lacewing.tamu.edu/Biblio/Main. Last accessed [Sep 1, 2023].
- Paradis E, Schliep K. 2019. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35(3):526-528. https://doi. org/10.1093/bioinformatics/bty633
- R Core Team. 2013. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Revell LJ. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3(2):217-223. https://doi. org/10.1111/j.2041-210x.2011.00169.x
- Ronquist F, Teslenko M, van der Mark P, et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61(3):539-542. https://doi.org/10.1093/sysbio/sys029
- Shi GH, Grimaldi DA, Harlow GE, et al. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretac. Res. 37:155-163.
- Simões TR, Caldwell MW, Pierce SE. 2020. Sphenodontian phylogeny and the impact of model choice in Bayesian morphological clock estimates of divergence times and evolutionary rates. BMC Biol. 18(1):191. https://doi. org/10.1186/s12915-020-00901-5
- Zhang C, Wang M. 2019. Bayesian tip dating reveals heterogeneous morphological clocks in Mesozoic birds. R. Soc. Open Sci. 6(7):182062. https:// doi.org/10.1098/rsos.182062
- Zhang C, Stadler T, Klopfstein S, et al. 2016. Total-evidence dating under the fossilized birth-death process. Syst. Biol. 65(2):228-249.