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A remarkable new genus of Nevrorthidae (Neuroptera, Osmyloidea) from mid-Cretaceous Kachin amber of northern Myanmar

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Abstract

A remarkable new genus and species of Nevrorthidae, *Sisyroneurorthus aspoeckorum* gen. et sp. nov., is described from mid-Cretaceous Kachin amber of northern Myanmar. This new species is the second Mesozoic representative of Nevrorthidae. The distal fusion of ScP and RA in the forewing of this new genus is shared by most Sisyridae. Given the probable sister-group relationship between Nevrorthidae and Sisyridae, our study sheds light on the evolution and morphological diversity of Nevrorthidae in the Mesozoic era.

Key Words

aquatic Neuroptera, Kachin amber, new genus, new species, taxonomy

Introduction

Nevrorthidae is a small and one of the most mysterious groups of Neuroptera, comprising 19 extant species in four genera from the Mediterranean region, the eastern part of Australia and East Asia (Aspöck et al. 2017). Their larvae are exclusively aquatic and generalist predators, inhabiting coarsely granular sands of clear and clean rivulets (Aspöck et al. 2017). Nevrorthidae, Sisyridae (spongillaflies) and Osmylidae (lance lacewings) constitute the superfamily Osmyloidea. This superfamily is considered the sister to all other extant Neuroptera, except for Coniopterygidae, based on recent phylogenomic studies (Winterton et al. 2018; Vasilikopoulos et al. 2020). The phylogenetic relationships amongst these three families are currently controversial. Sisyridae is recognised as a sister taxon to the clade "Nevrorthidae + Osmylidae" (Engel et al. 2018; Winterton et al. 2018) or Osmylidae is sister to the other two families (Vasilikopoulos et al. 2020).

Although it is suggested that these three families arose during the Late Permian and Early Triassic (Winterton et al.

2018; Vasilikopoulos et al. 2020), the fossil records of Nevrorthidae are rare. To date, ten species have been described from the Cretaceous to the Miocene (Wichard 2016, 2017; Lu et al. 2018). Hitherto, *Cretarophalis patrickmuelleri* Wichard, 2017, from the mid-Cretaceous amber of northern Myanmar is the only known species of Nevrorthidae from the Mesozoic. The Middle Jurassic neuropteran larvae recently described and assigned as Nevrorthidae by Du et al. (2023) are not a definite member of this family although it may belong to an extinct family of Osmyloidea.

This paper describes a remarkable new genus and species of Nevrorthidae from mid-Cretaceous Kachin amber of northern Myanmar. Our study sheds light on the potential diversity of Nevrorthidae in the Mesozoic era.

Materials and methods

The holotype is deposited in the Entomological Museum, China Agricultural University (CAU), Beijing, under the collection number CAU-BA-NH-22001.

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The specimen originates from Hukawng Valley, Kachin State, northern Myanmar (26°20'N, 96°36'E) (Cruickshank and Ko 2003; Grimaldi and Ross 2017). This amber deposit has been considered as the mid-Cretaceous (late Albian to the early Cenomanian) or slightly older (see Balashov (2021)). We confirm that the amber specimen reported herein was collected and purchased prior to June 2017. Therefore, it is free of ethical concerns regarding the current acquisition of amber from the Kachin region.

The third (YT) and second (SY) authors polished the amber piece using waterproof sandpapers of different grain sizes, subsequently followed by plastic buffing cloths with an abrasive compound. The observation was made using a Nikon SMZ 800 stereomicroscope. Photographs were taken using a Canon 80D digital camera with a Canon MP-E 65 mm macro lens (F2.8, $1-5\times$), with the aid of a Canon MT-24EX twin flash. The amber specimen was completely submerged in clove oil when it was photographed to increase the visibility of the inclusion. Helicon Focus 8.1.0 was used for image stacking. All figures were edited and assembled with Adobe Photoshop and Illustrator CC 2022.

The wing venation terminology generally follows Breitkreuz et al. (2017). Although some authors interpreted the posterior-most branch of the RP (radius posterior) as MA (media anterior) in both fore- and hind-wing (*sensu* Kukalová-Peck 1991; Kukalová-Peck and Lawrence 2004), we here consider it as a part of the RP, following Breitkreuz et al. (2017) and Winterton et al. (2019). The abbreviations of morphological terms used for wing venations are as follows: A1–A3, first to third anal vein; CuA, cubitus anterior; CuP, cubitus posterior; MA, media anterior; MP, media posterior; RA, radius anterior; RP, radius posterior; ScP, subcostal posterior. The terminology of the terminalia follows Lu et al. (2018).

Systematic palaeontology

Order Neuroptera Linnaeus, 1758 Superfamily Osmyloidea Leach, 1815 Family Nevrorthidae Nakahara, 1915

Genus Sisyroneurorthus gen. nov.

https://zoobank.org/AA446547-70EC-4549-A734-76E156C4445B Figs 1–4

Type species. Sisyroneurorthus aspoeckorum sp. nov., here designated.

Diagnosis. *Sisyroneurorthus* gen. nov. can be distinguished from the other nevrorthid genera by the combination of the following characters. Forewing: costal crossveins simple; ScP fused with RA at distal fourth; CuA and CuP diverging well distad 1m-cu; cua-cup crossvein absent; a long oblique crossvein present between CuP and A1. Hind-wing: CuA with pectinate branching on distal half, all branches simple.

Etymology. The new generic name is a combination of "*Sisyra*" (Greek, the name of the type genus of Sisyridae) and "*Neurorthus*" (Greek, the common suffix of the generic name of Nevrorthidae) with reference to the mosaic characters with Sisyridae and Nevrorthidae in the new genus.

Remarks. This new genus is placed in Nevrorthidae by the presence of three radial crossveins and the long distal half of CuA with 10 branches and nearly parallel with the posterior wing margin in the hind-wing. Interestingly, the new genus shares the distal fusion of the forewing ScP and RA due to the terminal curve of ScP with many species of Sisyridae. Wichard et al. (2009) use the fusion/separation of ScP and RA to distinguish Sisyridae and Nevrorthidae in their key to the aquatic Neuroptera in the Eocene Baltic amber. However, the fusion of ScP and RA in some sisyrids, such as Sisyrina Banks, 1939, Prosisyrina Perkovsky & Makarkin, 2015 and Paleosisyra electrobaltica Wichard, Gröhn & Seredszus, 2009 is atypical because the apical part of ScP is abruptly curved towards RA and the short terminal section connecting to RA can be also interpreted as a crossvein (e.g. 2scp-r in Makarkin and Perkovsky (2016) or 2scp-ra in Yang and Liu (2021)). This feature is just the state present in Sisyroneurorthus gen. nov. and should not be used to place the new genus in Sisyridae. Moreover, all known sisyrids have only two radial crossveins, but lack 1ra-rp in the hind-wing. They also have fewer (usually five or six) branches of hind-wing CuA.

The new genus is most similar to the contemporary genus *Cretarophalis* Wichard, 2017 by having simple forewing costal crossveins and simple hind-wing CuA branches. However, it differs from the latter genus by the configuration of ScP, which is terminally curved towards RA (in *Cretarophalis*, ScP runs straight terminally), the position of the crossvein between Cu and A1 (2cu-a1), which is distad separation of CuA and CuP (in *Cretarophalis* 2cu-a1 proximad separation of CuA and CuP).

Sisyroneurorthus aspoeckorum sp. nov.

https://zoobank.org/C9496131-33DA-46E8-9579-276CB5B291BF Figs 1–4

Type material. *Holotype*, an incomplete female adult (Fig. 1), one-third of left fore- and hind-wings lost due to over-polishing, preserved in approximately $9 \text{ mm} \times 5 \text{ mm} \times 4 \text{ mm}$ parallelepiped-shaped, yellowish, somewhat cloudy amber piece; specimen accession number CAU-BA-NH-22001, deposited in the Entomological Museum, China Agricultural University (CAU), Beijing.

Type locality and horizon. Hukawng Valley (26°21'33.41"N, 96°43'11.88"E), Kachin State, northern Myanmar; mid-Cretaceous, upper Albian to lower Cenomanian.

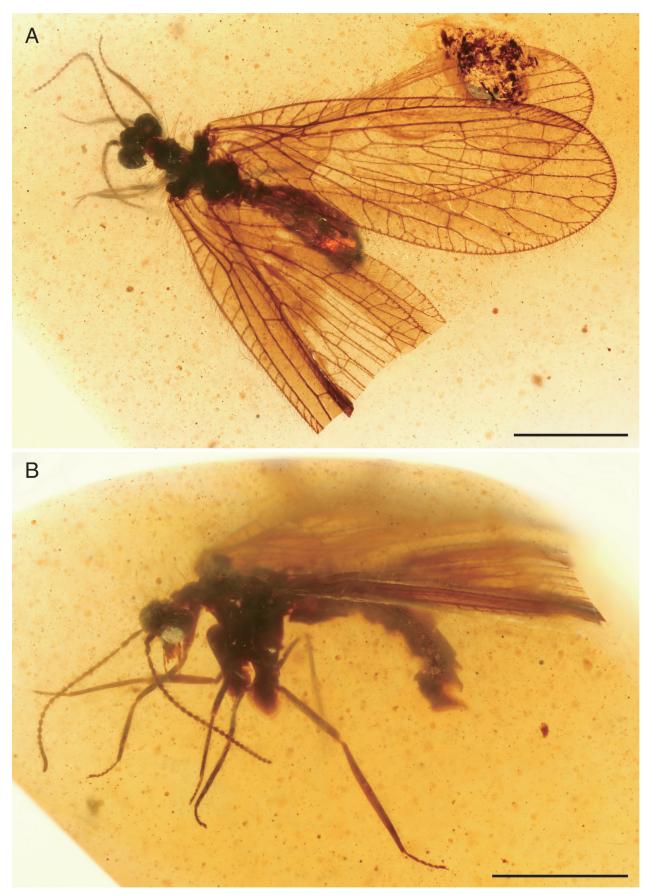


Figure 1. Habitus of *Sisyroneurorthus aspoeckorum* gen. et sp. nov., holotype female (CAU-BA-NH-22001) in mid-Cretaceous Kachin amber. **A.** Dorsal view; **B.** Left lateral view. Scale bars: 1.0 mm.

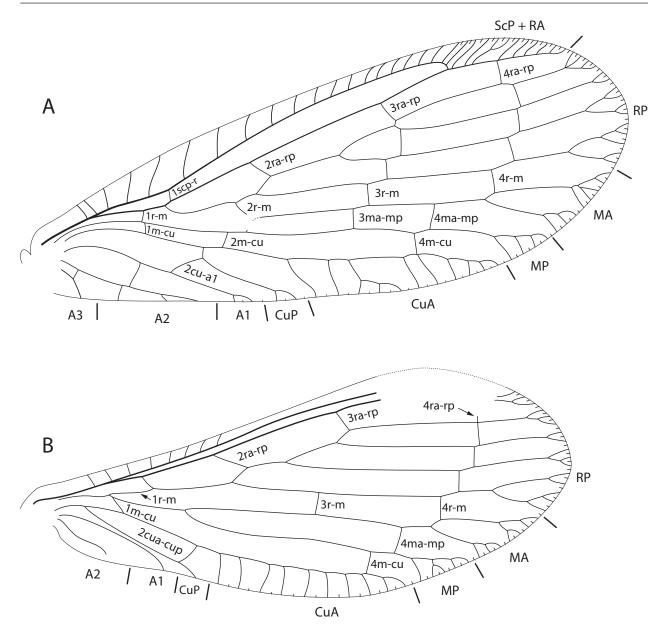


Figure 2. Wing venation of *Sisyroneurorthus aspoeckorum* gen. et sp. nov., holotype female (CAU-BA-NH-22001) in mid-Cretaceous Kachin amber. A. Right forewing; B. Right hind-wing. Abbreviations. A (a) – anal vein; A1–A3 – first to third anal vein; Cu (cu) – cubitus; CuA – cubitus anterior; CuP – cubitus posterior; M (m) – media: MA – media anterior; MP – media posterior; R (r) – radius; RA – radius anterior; RP – radius posterior; Sc (sc) – subcosta; ScP – subcosta posterior. Scale bar: 0.5 mm.

Etymology. The new species is dedicated to Dr. Ulrike Aspöck and Dr. Horst Aspöck for their outstanding contributions to the systematics of Nevrorthidae.

Diagnosis. As for the genus (*vide supra*).

Description. *Body.* Length ca. 2.4 mm as preserved (measured from vertex to apex of the abdomen).

Head (Fig. 3A–C). Vertex moderately domed, covered with thin setae. Eyes large, protruding laterally. Antennae: scapus relatively long, ca. four times as long as wide; pedicellus half length of scape; both scattered with thin setae; flagellum moniliform, composed of 24 flagellomeres, each with scattered fine setae (Fig. 3A). Maxillary palpi with 4 palpomeres, terminal palpomere fusiform, acutely tapering at tip; labial palpi poorly preserved (Fig. 3B, C). *Thorax.* Pronotum short, slightly longer than head, ca. 1.3 times as long as wide, lateral margins with long thin setae on several small processes. Meso- and metathorax covered with thin setae.

Legs slender, covered with dense thin setae; tarsus five segmented, tarsomeres 1 and 5 almost same length and slightly longer than each of remaining tarsomeres.

Wings. Forewing (Fig. 2A) hyaline, elongated oval, ca. 3.7 mm long, ca. 1.4 mm wide (right forewing). Distinct trichosors present on one-third apical wing margin (Fig. 3D), obscured trichosors on posterior margin (Fig. 3E); thin setae sparsely present on dorsal and ventral surfaces of longitudinal veins. Costal space distinctly broad near wing base, narrowed distally; all subcostal veinlets simple.

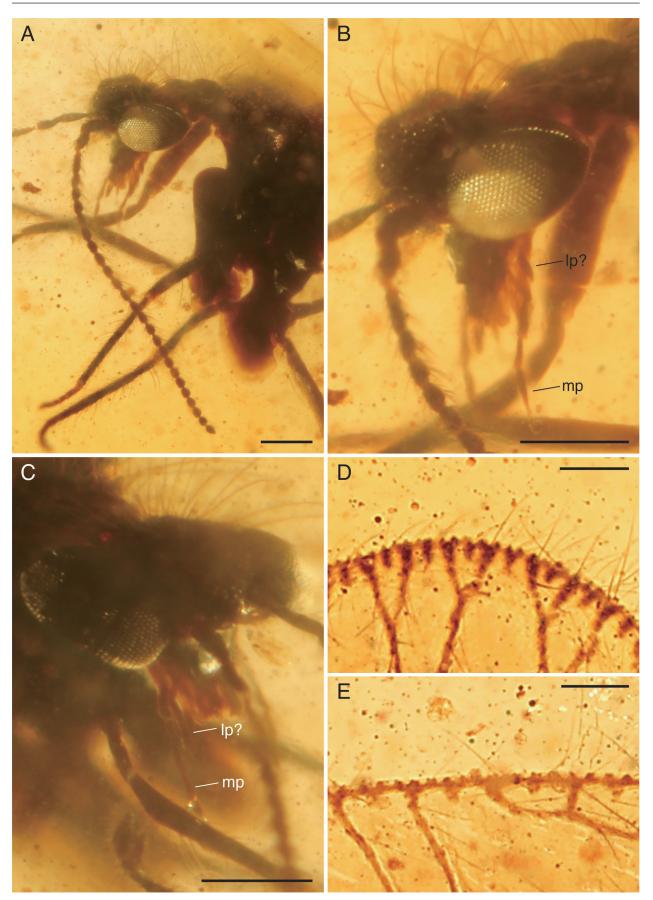


Figure 3. Details of *Sisyroneurorthus aspoeckorum* gen. et sp. nov., holotype female (CAU-BA-NH-22001) in mid-Cretaceous Kachin amber. **A.** Left anterolateral view of head and antenna; **B.** Left anterolateral view of mouthparts; **C.** Right anterolateral view of mouthparts; **D.** Distinct trichosors present on apical wing margin in right forewing; **E.** Obscured trichoshors on posterior margin in right forewing. **Abbreviations. lp** – labial palpus; **mp** – maxillary palpus. Scale bars: 0.2 mm (**A–C**); 0.1 mm (**D, E**).

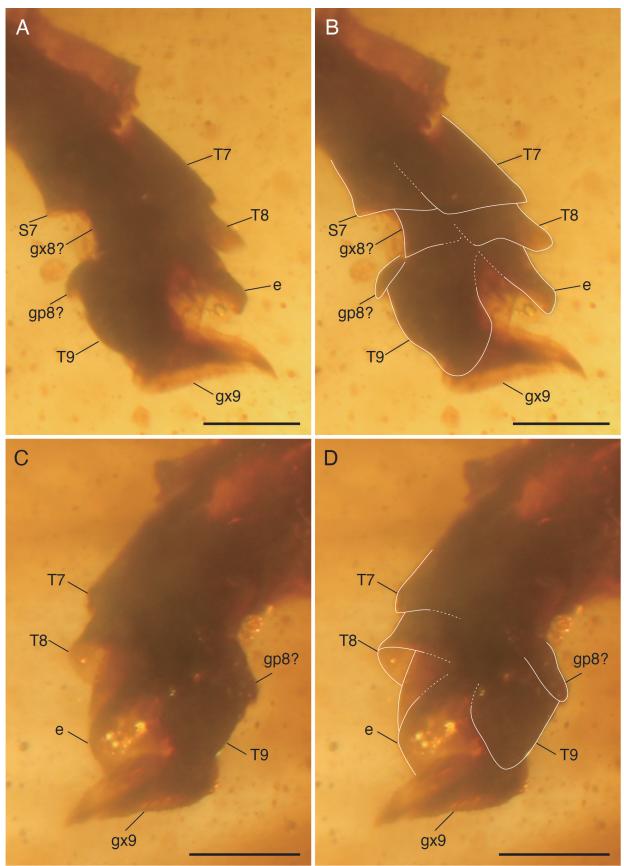


Figure 4. Terminalia of *Sisyroneurorthus aspoeckorum* gen. et sp. nov., holotype female (CAU-BA-NH-22001) in mid-Cretaceous Kachin amber. **A.** Left lateral view of terminalia; **B.** Left lateral view of terminalia with white line indicating each segment, go-napophyses and gonocoxite; **C.** Right ventrolateral view of terminalia; **D.** Right ventrolateral view of terminalia with white line indicating each segment and gonapophyses. **Abbreviations. e** – ectoproct; **gp** – gonapophyses; **gx** – gonocoxite; **S** – sternum; **T** – tergum. Scale bars: 0.2 mm.

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ScP fused with RA at distal fourth by abrupt curve terminally. Subcostal space slightly widened distad. Proximal crossvein (1scp-r) located near origin of RP. RP divided into four branches, each of which has marginal branches, third (median) gradate series present, composed of two crossveins. Fourth (outer) gradate series present, composed of three crossveins. Three ra-rp crossveins (2ra-rp, 3ra-rp and 4ra-rp) present. M divided into MA and MP; base of MA rather weak; two medial crossveins (3ma-mp and 4ma-mp) present. Four r-m crossveins (1r-m, 2r-m, 3r-m and 4r-m) present. Cu divided into CuA and CuP; CuA with nine pectinate branches, basal third branch trifurcated marginally; CuP with only a marginal fork; cua-cup crossvein absent. Three m-cu crossveins (1m-cu, 2m-cu and 4m-cu) present. One cu-a crossvein (2cup-a1) present, oblique, anteriorly connecting base of CuP. Three anal veins present; A1 with only a marginal fork; A2 with three short marginal branches; A3 simple; two crossveins (1a1-a2 and 1a2-a3) present.

Hind-wing (Fig. 2B) hyaline, elongated oval, ca. 3.3 mm long, ca. 1.3 mm wide (right hind-wing); not visible at distal third of anterior margin due to debris and poor preservation. Trichosors present from apical area to posterior wing margin; thin setae sparsely present on dorsal and ventral surfaces of longitudinal veins. Costal space narrowed; all subcostal veinlets simple. RP divided into four branches, each of which has marginal branches, there is only one gradate visible, composed of three crossveins. Three ra-rp crossveins (2ra-rp, 3ra-rp and 4ra-rp) present. M divided into MA and MP, one medial crossvein (4mamp) present. Three r-m crossveins (1r-m, 3r-m and 4r-m) present, basal 1r-m slightly long and weakly sinuate. Cu divided into CuA and CuP; CuA with distal half nearly parallel with posterior wing margin and bearing 10 pectinate simple branches; CuP simple; one cua-cup crossvein (2cua-cup) present. Two m-cu crossveins (1m-cu and 4mcu) present. A1 and A2 simple, cu-a crossvein absent.

Abdomen (Figs 1, 4). Poorly preserved, terminal segment unclear. Tergum 9 (Fig. 4) with lateral parts strongly produced posteriad. Gonocoxite 9 (Fig. 4) visible, well developed, flat, almost vertically directed dorsal, with apex slightly curved in lateral view. Ectoproct subtrapezoidal in lateral view.

Discussion

The presently described new nevrorthid represents the second genus and species of this enigmatic lacewing family from the Mesozoic, following the discovery of *Cretarophalis* (Wichard 2017). These two nevrorthid genera from the Kachin amber are still the oldest fossils of Nevrorthidae known to date. It is notable that these two genera share several apomorphic characters states, such as the relatively distal origin of the forewing CuP, the absence of the forewing cua-cup, the hind-wing CuA with all branches simple and the female tergum 9 with lateral parts strongly produced posteriad (Lu et al. 2018). Unfortunately, male specimens of the Cretaceous nevrorthids have not yet been

found. Therefore, their phylogenetic relationships with the Eocene Baltic amber and extant counterparts could not be inferred by lack of the informative male genital characters (Aspöck et al. 2017; Lu et al. 2018). Nevertheless, the present finding further supports a sister-group relationship between Nevrorthidae and Sisyridae. Lu et al. (2018) pointed out that the female tergum 9 strongly produced posteriad, shared by Cretarophalis and Sisyridae, may provide evidence supporting the close relationship of these two aquatic lacewing families. The distal fusion of ScP and RA in Sisyroneurorthus gen. nov. is another character shared by Sisyridae. Thus, given the probable sister-group relationship of Nevrorthidae and Sisyridae, whether these Cretaceous nevrorthids represent a stem-group of Nevrorthidae + Sisyridae or a transitional lineage between these two families needs critical evaluation.

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References

- Aspöck U, Aspöck H, Liu X (2017) The Nevrorthidae, mistaken at all times: Phylogeny and review of present knowledge (Holometabola, Neuropterida, Neuroptera). Deutsche Entomologische Zeitschrift 64(2): 77–110. https://doi.org/10.3897/dez.64.13028
- Balashov I (2021) The first records of mollusks from mid-Cretaceous Hkamti amber (Myanmar), with the description of a land snail, *Euthema myanmarica* n. sp. (Caenogastropoda, Cyclophoroidea, Diplommatinidae). Journal of Paleontology 95(5): 994–1003. https://doi.org/10.1017/jpa.2021.26
- Banks N (1939) New genera and species of neuropteroid insects. Bulletin of the Museum of Comparative Zoology 85: 439–504.
- Breitkreuz LCV, Winterton SL, Engel MS (2017) Wing tracheation in Chrysopidae and Other Neuropterida (Insecta): A resolution of the confusion about vein fusion. American Museum Novitates 3890(3890): 1–44. https://doi.org/10.1206/3890.1
- Cruickshank RD, Ko K (2003) Geology of an amber locality in the Hukawng Valley, Northern Myanmar. Journal of Asian Earth Sciences 21(5): 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5
- Du X, Niu K, Bao T (2023) Giant Jurassic dragon lacewing larvae with lacustrine palaeoecology represent the oldest fossil record of larval neuropterans. Proceedings of the Royal Society B 290: 20222500. https://doi.org/10.1098/rspb.2022.2500
- Engel MS, Winterton SL, Breitkreuz LCV (2018) Phylogeny and evolution of Neuropterida: Where have wings of lace taken us? Annual Review of Entomology 63(1): 531–551. https://doi.org/10.1146/annurev-ento-020117-043127
- Grimaldi DA, Ross AJ (2017) Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. In: Fraser NC, Sues

HD (Eds) Terrestrial Conservation Lagerstätten: Windows Into the Evolution of Life on Land. Dunedin Academic Press, Edinburgh, 287–342.

- Kukalová-Peck J (1991) Fossil history and the evolution of hexapod structures. In: Naumann ID (Ed.) The Insects of Australia: a Textbook for Students and Research Workers (2nd edn., Vol. 1). Cornell University Press, Ithaca, 141–179.
- Kukalová-Peck J, Lawrence JF (2004) Relationships among coleopteran suborders and major endoneopteran lineages: Evidence from hind wings characters. European Journal of Entomology 101(1): 95–144. https://doi.org/10.14411/eje.2004.018
- Leach WE (1815) Entomology. In: Brewster D (Ed.) Edinburgh Encyclopaedia (Vol. 9. Pt. 1). Blackwood, Edinburgh, 57–172.
- Linnaeus C (1758) Systema Naturae per Regna Tria Naturae Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis (10th edn. Vol. 1). Salvii, Holmiae, 824 pp. https:// doi.org/10.5962/bhl.title.542
- Lu X, Xia F, Wang B, Aspöck U, Liu X (2018) Taxonomic notes on *Cretarophalis patrickmuelleri* Wichard, 2017 (Insecta: Neuroptera: Nevrorthidae) from the mid-Cretaceous of Myanmar, and its phylogenetic significance. Zootaxa 4370(5): 591–600. https://doi. org/10.11646/zootaxa.4370.5.10
- Makarkin VN, Perkovsky EE (2016) An interesting new species of Sisyridae (Neuroptera) from the Upper Cretaceous Taimyr amber. Cretaceous Research 63: 170–176. https://doi.org/10.1016/j.cretres.2016.03.010
- Nakahara W (1915) On the Hemerobiinae of Japan. Annotationes Zoologicae Japonenses 9: 11–48.
- Perkovsky EE, Makarkin VN (2015) First confirmation of spongillaflies (Neuroptera: Sisyridae) from the Cretaceous. Cretaceous Research 56: 363–371. https://doi.org/10.1016/j.cretres.2015.06.003

- Vasilikopoulos A, Misof B, Meusemann K, Lieberz D, Flouri T, Beutel RG, Niehuis O, Wappler T, Rust J, Peters RS, Donath A, Podsiadlowski L, Mayer C, Bartel D, Böhm A, Liu S, Kapli P, Greve G, Jepson JE, Liu X, Zhou X, Aspöck U, Aspöck H (2020) An integrative phylogenomic approach to elucidate the evolutionary history and divergence times of Neuropterida (Insecta: Holometabola). BMC Evolutionary Biology 20(1): 1–64. https://doi.org/10.1186/ s12862-020-01631-6
- Wichard W (2016) Overview and descriptions of Nevrorthidae in Baltic amber (Insecta, Neuroptera). Palaeodiversity 9(1): 95–111. https:// doi.org/10.18476/pale.v9.a7
- Wichard W (2017) Family Nevrorthidae (Insecta, Neuroptera) in mid-Cretaceous Burmese amber. Palaeodiversity 10(1): 1–5. https:// doi.org/10.18476/pale.v10.a1
- Wichard W, Gröhn C, Seredszus F (2009) Aquatic Insects in Baltic Amber. Kessel, Remagen, 336 pp.
- Winterton SL, Lemmon A, Gillung JP, Garzon IJ, Badano D, Bakkes DK, Breitkreuz LCV, Engel MS, Lemmon EM, Liu XY, Machado RJP, Skevington JH, Oswald JD (2018) Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). Systematic Entomology 43(2): 330–354. https://doi.org/10.1111/syen.12278
- Winterton SL, Martins CC, Makarin V, Ardila-Camacho A, Wang Y (2019) Lance lacewings of the world (Neuroptera: Archeosmylidae, Osmylidae, Saucrosmylidae): review of living and fossil genera. Zootaxa 4581(1): 1–99. https://doi.org/10.11646/zootaxa.4581.1.1
- Yang Y, Liu X (2021) New spongillaflies of the genus Sisyrina Banks, 1939 (Neuroptera: Sisyridae) from the Oriental faunal region. Zootaxa 5052(4): 552–566. https://doi.org/10.11646/zootaxa.5052.4.5