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Taxonomic notes on dustywings of Aleuropteryginae (Insecta, Neuroptera, Coniopterygidae) from the mid-Cretaceous Burmese amber



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ABSTRACT

Two new genera and three new species of the dustywings subfamily Aleuropteryginae are described from the Burmese amber (lowermost Cenomanian, mid-Cretaceous). *Cycloconis maculata* gen. et sp. nov. is tentatively placed in the tribe Fontenelleini and appears to be closely related to *Libanoconis* Engel, 2002, but it can be distinguished from the latter genus by the forks of forewing RP + MA and MP subequal in length and the trifurcated hind wing MP. *Burmaleuropteryx meinanderi* gen. et sp. nov. resembles *Garnaconis* Perrichot & Nel, 2014 (both genera with unclear placement of tribe), but can be separated from the latter genus by the forks of stiff setae along distal and posterior margins of wings. *Achlyoconis jiae* sp. nov. is distinguished from *Achlyoconis heptatrichia* Engel, 2016 by the larger body size, the forewing point between forewing RP and MA. *Achlyoconis heptatrichia* Engel, 2016 is also redescribed based on a series of new material, and its male genitalia is described in detail.

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1. Introduction

Coniopterygidae (dustywings) is a distinctive family of Neuroptera and characterized by the minute body-size, the waxy covering, and the reduction of wing venation. Currently, there are 571 described species in the world (Sziráki, 2011; Engel, 2016; Oswald and Machado, 2018). The phylogenetic position of Coniopterygidae has been controversial for a long time (Aspöck et al., 2001; Haring & Aspöck, 2004; Aspöck & Aspöck, 2008; Zimmermann et al., 2009; Randolf et al., 2017), while recent molecule-based phylogenetic studies suggested that this family is the sister group of the lineage comprising all other extant lacewing families and probably had been diverged during the late Permian (Winterton et al., 2010, 2017; Misof et al., 2014; Wang et al., 2017).

The oldest fossil record of Coniopterygidae refers to Juraconiopteryx zherichini Meinander (1975), described based on an

* Corresponding author. E-mail address: xingyue_liu@yahoo.com (X. Liu). incomplete compression fossil from the Upper Jurassic of Kazakhstan (Karatau). Almost all remaining fossils of the family are found in most major amber deposits of the Cretaceous and Cenozoic (Grimaldi et al., 2013; Engel, 2016), as follows: Lebanon [Bkassine (Jouar Ess Sour) (South Lebanon), Mdeyrij-Hammana (Central Lebanon), Lower Cretaceous, lower Barremain: Whalley 1980; Azar et al., 2000; Nel et al., 2005; Maksoud et al., 2017]; Spain (Cantabria, Lower Cretaceous, Albian: Pérez-de la Fuente, 2012); France (Charente-Maritime, Lower Cretaceous, Albian: Nel et al., 2005; Vendée, Upper Cretaceous, Cenomanian-Santonian: Perrichot et al., 2014; Alsace, Oligocene: Nel, 1990); Myanmar (Kachin, mid-Cretaceous, lowermost Cenomanian: Engel, 2004, 2016; Sziráki, 2016, 2017; Liu & Lu, 2017); U.S.A. (New Jersey, mid-Cretaceous, Turonian: Grimaldi, 2000; Engel, 2002); Russia (Taimyr Peninsula, Upper Cretaceous, Santonian: Meinander, 1975; Makarkin & Perkovsky, 2017, 2018); Canada (Alberta, Upper Cretaceous, Campanian: McKellar et al., 2008); India (Gujarat, Eocene: Grimaldi et al., 2013); France (Oise, Les Quesnoys, Eocene: Nel et al., 2005); Baltic and the Ukraine (Eocene: Enderlein, 1910, 1930; Meinander, 1975; Dobosz & Krzemiński, 2000;



Kupryjanowicz & Makarkin, 2008; Engel, 2010); and the Dominican Republic (Miocene: Meinander, 1998; Engel & Grimaldi, 2007; Grimaldi et al., 2013) (See Table 1). Among them, 10 genera and 17 species are described from Cretaceous ambers.

The palaeofauna of Coniopterygidae from the mid-Cretaceous of Myanmar was relatively rich. Currently, five genera and six species have been described from the Burmese amber (Engel, 2004, 2016; Sziráki, 2016, 2017; Liu & Lu, 2017). There are two species of Aleuropteryginae, three species of Coniopteryginae, and a species representing its own subfamily, i.e. Cretaconiopteryginae, which is only known from the Burmese amber (Liu & Lu, 2017).

In this paper we present new information on the Burmese amber dustywings of the subfamily Aleuropteryginae, some new data refer to described species. The present findings enrich the knowledge on palaeodiversity and early evolution of the Mesozoic dustywings.

2. Material and methods

The amber specimens herein described are from the Hukwang Valley in Tanai Township, Myikyina District of Kachin State, northern Myanmar (Kania et al., 2015: fig. 1). The age of this deposit has been investigated and dated to be 98.8 \pm 0.6 Ma (earliest

Table 1

Fossil species of Coniopterygidae.

Cenomanian) by U–Pb dating of zircons from the volcanoclastic matrix of the amber (Shi et al., 2012).

The specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIPG), Chinese Academy of Sciences, Nanjing; the Century Amber Museum (CAM), Shenzhen; and the Three Gorges Entomological Museum (EMTG), Chongqing.

Photographs and drawings were taken and made by using a Zeiss SteREO Discovery V12 stereo microscope system and a Leica DM 2000 optical microscope with Nikon D90 digital camera. The figures were prepared with Adobe Photoshop CS4®. Terminology of wing venation generally follows Aspöck et al. (1980). We did not use the terminology of wing venation of Meinander (1972) as it lacks homology with other lacewing families, although this wing venation system were frequently used in many papers on Coniopterygidae (e.g., Azar et al., 2000; Engel, 2016). Breitkreuz et al. (2017) presented an alternative interpretation on the homology of wing venation in Neuropterida based on vein tracheation, particularly pointing out that the MA is not fused RP at wing base. Nevertheless, in this paper we still consider the basal fusion between RP and MA. The presently used vein nomenclature is given below with comparison of that used by Meinander (1972) in corresponding parentheses. Terminology of genitalia follows Aspöck and Aspöck (2008).

	Species	Age	Locality
Family Coniopterygidae Burmeister, 1839			
Subf	family Cretaconiopteryginae Liu & Lu, 2017		
1	Cretaconiopteryx grandis Liu & Lu (2017)	Upper Cretaceous (lowermost Cenomanian)	Kachin, Myanmar
Subi	amily Aleuropteryginae Enderlein, 1905		
2	Juraconiopteryx zherichini Meinander (1975)	Upper Jurassic (Oxfordian)	Karatau, Kazakhstan
3	Achlyoconis heptatrichia Engel (2016)	Upper Cretaceous (lowermost Cenomanian)	Kachin, Myanmar
4	Achiyoconis jiae sp. nov.	Upper Cretaceous (lowermost Cenomanian)	Kachin, Myanmar
5	Alboconis cretacica Nel et al. (2005)	Lower Cretaceous (Albian)	Charente-Maritime, France
6	Apoglaesoconis ackermani Grimaldi (2000)	Upper Cretaceous (Turonian)	New Jersey, U.S.A.
/	Apoglaesoconis luzzii Grimaldi (2000)	Upper Cretaceous (Turonian)	New Jersey, U.S.A.
8	Apoglaesoconis swolenskyl Grimaldi (2000)	Upper Cretaceous (Turonian)	New Jersey, U.S.A.
9	Apoglaesoconis cherylae Engel (2002)	Upper Cretaceous (Turonian)	New Jersey, U.S.A.
10	Burmaleuropteryx meinanaeri gen. et sp. nov.	Upper Cretaceous (lowermost Cenomanian)	Kachin, Myanmar
11	Cycloconis maculata gen. et sp. nov.	Upper Cretaceous (lowermost Cenomanian)	Kachin, Myanmar Mandéa France
12	Garnaconis aupeorum Perrichot & Nei in Perrichot et al. (2014)	Upper Cretaceous (Cenomanian–Santonian)	Vendee, France Kashin, Muanmar
13	Glassocomis ballopleryx Eliger (2004)	Upper Cretaceous (Turopian)	New Jorgey, LLS A
14	Glassocomis mediculu Grinialdi (2000)	Upper Cretaceous (Conjacian, Santonian)	New Jersey, U.S.A.
10	Glassoconis cretica Methaliael (1973)	Upper Cretaceous (Contacian–Santonian)	Taimur Doningula, Russia
17	Libanoconis fadiacra Whallov (1080)	Lower Cretaceous (Jower Parremian)	Pleassing (Jouar Ess Sour) and Mdourij
17	Libunoconis Judiuciu Whaney (1980)	Lower Cretaceous (lower Barrennan)	Hammana, Lohanon
18	Libanoconis siberica Makarkin & Perkovsky (2018)	Upper Cretaceous (upper Cenomanian)	Taimur Deningula, Russia
10	Archiconiocompsa prisca Enderlein (1010)	Focene (Lutetion)	Poland or Russia (Baltic amber): Rivne Ukraine
20	Archiconis electrica Enderlein (1910)	Focene (Lutetian)	Poland or Russia (Baltic amber)
20	Ceroconiocompsa ostara Engel (2010)	Focene (Lutetian)	Poland or Russia (Baltic amber)
21	Pararchiconis quievreuxi Nel (1990)	Oligocene (Rupelian)	Alsace France
22	Spiloconis eominuta Crimaldi & Engel in Crimaldi et al. (2013)	Focene (Vpresian)	Cuiarat India
23	Spiloconis commune drimaner (1998)	Miocene (Burdigalian)	Dominican Republic
25	Spiloconis glacsana memanaer (1998)	Miocene (Burdigalian)	Dominican Republic
26	Neoconis naleocaribis Grimaldi & Engel in Grimaldi et al. (2013)	Miocene (Burdigalian)	Dominican Republic
Subfamily Conjoptervginae Burmeister, 1839			
27	Libanosemidalis hammanaensis Azar et al. (2000)	Lower Cretaceous (lower Barremian)	Bkassine (Jouar Ess Sour) and Mdeyrij- Hammana, Lebanon
28	Paranimboa litotes Engel (2016)	Upper Cretaceous (lowermost Cenomanian)	Kachin, Myanmar
29	Paranimboa groehni Sziráki (2016)	Upper Cretaceous (lowermost Cenomanian)	Kachin, Myanmar
30	Phthanoconis burmitica Engel (2004)	Upper Cretaceous (lowermost Cenomanian)	Kachin, Myanmar
31	Coniontervx timida Hagen in Berendt (1856)	Eocene (Lutetian)	Poland or Russia (Baltic amber)
32	Conjopteryx antiquua Engel and Grimaldi (2007)	Miocene (Burdigalian)	Dominican Republic
33	Coniopteryx enderleini Meunier (1910a,b)	Pleistocene (Calabrian)	Togo
34	Gallosemidalis eocenica Nel et al. (2005)	Eocene (Ypresian)	Paris. France
35	Hemisemidalis kulickae Dobosz & Krzemiński (2000)	Eocene (Lutetian)	Poland or Russia (Baltic amber)
36	Parasemidalis sharovi Meinander (1975)	Eocene (Lutetian)	Poland or Russia (Baltic amber)
37	Semidalis fritschi Enderlein (1930)	Eocene (Lutetian)	Poland or Russia (Baltic amber)
38	Semidalis copalina Meunier (1910a),b	Pleistocene (Calabrain)	Madagascar

Abbreviations used for wing veins are as following (Words in bracket were used in Meinander, 1972): A, anal vein; C, costa; Cu, cubitus; CuA (Cu1), cubitus anterior; CuP (Cu2), cubitus posterior; M, media; MA (R4+5), media anterior; MP (M), media posterior; R, radius; RA (R1), radius anterior; RP (R2+3), radius posterior; ScP (Sc), subcosta posterior.

3. Systematic palaeontology

Class Insecta Linnaeus, 1758 Order Neuroptera Linnaeus, 1758 Family Coniopterygidae Burmeister, 1839 Subfamily Aleuropteryginae Enderlein, 1905 Tribe Fontenelleini Carpentier & Lestage, 1928

Genus *Achlyoconis* Engel, 2016 (Figs. 1–5)

Achlyoconis Engel, 2016: 4. Type species: Achlyoconis heptatrichia Engel, 2016: 4.

Revised diagnosis. Minute to medium-sized dustywings (forewing length 1.6-3.0 mm). Antenna with 22-29 flagellomeres; scape about twice as long as wide. Wing membrane hyaline, usually with four or five pigmented spots on forewing. Forewing ScP2 not curved anteriorly toward ScP1; origin of RP + MA near wing midlength; RP simple, with crossvein between RA and RP + MA (i.e. ra-rp or ra-rp + ma) distinctly distad proximal section of ScP2; MA simple, proximally angulately curved, with curving point connected with anterior-most branch of MP by a crossvein (ma-mp) or fused with the latter vein; MP with 6-8 distinctive thickenings bearing specialized setae; MP trifurcate; separation between CuA and CuP on wing margin nearly twice than that of marginal separation between MP2 and CuA; cua-cup present proximad mp-cua; one or two cup-a1 crossveins; a1-a2 present. Hind wing venation in general similar to that of forewing; RP + MA origin near wing base; MP and Cu parallel and separated by distinct membrane. Abdominal plicaturaes present.

Achlyoconis heptatrichia Engel, 2016. (Figs. 1–5)

Achlyoconis heptatrichia Engel, 2016: 4.

Revised diagnosis. Forewing length 1.6–2.4 mm. Antenna with 22–27 flagellomeres. Forewing with five pigmented spots. Forewing ra-rp distinctly distad branching point between RP and MA; mp-cua present; two cup-a1 crossveins present. Hind wing ScP proximally with series of small, hamuli-like setae.

Redescription. Male. Body length 1.2–1.8 mm; integument brown.

Head nearly as long as wide, with prominent compound eyes; eye height/head height ratio ca. 0.50–0.67; frons well-sclerotized between antennal insertions, anteriorly with a pair of small projections; gena slightly elongated; vertex distinctly domed. Antenna with scape stouter than pedicel and flagellomeres, about twice as long as wide; flagellum moderately setose, with 22–27 flagellomeres, each flagellomere subquadrate, but terminal flagellomere bullet-shaped. Terminal maxillary palpomere subtriangular, much longer and broader than preceding palpomeres; terminal labial palpomere ovoid, much longer and broader than preceding palpomeres.

Prothorax much narrower and shorter than meso- and metathorax. Legs slender, with short setae; pro- and mesotibiae nearly equal in length to pro- and mesofemora; metatibia much longer than metafemur; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of remaining tarsomeres; tarsomere 4 apically expanded; pretarsal claws short, simple; arolium absent.

Forewing length 1.6-2.4 mm; membrane hyaline, more or less brownish throughout, with five ovoid, pigmented spots, respectively located at proximal section of MA, stem of MP1, rp + ma-mp, cua-cup, and a1-a2, but spot at proximal section of MA sometimes reduced; costal space proximally with two costal crossveins; ScP largely parallel to costal margin, distally feebly curved posteriad. ScP2 separating nearly at distal 1/5-1/6, and not curved anteriorly toward ScP1; origin of RP + MA near wing midlength; RP simple, with ra-rp distinctly distad proximal section of ScP2 as well as branching point between RP and MA; MA simple, proximally angulately curved, with curving point connected with anteriormost branch of MP by a short crossvein (ma-mp) or fused with the latter vein; MP with 6–7 distinctive thickenings bearing stiff setae; MP trifurcate into a forked MP1 and a simple MP2; mp-cua present proximad rp + ma-mp; separation between CuA and CuP on wing margin nearly twice that of marginal separation between MP2 and CuA; cua-cup present proximad mp-cua; distance between rp + ma-mp and mp-cua shorter than that between mp-cua and cua-cup; two cup-a1 crossveins; A1 simple, A2 with a short proximal branch reaching wing margin; a1-a2 present.

Hind wing length 1.2–2.2 mm, wing shape similar to forewing, immaculate; ScP proximally with series of small, hamuli-like setae; venation in general similar to that of forewing; RP + MA origin near proximal quarter of wing length; rp + ma-mp present near origin of RP + MA; MP and Cu parallel and separated by distinct membrane; separation between CuA and CuP on wing margin nearly twice that of marginal separation between MP2 and CuA; cua-cup and cup-a1 present near wing base.

Abdomen greatly tapering to narrow apical segments; plicatures present on segments 2–6, but some of them not clearly visible in some individuals. Genitalia covered with sparse long setae (clearly visible only in EMTG BU001199). Tergum 9 not fused with and slightly longer than sternum 9+hypandrium?, posterolaterally fused with ectoprocts; sclerotized apodeme between tergum 9 and ectoprocts extending anteromedially, ventrally fused with putative gonocoxities 9, which bear eight differently lengthed, medially curved, stout spines; anus opening present beneath median part of ectoprocts; sternum 9+hypandrium? nearly rectangular, posterolaterally with a pair of obtuse processes; putative gonapophyses 10 (parameres) slenderly elongate and arcuately curved laterally, posterior half gradually widened, terminally trifurcated into two digitiform and one spinous processes; rods of penis (putative gonostyli 10) slender, distinctly not fused together, posteriorly enlarged, laterally with an anteriorly directed digitiform process, and terminally spinous and slightly curved medially.

Female. Body length 1.7–2.4 mm; forewing length 2.1–2.4 mm, hind wing length 1.8–2.2 mm. Morphology mostly similar to male. Abdomen tapering posteriad, especially in segment 7–9, with length and width much shorter than other segments. Putative gonocoxites 9 and ectoprocts subtriangular.

Materials examined. NIGP 169963 (Fig. 1A, B), amber piece preserving a complete adult (abdominal apex obscure), it is polished in the form of nearly rectangular, transparent cabochon, with length × width about 15.01 × 10.92 mm, height about 3.33 mm. NIGP 169964 (Fig. 1C, D), amber piece preserving a complete female adult, it is polished in the form of elliptical, transparent cabochon, with length × width about 22.94 × 14.39 mm, height about 5.95 mm. NIGP 169965 (Fig. 1E, F), amber piece with a partly preserved male adult is polished in the form of short, clavate cabochon, semitransparent, with length × width about 13.34 × 3.95 mm, height about 3.45 mm. NIGP 169966 (Fig. 2A, B), amber piece



Fig. 1. Achlyoconis heptatrichia Engel. A-B. NIGP 169963, sex unknown. A. Habitus photo, ventral view; B. Photo of mid part of forewing, arrows indicate stiff setae on stem of MP; C-D. NIGP 169964, female; C. Habitus photo, lateral view. D. Photo of mid part of forewing, arrows indicate stiff setae on stem of MP; E-F. NIGP 169965, male; E. Habitus photo, dorsal view; F. Photo of mid part of forewing, arrows indicate stiff setae on stem of MP.

preserving a clear complete male adult of *A. heptatrichia* and a midge, it is polished in the form of ellipsoidal transparent cabochon, with length × width about 17.99 × 16.72 mm, height about 10.07 mm. NIGP 169967 (Fig. 2C, D), amber piece preserving a complete female adult, it is polished in the form of elliptical cabochon, transparent, with length × width about 20.09 × 14.94 mm, height about 5.19 mm. EMTG BU001474 (Fig. 2E, F), amber piece with a complete male adult and a psocid, a beetle, and 17 parasitoid wasps, it is polished in the form of ovoid cabochon, transparent, with length × width about 20.79 × 10.37 mm, height about 7.41 mm. EMTG BU001934 (Fig. 3A, B), amber piece preserving a complete female adult, it is polished in the form of trapezoid cabochon, transparent, with length × width about 16.99 × 7.20 mm, height about 6.03 mm. EMTG BU001199



Fig. 2. Achlyoconis heptatrichia Engel. A-B. NIGP 169966, male; A. Habitus photo, ventral view; B. Photo of mid part of forewing, arrows indicate stiff setae on stem of MP; C-D. NIGP 169967, female; C. Habitus photo, ventral view; D. Photo of mid part of forewing, arrows indicate stiff setae on stem of MP; E-F. ETMG BU001474, male; E. Habitus photo, lateral view; F. Photo of mid part forewing, arrow indicate stiff setae on stem of MP.

(Figs. 3C–G, 4, 5), amber piece preserving a complete male adult, it is polished in the form of rounded cabochon, transparent, with length \times width about 18.90 \times 15.70 mm, height about 4.21 mm. *Remarks.* Engel (2004) described a Burmese amber dustywing species, i.e. *Glaesoconis baliopteryx* Engel (2004). The arguments for the placement of this species into the genus *Glaesoconis* Meinander, 1975 (Aleuropteryginae: Fontenelleini) include the possession of more than 20 flagellomeres, three branches of forewing MP which lacks stiff setae on its stem, and the branching of MP strongly distad basal rp + ma-mp. However, as pointed in Engel (2004), this species can be distinguished from the other *Glaesoconis* species by the distinctly spotted forewing and the extremely short ma-mp (= distalmost r-m crossvein in Engel, 2004) that is shorter than the proximal section of MA (= R4+5 in Engel, 2004). However, it is notable that *Achlyoconis heptatrichia* shares most morphological characters (i.e. the body size, the head shape, the number of flagellomeres, and the wing venations and marking patterns) with *G. baliopteryx* except for the forewing MP with seven stiff setae. The eight specimens herein examined in morphology fit well with the holotype of *A. heptatrichia*, particularly bearing 6–8 stiff setae on



Fig. 3. Achlyoconis heptatrichia Engel. A-B. ETMG BU001934, female; A. Habitus photo, lateral view; B. Photo of proximal half of forewing, arrows indicate stiff setae on stem of MP; C-G. ETMG BU001199, male; C. Habitus photo, dorsal view; D. Photo of proximal half of forewing, arrows indicate stiff setae on stem of MP; E. Habitus photo, ventral view; F-G. Photo of genitalia; F. Dorsal view; G. Ventral view. T: tergum; S: sternum; a: anus; epr: ectoproct; hyp: hypandrium; gp: gonapophysis; gst: gonostylus; gx: gonocoxite.

stem of forewing MP. However, we did not find any specimen lacking the stiff setae on forewing MP. So far, there has been no case that two dustywing genera have identical diagnostic characters except for presence/absence of stiff setae on forewing MP. Actually, the series of stiff setae on forewing MP of *Achlyoconis* is not easy to be recognized because the vein thickening is rather weak, which may mislead an interpretation of absence of these setae in *G. baliopteryx*. Makarkin & Perkovsky (2017) also indicated that this species may actually not belong to *Glaesoconis* and need to be reexamined to more firmly establish its generic attribution. Therefore, *G. baliopteryx* probably belongs to *Achlyoconis*. Nevertheless, formal taxonomic treatment will have to be made when we examine the type of *G. baliopteryx*. As described in Engel (2016), there are five ovoid, pigmented spots at proximal section of MA, stem of MP1, rp + ma-mp, cua-cup and a1-a2 in the forewing of *A. heptatrichia*. However, we found that the spot at proximal section of MA is reduced or poorly visible in most specimens of our materials (i.e. NIGP 169965, NIGP 169966, NIGP 169967, NIGP 169963, ETMG BU001474, ETMG BU001943).

Achlyoconis jiae Li, Wang & Liu, sp. nov. (Figs. 6 and 7) urn:lsid:zoobank.org:act:B97F9FA9-F3A3-45BF-B3F0-2760B5BCDB03

Type material. Holotype. CAM BA-0013 (Figs. 6 and 7), amber piece preserving a complete adult female of *Achlyoconis jiae* sp. nov. and a





Fig. 4. Achlyoconis heptatrichia Engel, ETMG BU001199, male. A. Drawing of forewing; B. Drawing of hind wing.

parasitoid wasp, it is polished in the form of an elliptical transparent cabochon, with length \times width about 13.07 \times 10.48 mm, height about 4.74 mm.

Locality and horizon. Amber deposits from the Hukwang Valley in Tanai Township, Myikyina District of Kachin State, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Etymology. The new species is dedicated to Mrs. Xiao Jia who kindly provided the specimen of this new species for our study.

Diagnosis. Forewing length 3.0 mm. Antenna with 29 flagellomeres. Forewing with four ovoid pigmented spots, a narrow short stripe present along ma-mp1. Eight weak subcostal veinlets on distal part of costal space; crossvein between RA and RP + MA distinctly distad proximal section of ScP2, but slightly proximad branching point between RP and MA; mp-cua present but reduced, short, indistinct, not reaching CuA; one cup-a1 crossvein. Hind wing ra-rp distinctly distad branching point of RP + MA, crossvein rp + ma-mp present, situated near midlength of wing; an oblique mp-cua present.

Description. Female. Body length 3.6 mm; integument pale brown.

Head slightly longer than wide, with prominent compound eyes; eye height/head height ratio ca. 0.46; frons well-sclerotized between antennal insertions; gena distinctly elongated; vertex feebly domed. Antenna with scape stouter than pedicel and flagellomeres, about twice as long as wide; flagellum moderately setose, with 29 flagellomeres, each flagellomere subquadrate, but terminal flagellomere bullet-shaped. Terminal maxillary

Fig. 5. Achlyoconis heptatrichia Engel, ETMG BU001199, male. A. Drawing of genitalia, dorsal view; B. Drawing of genitalia, ventral view; C. Drawing of gonapophysis 10 (paramere); D. Drawing of gonostyli 10 (penis). T: tergum; S: sternum; a: anus; epr: ectoproct; hyp: hypandrium; gp: gonapophysis; gst: gonostylus; gx: gonocoxite.

palpomere and terminal labial palpomere both subtriangular, much longer and broader than preceding palpomeres.

Prothorax much narrower but slightly longer than meso- and metathorax. Legs slender, with short setae; pro- and mesotibiae slightly shorter than pro- and mesofemora; metatibia slightly longer than metafemur; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of remaining tarsomeres; tarsomere 4 expanded distad; pretarsal claws short, simple; arolium absent.

Forewing length 3.0 mm; membrane hyaline, slightly brownish, with four ovoid, pigmented spots, respectively located at stem of MP1, rp + ma-mp, cua-cup, and a1-a2, in addition a narrow short stripe present along ma-mp1; costal space proximally with two costal crossveins, eight weak costal crossveins on distal part of costal space; ScP largely parallel to costal margin on proximal half, but distally very close to C and feebly curved posteriad, ScP2 separating nearly at distal 1/5, and not curved anteriorly toward ScP1; origin of RP + MA near wing midlength; RP simple, with crossvein between RA and RP + MA distinctly distad proximal section of ScP2 but slightly proximad branching point between RP and MA; MA simple, proximally angulately curved, with curving point connected with anterior-most branch of MP by a crossvein (ma-mp); rp + ma-mp present, not reaching the stem of MP; MP



Fig. 6. Achlyoconis jiae sp. nov., holotype, CAM BA-0013, female. A. Habitus photo, dorsal view; B. Habitus photo, ventral view; C. Head, dorsal view; D. Genitalia, lateral view; E. Photo of mid part of forewing, arrows indicate stiff setae on stem of MP; F. Photo of stiff setae (indicated by arrows) on stem of MP.

with seven distinctive thickenings bearing stiff setae; MP trifurcate into a forked MP1 and a simple MP2; mp-cua present, but indistinct, short, not reaching CuA; separation between CuA and CuP on wing margin nearly twice that of marginal separation between MP2 and CuA; cua-cup present at midlength of CuA, but not reaching CuP; one cup-a1 crossvein; A1 simple, A2 with a short proximal branch reaching wing margin; a1-a2 present.

Hind wing length 2.6 mm, wing shape similar to forewing, immaculate; ScP proximally without hamuli-like setae; venation in general similar to that of forewing; one costal crossvein present proximally; RP + MA origin near proximal 1/5 of wing length; crossvein between RA and RP + MA distinctly distad branching point of RP + MA; MP and Cu parallel and separated by distinct membrane; rp + ma-mp present, situated near midlength of wing; an oblique mp-cua present. Abdomen distinctly tapering distad; plicatures visible on segments 3–5. Genitalia obscure. Male. Unknown.

Remarks. The new species is placed in *Achlyoconis* based on the presence of seven stiff setae on thickenings of forewing MP as well as the wing venation largely similar to the type species of *Achlyoconis*. However, the new species can be distinguished from *A. heptatrichia* by the larger body size (female forewing length 3.0 mm), the forewing with four pigmented spots, the presence of eight weak costal crossveins on distal part of forewing costal space, and the crossvein between RA and RP + MA slightly proximad branching point between RP and MA in the forewing. In *A. heptatrichia* the body size is relatively small (forewing length 2.1–2.4 mm), the forewing has five pigmented spots, the distal part



Fig. 7. Achlyoconis jiae sp. nov., CAM BA-0013, holotype, female. A. Drawing of forewing; B. Drawing of hind wing.

of forewing costal space lacks crossveins, and the forewing ra-rp crossvein is present distad branching point of RP + MA (i.e. connecting to RP).

Genus Cycloconis Li, Wang & Liu, gen. nov.

(Figs. 8 and 9)

urn:lsid:zoobank.org:act:E41B5C8C-1811-4F79-AD07-79E29A3880A9

Type species. Cycloconis maculata sp. nov.

Etymology. The new generic name is a combination of "cyclo-" (Greek, meaning "round", in reference to the round distal margin of wings of the new species) and "konis" (Greek, meaning "dust", a common suffix of the generic name of dustywings). The gender of the name is feminine.

Diagnosis. Minute dustywings. Antenna with 19 flagellomeres; scape approximately twice as long as wide. Wings relatively broad. Forewing with pigmented spots; ScP distally very close to C and strongly curved posteriad, ScP2 also curved posteriad; origin of RP + MA near wing midlength; crossvein between RA and RP + MA distinctly distad proximal section of ScP2; RP proximally angulately curved, MA not strongly angling anterior at connecting point of mamp; RP + MA with branching point far proximad ma-mp, and approximately at same level to first fork of MP (i.e., their forks nearly equal in length); stem of MP without stiff setae, trifurcated into a forked MP1 and a simple MP2; rp + ma-mp present near origin of RP + MA, and far from initial branching point of MP; mp-cua present slightly distad rp + ma-mp. Hind wing venation similar to that of forewing, RP + MA origin near wing base; MP trifurcated into a forked MP1 and a simple MP2.

Remarks. This new genus appears similar to *Libanoconis* Engel, 2002 from the Lower Cretaceous Lebanon amber in having some similar



Fig. 8. Cycloconis maculata gen. et sp. nov., holotype, NIGP 169968, female, habitus photo.



Fig. 9. Cycloconis maculata gen. et sp. nov., holotype, NIGP 169968, female. A. Drawing of forewing; B. Drawing of hind wing.

forewing characters, i.e., MA not strongly angling anteriorly at connecting point of ma-mp, and MP trifurcated and without stiff setae. However, the new genus can be distinguished from Libanoconis by the following forewing characters: 1) presence of pigmented spots [forewing immaculate in Libanoconis], 2) fork of RP + MA nearly equal in length to the fork of MP [these two forks differently lengthed in *Libanoconis*], 3) rp + ma-mp far from initial branching point of MP [rp + ma-mp close to initial branching point of MP in *Libanoconis*], 4) mp-cua present distad rp + ma-mp [mpcua proximad rp + ma-mp in Libanoconis]. Moreover, Makarkin & Perkovsky (2018) mentioned that the bifurcated hind wing MP is a significant character for distinguishing Libanoconis from most other Cretaceous aleuropterygine genera except Garnaconis Perrichot & Nel, 2014 and Burmaleuropteryx gen. nov. Therefore, this new genus is apparently different from *Libanoconis* because of its trifurcate MP in the hind wing.

Cycloconis maculata Li, Wang & Liu, sp. nov.

(Figs. 8 and 9)

urn:lsid:zoobank.org:act:1B63A93D-0F3F-48CB-B335-1C7CEDEBA065

Type material. Holotype. NIGP 169968 (Figs. 8 and 9), amber piece preserving a complete adult female of *Cycloconis maculata* sp. nov. and two heteropterans, it is polished in the form of a subquadrate transparent cabochon, with length \times width about 16.53 \times 10.32 mm, height about 6.28 mm.

Locality and horizon. Amber deposits from the Hukwang Valley in Tanai Township, Myikyina District of Kachin State, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Etymology. The specific epithet "maculata" refers to presence of pigmented spots on the forewing of the new species.

Diagnosis. Same as for genus.

Description. Female. Body length 2.2 mm; integument brownish.

Head capsule longer than wide, compound eyes small (eye height/head height ratio ca. 0.40). Antenna with scape stouter than pedicel and flagellomeres, about twice as long as wide; 19 flagellomeres, first flagellomere slightly longer than others, covered by short setae. Terminal maxillary palpomere subtriangular, much longer and broader than preceding palpomeres; terminal labial palpomeres.

Prothorax narrower and shorter than meso- and metathorax. Legs slender, with short setae, pro- and mesotibiae nearly equal in length to pro- and mesofemora; metatibia nearly equal in length to metafemur; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of remaining tarsomeres; pretarsal claws short, simple; arolium absent.

Forewing length 2.3 mm, relatively broad, with rounded distal margin; membrane hyaline, with two pigmented spots, respectively located at rp + ma - mp and near branching point of RP + MA; costal space proximally with two costal crossvein; ScP largely parallel to costal margin, distally very close to C and strongly curved posteriad, ScP2 also curved posteriad; origin of RP + MA near wing midlength; crossvein between RA and RP + MA distinctly distad proximal section of ScP2; RP angulately curved at ra-rp, MA not strongly angling anteriorly at connecting point of ma-mp; RP + MAwith branching point far proximad ma-mp, and approximately at same level to first fork of MP (i.e., their forks nearly equal in length); stem of MP lacking stiff setae, distally trifurcate into a forked MP1 and a simple MP2; rp + ma-mp present near origin of RP + MA, and far from initial branching point of MP; mp-cua present slightly distad rp + ma-mp; separation between CuA and CuP on wing margin over twice that of marginal separation between MP2 and CuA; cua-cup absent; A1 simple, A2 with a short proximal branch connecting wing margin.

Hind wing length 2.2 mm, wing shape and venation generally similar to that of forewing; RP + MA origin near wing base; MP trifurcated into a forked MP1 and a simple MP2; mp-cua present near initial branching point of Cu; MP and Cu separated by distinct membrane, but CuA and MP2 approaching to each other at wing margin; CuA and CuP parallel, cup-a1 present distad initial branching point of Cu.

Abdomen tapering distad; plicatures invisible. Genitalia poorly visible.

Male. Unknown.

Tribe Incertae sedis

Genus Burmaleuropteryx Bai, Wang & Liu, gen. nov.

(Figs. 10 and 11)

urn:lsid:zoobank.org:act:078CCB6C-A4AF-4052-9480-B33836C27139

Type species. Burmaleuropteryx meinanderi sp. nov.

Etymology. The new generic name is a combination of Burma (in reference to the new genus currently known only from the Burmese amber) and *Aleuropteryx* (the generic name of the type genus of Aleuropteryginae, in reference to the placement of the new genus in this subfamily). The gender of the name is feminine.

Diagnosis. Minute dustywings (forewing length 1.15 mm). Antenna with 17 flagellomeres; scape nearly as long as wide. Wing membrane hyaline, immaculate. Forewing proximally narrow, but distinctly broadened distad: costal crossveins absent: crossvein between RA and RP + MA slightly distad proximal section of ScP2, but proximad branching point between RP and MA; RP + MA originating slightly proximad midpoint of wing; MP bifurcate; crossvein between RP + MA and MP respectively connected to stem of RP + MA and MP1; two stiff setae present along stem of MP; mpcua crossvein present; cua-cup present nearly at proximal 1/3 of wing, slightly distad m-cua; two widely apart cup-a1 present, 2cup-a1 aligned with mp-cua and cua-cup; a1-a2 present. Hind wing venation in general similar to that of forewing; crossvein between RA and RP + MA slightly proximad proximal section of ScP2; RP + MA origin near wing base; MP and Cu parallel and separated by distinct membrane.

Remarks. The new genus appears to be closely related to *Garnaconis* Perrichot & Nel, 2014 from the Upper Cretaceous Vendean amber in having a combination of the following similar characters: 1) antenna with 17 flagellomeres, 2) forewing costal crossveins absent, 3) radial crossvein slightly proximad branching point between RP and MA in both fore- and hind wings, 4) forewing MP bifurcate, with two stiff setae along its stem, 5) only one crossvein present between forewing RP + MA and MP. However, the new genus can be distinguished from *Garnaconis* by the position of rp + ma-mp that is proximad branching point between RP and MA, the presence of forewing cua-cup, and the lack of stiff setae along distal and posterior margins of wings. In *Garnaconis* the rp + ma-mp in both fore- and hind wings is connected to MA, the forewing cua-cup is absent, and a row of widely spaced macro setae is present along the wing margin until the basal section of posterior margins.

Burmaleuropteryx meinanderi Bai, Wang & Liu, sp. nov. (Figs. 10 and 11)

urn:lsid:zoobank.org:act:48412C92-5733-4819-8953-667B5201CA62

Type material. Holotype. NIGP 169969 (Figs. 10 and 11), the amber preserving a complete adult female of Burmaleuropteryx meinanderi sp. nov. is polished in the form of subtriangular transparent



Fig. 10. Burmaleuropteryx meinanderi gen. et sp. nov., holotype, NIGP 169969, female. A. Habitus photo, lateral view; B. Photo of head, lateral view; C. Photo of mesotibia and mesotarsus; D. Photo of costal margin of left hind wing, showing stiff setae; E. Photo of mid part of forewing, showing two stiff setae (indicated by arrows) on stem of MP.

cabochon, with length \times width about 18.97 \times 15.15 mm, height about 2.93 mm.

Locality and horizon. Amber deposits from the Hukwang Valley in Tanai Township, Myikyina District of Kachin State, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Etymology. The new species is dedicated the late Dr. Martin Meinander in memory of his tremendous contributions on the systematics of Coniopterygidae.

Diagnosis. Same as for genus.

Description. Female. Body length 1.0 mm; integument dark brown.

Head nearly as long as wide, with prominent compound eyes, eye height/head height ratio ca. 0.54; frons sclerotized between antennal insertions; vertex feebly domed. Antenna with scape and pedicel stouter than flagellum, similar in shape, and as long as wide; flagellum with minute setae and with 17 flagellomeres, flagellomere subquadrate, but terminal flagellomere bullet-shaped. Terminal maxillary palpomere and terminal labial palpomere both subtriangular, much longer and broader than preceding palpomeres.

Prothorax much shorter than head, and distinctly smaller than meso- and metathorax. Legs relatively short, with many prominent trichobothria on tibiae; protibia slightly shorter than profemur, while meso- and metatibiae slightly longer than meso- and meta-femora; tarsus five-segmented; tarsomere 1 longest, nearly equal to combined lengths of tarsomeres 2–4; tarsomere 4 apically expanded; pretarsal claws short, simple; arolium absent.

Forewing length 1.15 mm, maximal width 0.46 mm; hyaline and immaculate; marginal setae visible at distal part of wing. Costal crossveins absent; ScP parallel with costal margin; crossvein between RA and RP + MA slightly distad proximal section of ScP2, but proximad branching point between RP and MA; RP + MA originating slightly proximad midpoint of wing, RP and MA respectively simple, without angulate curving; MP bifurcate; crossvein between RP + MA and MP respectively connected to stem of RP + MA and MP1; two stiff setae present along stem of MP; m-cua and mp-cua present; Cu diverging deeply into long, simple and posteriorly curved CuA and CuP; cua-cup present nearly at proximal 1/3 of wing, slightly distad m-cua; two widely apart cup-a1 present, 2cup-a1 aligned with m-cua and cua-cup; A1 simple, A2 with a short branch reaching wing margin; a1-a2 present.



0.5mm

Fig. 11. Burmaleuropteryx meinanderi gen. et sp. nov., holotype, NIGP 169969, female. A. Drawing of left forewing; B. Drawing of right forewing; C. Drawing of left hind wing; D. Drawing of right hind wing.

Hind wing length 0.95 mm, maximal width 0.36 mm; hyaline and immaculate. Venation in general similar to that of forewing; crossvein between RA and RP + MA slightly proximad proximal section of ScP2; RP + MA origin near wing base; MP and Cu parallel and separated by distinct membrane.

Abdomen robust, distinctly tapering posteriad; plicatures invisible. Visible sclerites of genitalia composed of a fused ecto-procts on dorsal portion, and a subtriangular sclerite (putative gonocoxite 9) in lateral view.

Male. Unknown.

4. Key to Cretaceous genera of Coniopterygidae

- Forewing MP with two branches (both MP1 and MP2 simple)
- 3. Forewing without stiff setae on stem MP 4

- 6. Forewing with two stiff setae proximally on stem of MP; MA partially fused with MP1 in both fore- and hind wing; antenna with 21–23 flagellomeres [New Jersey: Turonian (Grimaldi, 2000: figs. 7-11)] *Apoglaesoconis* Grimaldi

- RP + MA simple, not branched; proximal section of forewing ScP2 strongly distad ra-rp [Myanmar: lowermost Cenomanian (Engel, 2016: fig. 4)] Paranimboa Engel
- Forewing branching point of RP + MA distad rp + ma-mp

- Forewing ra-rp connected to RP, having four dark spot; antenna with 20 flagellomeres [Archingeay: Albian (Nel et al., 2005: fig. 8)] Alboconis Nel et al.

5. Discussion

As mentioned above in the remarks of A. heptatrichia, G. baliopteryx may actually belong to Achlyoconis. Engel (2016) described that the wing background color of A. heptatrichia is dark brown, while that in *G. baliopteryx* are hyaline as described in Engel (2004). However, the specimens of A. heptatrichia we examined show distinctly variable wing background color. There are three specimens with more or less dark wing background color (NIGP 169963, NIGP 169964, and ETMG BU001474; see Figs. 1A-D, 2E, F), and particularly in NIGP 169963 (Fig. 1A, B) the wing background color is dark brown and fit well with that in the holotype of A. heptatrichia. Nevertheless, in the rest of our materials the wing background color is hyaline (NIGP 169965, Fig. 1E, F; NIGP 169966, Fig. 2A, B; NIGP 169967, Fig. 2C, D; EMTG BU001934, Fig. 3A, B; EMTG BU001199, Fig. 3C–E). Although the change of the wing background color might refer to individual variation, evidence from NIGP 169963 and ETMG BU001474 suggests that the dark brown wing background color might not be natural to the species but caused during preservation of the amber. The two specimens both show unnatural loss of color in their wings. In NIGP 169963, a hyaline region is present along proximal sections of MP and Cu of right forewing (Fig. 1A, B), while in ETMG BU001474 hyaline regions are present at middle of forewings (Fig. 2E, F). Consequently, wing background color of dustywings in amber may not be a good character for species identification

The development of forewing ma-mp was often used as a diagnostic character to distinguish species. In the specimens of *A. heptatrichia* we examined, the length of forewing ma-mp apparently varies among individuals. In most specimens, the length of forewing ma-mp is 0.07–0.12 mm, while in ETMG BU001199 it is just ca. 0.01 mm. Notably, in NIGP 169966 and ETMG BU001474 forewing MA is touching or fused with MP1 for a short distance (Fig. 2A, E). Nevertheless, the hind wing ma-mp is present and nearly equal in length among individuals. The fusion of MA and MP1 is also present in *Apoglaesoconis* Grimaldi in both fore- and hind wings, and the length of this fusion is one of the most important characters to distinguish the three species of this genus. However, considering the intraspecific variation of MA, MP1 and ma-mp crossvein in *Achlyoconis*, the reliability using length of fusion between MA and MP1 for species delimitation needs further evaluation.

The new genus *Cycloconis* gen. nov. appears to be closely related to a group of Cretaceous genera that possess trifurcated forewing MP, including *Glaesoconis* Meinander, *Apoglaesoconis* Grimaldi, *Libanoconis* Engel, and *Achlyoconis* Engel. Moreover, *Cycloconis* gen. nov. might be closer to *Libanoconis* due to the forewing MA not angling at connecting point of ma-mp and the lack of the thickenings and stiff setae on the stem of forewing MP. Makarkin & Perkovsky (2018) claimed that the hind wing MP in all known species of *Libanoconis* is bifurcate. However, the anterior and proximal portions of hind wing are poorly preserved in *L. siberica*. Actually, the distal section of hind wing CuA as interpreted in *L. siberica* (see Makarkin & Perkovsky, 2018: fig. 4B) resembles the hind wing MP2 of *Cycloconis* gen. nov. in position and direction. Besides, based on the drawing of *Libanoconis fadiacra* (Nel et al., 2005: fig. 5), the hind wing of this species strongly overlaps with the forewing, and the branching number of hind wing MP is hard to determine. Thus, whether the hindwing MP is bifurcated or not needs to be clarified in the future.

The five Cretaceous genera aforementioned with trifurcated forewing MP are currently placed in the aleuropterygine tribe Fontenelleini. Extant Fontenelleini is characterized mainly by the frons with large unsclerotized area including antennal sockets and extending downwards medially to clypeus, and most extant genera of Fontenelleini except Pseudoconis Meinander and Vartiana Aspöck & Aspöck have closely spaced hind wing MP and CuA. Thus, these Cretaceous genera are distinctly different from the extant genera of Fontenelleini because of the largely sclerotized frons, the trifurcate forewing MP, and the widely separated hind wing MP and CuA. However, as mentioned in Engel (2016), superficial similarity is also observed between these Cretaceous dustywings and some extant genera of Fontenelleini. One of such cases noted in Engel (2016) refers to Achlyoconis and Heliconis Enderlein, and in both genera the scape is relatively short and the forewing MA resembles a branch of MP. Here, it is also notable that in an extant species of Fontenelleini, i.e., Pseudoconis maculipennis Meinander (1972), the hind wing MP is also trifurcated (Meinander, 1972: fig. 91F). Moreover, P. maculipennis and another extant species of Fontenelleini [Helicoconis (Capoconis) capensis Enderlein, 1914] possess a few costal crossveins on distal part of forewing costal space, which is shared by A. jiae sp. nov. Nevertheless, this trait is also present in Cretaconiopteryx grandis Liu & Lu (2017) (Subfamily Cretaconiopteryginae) that might represent the basalmost dustywing known so far. Trace of distal forewing costal crossveins in Coniopterygidae is probably plesiomorphic. But as this trait is only found in relatively large-sized dustywings (forewing length ca. 3.0 mm in A. jiae sp. nov., ca. 2.9–3.9 mm in H. (Capoconis) capensis, ca. 4.8 mm in *P. maculipennis*, and ca. 6.5 mm in *C. grandis*), it may also be a re-expression associated with the large-sized wings.

Interestingly, the male genitalia of *A. heptatrichia* (Fig. 5) and *P. maculipennis* (Meinander, 1972: figs. 91B, C) possess generally similar configuration, especially the rods of penis (gx10) apparently not fused together in both species. In most species of extant Fontenelleini the penis are separated anteriorly but posteriorly fused into a tube (see Meinander, 1972: figs. 55-91). In all known species of extant Coniopterygidae, the male tergum and sternum 9 are generally fused into a well-sclerotized ring (Meinander, 1972). However, the male tergum and sternum 9 are clearly separated in *A. heptatrichia*, being a plesiomorphic condition.

6. Conclusions

The new taxa herein described enrich the palaeodiversity of dustywings from the Upper Cretaceous of Myanmar. The probable close relationships between *Cycloconis* gen. nov. and *Libanoconis* as well as between *Burmaleuropteryx* gen. nov. and *Garnaconis* indicate certain palaeofaunal connections of dustywings among the locations they occurred, i.e. the mid-Cretaceous of Myanmar, the Lower Cretaceous of Lebanon, the Upper Cretaceous of France, etc. Moreover, the new materials facilitate critical evaluation on the morphological variation within species, such as the wing color and the configuration of forewing ma-mp, and the illustrated male genitalia of a Cretaceous dustywing provide important information for understanding the phylogenetic status of these extinct taxa.

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References

- Aspöck, U., Aspöck, H., 2008. Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). Systematic Entomology 33, 97–127.
- Aspöck, H., Aspöck, U., Hölzel, H., 1980. Die Neuropteren Europas: eine zusammenfassende Darstellung der Systematik, Ökologie und Chorologie der Neuropteroidea (Megaloptera, Raphidioptera, Planipennia) Europas. Goecke & Evers, Krefeld 2 vols, 495 & 355 pp.
- Aspöck, U., Plant, J.D., Nemeschkal, H.L., 2001. Cladistic analysis of Neuroptera and their systematic position within the Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera). Systematic Entomology 26, 73–86.
- Azar, D., Nel, A., Solignac, M., 2000. A new Coniopterygidae from Lebanese amber. Acta Geológica Hispánica 35, 31–36.
- Breitkreuz, L.C.V., Winterton, S.L., Engel, M.S., 2017. Wing tracheation in Chrysopidae and other Neuropterida (Insecta): a resolution of the confusion about vein fusion. American Museum Novitates 3890, 1–44.
- Dobosz, R., Krzeminski, W., 2000. A new species of the Coniopterygidae (Neuroptera) from Baltic amber. Polskie Pismo Entomologiczne 69, 219–224.
- Enderlein, G., 1910. Über die Beziehungen der fossilen Coniopterygiden zu den recenten und über Archiconiocompsa prisca nov. gen. nov. spec. Zoologischer Anzeiger 35, 673–677.
- Enderlein, G., 1930. Die Klassifikation der Coniopterygiden auf Grund der recenten und fossilen Gattungen. Archiv f
 ür Klassifikatorische Phylogenetische Entomologie 1, 98–114.
- Engel, M.S., 2002. A new dustywing (Neuroptera: Coniopterygidae) in Turonian amber from New Jersey, with a reassessment of Glaesoconis in Neocomian amber from Lebanon. Journal of the Kansas Entomological Society 75, 38–42.
- Engel, M.S., 2004. The dustywings in Cretaceous Burmese amber (Insecta: Neuroptera: Coniopterygidae). Journal of Systematic Paleontology 2, 133–136.
- Engel, M.S., 2010. A new genus of dustywings allied to Archiconiocompsa in Baltic amber (Neuroptera: Coniopterygidae). Transactions of the Kansas Academy of Science 113, 145–150.
- Engel, M.S., 2016. Two new genera of Cretaceous dustywings in amber from northern Myanmar (Neuroptera: Coniopterygidae). Novitates Paleoentomologicae 17, 1–16.
- Engel, M.S., Grimaldi, D.A., 2007. The neuropterid fauna of Dominican and Mexican amber (Neuropterida: Megaloptera, Neuroptera). American Museum Novitates 3587, 1–58.
- Grimaldi, D., 2000. A diverse fauna of Neuropterodea in amber from the Cretaceous of New Jersey. In: Grimaldi, D. (Ed.), Studies on Fossils in Amber, With Particular Reference to the Cretaceous of New Jersey. Backhuys Publishers, Leiden, pp. 259–303.
- Grimaldi, D., Engel, M.S., Nascimbene, P.C., Singh, H., 2013. Coniopterygidae (Neuroptera: Aleuropteryginae) in amber from the Eocene of India and the Miocene of Hispaniola. American Museum Novitates 3770, 20–39.
- Haring, E., Aspöck, U., 2004. Phylogeny of the Neuropterida: A first molecular approach. Systematic Entomology 29, 415–430.
- Kania, I., Wang, B., Szwedo, J., 2015. *Dicranoptycha* Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Cenomanian Burmese amber. Cretaceous Research 52, 522–530.
- Kupryjanowicz, J., Makarkin, V.N., 2008. Archiconiocompsa prisca Enderlein (Neuroptera: Coniopterygidae): the first neuropteran fossil in Rovno amber (Ukraine). Entomologica Fennica 19, 25–31.
- Liu, X.Y., Lu, X.M., 2017. A remarkable new genus of Cretaceous dustywings (Neuroptera: Coniopterygidae) in amber from northern Myanmar. Zoological Systematic 42, 380–389.
- Makarkin, V.N., Perkovsky, E.E., 2017. A new species of *Glaesoconis* Meinander (Neuroptera: Coniopterygidae) from the Santonian Taimyr amber. Cretaceous Research 75, 120–124.

- Makarkin, V.N., Perkovsky, E.E., 2018. New Coniopterygidae (Neuroptera) from the upper Cenomanian Nizhnyaya Agapa amber, northern Siberia. Cretaceous Research 93, 107–113.
- Maksoud, S., Azar, D., Granier, B., Gèze, R., 2017. New data on the age of the Lower Cretaceous amber outcrops of Lebanon. Palaeoword 26, 331–338.
- McKellar, R.C., Wolfe, A.P., Tappert, R., Muehlenbachs, K., 2008. Correlation of Grassy Lake and Cedar Lake ambers using infrared spectroscopy, stable isotopes, and palaeoentomology. Canadian Journal of Earth Sciences 45, 1061–1082.
- Meinander, M., 1972. A revision of the family Coniopterygidae (Planipennia). Acta Zoologica Fennica 136, 1–357.
- Meinander, M., 1975. Fossil Coniopterygidae (Neuroptera). Notulae Entomologicae 55, 53-57.
- Meinander, M., 1998. Coniopterygidae (Neuroptera) in amber from the Dominican Republic. Journal of Neuropterology 1, 33–36.
- Meunier, F., 1910a. Un Coniopterygidae du copal récent de Togo. Annales de la Société Scientifique de Bruxelles 34, 198–199.
- Meunier, F., 1910b. Un Coniopterygidae du copal récent de Madagascar. Bulletin de la Societe Entomologique de France 1910, 164–166.
- Misof, B., Liu, S.L., Meusemann, K., Peters, R.S., Donath, A., et al., 2014. Phylogenomics resolves the timing and pattern of insect evolution. Science 346, 763–767.
- Nel, A., 1990. Nouveaux insectes neuroptéroïdes fossiles de l'Oligocène de France (Neuroptera et Megaloptera). Bulletin du Muséum National d'Histoire Naturelle, Paris 12, 327–349.
- Nel, A., Perrichot, V., Azar, D., 2005. New and poorly known fossil Coniopterygidae in Cretaceous and Cenozoic ambers (Insecta: Neuroptera). Annales Zoologici 55, 1–7.
- Oswald, J.D., Machado, R.J.P., 2018. Biodiversity of the Neuropterida (Insecta: Neuroptera, Megaloptera and Raphidioptera). Insect Biodiversity: Science and Society 2, 627–671.
- Pérez-de la Fuente, R., 2012. Paleobiología de los artrópodos del ámbar cretácico de El Soplao (Cantabria, España). Unpublished PhD thesis. Universitat de Barcelona, p. 109.
- Perrichot, V., Garrouste, R., Azar, D., Néraudeau, D., Nel, A., 2014. A new genus of dustywings (Neuroptera: Coniopterygidae) in late cretaceous Vendean amber. Paleontological Contributions 10, 25–29.
- Randolf, S., Zimmermann, D., Aspöck, U., 2017. Head anatomy of adult Coniopteryx pygmaea Enderlein, 1906: Effects of miniaturization and the systematic position of Coniopterygidae (Insecta: Neuroptera). Arthropod Structure & Development 46, 304–322.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L., Li, X.H., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163.
- Sziráki, G., 2011. Coniopterygidae of the World: Annotated Ccheck-list and Identification Keys for Living Species, Species Groups, and Supraspecific Taxa of the Family. Lambert Academic Publishing, Saarbrücken, Germany, p. 264.
- Sziráki, D., 2016. A new dusty lacewing genus and species (Neuroptera: Coniopterygidae) from Cretaceous Burmese amber. Folia Historico Naturalia Musei Matraensis 40, 89–93.
- Sziráki, G., 2017. Taxonomic position of *Paranimboa groehni* Sziráki, 2016, with remarks on the Cretaceous genus *Paranimboa* Engel, 2016 (Neuroptera, Coniopterygidae). Folia Historico Naturalia Musei Matraensis 41, 181–182.
- Wang, Y.Y., Liu, X.Y., Garzán-Orduña, I.J., Winterton, S.L., Yan, Y., Aspöck, U., Aspöck, H., Yang, D., 2017. Mitochondrial phylogenomics illuminates the evolutionary history of Neuropterida. Cladistics 33, 617–636.
- Whalley, P.E.S., 1980. Neuroptera (Insecta) in amber from the Lower Cretaceous of Lebanon. Bulletin of the British Museum. Natural History. Geology Series 33, 157–164.
- Winterton, S.L., Hardy, N.B., Wiegmann, B.M., 2010. On wings of lace: Phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. Systematic Entomology 35, 349–378.
- Winterton, S.L., Lemmon, A.R., Gillung, J.P., Garzon, I.J., Badano, D., Bakkes, D.K., Breitkreuz, L.C.V., Engel, M.S., Lemmon, E.M., Liu, X.Y., Machado, R.J.P., Skevington, J.H., Oswald, J.D., 2017. Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). Systematic Entomology 43, 330–354.
- Zimmermann, D., Klepal, W., Aspöck, U., 2009. The first holistic SEM study of Coniopterygidae (Neuroptera) — structural evidence and phylogenetic implications. European Journal of Entomology 106, 651–662.