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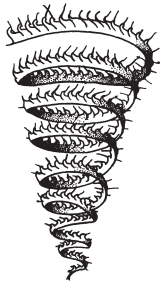
## **A New Genus of Dustywings (Neuroptera: Coniopterygidae) in Late Cretaceous Vendean Amber**

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# Paleontological Contributions

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## A NEW GENUS OF DUSTYWINGS (NEUROPTERA: CONIOPTERYGIDAE) IN LATE CRETACEOUS VENDEAN AMBER

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### ABSTRACT

A new genus and species of Coniopterygidae is described from a female preserved in Late Cretaceous (Cenomanian to Santonian) amber of Vendée, in northwestern France. *Garnaconis dupeorum* Perrichot & Nel, n. gen. and sp., displays intermixing features between Aleuropteryginae and Coniopteryginae as currently defined, making its accurate phylogenetic placement difficult. It is tentatively placed in the Aleuropteryginae. A new practical key to the Mesozoic genera of dustywings is proposed.

Keywords: Insecta, Neuropterida, Aleuropteryginae, Mesozoic, France

### RÉSUMÉ

Un nouveau genre et une nouvelle espèce de Coniopterygidae sont décrits d'après une femelle préservée dans l'ambre du Crétacé supérieur (Cénomanien à Santonien) de Vendée, nord-ouest de la France. *Garnaconis dupeorum* Perrichot & Nel n. gen. et sp., montre une mosaïque de caractères des deux sous-familles Aleuropteryginae et Coniopteryginae telles que définies actuellement, rendant sa position phylogénétique relativement incertaine. Il est ainsi provisoirement placé au sein des Aleuropteryginae. Une nouvelle clé des genres de Coniopterygidae mésozoïques est proposée.

Mots-clés: Insecte, Neuropterida, Aleuropteryginae, Mésozoïque, France

### INTRODUCTION

Fossil dustywings are almost exclusively found in amber, with 24 species known in 15 genera (10 extinct) from the Neogene Dominican and Mexican ambers, the Palaeogene Baltic, Ukrainian, Indian, and Parisian ambers, and the Cretaceous ambers from Siberia, New Jersey, France, Myanmar, and Lebanon (see the detailed list in Engel & Grimaldi, 2008: appendix 1; and updates in Kupryjanowicz & Makarkin, 2008, Engel, 2010, and Grimaldi & others, 2013). Only two additional, monotypic genera are known as compression fossils, from the Oligocene of France (Nel, 1991) and the Jurassic of Kazakhstan (Meinander, 1975). Two subfossil species were also described from African copal (Meunier, 1910a, 1910b) but are likely synonymous with extant species (Engel, 2004). Finally, several

specimens have been reported from Campanian Canadian amber (McKellar & others, 2008) and Albian Spanish amber (Pérez-de la Fuente, 2012), but have yet to be described.

Cretaceous dustywings mostly belong in the Aleuropteryginae, with ten species known in four genera. The Coniopteryginae are known by only two monotypic genera (see the key to Cretaceous genera below).

Herein we report the discovery of a new Coniopterygidae from the Mesozoic, based on a fossil inclusion from Late Cretaceous amber of France.

### MATERIAL AND METHODS

The specimen is entombed in a piece of Vendean amber, which derives from a deposit that briefly outcropped between 2002 and 2005

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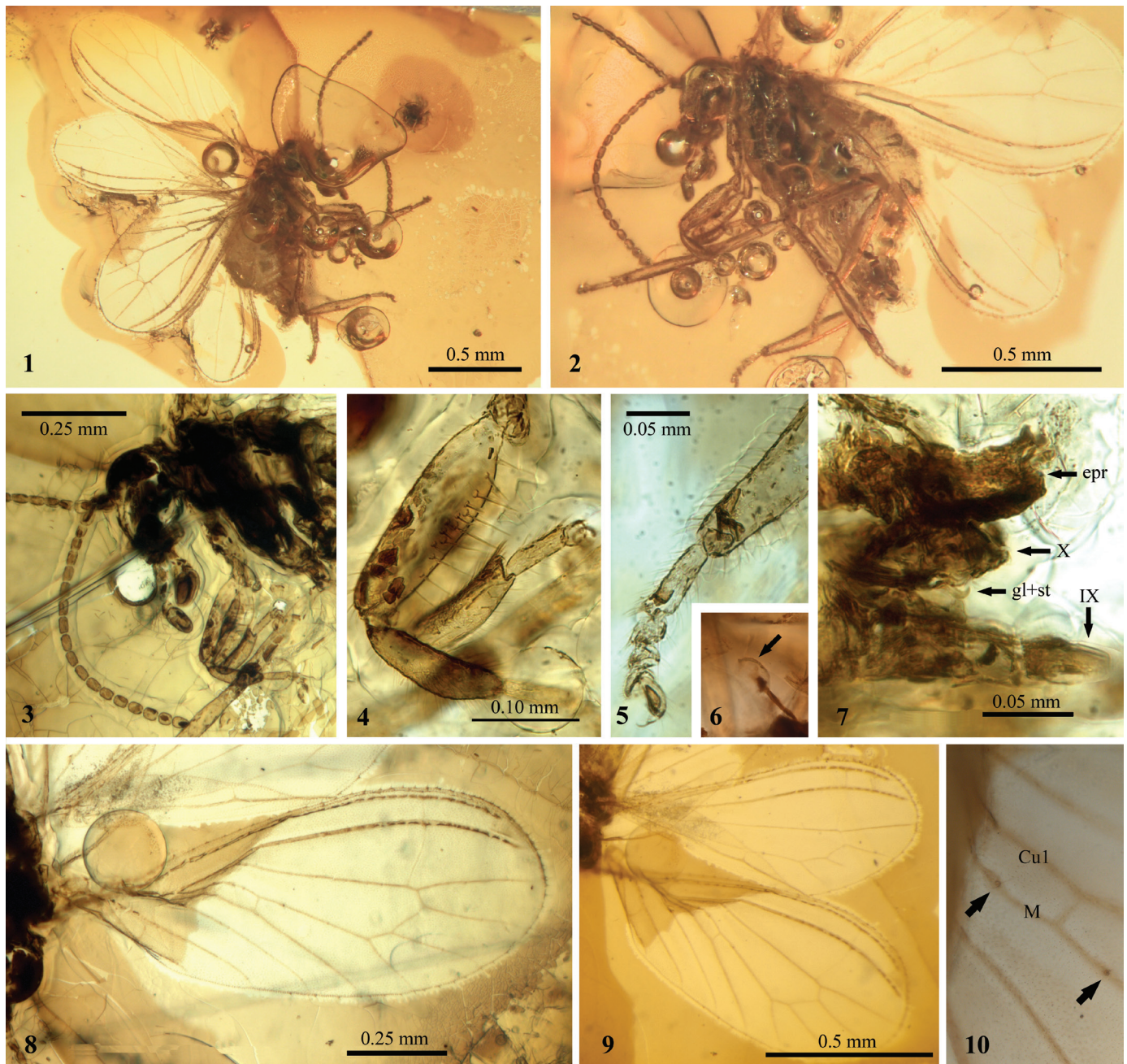


Figure F1. Photomicrographs of *Garnaconis dupeorum* Perrichot & Nel, n. gen. and sp., holotype female IGR.GAR-2, in Late Cretaceous Vendean amber. 1, 2, profile views; 3, head and mesosoma in left profile view, as preserved after embedding in Canada balsam; 4, fore femur; 5, hind tarsi; 6, plicature on fourth abdominal segment (arrow); 7, genitalia with indication of the 9th segment (IX), ectoproct (epr), 10th sternite (X), and gonapophyses laterales with two curved setae visible (gl+st); 8, left forewing; 9, left hindwing (above) and forewing (below); 10, forewing median area with indication of the two stiff setae.

during construction along the D32 road between La Garnache and Challans, in the department of Vendée, northwestern France. The exact dating of the amber-bearing stratum remains uncertain within the Middle Cenomanian–Early Santonian interval (97–85 Ma), and a discussion with more details on the geology and paleoenvironment of this deposit will be provided elsewhere (see preliminary account in Perrichot & Néraudeau, 2014: 10A in this volume).

The clear yellow amber sliver containing the specimen was originally 7×5×4 mm in size and was polished to maximize close views; polishing used emery papers at different grits (1200 and 2500) on a water-fed grinder. Because some structures were still hidden by large air bubbles, a razor blade was used to remove precise portions with bubbles and the remaining piece was included in Canada balsam between cover glasses; unfortunately the balsam diffused within the amber matrix and caused irreversible damages (lightening

and/or blurring) to the inclusion cuticle (e.g., Fig. F1.3, F1.7), so embedding of fossiliferous Vendean amber in this natural medium must be strictly avoided and instead, epoxy-embedding should be preferred. Photographs were taken with a Canon 5D Mark II camera attached to Leica microscopes, and HeliconFocus 4.45 software was used to produce multifocus z-stacks so as to achieve sharp focus throughout the images.

We use the morphological terminology proposed by Meinander (1972).

## SYSTEMATIC PALEONTOLOGY

Family CONIOPTERYGIDAE Burmeister, 1839  
Subfamily ALEUROPTERYGINAE Enderlein, 1905  
Genus GARNACONIS Perrichot & Nel, new genus

*Type species.*—*Garnaconis dupeorum*, new species, by original and monotypic designation.

*Etymology.*—The new genus-group name is a combination of the name Garnache (the town near which the amber deposit originates) and the Greek *konis* (meaning dust), a common suffix for dustywing genera.

*Diagnosis.*—Female. Antenna with 17 flagellomeres. Forewing entirely fuscous, without any clouds over crossveins; crossveins sc-r and r-rs aligned, r-rs meeting Rs distinctly basad fork of  $R_{2+3}$ – $R_{4+5}$  (i.e., r-rs connected to Rs); no crossvein between Rs and M (i.e., only distal crossvein r-m between  $R_{4+5}$  and  $M_{1+2}$ ), about 2.5× as long as basal abscissa of  $R_{4+5}$ ; medial vein with two branches, with thickened setigerous spot on each side of m-cu; Cu2 with one thickened setigerous spot distal to crossvein cua-cua2. Small plicatures visible at least on third and fourth abdominal segments. Abdominal segment 9 very long.

### GARNACONIS DUPEORUM, Perrichot & Nel, new species Figures F1–F2

*Type material.*—Holotype female IGR.GAR-2, in Late Cretaceous (Middle Cenomanian to Late Santonian, 97–85 Ma) Vendean amber; deposited in the Geological Department and Museum of the University Rennes 1, France.

*Type locality.*—La Robinière, departmental road D32, about 2.5 km south-west of La Garnache, Vendée, France.

*Etymology.*—The specific epithet is a patronym honoring Fanny and André Dupé who collected this and most of the Vendean amber material.

*Diagnosis.*—As for the genus (see above).

*Description.*—Body length ca. 0.8 mm (measured from tip of the head to tip of genitalia). Head (Fig. F1.2, F1.3) hypognathous, elongate, ca. 0.24 mm long. Compound eyes well developed and oval, smallest diameter 0.07 mm, largest diameter 0.09 mm. Interocular distance equal to smallest eye diameter. Antenna 0.74 mm long, with all articles bearing scattered sensilla (Fig. F1.3); flagellomeres cylindrical, f1–f13 about twice as long as broad, f14–f17 about 1.6 × as long as broad; f1 and f2 not distinctly longer than following flagellomeres, f1 0.02 mm long, 0.01 mm wide. Maxillary palps five-segmented, about 0.19 mm long; third segment slightly longer than first, second, and fourth; fifth segment particularly swollen basally, distinctly larger than others,

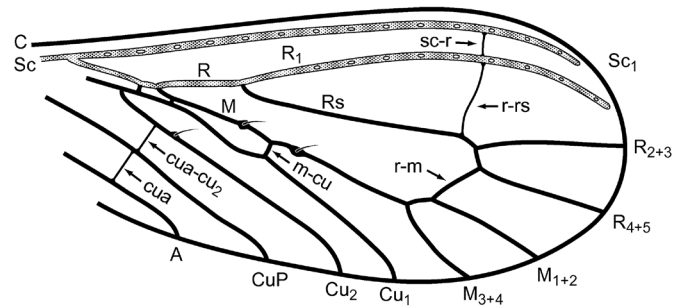


Figure F2. Forewing of *Garnaconis dupeorum* Perrichot & Nel, n. gen. and sp., holotype female IGR.GAR-2, in Late Cretaceous Vendean amber.

0.07 mm long and 0.02 mm wide. Galea and lacinia obscured. Labial palps three-segmented, with third segment very large, 0.1 mm long, distinctly larger than first two segments. Thorax 0.27 mm long. Prothorax short, 0.12 mm long. Mesothorax 0.1 mm long, bearing two prominent tubercles dorsally, and two distinct lateral shoulders basad forewings. Metathorax 0.05 mm long. Forewing (Figs. F1.8–F1.10, F2) 1.1 mm long, 0.48 mm wide;  $Sc_1$  long and parallel to costal margin in its basal two thirds; fork  $Sc_1$  and  $Sc_2$  (or sc-r) at 0.82 mm from wing base; sc-r 0.85 mm long, aligned with r-rs at 0.26 mm from wing apex; R branching off from R+M at 0.2 mm from wing base, then bifurcating into  $R_1$  and  $R_s$  after a distance of 0.17 mm;  $R_s$  0.41 mm long before its fork;  $R_{2+3}$  0.27 mm long; crossvein r-rs slightly sinuate, 0.15 mm long, basal to fork of  $R_{2+3}$ – $R_{4+5}$ ; distance between base of  $R_{4+5}$  and its apex 0.26 mm; M 0.48 mm long before its fork into  $M_{1+2}$  and  $M_{3+4}$ ;  $M_{1+2}$  curved; crossvein rs-m connected to  $M_{1+2}$  0.05 mm distally of fork of  $M_{1+2}$ – $M_{3+4}$ ; M setae approximately equidistant on each side of m-cu (Fig. F1.10);  $M_{3+4}$  weakly curved, 0.15 mm long; Cu bifurcating into  $Cu_1$  and  $Cu_2$  0.12 mm from wing base;  $Cu_1$  curved, reaching wing margin 0.74 mm from wing base;  $Cu_2$  curved, distal half nearly parallel to  $Cu_1$ , reaching wing margin 0.63 mm from wing base; no visible crossvein between  $Cu_1$  and  $Cu_2$ ; crossveins cua-cua<sub>2</sub> and cua nebulous. Hind wing (Fig. F1.9) slightly shorter than forewing, 0.98 mm long, 0.41 mm wide;  $Sc_1$  rather long and parallel to costal margin, approaching costal margin 0.95 mm from wing base; fork of  $R_1$ – $R_s$  not clearly visible but in a very basal position, just distal base of M;  $R_s$  bifurcating into  $R_{2+3}$  and  $R_{4+5}$  0.79 mm from wing base;  $R_{2+3}$  slightly curved, 0.19 mm long; r-rs 0.13 mm long, basad fork of  $R_s$ ; distance between base of  $R_{4+5}$  and tip of  $R_{4+5}$  0.16 mm; M (0.5 mm long before its fork) branching off from R+M very basally; M and Cu distinctly separated, not touching;  $M_{1+2}$  slightly curved; crossvein between  $R_{4+5}$  and  $M_{1+2}$  0.07 mm from base of  $M_{1+2}$ ;  $M_{3+4}$  0.11 mm long; Cu bifurcating into  $Cu_1$  and  $Cu_2$  very basally;  $Cu_1$  curved; a crossvein m-cu present;  $Cu_2$  curved, nearly parallel to  $Cu_1$ . Legs slender and densely covered by microtrichiae; fore femur with 13–14 stiff erect setae on posterior surface (Fig. F1.4); tibiae rather long, covered with regular rows of regularly spaced setae; tarsi five-segmented, covered with setae (Fig. F1.5); first tarsomere long, slightly shorter than remaining tarsomeres; second and third tarsomeres nearly equal in length; fourth tarsomere shorter than others, broad and dorsally hollowed around base of fifth tarsomere; fifth tarsomere

elongated. Abdomen flattened and probably deformed by air bubbles, 0.46 mm long, 0.23 mm wide, including genitalia; a plicature visible at least on the third and fourth abdominal segments (Fig. F1.6), with a dark spot inside abdomen corresponding to each of them. Genitalia (Fig. F1.7) partly obscured and delicate to interpret because these organs are much internalized in the Coniopterygidae, male or female. Nevertheless, it seems most likely that they correspond to female genitalia for their striking similarities with those of a female *Coniocompsa* (see Meinander, 1972: fig. 45 C); the main diagnostic character is the very elongate segment 9 (s9) that extends far beyond the gonapophyses laterales (gl) which bear strongly curved setae; other genital structures are hidden inside abdomen.

#### Key to Cretaceous genera of Coniopterygidae (modified from Engel, 2004)

1. Media in forewing with three branches ..... 2  
Media in forewing with two branches ..... 4
2. Forewing without stiff setae proximally on media ..... 3  
Forewing with two stiff setae situated on thickenings of media (Late Cretaceous) ..... *Apoglaesoconis* Grimaldi
3. Antennae with 25 or more flagellomeres (25–30 where known);  $R_{4+5}$  distinctly angling anteriorly at distalmost rs-m crossvein; media branching strongly distad of basal r-m crossvein (Early–Late Cretaceous) ..... *Glaesoconis* Meinander  
Antennae with less than 20 flagellomeres;  $R_{4+5}$  not angling anteriorly at distalmost r-m crossvein, instead continuing straight to wing margin; media branching at basal r-m crossvein (Early–Late Cretaceous) ..... *Libanoconis* Engel
4. Forewing crossveins r-rs, r-m, and  $cu_1$ - $cu_2$  absent;  $R_{4+5}$  not connected to  $M_{1+2}$ ; m- $cu_1$  near bifurcation of M ..... *Phthanoconis* Engel  
Forewing crossveins r-rs, r-m present,  $cu_1$ - $cu_2$  present or absent;  $R_{4+5}$  connected to  $M_{1+2}$ ; m- $cu_1$  strongly basad bifurcation of M ..... 5
5. Forewing crossvein r-rs meeting bifurcation of Rs; 2r-m subequal to basal abscissa of  $R_{4+5}$ ;  $cu_1$ - $cu_2$  present; 24 flagellomeres (Early Cretaceous) ..... *Libanosemidalis* Azar, Nel, & Solignac  
Forewing crossvein r-rs not meeting Rs at bifurcation  $R_{2+3}$ - $R_{4+5}$ ; antennae with 20 or less flagellomeres ..... 6
6. Forewing crossvein r-rs meeting Rs distinctly basad bifurcation  $R_{2+3}$ - $R_{4+5}$  (i.e., connected to Rs); only one crossvein between Rs and M;  $cu_1$ - $cu_2$  absent; 17 flagellomeres (Late Cretaceous) ..... *Garnaconis* n. gen.  
Forewing crossvein r-rs meeting  $R_s$  strongly distad bifurcation  $R_{2+3}$ - $R_{4+5}$  (i.e., connected to  $R_{2+3}$ ); two crossveins between Rs and M;  $cu_1$ - $cu_2$  absent; 20 flagellomeres (Early Cretaceous) ..... *Alboconis* Nel, Perrichot & Azar

## DISCUSSION

Until now there has been no clear phylogenetic analysis of the Coniopterygidae, except for the preliminary proposal of Meinander (1972). *Garnaconis* n. gen. has only one radio-medial crossvein on forewing, a character currently considered as proper to Coniopteryginae (Meinander, 1972). Nevertheless, *Garnaconis* n. gen. has the hind wing base of Rs very close to that of M, which is a character present in Aleuropteryginae and in *Flintoconis* Sziráki, second bruceiserine genus, while *Bruceiser* Navás, has highly modified fore

and hind wing venation delicate to interpret (Riek, 1975). The polarity of this character remains controversial because even the sister-group relationships of Coniopterygidae within the Neuroptera remain debatable: Aspöck, Plant, and Nemeschkal (2001) supported a ‘Coniopterygidae + Sisyridae’ clade, while Haring and Aspöck (2004) and Aspöck and Aspöck (2008) supported a ‘Coniopterygidae + dilarid clade’ (see summary in Aspöck & Aspöck, 2007); Winterton, Hardy, and Wiegmann (2010) found Coniopterygidae as sister group of all other Neuroptera; Beutel, Friedrich, and Aspöck (2010) considered that the position of this family remains uncertain; Zimmermann and others (2011) considered them as sister group to the clade (Mantispidae + (Dilaridae + (Rhachiberothidae + Berothidae))); while Aspöck, Haring, & Aspöck (2012) proposed them as sister group of the (Dilaridae + (Mantispidae + (Rhachiberothidae + Berothidae))). Note that this last hypothesis, as for the sisyrid or dilarid hypotheses, is congruent with a basal position of Rs as a plesiomorphy for the Coniopterygidae.

*Garnaconis* n. gen. also shows a plicature at least on the third and fourth abdominal segments (see Fig. F1.5). Meinander (1972) considered the presence of abdominal plicatures as a potential synapomorphy of the Aleuropteryginae. They are also present in Bruceiserinae. But Zimmermann, Klepal, and Aspöck (2009) hypothesized the following relationships between the three subfamilies: (Bruceiserinae + Coniopteryginae) + Aleuropteryginae, on the basis of potential synapomorphies in the larvae. They concluded that the presence of abdominal plicatures could rather be a plesiomorphy. *Garnaconis* n. gen. also has the two stiff setae on median vein, a character considered by Meinander (1972:17-18) as an apomorphy of the Aleuropteryginae, absent in Coniopteryginae. Note that *Flintoconis* has no ‘outstanding setae of M’, but ‘somewhat stronger bristle at about the basal third of M’ that could correspond to a ‘remnant of one of these stiff setae (Sziráki, 2007), while *Bruceiser* seems to have no clear specialized setae on M. The genital appendages of *Garnaconis* n. gen., although showing similarities with those of the females *Coniocompsa* (Aleuropteryginae), are too obscured to be safely used because many diagnostic features (Aspöck & Aspöck, 2008; Zimmermann, Klepal, & Aspöck 2009) are not visible. Consequently, *Garnaconis* n. gen. could be attributed to the Aleuropteryginae in the basis of the set of characters considered by Meinander (1972) as apomorphic to this subfamily. Nevertheless the polarity of these characters remains debatable because of the lack of a more recent phylogenetic analysis of the family. The present attribution to the Aleuropteryginae is tentative and will need verification when such analysis will become available.

Among the Cretaceous Coniopteryginae, *Libanosemidalis* shares with *Garnaconis* the hind wing with vein Rs branching from R very near the wing base, but *Libanosemidalis* has no stiff setae on M and no plicature. The second Mesozoic coniopterygine genus *Phthanoconis* has a hind wing Rs branching far from wing base, as in modern representatives of the subfamily. *Garnaconis* n. gen. also differs from other Cretaceous dustywings except *Libanosemidalis*, *Phthanoconis*, and *Alboconis*, by the presence of only two (as opposed to three) terminal branches of the media on the forewing. It differs from *Libanosemidalis* and *Alboconis* by the number of antennal flagellomeres, which is 17 in *Garnaconis*, as opposed to 24 in *Libanosemidalis*, and 20 in *Alboconis* – erroneously mentioned with 18 flagellomeres in the

original description by Nel, Perrichot, & Azar (2005); the vertex not prominent; and the forewing with Rs branching into  $R_{2+3}$  and  $R_{4+5}$  distally of crossvein r-rs.

The new fossil adds significantly to the scant geological record of dustywings, and it displays intermingled features of both Aleuropteryginae and Coniopteryginae as currently defined, such that it might help to refine the limits of both subfamilies once incorporated in a phylogenetic analysis.

## ACKNOWLEDGEMENTS

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## REFERENCES

- Aspöck, U., & H. Aspöck. 2007. Verbliebene Vielfalt vergangener Blüte. Zur Evolution, Phylogenie und Biodiversität der Neuropterida (Insecta: Endopterygota). *Denisia* 20:451–516.
- Aspöck, U., & H. Aspöck. 2008. Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). *Systematic Entomology* 33(1):97–127.
- Aspöck, U., E. Haring, & H. Aspöck. 2012. The phylogeny of the Neuropterida: long lasting and current controversies and challenges (Insecta: Endopterygota). *Arthropod Systematics & Phylogeny* 70:119–129.
- Aspöck, U., J. D. Plant, & H. L. Nemeschkal. 2001. Cladistic analysis of Neuroptera and their systematic position within Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera). *Systematic Entomology* 26(1):73–86.
- Beutel, R.G., F. Friedrich, & U. Aspöck. 2010. The larval head of Nevrothidae and the phylogeny of Neuroptera (Insecta). *Zoological Journal of the Linnean Society* 158(3):533–562.
- Burmeister, H. 1839. *Handbuch der Entomologie*. 2. Band. 2. Abt. Reimer, Berlin. 771.
- Enderlein, G. 1905. Klassifikation der Neuropteren-familie Coniopterygidae. *Zoologischer Anzeiger* 29:225–227.
- Engel, M. S. 2004. The dustywings in Cretaceous Burmese amber (Insecta: Neuroptera: Coniopterygidae). *Journal of Systematic Palaeontology* 2(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(3-4):145–150.
- Engel, M. S., & D. A. Grimaldi. 2008. Diverse Neuropterida in Cretaceous amber, with particular reference to paleofauna of Myanmar (Insecta). *Nova Supplementa Entomologica* 20:1–86.
- Grimaldi, D., M. S. Engel, P. C. Nascimbene, & H. Singh. 2013. Coniopterygidae (Neuroptera: Aleuropteryginae) in amber from the Eocene of India and the Miocene of Hispaniola. *American Museum Novitates* 3770:20–39.
- Haring, E., & U. Aspöck. 2004. Phylogeny of the Neuropterida: a first molecular approach. *Systematic Entomology* 29:415–430.
- Kupryjanowicz, J. & V. N. Makarkin. 2008. *Archiconiocompsa prisca* Enderlein (Neuroptera: Coniopterygidae): the first neuropteran fossil in Rovno amber (Ukraine). *Entomologica Fennica* 19(1):25–31.
- McKellar, R., A. P. Wolfe, R. Tappert, & K. Muehlenbachs. 2008. Correlation of Grassy Lake and Cedar Lake ambers using infrared spectroscopy, stable isotopes, and palaeoentomology. *Canadian Journal of Earth Sciences* 45(9):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.
- Meunier, F. 1910a. Un Coniopterygidae du copal récent du Togo. *Annales de la Société Scientifique de Bruxelles* 34:198–199.
- Meunier, F. 1910b. Un Coniopterygidae du copal récent de Madagascar. *Bulletin de la Société Entomologique de France* 1910:164–166.
- Nel, A. 1991. Nouveaux insectes neuroptéroïdes fossiles de l'Oligocène de France (Neuroptera et Megaloptera). *Bulletin du Muséum National d'Histoire Naturelle (C)* 12(3-4):327–349.
- Nel, A., V. Perrichot, & D. Azar. 2005. New and poorly known fossil Coniopterygidae in Cretaceous and Cenozoic ambers (Insecta: Neuroptera). *Annales Zoologici* 55:1–7.
- Pérez-de la Fuente, R. 2012. Paleobiología de los artrópodos del ámbar cretácico de El Soplao (Cantabria, España). Unpublished PhD thesis, Universitat de Barcelona, 109 p. + annexes.
- Perrichot, V., & D. Néraudeau. 2014. Introduction to thematic volume "Fossil arthropods in Late Cretaceous Vendean amber (northwestern France)". *Paleontological Contributions* 10A:1–4.
- Riek, E.F. 1975. On the phylogenetic position of *Brucheiser argentinus* Navas, 1927 and description of a second species from Chile (Neuroptera). *Studies on the Neotropical Fauna* 10:117–126.
- Sziráki, G. 2007. Studies on Brucheiserinae (Neuroptera: Coniopterygidae), with description of the second genus of the subfamily. *Acta Zoologica Academiae Scientiarum Hungaricae* 53 (Suppl. 1):231–254.
- Tjeder, B. 1957. Neuroptera - Planipennia. The lacewings of southern Africa. 1. Introduction and families Coniopterygidae, Sisyridae and Osmylidae. *South African Animal Life* 4:95–188.
- Winterton, S. L., N. B. Hardy, & B. M. Wiegmann. 2010. On wings of lace: phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. *Systematic Entomology* 35(3):349–378.
- Zimmermann, D., W. Klepal, & U. Aspöck. 2009. The first holistic SEM study of Coniopterygidae (Neuroptera) – Structural evidence and phylogenetic implications. *European Journal of Entomology* 106(4):651–662.
- Zimmermann, D., S. Randolph, B. D. Metscher, & U. Aspöck. 2011. The function and phylogenetic implications of the tentorium in adult Neuroptera (Insecta). *Arthropod Structure & Development* 40:571–582, DOI: 10.1016/j.asd.2011.06.003.