

A new extraordinary neuropterid family from the Lower Cretaceous Crato Formation of Brazil: a new insect order? (Insecta, Neuropterida)

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Abstract

A new, highly specialized family, Rafaelidae, is proposed for two new lacewing-like species from the Lower Cretaceous Crato Formation in the Araripe Basin, Brazil. They have body and wing venation characters that are unique within the neuropterid insects, i.e., head, ovipositor, organization of the radial and median veins and structure of the subcostal vein. This new family cannot be attributed to any known insect order with certainty. These discoveries support the hypothesis of a considerable morphological disparity between neuropterid insects during the Early Cretaceous, as for the Odonatoptera.

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1. Introduction

The Neuroptera fauna of the Brazilian Early Cretaceous is one of the richest and diverse known (for a review, see Martins-Neto, 2000). Nevertheless, some very curious taxa from the Araripe Formation still await description. The following new family (first figured as an “erratic lacewing” in Bechly, 1998, p. 98) is certainly one of the most remarkable fossil insect taxa from this outcrop because of the very unusual wing venation and body morphology, showing numerous important autapomorphies. It is of great interest for estimating the diversity and morphological disparity of the Early Cretaceous entomofauna.

All of these fossils come from the laminated limestones of the Nova Olinda Member of the Crato Formation (Early Cretaceous, Late Aptian/Early Albian) in the Araripe Basin, Ceara State, northeast Brazil.

2. Systematic palaeontology

We follow the wing venation terminology of Kukalová-Peck and Lawrence (2004), widely inspired by that of New (1990). Abbreviations are as follows: Sc, subcostal vein; RA, radius anterior; RP, radius posterior; MA, media anterior; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; AA, analis anterior; AP, analis posterior.

Superorder: Neuropterida

Order: incertae sedis

Family: Rafaelidae fam. nov.

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Type genus. *Rafaelia* gen. nov.

Diagnosis. This family has a highly specialized wing venation, with numerous autapomorphies. Fore wing: ScP ending on C basal of apex of RA, then RA fused with C + ScP, without any cross-veins in the small area between C + ScP and RA (autapomorphy, visible in specimens B 124 and alate specimen from Museum für Naturkunde in Berlin); RP with a strong anterior curve in its distal part (autapomorphy); RP with only four branches; presence of well-defined large, broad areas, distally closed by cross-veins stronger than others or by main veins meeting in one point (autapomorphy), these areas being between RP2 and RP3, between RP, RP4, and MA, between MA and MP, and between MP and CuA; RP, MA, and MP emerging from R + M at the same point (autapomorphy); MP perpendicular to R and Cu at its base, touching Cu at one point and distally nearly parallel to MA and Cu (autapomorphy). Hind wing: Sc not closely parallel along length with R, but very short, strongly diverging from R and ending in costal margin near wing base (autapomorphy or synapomorphy with Raphidioptera); MA emerging from R (+ MA) well basal of RP; RP emerging from R in a very distal position; RP with only three main branches; presence of well-defined, large, broad areas, similar to those of fore wing, at least between R and MA, MA and MP, and MP and CuA (autapomorphy). Furthermore, fore wing is clearly longer than hind wing.

Remarks. In all known Neuroptera s.s. (= Planipennia), except for the highly specialized and very different Coniopterygidae, the vein Sc is closely parallel to R in both the fore and hind wings, and the veins MA and RP have a common stem in the fore wing (New, 1990).

Genus *Rafaelia* gen. nov.

Derivation of name. After Dr. Rafael G. Martins-Neto, a specialist in fossil Neuroptera from the Crato Formation.

Type species. *Rafaelia maxima* sp. nov., by present designation.

Species included. The type species only.

Diagnosis. As for the family.

Rafaelia maxima sp. nov.

Figs. 1–3

Derivation of name. After the large size of this species.

Material. Holotype specimen WDC-CCFB-001, paratype specimen WDC-CCFB-002, Wyoming Dinosaur Center-Crato, Wyoming, USA.

Diagnosis. Fore wing with distal anterior curve of RP weakly pronounced; bases of branches of RP not strongly approximate; no straight secondary longitudinal vein between

RP and MA; a strong cross-vein between RP4 and MA at narrowest point.

Description. Body very poorly preserved, with the head and thorax indistinct, abdomen large and elongate, with a rather long structure (sclerotized ovipositor or abdomen prolonged in an apical tube), visible in the two specimens, head ca. 5.0 mm wide, thorax 10.0 mm wide, abdomen 36.0 mm long, 12.0 mm wide.

Fore wing very long and rather narrow, 60.0 mm long in holotype, 58.0 mm in paratype, 12.5 mm wide, with its posterior margin partly missing; costal area narrow, 1.0 mm wide, with numerous cross-veins (27 preserved between wing base and fusion of Sc and RA and 12 distal of this point); Sc and RA long, parallel; RA fused with C + ScP 53.3 mm from wing base and 10.5 mm from wing apex, with few cross-veins between them; RP separating from RA 11.2 mm from wing base, in the basal 20% of the wing; a very strong concave vein, 2.0 mm long, perpendicular to RA and to convex CuA at the origin of RA and MA, which we interpret as the concave MP that separates from R at the same point as RP and MA, reaches CuA, and immediately separates from it (Figs. 2, 4); bases of RP (concave vein) and MA (convex vein) at the same point; RP almost parallel along length to RA, with numerous short cross-veins between them; RP with only four posterior branches, all in a very distal position; RP very strongly curved and strongly approximating RA in its distal part, just before fusion of RA with Sc; RP1 ending in RA + Sc; three secondary zigzagged longitudinal veins between RP1 and RP2; RP2 basally straight, but making an abrupt angle distally, and with a strong cross-vein between it and third branch of RP at this point; a broad area between RP2 and RP3 basal to this point, with three rows of cells; third branch of RP sigmoidal; RP4 with a strong angle and apparently ending in MA, delimitating a long and broad area between MA, RP and RP4; RP4 distally forked, with a broad area and a secondary zigzagged longitudinal vein between its branches; MA simple, straight for 36.1 mm, with a strong angle distally; concave MP simple; MP parallel to MA and straight but with a pronounced distal angle, then ending on posterior wing margin nearly at right angle; a long, broad area delimited by MA, MP and strong cross-vein between them, with two rows of cells and a secondary longitudinal vein in it; Cu convex, straight, strongly approximating MP rather near its base, and progressively diverging from it distally; CuP and CuA separating 15.0 mm from wing base; a closed area between MP and CuA, 35.1 mm long and 1.7 mm wide; CuA divided into two branches in apical 66% of the wing, 39.8 mm from wing base; CuP basally straight, closely parallel to CuA, distally divided into two posterior branches; a broad area between Cu and anal vein, crossed by numerous parallel cross-veins; AA simple and straight; AP also straight, but more poorly preserved; anal area very narrow.

Hind wing distinctly shorter than fore wing, only ca. 37.0 mm long, ca. 11.0 mm wide; posterior margin poorly preserved in both hind wings; a strong but short, simple vein corresponding to Sc reaches costa 6.7 mm from wing

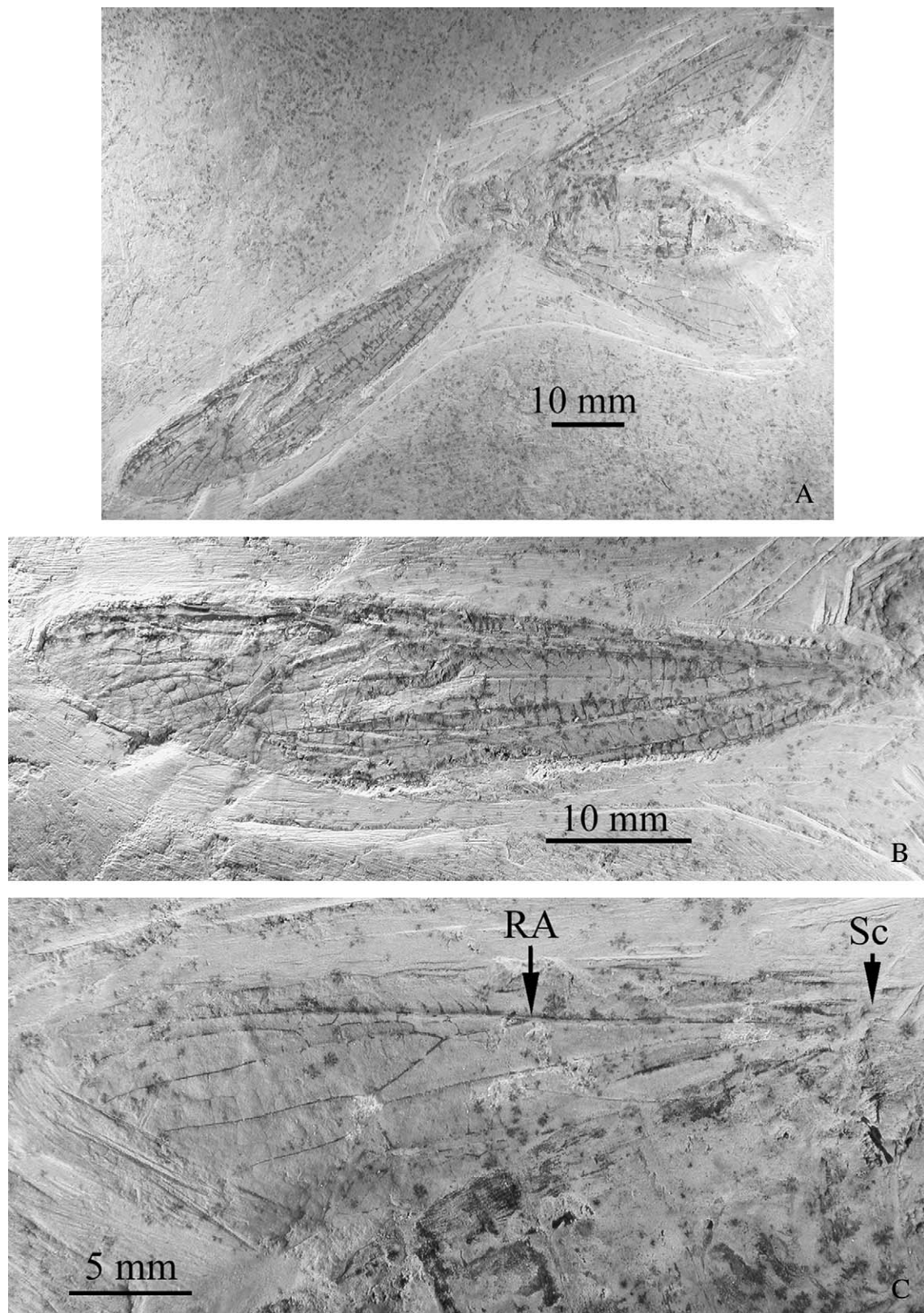


Fig. 1. *Rafaelia maxima* sp. nov., holotype, WDC-CFB-001; photographs of, A, general habitus, B, fore wing, and C, hind wing.

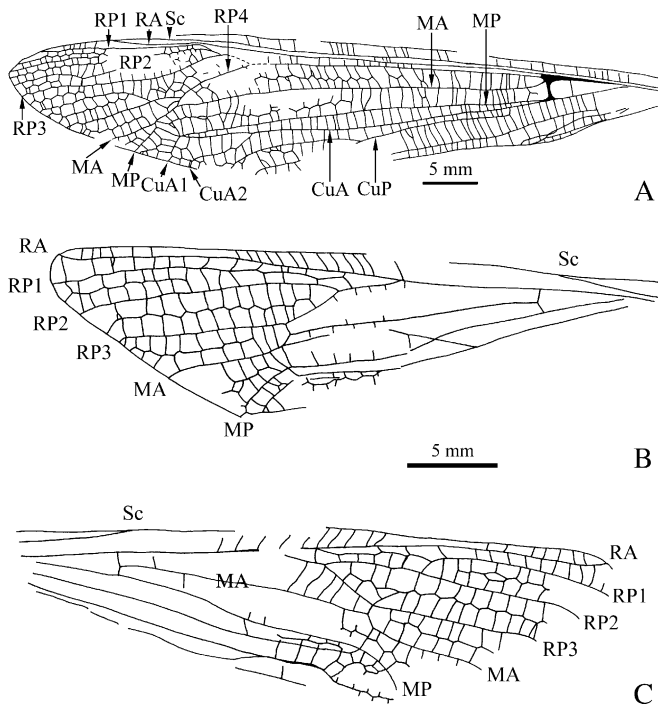


Fig. 2. *Rafaelia maxima* sp. nov., holotype; drawings of, A, fore wing, B, left hind wing, C, right hind wing.

base, with apparently no cross-vein between them (Figs. 3, 5); a series of cross-veins between RA and costa (Fig. 6), those in basal two thirds being sigmoidal and those in distal part of wing straight; RP separating from R very far from wing base, at 20.5 mm from wing apex; RP with three main branches, RP1 emerging anteriorly on RP2, with a zigzagged longitudinal vein between RA and RP1; two rows of cells and a zigzagged longitudinal vein between RP1 and RP2 and between RP2 and RP3; RP1 and RP2 more or less straight but RP3 with a pronounced angle and a strong cross-vein between it and MA, closing a broad area between MA, R, RP, and RP3; MA separating from R 7.8 mm from wing base; MA simple, straight for 14.8 mm, and with two pronounced angles distally; MP simple, straight in basal part but curved near its apex; veins of posterior part of wings more poorly preserved, but CuA, CuP and probably AA straight in their main course and more or less parallel.

Rafaelia minima sp. nov.

Figs. 4–6

Derivation of name. After the small size of the type specimen of this species.

Material. Holotype specimen SMNK 2359, Landessammlungen für Naturkunde Karlsruhe, Germany (a thorax with the four wings attached). Paratype specimens: B 124, Tokyo University of Agriculture, Japan (a fore wing apex); specimen without number, SMNS, Stuttgart, Germany (a fore wing apex); nearly complete specimen without number, Museum für Naturkunde, Berlin, Germany.

Diagnosis. Fore wing with distal anterior curve of RP more pronounced than in *R. maxima*; bases of branches of RP more strongly approximate than in *R. maxima*; a straight secondary longitudinal vein between RP and MA; no strong cross-vein between RP4 and MA at narrowest point.

Description. Holotype: body very poorly preserved with the thorax indistinct, ca. 10.0 mm long, 9.0 mm wide; only the fore wings are well preserved, fragments of the hind wings are visible but useless for study. Organization of the fore wing venation is very similar to that of *Rafaelia maxima* (Fig. 5A, B); the main differences are listed below.

Fore wing 44.0 mm long, 10.0 mm wide, distinctly shorter than that of *R. maxima*; distal curve of RP distinctly more pronounced than in *R. maxima*, with the bases of branches of RP more strongly approximate; a long, straight, longitudinal secondary vein in area between RP and MA, closely parallel to MA, 18.8 mm long; RP4 touching MA at one point.

Paratype B 124: apical half of a fore wing, showing same pattern as the holotype, but distinctly longer (length of preserved part 56 mm, probable total length ca. 60 mm). In this specimen, the apical fusion of ScP with C is clearly visible (arrowed in Fig. 6A), then RA ends on C + ScP, without any cross-veins in the small area between C + ScP and RA.

Paratype SMNS (Fig. 6B): apical half of a fore wing shows the same pattern as the holotype, but is probably longer (length of preserved part 48.6 mm).

Paratype in Berlin collection (Fig. 6C): the body structures are better preserved than in the other specimens. Fore wing venation is identical to that of the holotype, but it is 53 mm long, longer. The apices of ScP and RA are organized as in specimen B 124. The head is rounded, transverse, narrower than thorax, 3.7 mm long, 6.2 mm wide, with very large rounded, nearly holoptic eyes, touching at one point, ocelli not visible, may be absent; mouth parts partly visible, with short mandibles; antennae not visible, may be very short. Thorax strong, 12.5 mm long, 10 mm wide. Fragments of fore legs and hind (?) tibiae and tarsi are visible. Hind legs very long and slender. Abdomen 18.7 mm long, 8.1 mm wide, without visible ovipositor (male?).

Note. One other specimen in the Museum für Naturkunde, Berlin is attributable to the Rafaelidae because its head structures are identical to those of other specimens in the museum, but its wings are apparently missing (Fig. 6D). It has long, slender legs, very large, nearly holoptic eyes, and male genital structures, but without any visible cerci.

Phylogenetic position. Because of their very similar and highly specialized wing venation and head structures, these six fossils are all attributed to the new family Rafaelidae, which is of uncertain position within the Pterygota. The ability to fold the wings over the abdomen proves that the Rafaelidae belongs to the pterygote clade Neoptera. The fossils show superficial similarities with the “orthopteroid” lineage in having an ovipositor, and in their wing venation, but they differ in the

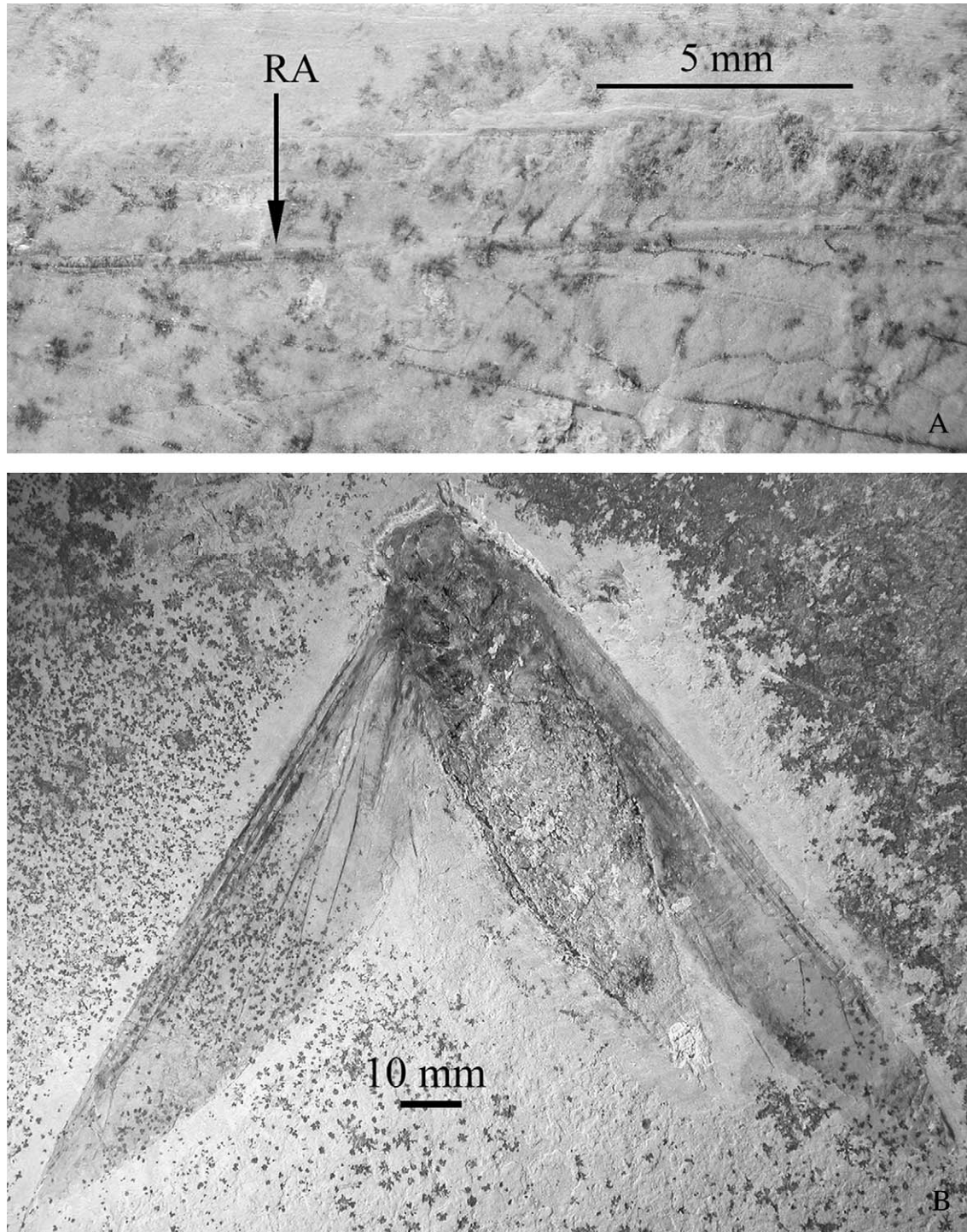


Fig. 3. *Rafaelia maxima* sp. nov. A, holotype, photograph of hind wing area between RA and costa. B, paratype, WDC-CFB-002, photograph of general habitus.

probable absence of cerci, and in having a long, common basal stem of Cu, with CuA and CuP separating distal of the base of M (Béthoux and Nel, 2002). The MA in the Rafaelidae is basally fused with the radius, which is typical of the Blattoneoptera, Hemineoptera, and Endoneoptera (sensu Kukalová-Peck and Lawrence, 2004, p. 107). The Blattoneoptera have a very different fore wing venation and a broad anojugal fan. Characters of the Endoneoptera (Haas and

Kukalová-Peck, 2001) are: fore wing ScP long and parallel to radial vein; basal portion of MP obscured, deep under radial vein; CuP weakly branched. The Rafaelidae have some features in common with neuropteroid insects, namely: veins ScP and RA closely parallel; numerous simple cross-veins in area between ScP and C; CuP separating from CuA at almost a right angle rather far from wing base. Their phylogenetic relationships within the group Neuropterida

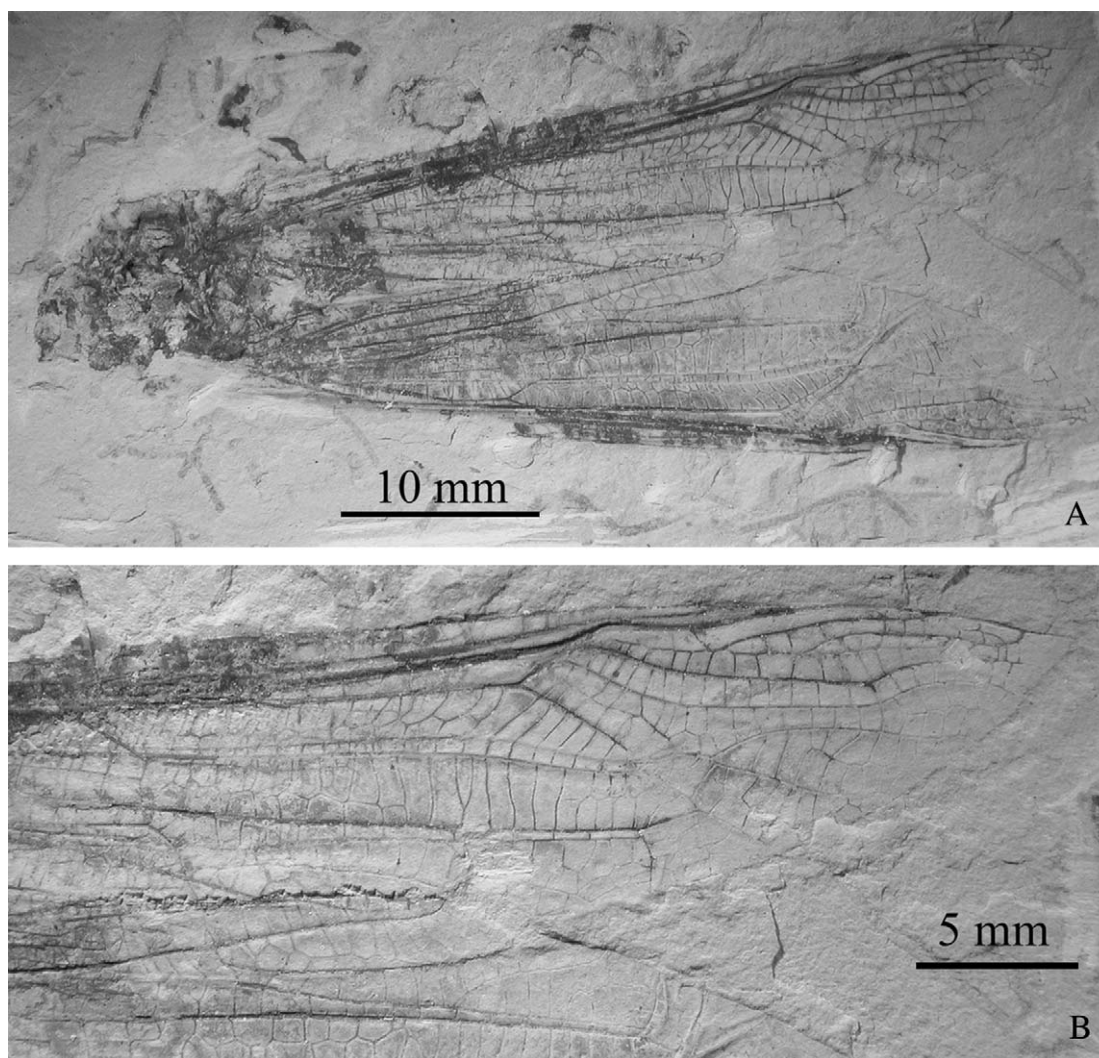


Fig. 4. *Rafaelia minima* sp. nov., holotype, SMNK 2359; photographs of, A, general habitus, and B, apical part of fore wing.

(Megaloptera + Raphidioptera + Neuroptera) are more difficult to determine because of the relatively poor preservation of the body structures, but MP, CuA, CuP and anal veins that are parallel for a long distance with numerous cross-veins between them are characters in common with the Neuroptera s.s. (e.g. Myrmeleontidae, Nymphidae, Polystoechotidae).

Within the Neuroptera, the wing venation is clearly not sufficient alone to establish phylogenetic relationships, especially for taxa with such unusual venation. The available phylogenetic analyses do not include wing venation characters: for example, the Nevrothidae and Sisyridae have very similar wing venations but they belong to very different clades. Following Aspöck et al. (2001) and Aspöck (2002), the Sisyridae are included in the Hemerobiiformia, and the Nevrothidae are considered to be the sister group of all other Neuroptera, even if, following Haring and Aspöck (2004), the Nevrothidae could be the sister group of the (Sisyridae + other Neuroptera).

We do not, therefore, think it is possible at this stage to propose a hypothesis of phylogenetic affinities for the Rafaelidae within the Neuroptera. Nevertheless, the family differs from most other Recent and fossil Neuropterida in head shape,

possible ovipositor (only present as a sympleisiomorphy in Raphidioptera and Neuroptera: Dilaridae), absence of a cross-vein in the small area between the apex of RA and C + ScP in the fore wing, very short ScP in the hind wing (derived similarity with Raphidioptera), and MA and RP emerging independently

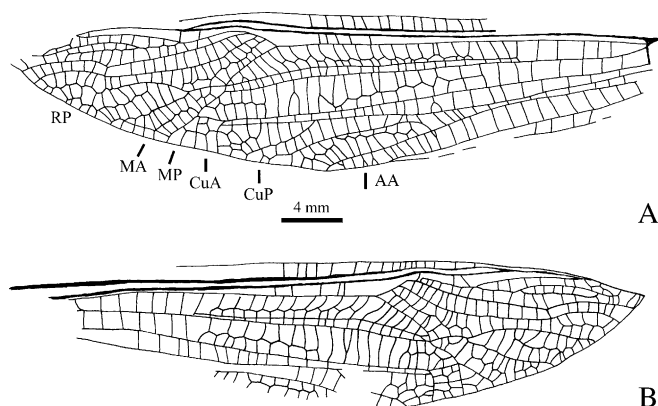


Fig. 5. *Rafaelia minima* sp. nov., holotype; drawings of, A, left, and B, right fore wings.

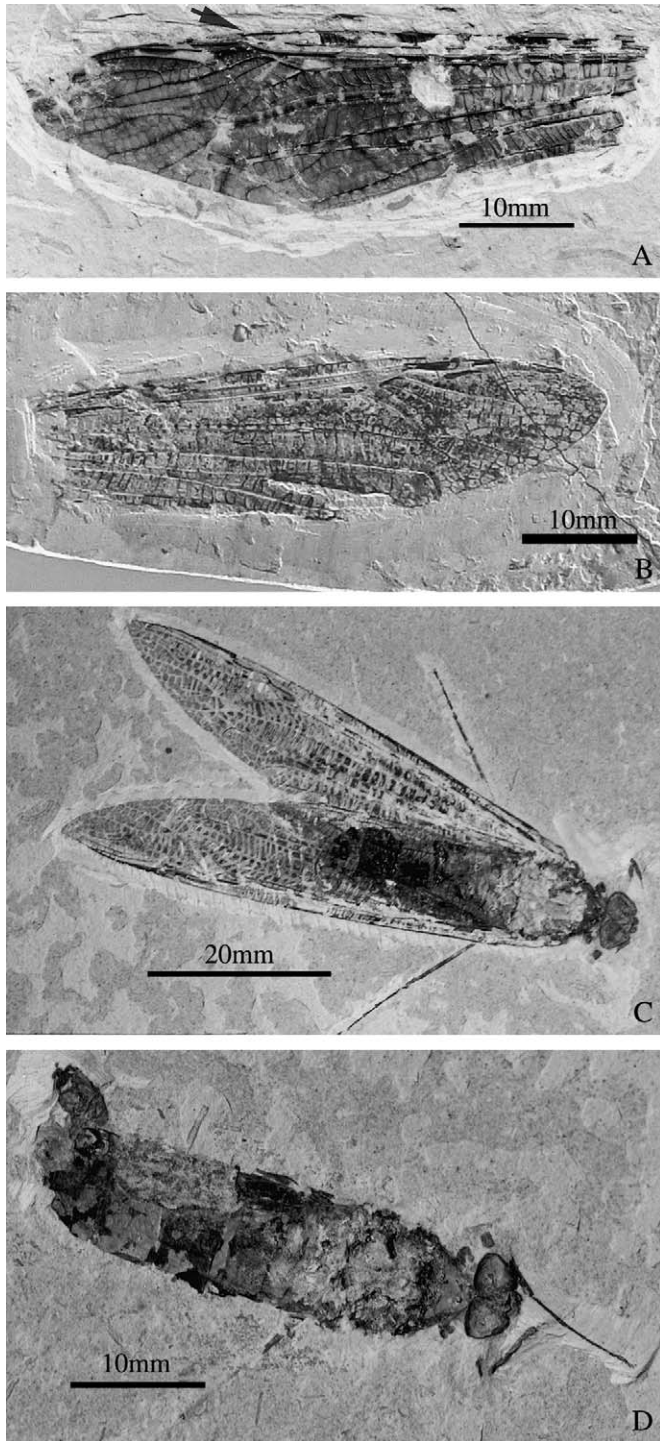


Fig. 6. *Rafaelia minima* sp. nov., photographs. A, paratype B 124, fore wing; arrow indicates point of fusion between ScP and C. B, paratype specimen SMNS. C, paratype specimen from Berlin Museum. D, Rafaelidae species undetermined, specimen from Berlin Museum.

from the radial vein in both fore and hind wings. This last character especially seems to exclude a position within the Neuropterida, because all known fossil and Recent members of this group have the media arising from the radius!

Despite these very original structures, we prefer to avoid erecting a new order for these insects for two reasons. If

the Rafaelidae belong to a new insect order, it could either be the sister group of the Raphidioptera or the sister group of the Neuropterida (or even the Neuropterida + Mecopterida), if we follow Kukalová-Peck and Lawrence (2004), but this would contradict the presence of several specialized characters shared between the Rafaelidae and some Neuroptera (shape of the median posterior, cubital and anal areas in fore and hind wings), even though these may not belong to the common ground plan and could, of course, easily be due to convergent evolution. Also, as genuine Megaloptera, Neuroptera and Mecoptera are known in Permian and Triassic deposits, this hypothetical order would be rather “cryptic” between the Permian and the Lower Cretaceous, but this does not exclude the possibility of such a Lower Cretaceous fossil, because the same outcrop has also yielded other unexpected examples of “cryptic” taxa (e.g., surviving relatives of Permian Protocoleoptera and Protereismatidae; Bechly, 2001, pp. 48, 49).

Nevertheless, there still exists the possibility that the Rafaelidae are just late Mesozoic Neuroptera with very specialized body and wing venation structures, or that they are neuropteroid-like stemgroup representatives of Raphidioptera. The Early Cretaceous appears to have been a time of major diversification and morphological disparity at family level in the Neuropterida. This is especially the case for the Chrysopoidea (Zhang, 1991; Martins-Neto, 2000; Ren, 2002; Nel et al., 2005). The present discoveries strongly support this hypothesis. A similar situation also occurs in the Odonatoptera, with the coexistence of extinct clades characterized by numerous autapomorphies with representatives of the Recent groups (Fleck and Nel, 2003; Fleck et al., 2003).

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References

- Aspöck, U., 2002. Phylogeny of the Neuropterida. *Zoologica Scripta* 31, 51–56.
- Aspöck, U., Plant, J.D., Nemeschkal, H.L., 2001. Cladistic analysis of Neuroptera and their position within Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera). *Systematic Entomology* 26, 73–86.
- Bechly, G., 1998. Santana — Die Schatzkammer fossiler Insekten. *Fossilien* 2, 95–99.
- Bechly, G., 2001. Rätselhafte Funde. In: Bechly, G., et al. (Eds.), *Ur-Geziefen — Die faszinierende Evolution der Insekten*. Stuttgarter Beiträge zur Naturkunde (C) 49, 46–50.
- Béthoux, O., Nel, A., 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa* 96, 1–88.
- Fleck, G., Bechly, G., Martínez-Delclòs, X., Jarzembowski, E.A., Coram, R., Nel, A., 2003. Phylogeny and classification of the Stenophlebiptera

- (Odonata, Epiproctophora). *Annales de la Société Entomologique de France, Nouvelle Série* 39, 55–93.
- Fleck, G., Nel, A., 2003. Revision of the Mesozoic family Aeschnidiidae (Odonata: Anisoptera). *Zoologica* 153, 1–180.
- Haas, F., Kukalová-Peck, J., 2001. Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within *Neoptera* (Insecta). *European Journal of Entomology* 98, 445–509.
- Haring, E., Aspöck, U., 2004. Phylogeny of the Neuropterida: a first molecular approach. *Systematic Entomology* 29, 415–430.
- Kukalová-Peck, J., Lawrence, J.F., 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. *European Journal of Entomology* 101, 95–144.
- Martins-Neto, R.G., 2000. Remarks on the Neuroptero fauna (Insecta, Neuroptera) from the Brazilian Cretaceous with keys for the identification of the known taxons. *Acta Geologica Hispanica* 35, 97–118.
- Nel, A., Martinez-Declos, X., Hutin, A., 2005. Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta, Neuroptera). *Annales de la Société Entomologique de France* 41, 29–68.
- New, T.R., 1990. Planipennia (lacewings). *Handbuch der Zoologie* 4 (30) (Arthropoda: Insecta), 1–132.
- Ren, D., 2002. A new lacewing family (Neuroptera) from the Middle Jurassic of Inner Mongolia, China. *Entomologia Sinica* 9, 53–67.
- Zhang, J.-F., 1991. A new family of Neuroptera (Insecta) from the late Mesozoic of Shandong, China. *Science in China (B)* 34, 1105–1111.