

New species of the Mesochrysopidae (Insecta, Neuroptera) from the Crato Formation of Brazil (Lower Cretaceous), with taxonomic treatment of the family

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Abstract

Two new species of the genus *Karenina* Martins-Neto belonging to the Mesozoic family Mesochrysopidae (*K. leilana* sp. nov. and *K. longicollis* sp. nov.) are described from the Nova Olinda Member, the lowest unit of the Lower Cretaceous Crato Formation, northeast Brazil. A detailed definition (diagnosis and description) of this family is provided, based on those genera most similar to the type genus, *Mesochrysopa* Handlirsch. The genera *Tachinymphes* Ponomarenko, *Siniphes* Ren and Yin, *Allopterus* Zhang, *Karenina* Martins-Neto and *Mesascalaphus* Ren et al. are added to it, whereas the genera *Osmylites* Haase (= *Nymphoides* Panfilov), *Chrysoleonites* Martynov, *Microsmylus* Panfilov and *Liasochrysa* Ansoerge and Schlüter are excluded. Allopteridae is regarded as a synonym of Mesochrysopidae. The phylogenetic position of the family is discussed. The occurrence of Mesochrysopidae in South America demonstrates that its widespread distribution included Gondwana.

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1. Introduction

The Mesochrysopidae is an extinct Mesozoic family whose status and composition were unclear hitherto. Unfortunately, this is a common feature of almost every extinct higher taxon of Neuroptera, and characterises the generally unresolved state of the systematics of the order. A more-or-less detailed definition of this family has not been provided previously; the type genus has not been re-examined since the classic work of Handlirsch (1906–1908). Therefore, the opinion of some authors on the heterogeneity (paraphyly) of this group was quite reasonable (Willmann and Brooks, 1991; Nel and Henrotay, 1994; Makarkin, 1997). Until now, it was treated either as

a separate family (e.g., Adams, 1956; Martynova, 1962; Makarkin, 1990, 1997; Carpenter, 1992; Makarkin and Archibald, 2003; Ponomarenko, 2003) or as a subfamily of the Chrysopidae (e.g., Adams, 1967; Schlüter, 1982, 1984; Séméria and Nel, 1990; Martins-Neto, 2000, 2003).

The family was erected by Handlirsch (1906–1908) for the two monotypic genera, *Mesochrysopa* Handlirsch, 1906 and *Mesotermes* Haase, 1890 from the Upper Jurassic of Solnhofen, Germany. Handlirsch also assumed that *Pseudomyrmeleon* Handlirsch, 1906, represented by one poorly preserved single specimen, also from Solnhofen, may belong to this family. Martynov (1927) described another Upper Jurassic genus, *Mesypochrysa* Martynov, 1927, from the southern Kazakhstan locality of Karatau, and placed it in the Mesochrysopidae. Later, Panfilov (1980) assigned five genera to it, also described from Karatau (*Chrysoleonites* Martynov, 1925, *Aristenymphes* Panfilov, 1980, *Macronympha* Panfilov, 1980, *Microsmylus* Panfilov, 1980 and *Nymphoides* Panfilov, 1980). Ansoerge and

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Schlüter (1990) added the new genus *Liassochrysa* Ansorge and Schlüter, 1990 from the Lower Jurassic of Dobbertin, Germany, and Nel and Henrotay (1994) described *Protoaristenympes* Nel and Henrotay, 1994 from the Lower Jurassic of Luxembourg. Recently, Ponomarenko (2003) synonymized *Nymphoides* and *Osmylites* Haase, 1890, and considered Osmylitidae to be a synonym of Mesochrysopidae.

In this paper we propose a detailed definition of the Mesochrysopidae as a monophyletic group based on those genera most similar to the type genus *Mesochrysope* Handlirsch, 1906, excluding from it some genera, namely *Osmylites* (= *Nymphoides*), *Chrysoleonites*, *Microsmylus*, and *Liassochrysa*, and adding others: *Tachinympes* Ponomarenko, 1992, *Siniphes* Ren and Yin, 2002, *Allopterus* Zhang, 1991, *Karenina* Martins-Neto, 1997, and *Mesascalaphus* Ren et al., 1995. The family Allopteridae is regarded as a synonym of Mesochrysopidae, whereas placing Osmylitidae and Mesochrysopidae in synonymy is not justified.

The family was hitherto known only from the Mesozoic of Eurasia. Our study shows, however, that it also occurs in the Lower Cretaceous of South America, being represented in the Brazilian Crato Formation by the genus *Karenina* with three species, two of which are new. Descriptions of the latter are provided below.

2. Material and methods

We examined two specimens for this study, found in one of the small quarries or stone yards in the Nova Olinda municipality; the precise locality is not known. Preparation was carried out using an aeroneedle (Selden, 2003) to remove minor amounts of matrix obscuring portions of the fossils. Drawings were made with a camera lucida attached to an Olympus SZH stereomicroscope, and digital photographs were taken with a Sony DCS-717 camera at 2560 × 1920 pixel resolution or a DIX digital camera attached to a Wild M8 stereozoom microscope. All wings in drawings are shown in standard form, with the apex to the right.

Wing venation terminology follows Comstock (1918), with a few exceptions in accordance with current usage in neuropterology (e.g., Comstock's M_{1+2} is our MA, Cu_1 is CuA); that of wing spaces follows Oswald (1993). Venation abbreviations used in the text and figures are as follows: 1A–3A, anal veins; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; M, media; MA, anterior branch of media; MP, posterior branch of media; R, radius; R1, first branch of radius; Rs, radial sector; Sc, subcosta.

3. Stratigraphy and depositional setting

The Crato Formation is a local stratigraphic unit of the Brazilian non-marine Cretaceous, extending over the Araripe sedimentary basin (Araripe Plateau), in the states of Ceará, Pernambuco and Piauí, northeast Brazil, about 7° south of the Equator. The most important outcrops are in the eastern part of the Araripe Plateau, especially near the towns of Crato, Santana do Cariri and Nova Olinda (see fig. 1 in Martins-Neto,

1992). The stratigraphy of the entire Araripe Basin, and of the Crato unit in particular, is unresolved (Martill, 1993). Many authors have considered the latter as the lower member of the Santana Formation, accounting for the similarities in rock types across the outcrops (e.g., da Silva, 1986; Maisey, 1990, 1991). The simple subdivision of the Santana Formation into three members (from bottom to top: Crato, Ipubi and Romualdo), however, does not correspond to the variety and sequence of sediments: the depositional environment, palaeobiology, fossil record and taphonomy differ considerably through the succession (FM pers. obs.). Martill (1993) elevated the Crato unit to formation level and subdivided it into three members, from bottom to top, the Nova Olinda, Barbalha and Jamacaru. This approach reflects more closely the dynamics and rapid evolution of the basin. Uncertainty remains, however, regarding the stratigraphy and definition of these units; detailed mapping is required to resolve their relationships. In this paper we use Martill's (1993) subdivision.

The Nova Olinda Member, the basal unit of the formation, is the richest in fossils. It is a 10–15-m sequence of finely laminated limestone. The laminae, which are 1–2 mm thick and can be followed for a great distance, are characteristic of a calm, anoxic, deep-water lagoon/lacustrine depositional environment (Martill, 1993). Its arthropod fauna is known for the quality of soft tissue preservation and for their colour patterns. Insects and arachnids are found in association with very rare myriapods, the gonorhynchiform fish *Dastilbe* Jordan, 1921, plant remains, wood, bird feathers, pterosaurs and other vertebrates. The insects are incredibly abundant, mostly represented by Orthoptera, Blattoda and Hemiptera; Neuroptera constitute roughly 10% of the insect fauna (FM pers. obs.), among which the superfamily Myrmeleontoidea is clearly dominant (Martins-Neto, 1997, 2000, 2003). The Nova Olinda Member sits directly over fluvial mudstone of the Batateira Formation followed by the overlying Barbalha Member, a sequence of limestones containing ostracods and conchostracans (Martill, 1993). The upper unit of the Crato Formation, the Jamacaru Member, consists of laminated limestones and shales containing conchostracans, freshwater bivalves, wood remains, the fish *Dastilbe* (including many occurrences of mass mortality of juveniles), and rare insects (FM pers. obs.).

The precise age of this formation is unresolved; however, it is generally recognized to be Late Aptian–Early Albian, approximately 110–120 Ma (Berthou, 1994), and so was deposited during the initial opening of the Atlantic Ocean (Maisey, 1991). The age of the Santana Formation, a younger stratigraphic unit, was determined by ostracod biostratigraphy as Albian (Braunn, 1966; Maisey, 1990; Berthou et al., 1994). The occurrence of early Angiosperm pollen recorded from the Santana Formation and the overlying Exu Formation confirms this age (Mabesoone and Tinoco, 1973; Maisey, 1990). The Crato Formation is therefore thought to be Late Aptian.

The fine preservation of the fossils results from the limonitic replacement, after pyrite, of organic tissues (Martill and Frey, 1995). In deep, anoxic waters, organic feeding bacteria cannot respire and consume organic matter, further facilitating detailed preservation. Rapid accumulation of sediments from

the nearby delta and therefore rapid burial further promoted fine-level fossilization of arthropod, plant and vertebrate material.

4. Systematic palaeontology

Order: Neuroptera Linnaeus, 1758

Family: Mesochrysopidae Handlirsch, 1906 (syn. Allopteridae Zhang, 1991, syn. nov.)

Diagnosis. Medium-sized to large, graceful neuropterans of somewhat myrmeleontoid appearance, with relatively narrow wings and body. The following combination of forewing character states is diagnostic: (1) trichosors absent (apomorphy, shared with several other families); (2) costal space narrow (apomorphy, shared with several other families); (3) not or only slightly expanded basally (apomorphy shared with several other families); (4) Sc, R1 fused apically (polarity unclear); (5) origin of Rs inclined at acute angle, $<30^\circ$ (polarity unclear); (6) stem of Rs from its origin to basal crossvein rs-ma straight, if present, otherwise to proximal branch of Rs (polarity unclear); (7) usually much longer than length of rs-ma (polarity unclear); (8) fork of apparent M in proximal half of wing present (plesiomorphy); (9) MA and MP diverged at angle of $>40^\circ$ (apomorphy, shared with most Chrysopidae and Mantispidae); (10) MA entering margin at or before wing mid-point (apomorphy, shared with Chrysopidae and most Mantispidae); (11) basal crossvein m-cu long (apomorphy, shared with several other families); (12) anterior tip of m-cu inclined toward wing apex, rarely perpendicular to Cu (polarity unclear); (13) jugal lobe strongly reduced or absent (putative apomorphy, shared with several other families) (see “Discussion” for more details).

Comparison. Family Mesochrysopidae is most similar to representatives of the families Chrysopidae, Osmylitidae (see “Discussion”), Myrmeleontoidea (i.e., Nymphidae, Myrmeleontidae, Araripeneuridae, if familial rank is confirmed, and Ascalaphidae) and Mantispidae, which differ from it by the following forewing character states: trichosors present in Nymphidae; costal margin markedly expanded basally in Chrysopidae, Osmylitidae, Mantispidae and Nymphidae; Sc and R1 not fused in the vast majority of Chrysopidae (but see “Discussion”) and Mantispidae; origin of Rs inclined at $>30^\circ$ in Chrysopidae, Mantispidae, most Myrmeleontidae and Ascalaphidae; stem of Rs slightly curved in some Osmylitidae and Mantispidae; stem of Rs from its origin to basal crossvein rs-ma short, comparable with length of basal crossvein rs-ma in Chrysopidae, Ascalaphidae, Myrmeleontidae and Araripeneuridae; fork of apparent M absent in Ascalaphidae, Myrmeleontidae and Araripeneuridae; MA and MP diverged at angle of $<40^\circ$ in Osmylitidae and Nymphidae; MA entering margin well distal to wing mid-point in Nymphidae, Ascalaphidae, Myrmeleontidae, Araripeneuridae and Osmylitidae; m-cu short in Osmylitidae and Mesozoic Mantispidae; m-cu inclined toward base (rarely perpendicular

to Cu) in Chrysopidae; jugal lobe well developed in Mantispidae and Mesozoic Chrysopidae.

Description. Antennae filiform. Wings lacking trichosors, nygmata; with distinct pterostigma (not detected in *Karenina longicollis*, not described in *Mesochrysopa*, unknown in *Protoaristenymphes* and *Tachinymphes*). Forewings elongate to broad oval, often with sub-acute apex, 18–48 mm long (length/width ratio 2.8–4.5). Costal space narrow, not or only slightly expanded basally. Sc, R1 fused apically (unknown in *Protoaristenymphes* and *Tachinymphes*). Sc + R1 entering margin at wing apex. Humeral veinlet simple, crossvein-like. Subcostal veinlets proximal to pterostigma not forked, rather sparsely spaced, inclined at nearly right angle to Sc. Veinlets of Sc + R1 simple (forked in *Macronympha*, *Aristenymphes* and possibly *Mesochrysopa*). Subcostal crossveins not detected (one basal crossvein present in *Protoaristenymphes*). Origin of Rs inclined at very acute angle. Stem of Rs straight or only slightly zigzagged distally; stem of Rs from its origin to basal crossvein rs-ma (if present) or to proximal branch of Rs usually much longer than length of rs-ma. Branches of Rs quite short, not forked except for marginal fork (if present). Crossveins between R1, Rs numerous or more or less regular. Long hypostigmal cell absent (present in *Macronympha*, *Aristenymphes* and *Mesochrysopa*, unknown in *Protoaristenymphes* and *Tachinymphes*). Radial crossveins arranged in two (*Protoaristenymphes*, *Macronympha*, *Aristenymphes*) to seven (*Allopterus*) regular gradate series or not forming gradate series (*Mesascalaphus*, partly *Karenina*). In radial space, two conspicuous longitudinal convergent folds present (*Mesochrysopa*, unnamed taxon: Martínez-Delclòs, 1989, fig. 13; probably absent in *Karenina*). Apparent M relatively short, basally fused with R for rather long distance, entering margin at or before wing mid-point. Fork of apparent M located far distal to wing base; MA, MP strongly diverged basally, widely spaced until reaching wing margin. MA gradually curved to wing margin, not branched (with only shallow marginal fork); basal crossvein connecting it with stem of Rs (somewhat distal to fork of M) present (*Protoaristenymphes*, *Macronympha*, *Aristenymphes*) or absent (other genera, not clear in *Mesascalaphus*). MP parallel to MA, varying in structure: running smoothly (*Protoaristenymphes*, *Macronympha*) or strongly zigzagged (*Karenina*, *Allopterus*) with 2–3 straight or 1–3 strongly zigzagged branches, or only with shallow marginal fork (*Siniphes*, *Allopterus*, one additional deeply branched fork in latter), connected basally (distal to fork of M) with CuA by long crossvein or touching it (*Allopterus*, *Karenina*). Mediocubital space basally broad; basal crossvein m-cu located at origin of apparent M, long, its anterior tip usually inclined towards wing apex. Cu divided into CuA, CuP rather close to wing base; CuA with few (1–3) pectinate branches, not zigzagged (*Protoaristenymphes*) to strongly zigzagged (*Karenina*); CuP with only marginal fork, rarely with two pectinate branches. Normally, two crossveins between CuA and CuP. Anal veins poorly developed, occupying restricted area; 1A at least with one fork; 2A and 3A very short, simple. Jugal lobe not developed or at most strongly reduced.

Hindwing 0.4 (*Allopterus*) to 0.9 (*Siniphes*) of forewing length, narrowed basally. In radial space two conspicuous longitudinal convergent folds present (*Mesochrysopa*; probably absent in *Karenina*). Venation similar to that of forewing (except strongly reduced in *Allopterus*) differing as follows: apparent M fused basally with R for lesser distance than in forewing, so appearing to originate from R base; CuA shorter, with a few short, simple, pectinate branches; CuP probably lost (at least in Cretaceous genera); 1A short, running parallel, close to hind margin (rather remote in *Mesochrysopa*), with a few very short, pectinate branches; 2A very short, simple; 3A not detected, probably lost (or extremely short).

Genera included. The family as defined here includes the following ten Mesozoic genera (12 species, Table 1) recorded from the upper Lower Jurassic (Toarcian) to upper Lower Cretaceous (Aptian) of Eurasia and South America: *Protoaristenymphes* [Lower Jurassic (Toarcian) of Luxembourg]; *Macronympha*, *Aristenymphes* [Upper Jurassic (Oxfordian/Kimmeridgian) of Kazakhstan]; *Mesochrysopa*, *Mesotermes* [Upper Jurassic (early Tithonian) of Germany]; *Allopterus*, *Mesascalaphus*, *Siniphes* [Lower Cretaceous of China]; *Tachinymphes* [Lower Cretaceous (early Valanginian) of Siberia]; and *Karenina* [Lower Cretaceous (Aptian) of Brazil]. Additionally, unnamed taxa reported as the representatives of Myrmeleontidae (Martínez-Delclòs, 1989, p. 71, fig. 13) or Chrysopidae (Martínez-Delclòs and Ruiz de Loizaga, 1993, p. 197, fig. 6; Martínez-Delclòs and Nel, 1995, p. 40, fig. IV-9, 4) from the Lower Cretaceous (Barremian) locality of “Las Hoyas” in Spain, belong to this family with certainty.

Remarks. Although the type genus *Mesochrysopa* may be a junior synonym of *Mesotermes* (Carpenter, 1932), the family name Mesochrysopidae is valid according to article 40.1 of the ICZN (1999).

Six long, clavate, thoracic appendages were considered to be present in *Mesascalaphus* (Ren et al., 1995, fig. 3-60). Most likely, however, these are the tibiae of the ventrally exposed specimen (Viktor Krivokhatsky, St. Petersburg, pers. comm. 1998).

The monotypic genus *Liaoximyia* Hong, 1988 (Lower Cretaceous of China), previously referred to the Myrmeleontidae by Hong (1988) and Ross and Jarzembowski (1993) most probably belongs to the Mesochrysopidae. The holotype of *L. sinica* Hong, 1988 is a very incomplete and crumpled specimen, leaving its family determination somewhat tentative. The forewing, however, possesses many character states suggesting a mesochrysopid affinity: costal space not narrowed basally, subcostal veinlets simple, subcostal crossveins absent, origin of Rs inclined at acute angle, stem of Rs straight, branches of Rs short and not forked (including loss of marginal forks). The only character state found in *L. sinica* that is absent in genera of the Mesochrysopidae is the presence of several crossveins between each pair of subcostal veinlets. Until a more complete specimen is found, the family affinity of this genus should be considered uncertain.

Table 1
Geological and geographic distribution of known species of Mesochrysopidae

Age	Species	Locality and horizon	References
Cretaceous			
K1	<i>Karenina breviptera</i> Martins-Neto, 1997	Nova Olinda or Santana do Cariri, Ceará State, Brazil; Crato Fm	Martins-Neto, 1997
K1	<i>Karenina longicollis</i> sp. nov.	Nova Olinda, Ceará State, Brazil; Crato Fm	This paper
K1	<i>Karenina leilana</i> sp. nov.	Nova Olinda, Ceará State, Brazil; Crato Fm	This paper
K1	<i>Allopterus luianus</i> Zhang, 1991	Laiyang, Shandong, China; Laiyang Fm	Zhang, 1991
K1	<i>Tachinymphes ascalaphoides</i> Ponomarenko, 1992	Baissa, Transbaikalia, Russia; Zaza Fm	Ponomarenko, 1992
K1	<i>Siniphes delicatus</i> Ren and Yin, 2002	Beipiao, Liaoning, China; Yixian Fm	Ren and Yin, 2002
K1	<i>Mesascalaphus yangi</i> Ren et al., 1995	Beipiao, Liaoning, China; Yixian Fm	Ren et al., 1995
Jurassic			
J3	<i>Mesochrysopa zitteli</i> (Meunier, 1898)	Solnhofen, Germany; Lithographic Limestone, Tithonian	Meunier, 1898; Handlirsch, 1906–1908; 1920–1921
J3	<i>Mesotermes heros</i> (Hagen, 1862)	Solnhofen, Germany; Lithographic Limestone of the Tithonian	Hagen, 1862; Carpenter, 1932; Nel and Henrotay, 1994
J3	<i>Aristenymphes perfecta</i> Panfilov, 1980	Karatau, South Kazakhstan; Karabastau Fm	Panfilov, 1980
J3	<i>Macronympha elegans</i> Panfilov, 1980	Karatau, South Kazakhstan; Karabastau Fm	Panfilov, 1980
J1	<i>Protoaristenymphes bascharagensis</i> Nel and Henrotay, 1994	Bascharage, Luxembourg; Posidonia Shales, Lower Toarcian	Nel and Henrotay, 1994

The genus *Pseudomyrmeleon* [monotypic: *P. extinctus* (Weyenbergh, 1869)] is very poorly known. Judging from the illustrations of Weyenbergh (1869, pl. 35, fig. 16) and Meunier (1897, pl. 7, fig. 9), it is represented by a very poorly preserved whole specimen, with all four wings outspread. No distinct characters may be detected beyond its general myrmeleontid appearance, with narrow and elongate wings and narrow costal space (similar to those of mesochrysopid genera). Handlirsch (1906–1908) assumed that this species “possibly belongs to the Mesochrysopidae” (p. 614). Carpenter (1992) referred it to Neuroptera incertae sedis “possibly related to Mesochrysopidae” (p. 356). Confirmation of the assignment of *P. extinctus* to this family requires re-examination of the type specimen.

Of the other seven genera formerly assigned to this family, none belongs to the Mesochrysopidae with certainty. *Mesypochrysa* and *Caririchrysa* Martins-Neto and Vulcano, 1989,

which are sometimes assigned to this taxon (e.g., Martins-Neto and Vulcano, 1989; Martins-Neto, 2003), are undoubtedly true chrysopids and were assigned to the Limaiinae, a subfamily of Chrysopidae, by Makarkin (1997).

The single species of *Microsmylus* (*M. foliformis* Panfilov, 1980) was assigned to the Mesochrysopidae (Panfilov, 1980). It is, however, represented by a single, fragmentary wing, and we find its family affinity to be unclear. We believe that it should be excluded from the Mesochrysopidae pending the recovery of more specimens, and consider it here as *Neuroptera incertae sedis*.

Liassochrysa (with *L. stigmatica* Ansoerge and Schlüter, 1990) probably belongs to another family. Examination of clear photographs of the holotype shows that the structure of the forewing pterostigma and venation are most similar to those of *Promantispa* Panfilov, currently assigned to the Mantispidae (Makarkin, unpublished).

The genus *Nymphoides* (with two species from the Jurassic of Siberia and Kazakhstan) was assigned to the Mesochrysopidae by Panfilov (1980) and Ponomarenko (1984). It was recently synonymized with *Osmylites* based on the examination of the type specimen of *O. excelsa* (Oppenheim, 1888) from Solnhofen (Ponomarenko, 2003). If the redescription of *Osmylites* by Ponomarenko (2003) is correct (the author himself is uncertain), this synonymy is justified. The forewing of *Osmylites* possesses some character states not characteristic of other genera of Mesochrysopidae, namely: costal space markedly expanded basally; apparent M lesser curved to hind margin, reaching it well after wing mid-point; CuA with regularly pectinate branching; 1A long and with few pectinate branches; end-twigging of branches of Rs and M rather well developed (i.e., with distal dichotomous branching, and very shallow marginal forks); crossveins rather rare and irregularly arranged. These character states are sufficient to exclude this genus from the Mesochrysopidae.

Chrysoleonites, with three species from the Upper Jurassic of Karatau, is quite similar to *Osmylites*, possessing nearly the same character states that allow the exclusion of that genus from Mesochrysopidae (see above). However, it superficially resembles genera of Nymphidae more than it does *Osmylites*, e.g., on account of the structure of the apical portion of its forewing and CuA, and its longer M (see Martynov, 1925, fig. 10a–c; Martynova, 1949, figs. 4, 5). There has been no general agreement as to the family placement of *Chrysoleonites*: Panfilov (1980) assigned it to the Mesochrysopidae and Carpenter (1992) to the Nymphitidae; Adams and Penny (1992) assumed that it might belong to the Nymphidae. In fact, many character states of this and another similar genus, *Baissoleon* Makarkin, 1990 from the Lower Cretaceous of Transbaikalia, are intermediate between those of Nymphidae and Mesochrysopidae, so they probably cannot be placed in either family with any degree of confidence (see “Discussion”).

Genus *Karenina* Martins-Neto, 1997

Type species. *Karenina breviptera* Martins-Neto, 1997; Lower Cretaceous, Crato Formation, Nova Olinda Member.

Species included. *K. breviptera*, *K. longicollis* sp. nov., *K. leilana* sp. nov., all from the Lower Cretaceous, Nova Olinda Member of the Crato Formation.

Diagnosis. Forewing: MP touching (or almost touching) CuA; venation in radial space at least partly reticulated; venation in MP, CuA spaces highly reticulated, so not possible to discriminate confidently longitudinal veins from crossveins. Hindwing elongate, 0.6–0.8 of forewing length; apex of wing sub-acute; M, Cu basally close.

Comparison. *Karenina* is most similar to *Allopterus* by forewing venation. In particular, these two genera share MP touching (or almost touching) CuA, distinguishing them from other genera of the family. *Allopterus* may be distinguished from *Karenina* by the following character states: forewing longitudinal veins in MP, CuA spaces easily discriminated from crossveins; forewing radial crossveins arranged into seven regular gradate series; hindwing approximately 0.4 of forewing length, with apex broadly rounded and venation highly specialized due to reduced size, atypical shape.

Description. Medium-sized mesochrysopid. Antennae less than one-half of forewing length. Pronotum elongate, 2–4 times longer than wide. Forewing 23–26 mm long, with sub-acute or rather rounded apex; costal gradate series in distal portion of costal space present (in *K. leilana* absent); long hypostigmatic cell absent; crossveins between stem of Rs, MA absent; venation in radial, medial and cubital spaces highly reticulated or (in radial space) with several irregular gradate series of crossveins; MA arched, entering margin at wing mid-point; MP touching CuA (connecting by short crossvein in forewings of *K. longicollis*); basal m-cu long; branches of MP and CuA strongly zigzagged; MP with only marginal fork or additionally with two long, zigzagged branches (impossible to identify confidently because of highly reticulated venation in medial, mediocubital and cubital spaces); CuA zigzagged, with only marginal fork or few branches; CuP short, with 1–2 short branches; 1A close, parallel to hind margin. Hindwing narrower, shorter than forewing, 0.6 (*K. breviptera*) to 0.8 (*K. longicollis*) of forewing length; venation (based on *K. longicollis*) similar to that of forewing, differing as follows: apparent M not arched; CuA nearly straight; M and Cu basally close; basal crossvein m-cu remote from wing base.

Karenina longicollis sp. nov.

Figs. 1–4

Derivation of name. Latin *longus*, long, and *collum*, neck, referring to the unusually long pronotum.

Material. Holotype SMNS 65505 (part only), deposited in the Staatliches Museum für Naturkunde, Stuttgart (Germany). A nearly complete specimen preserved in dorsal aspect (with clearly visible concavity/convexity relationships of veins), collected near Nova Olinda, Ceará State, Brazil; Lower Cretaceous Crato Formation, Nova Olinda Member.

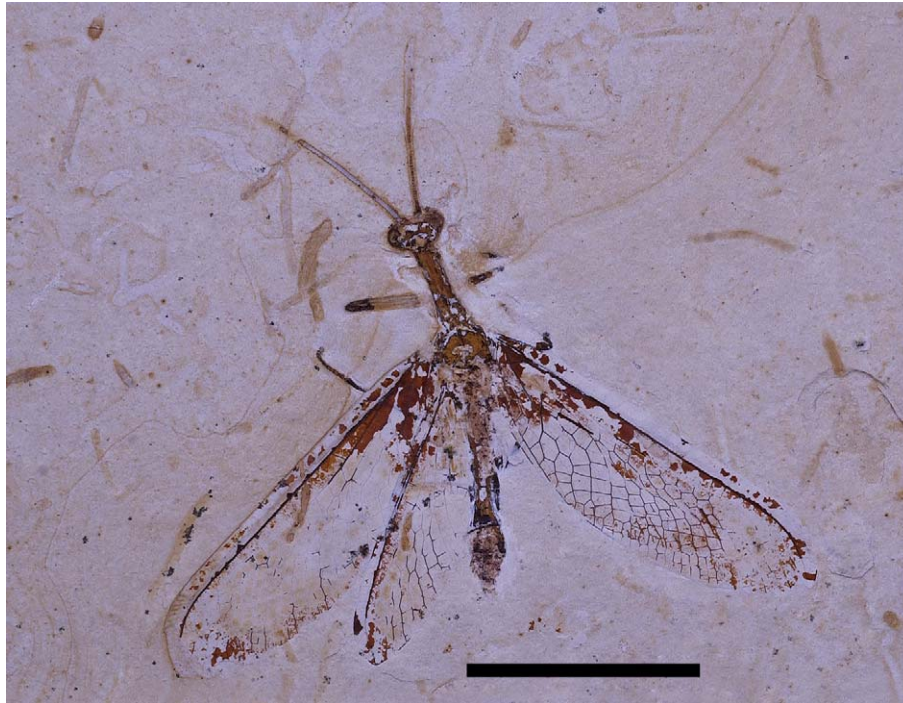


Fig. 1. *Karenina longicollis* sp. nov., SMNS 65505. Scale bar represents 10 mm.

Diagnosis. Pronotum four times longer than wide. Forewing elongate, length/width ratio 3.7; crossveins between veinlets in apical portion of costal space present; MP and CuA connected by short crossvein. Hindwing long, 0.8 of forewing length.

Comparison. Two other species of the genus may be distinguished from *Karenina longicollis* by following forewing character states: pronotum shorter (2–3 times longer than wide in *K. breviptera*); forewings broader (length/width ratio

2.8 in *K. leilana*); crossveins between veinlets of Sc + R1 in apical portion of costal space absent in *K. leilana*; MP touching CuA in *K. breviptera*. Hindwing approximately 0.6 of forewing length in *K. breviptera*.

Description. Head transverse (dorsal view), twice wider than long, 2×4 mm, with prominent compound eyes, each 1×1.5 mm. Ocelli absent or not preserved. Antennae 12 mm, widely spaced, filiform. Scape short, transverse; flagellum composed of 35 equal, short segments; left antenna only visible as impression in matrix. Pronotum unusually long, 4.5 times longer than wide, 5.2×1.2 mm. Thorax (excluding pronotum) 5.5×3.5 mm, oval, robust: mesothorax large rounded, metathorax short; exoskeleton not preserved. Abdomen 19 mm long; width of first segment twice that of length, 1×2 mm; second and third segments square, 1.5×1.5 mm; segments IV–V slightly elongate; other segments indistinct; exoskeleton partly not preserved. No legs entirely preserved. Foreleg: femur rather stout, 5×1.5 mm. Midleg or hindleg: tibia long, slender, apically not bearing spines or long setae; tarsus five-segmented, basitarsus 1.3 mm long, other four segments together 1.4 long; claws distinct, rather short.

Forewing oval with slightly pointed apex, 26 mm long, 7 mm wide (length/width ratio 3.7). Sc distally fused with R1; Sc + R1 curving backwards, terminating at wing apex. Costal space narrow, 0.6 mm wide, composed of approximately 50 cells, with subcostal veinlets widely spaced becoming increasingly closely spaced to pterostigmal region; between veinlets of Sc + R1 a few crossveins form costal gradate series. Humeral veinlet simple, crossvein-like. Pterostigma absent or not discernible. No crossveins between Sc

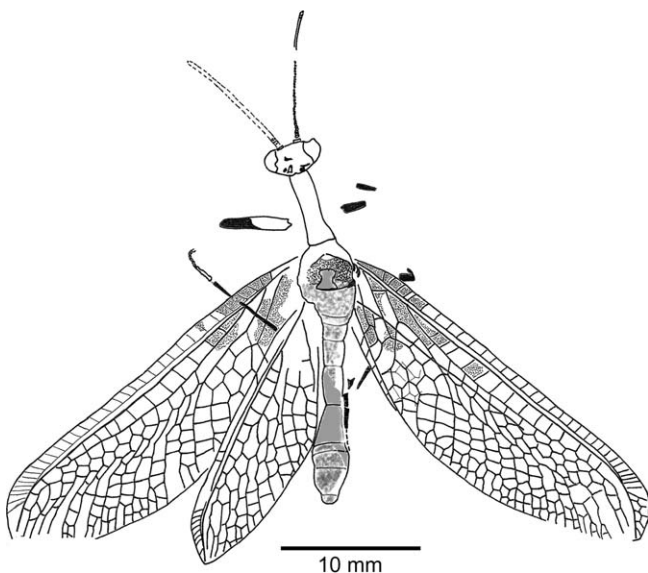


Fig. 2. *Karenina longicollis* sp. nov., dorsal aspect, camera lucida drawing of SMNS 65505.

and R1 detected. Stem of Rs straight, slightly zigzagged distally; its origin situated at 4.5 mm from wing base, inclined at acute angle to R1. R1 space most dilated at proximal third, narrowed distad, 1.1 mm maximum wide, with at least 19 cells. Rs with 12–13 zigzagged branches, not forked before marginal forks, which are rather deep and wide, each with crossvein connected to two branches of fork. Radial crossveins numerous forming several irregular gradate series, partly venation in radial space rather highly reticulated. No crossvein between stem of Rs and apparent M. Origin of apparent M at 1 mm from wing base at level of humeral veinlet. Apparent M moderately convex, divided into MA and MP at approximately 5 mm from wing base; MA smooth, slightly convex basally, slightly zigzagged distally, entering wing margin slightly before wing mid-point, with rather shallow but wide marginal fork. MP zigzagged, slightly convex basally, with only one marginal fork (alternatively, additionally with two long, zigzagged branches; impossible to identify these confidently because of highly reticulated venation in medial to cubital spaces). Crossveins in medial space fairly numerous, not arranged in regular series. Basal crossvein m-cu located slightly distal to origin of apparent M, oblique, long. Cu originated at wing base, probably not fused with R basally, divided into CuA and CuP slightly distal to crossvein m-cu. CuA straight, moderately convex basally (before distal crossvein cua-cup), strongly zigzagged after, with only one shallow, wide fork (alternatively, also with two branches each having wide marginal fork). CuA connected with MP by short crossvein in left wing and by very short crossvein in right wing (almost touching it). CuP short, with one wide marginal fork. Basal crossvein cua-cup almost perpendicular to both CuA and CuP; distal crossvein cua-cup very oblique, appearing as continuation of distalmost portion of CuP. Two crossveins between CuP and 1A. Anal space poorly preserved, very restricted. 1A and 2A incomplete, almost parallel to hind margin. 3A not preserved. No conspicuous longitudinal folds in radial space visible.

Hindwing 21 mm long, 6 mm wide, narrowed to wing base, with sub-acute apex. Venation similar to forewing. No costal crossveins detected. Sc fused with R1 apically; Sc + R1 entering margin at wing apex. Rs with 7–8 zigzagged branches (in left wing). Radial crossveins in anterior portion of space forming two rather regular gradate series, venation posteriorly in radial space reticulated, not forming gradate series. Apparent M originates near wing base, divided into MA and MP opposite to origin of Rs forming more acute angle than in forewing. MA simple, with only shallow marginal fork; MP deeply forked, posterior fork with abnormal configuration; not touching CuA, connected with it by long crossveins. Between M and Cu at least three crossveins; basal crossvein shifted far distal. CuA originated near origin of apparent M, rather short, almost straight, with three short, pectinate branches. CuP apparently absent. Only one partial 1A well preserved in anal space. No conspicuous longitudinal folds in radial space visible.

Karenina leilana sp. nov.
Figs. 5, 6

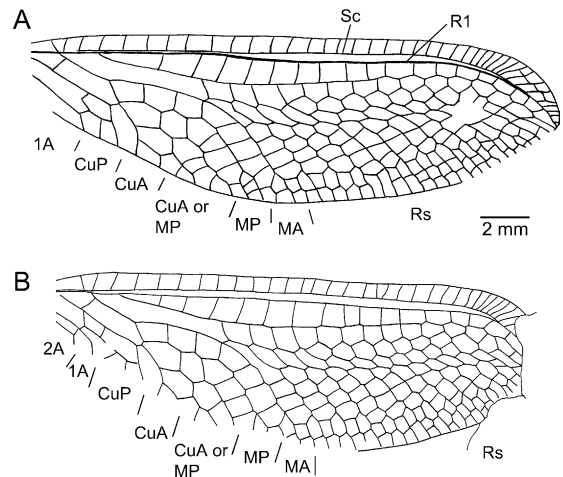


Fig. 3. *Karenina longicollis* sp. nov. A, right forewing, camera lucida drawing of SMNS 65505. B, left forewing, camera lucida drawing of SMNS 65505.

Derivation of name. In memory of a dear childhood friend of FM, Leila Dal Martello, who died not long ago.

Material. Holotype SMNS 65506 (only part), deposited in the Staatliches Museum für Naturkunde, Stuttgart (Germany). Two complete forewings articulated to a very poorly preserved thorax, collected near Nova Olinda, Cearà State, Brazil; Lower Cretaceous Crato Formation, Nova Olinda Member.

Diagnosis. Forewings relatively wide, length/width ratio 2.8; crossveins between veinlets of Sc+R1 in apical portion of costal space absent; venation in radial space rather highly reticulated; MP touching CuA; Sc and R1 fused distal to pterostigma.

Comparison. Two other species of genus may be distinguished from *Karenina leilana* by the following forewing character states: forewings elongate (length/width ratio 3.7 in *K. longicollis*); crossveins between veinlets of Sc+R1 in apical portion of costal space present; MP and CuA connected by short crossvein in *K. longicollis*; Sc and R1 fusion within pterostigma in *K. breviptera*.

Description. Forewing broad oval, with rather rounded apex, 23 mm long, 8.1 mm wide (length/width ratio 2.8). Costal space narrow, 0.6 mm wide, slightly expanded toward apex.

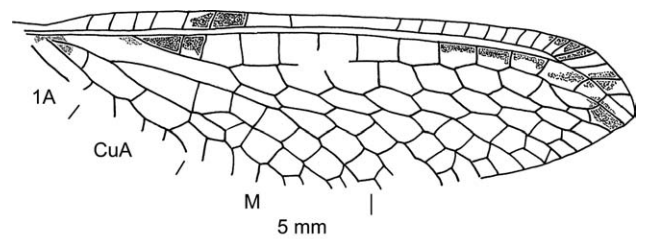


Fig. 4. *Karenina longicollis* sp. nov., left hindwing, camera lucida drawing of SMNS 65505.

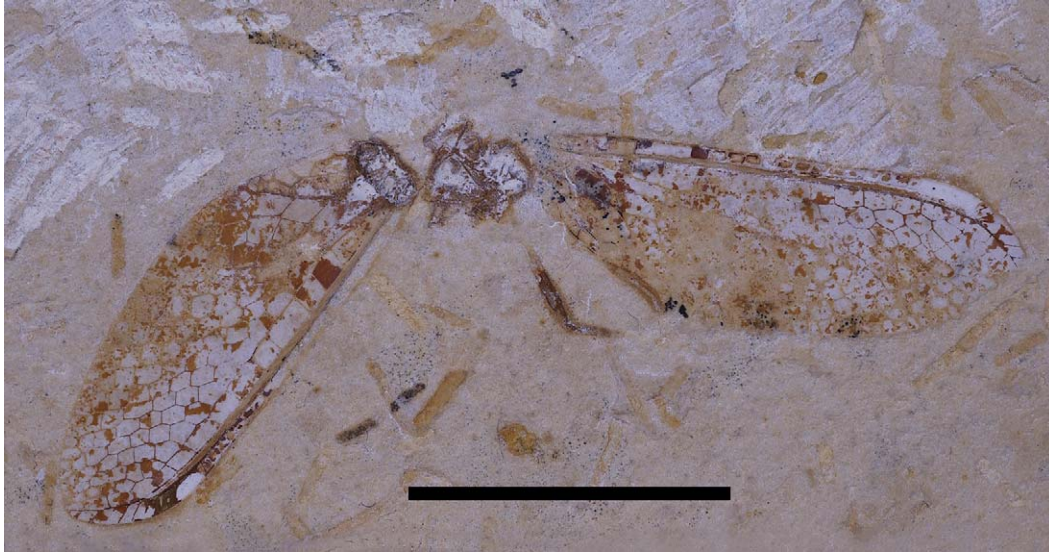


Fig. 5. *Karenina leilana* sp. nov., SMNS 65506. Scale bar represents 10 mm.

Subcostal veinlets simple (except one apical veinlet of Sc + R1, which is shallowly forked), proximal to pterostigma inclined to Sc at right angle, becoming gradually oblique towards wing apex, forming 23 cells in distal half of wing. Crossveins in costal and subcostal spaces not detected. Pterostigma occupying at least seven elongate cells, dark-pigmented. Sc and R1 fused distal to pterostigma. Sc + R1 entering wing margin at apex. Sixteen crossveins between Rs and R1 forming 17 cells, shorter basad, longer distad. Long hypostigmatic cell absent. Rs with ten zigzagged branches, not forked or only with one marginal fork. Venation in radial space rather highly reticulated forming pattern of polygons, most hexagonal. Base of M not preserved. Apparent M forked distal to origin of RS. MA not branched (only shallow marginal fork present), slightly zigzagged, arched entering margin at wing mid-point. MP similar to MA but more strongly zigzagged, touching CuA near its origin. Basal crossvein m-cu long, shifted far distal when compared with that of all other mesochrysoptids [alternatively, actual basal crossvein m-cu not preserved (obscured by matrix), present crossvein is additional]. CuA strongly zigzagged, short, with two very short branches (alternatively, with two more long branches, one of which having a shallow, wide fork; impossible to identify these confidently because of highly reticulated venation in medial to cubital spaces). CuP

short, with shallow, wide fork. Three crossveins between CuA and CuP. 1A close, parallel to margin, with at least one short branch; 2A and 3A not preserved. Wing preserved very flat, so impossible to determine concavity/convexity relationships of veins, or presence/absence of longitudinal folds in radial space.

5. Discussion

The genus *Karenina* from the Crato Formation was previously assigned to Ascalaphidae (Martins-Neto, 1997). Indeed, the mesochrysoptid affinity of the type species (*K. breviptera*) is not obvious, based on the description of the holotype, because of incomplete preservation. The two new species described here provide character states, particularly of venation of the fore and hindwings, that clearly confirm the mesochrysoptid affinity of this genus. The forewing venation of *Karenina* is most similar to that of *Allopterus*. The latter was separated by Zhang (1991), and placed in the monotypic family Allopteridae, based mainly on the great differences in size of the fore and hindwings (due to brachyptery), and the peculiar shape and reduced venation of the hindwing. Brachyptery occurs at times within extant taxa of Hemerobiidae (e.g., in *Nusalala* Navás; Oswald, 1996), where this condition is not found to be sufficient reason to create a new family for them. However, the hindwing venation of *Karenina* is most similar to that of *Siniphes* and *Tachinymphes* (which are almost identical to each other), whose mesochrysoptid affinities are clear. Although the drawing of the hindwing of the type species of the family (*Mesochrysopa zitteli* Meunier) might be inaccurate in some details (Handlirsch, 1920–1921, fig. 164), it shows that all of the main features are shared by these three genera (e.g., similar wing shape and relative size; Sc and R1 fused; branches of Rs short and each with only one marginal fork; M short, entering wing margin at or before mid-point, MA lacking a deep fork; CuA short, with few

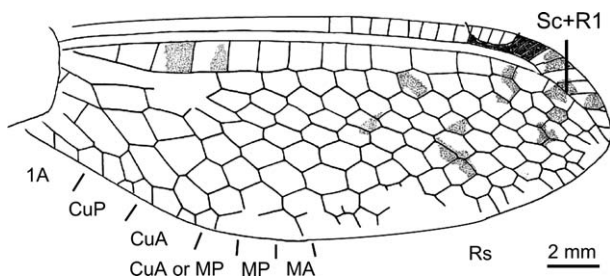


Fig. 6. *Karenina leilana* sp. nov., forewing, camera lucida drawing of SMNS 65506.

branches). The forewing venation of *M. zitteli* is also very similar to that of *Siniphes* (and therefore *Tachinymphes*: the forewing of the latter is not complete) on account of its principal characters (cf. Handlirsch, 1920–1921, fig. 164; Ren and Yin, 2002, fig. 4). On the other hand, the venation of *M. zitteli* very much resembles that of three genera from older Jurassic strata (*Protoaristenymphes*, *Macronympha*, *Aristenymphes*), which are more similar to each other (particularly with respect to the presence of a crossvein between stem of Rs and MA and long hypostigmatic cell, and forked veinlets of Sc + R1) than they are to other (younger) mesochrysopterid genera.

Based on individual characters of the wing, monophyly cannot be established with confidence for the Mesochrysopteridae. The venation of many of the more primitive families is generalised within the order: e.g., Sisyridae, Nevrothidae, Polystoechotidae, Ithonidae and Dilaridae. However, that of the Mesochrysopteridae is clearly derived with regard to these. Although the apomorphic character states (e.g., 1–3, 9–11, 13) clearly separate the Mesochrysopteridae from these families, they do occur in others within the order. As the higher-level phylogeny of the Neuroptera is currently poorly resolved, the putative polarities of the venational character states considered here are tentative; it is, therefore, not clear whether their co-occurrences in these families are homoplasious, or whether they indicate monophyly of a clade that includes them. The wings of Mesochrysopteridae are better characterised by combinations of character states. For example, the structure of the basal part of Rs (character states 5–7 together) occurs in all genera of this family and may be considered autapomorphic (and, therefore, supports the monophyly of this family); although it is found in other families, it occurs only rarely, in single genera.

Although a detailed phylogenetic analysis of Mesochrysopteridae and related groups (e.g., Chrysopidae and Osmyliidae) is outside of the scope of this paper, we briefly outline here the possible phylogenetic position of this family.

The Mesochrysopteridae is usually regarded as most closely related to the Chrysopidae, and is often included in it as a subfamily (Adams, 1967; Schlüter, 1984; Séméria and Nel, 1990; Martins-Neto, 2003). Of the genera currently considered to be Mesochrysopteridae, the oldest (*Protoaristenymphes*, *Macronympha*, *Aristenymphes*) resemble Chrysopidae somewhat whereas the younger taxa are very different. Mesochrysopterids (particularly younger genera) show greater superficial resemblance to the myrmeleontoids, and some (*Siniphes*, *Tachinymphes*, *Mesascalaphus*, *Karenina*) have previously been assigned to this group (Ponomarenko, 1992; Ren et al., 1995; Martins-Neto, 1997; Ren and Yin, 2002). The main differences between Mesochrysopteridae and Chrysopidae are given above, in the comparison section of the former. It should be noted that the venation in the basal portion of the forewing in these two families is very similar; even the number and arrangement of their crossveins are nearly identical except in the more derived genera, such as *Karenina*. The venation in the apical portion of the oldest members of the Mesochrysopteridae is, however, very different [i.e., Sc and R1 are clearly fused; costal space comparatively broad (narrow in Chrysopidae);

veinlets of Sc + R1 forked (never forked in Chrysopidae); long hypostigmatic cell present (long hypostigmatic cell absent in the vast majority of Chrysopidae)]. In the known specimens of *Mesypochrysa* (the most speciose Mesozoic chrysopid genus), Sc cannot be traced to its termination, as it is lost in the heavily pigmented pterostigma. However, in the few species in which this portion is more or less clearly visible, Sc and R1 appear to be fused; at least this has been detected in one specimen of Lower Cretaceous Chrysopidae (Makarkin, 1997, fig. 13). Different evolutionary trends are also apparent within Mesochrysopteridae and Chrysopidae concerning MP: a tendency to be fused with CuA in the most derived mesochrysopterids (*Karenina*, *Allopterus*), and a tendency to be fused with MA in derived chrysopids (Chrysopinae).

Adams (1956, p. 72) mentioned that “*Mesochrysopta* ... is to be considered as a specialized side-branch of the chrysopid stem”. At present, given current, more complete knowledge of fossil history of these groups, we assert that the Mesochrysopteridae and Chrysopidae are two distinct, monophyletic taxa at family rank, and may be sister taxa. At least, Chrysopidae is clearly the most closely related extant taxon to Mesochrysopteridae. The Chrysopidae is generally accepted to belong to the heterogeneous suborder Hemerobiiformia (or the superfamily Hemerobiodea of older authors). The actual position of Chrysopidae within the Hemerobiiformia remains uncertain; the family is considered to be a sister group of all other Hemerobiiformia excluding the clade Ithonidae + Polystoechotidae (Aspöck, 1992), or to be a sister group of Osmyliidae (Aspöck et al., 2001), although the Osmyliidae are morphologically rather distant from the Chrysopidae, by both their larval and imaginal features. Formerly, the Chrysopidae was considered to be most closely related to the Hemerobiidae (e.g., Henry, 1982; Tauber and Adams, 1990), but the superficially similar larvae of these two families in fact have no known synapomorphies (Aspöck, 1992), and the imagoes are strongly dissimilar.

MacLeod (1964, p. 194), in his detailed work on the head capsule structure of larval Neuroptera, stated that the larva of Chrysopidae, “though still of the hemerobioid type, shows certain of the features usually associated with myrmeleontoid larval heads”, mainly in the structure of the tentorium. However, cladistic analysis of the extant taxa shows that the position of the Chrysopidae is far from the lineage leading to the suborder Myrmeleontiformia (Aspöck et al., 2001). It is not possible, however, to understand clearly the phylogeny of the order based only on extant representatives, as neuropterans were most diverse in Jurassic/Cretaceous times. Ponomarenko (1992) was of the opinion that a group of the Mesozoic genera similar to *Chrysoleonites* might be ancestral to both “chrysopoid” (i.e., Mesochrysopteridae and Chrysopidae) and “myrmeleontoid” lineages, an idea that might be helpful in resolving the phylogenetic position of the Mesochrysopteridae. Nel and Henrotay (1994), in their cladistic analysis of Mesozoic chrysopid-like genera, found a clade consisting of *Chrysoleonites*, *Baissoleon* and *Nymphoides* (= *Osmylites*) to be monophyletic and the sister group of a clade consisting of the genera of the Mesochrysopteridae and Chrysopidae. This group of genera possesses some character states intermediate

in form between Nymphidae and Mesochrysopidae (e.g., by the structure of the main veins Rs, M, Cu), and is usually named “Nymphitidae” (Martynova, 1949; Makarkin, 1990). The true status of the family Nymphitidae, however, has not been entirely clear, as the type genus was inadequately described; the type specimen (*Nymphites priscus* Weyenbergh) is most probably a member of Nymphidae (Makarkin and Archibald, research in progress), and thus the Nymphitidae may be a subjective synonym of the latter. If *Chrysoleonites*, *Baissoleon* and *Osmylites* do form a monophyletic unit at family level (we think this is rather likely) then this taxon should be named Osmylitidae. Recently, Ponomarenko (2003) synonymized Osmylitidae and Mesochrysopidae but we suspect that these families are distinct; however, the composition and status of Osmylitidae is unclear at present.

If representatives of the Osmylitidae, as treated here, are related to both Mesochrysopidae and Nymphidae, then the clade Nymphidae + Osmylitidae + Mesochrysopidae + Chrysopidae might be monophyletic. The monophyly of Myrmeleontoidea, excluding Psychopsidae (i.e., the clade Nymphidae + Myrmeleontidae + Ascalaphidae + Nemopteridae), appears to be well founded (e.g., Mansell, 1992; Oswald, 1995, but see alternative view in Aspöck et al., 2001). Nymphidae, as the most primitive extant family of the clade Myrmeleontoidea [excluding Psychopsidae] + Osmylitidae + Mesochrysopidae + Chrysopidae, possesses trichosors, a plesiomorphic character at the order level, whereas all other families of this clade do not (except perhaps Osmylitidae: the presence of trichosors in this family has not been detected, but we think they may have been present). A secondary origin of trichosors seems very improbable; therefore, a stem species of this possible clade should possess this character. If our assumption is correct, then this hypothetical species should occur in Early Jurassic or Late Triassic deposits and have a venation most similar to that of Osmylitidae (e.g., *Osmylites* or *Chrysoleonites*), and possess trichosors. The oldest representative so far of this possible clade is the mesochrysopid genus *Protoaristenymphes* from the Upper Lias (Nel and Henrotay, 1994), which has comparatively regular venation and lacks trichosors; the oldest known fossil wings within the clade that possess trichosors are Late Jurassic (pers. obs.).

Of the families of Myrmeleontoidea, the most specialized Mesochrysopidae (like *Karenina*) strongly resemble Ascalaphidae, particularly with respect to the reticulation of their venation. They share many character states (e.g., Sc and R1 fused apically, costal space narrow, subcostal veinlets simple, pterostigma present, long hypostigmal cell absent); however, most of their fundamental character states are very different, especially the structure of M and Cu. In the forewing, M does not have an apparent fork, but there is an oblique vein from M to CuA, which is generally accepted to be MP, distad entirely fused with CuA; and the CuA space has a large triangular area enclosed by the distal portion of CuA (or CuA + MP) and basalmost branch of CuA (in Myrmeleontidae and Nemopteridae these features are similarly configured). Therefore the resemblance between the Mesochrysopidae and Ascalaphidae is probably only superficial.

The Mesochrysopidae also resemble Myrmeleontidae in that they share longitudinal folds in radial space. The wings of the latter possess a single medial longitudinal fold, which is often accompanied by a false longitudinal vein formed by bending of the branches of Rs and the crossveins connecting them, called the “anterior Banksian line” (New, 1985; Krivokhatsky, 1998). In the few species of Mesochrysopidae in which this character is recorded, there are two conspicuous longitudinal folds, which are also accompanied by false longitudinal veins formed mainly by series of strongly inclined crossveins connecting the branches of Rs. However, the majority of mesochrysopid species have not yet been examined for the presence or absence of this character. Until a comprehensive comparative study of this structure is carried out, we refrain from using the name “Banksian lines” to describe the structures found in these mesochrysopids, because they might be not homologous with those of the Myrmeleontidae.

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