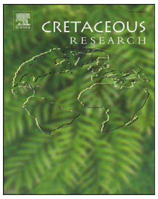
Cretaceous Research 78 (2017) 149–160

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes



Taxonomic study of the Cretaceous lacewing family Babinskaiidae (Neuroptera: Myrmeleontoidea: Nymphidoidae), with description of new taxa

Vladimir N. Makarkin [a], [*], Sam W. Heads [b], Sonja Wedmann [c]

[a] Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, 960022, Russia
[b] Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, 1816 South Oak Street, Champaign, IL, 61820, USA
[c] Senckenberg Research Institute, Messel Research Station, Markstr. 35, D-64409, Messel, Germany

ARTICLE INFO

Article history:
Received 19 April 2017
Received in revised form
12 June 2017
Accepted in revised form 13 June 2017
Available online 15 June 2017

Keywords:
Crato Formation
Baissa
Burmese amber
Nymphidoidae
Babinskaiidae

ABSTRACT

The Cretaceous lacewing family Babinskaiidae comprises nine species in seven genera, of which two new genera and one new species are described herein: *Parababinskaia elegans* gen. et sp. nov. from the late Aptian Crato Formation of Brazil, and *Pseudobabinskaia* gen. nov. (with the only species *Pseudobabinskaia martinsnetoi* Lu et al., 2017, comb. nov.) from mid-Cretaceous Burmese amber. The reduction of the veins AA2 and AA3 in the hind wing is an autapomorphy of the family. Babinskaiidae are most closely related to Nymphidae, and have probably evolved as a side branch of these. The superfamily Myrmeleontoidea is divided into two epifamilies: Nymphidoidae whose MP (or M) is long, not fused with CuA, and trichosors are present (Nymphidae, Babinskaiidae), and Myrmeleontoidae whose MP is crossvein-like, then fused with CuA, and trichosors are lost (Araripeneuridae, Ascalaphidae, Myrmeleontidae, Nemopteridae, Palaeoleontidae). The aligned crossveins 1r-m and 1m-cu in the forewing is probably the only venational autapomorphy of the Myrmeleontoidea.

1. Introduction

The Myrmeleontoidea, which comprise the largest extant neuropterans, include four extant families (Nymphidae, Nemopteridae, Ascalaphidae, and Myrmeleontidae), and three extinct (†Babinskaiidae, †Palaeoleontidae, and †Araripeneuridae). The fossil record shows that the superfamily diversified during the Early Cretaceous as only one myrmeleontoid family (i.e., Nymphidae) was present with several genera in the Jurassic (e.g., Carpenter, 1929; Makarkin et al., 2013; Shi et al., 2013). This early diversification is poorly documented, but at least four families were already represented by the end of the Barremian (i.e., Nymphidae, †Babinskaiidae, †Palaeoleontidae, and †Araripeneuridae). The Nemopteridae are known from the late Aptian Crato Formation of Brazil, but Mesozoic fossils of Ascalaphidae and Myrmeleontidae are unknown.

The family Babinskaiidae is small comprising until now eight species in five genera known from eleven specimens from the Lower Cretaceous Crato Formation of Brazil, the Baissa locality of Siberian Russia, and mid-Cretaceous Burmese amber (Martins-Neto and Vulcano, 1989a,b; Ponomarenko, 1992a; Martins-Neto, 1994, 1997, 1998; Makarkin, 2016b; Lu et al., 2017). The taxon was established as a subfamily of Nymphidae by Martins-Neto and Vulcano (1989a), and slightly later it was elevated to family level (Martins-Neto, 1992). Babinskaiids are the smallest myrmeleontoids, with forewings 9–12.7 mm long.

Until recently, Babinskaiidae were known mainly from the Crato Formation. These species were inaccurately described and need reexamination. Unfortunately, the types and other published specimens are deposited in Brazilian institutions or personal collections, and are now inaccessible for study. However, we found and studied two new specimens of this family from the Crato Formation in collections in the U.S.A. and Germany. One of them belongs to a known species, *Nelia maculata* Martins-Neto and Vulcano 1989b, and the other represents a new genus and species, *Parababinskaia elegans* gen. et sp. nov. Also, we re-examined the type of *Baisonelia vitimica* Ponomarenko, 1992a from the Baissa locality. Unfortunately, we were not able to examine any specimens of the type genus *Babinskaia* Martins-Neto and Vulcano 1989a, which are known from two incompletely preserved specimens belonging to two species from the Crato Formation.

---

[*] Corresponding author.
E-mail address: vnmakarkin@mail.ru (V.N. Makarkin).

http://dx.doi.org/10.1016/j.cretres.2017.06.007
0195-6671/© 2017 Elsevier Ltd. All rights reserved.

Table 1
List of species of Babinskaiidae.

	Species	Age	Locality
1	*Baisonelia vitimica* Ponomarenko, 1992a	Barremian	Baissa, Russia
2	*Babinskaia formosa* Martins-Neto et Vulcano, 1989a	Upper Aptian	Crato Formation, Brazil
3	*Babinskaia pulchra* Martins-Neto et Vulcano, 1989a	Upper Aptian	Crato Formation, Brazil
4	*Neliana maculata* (Martins-Neto et Vulcano, 1989b)	Upper Aptian	Crato Formation, Brazil
5	*Neliana impolluta* Martins-Neto, 1997	Upper Aptian	Crato Formation, Brazil
6	*Parababinskaia elegans* gen. et sp. nov.	Upper Aptian	Crato Formation, Brazil
7	*Electrobabinskaia burmana* Lu et al., 2017	Upper Albian/lower Cenomanian	Burmese amber, Myanmar
8	*Burmobabinskaia tenuis* Lu et al., 2017	Upper Albian/lower Cenomanian	Burmese amber, Myanmar
9	*Pseudobabinskaia martinsnetoi* (Lu et al., 2017), comb. nov.	Upper Albian/lower Cenomanian	Burmese amber, Myanmar

Recently, this family was discovered in Burmese amber (Makarkin, 2016b; Lu et al., 2017). We know of seven specimens, one of which was reported by Xia et al. (2015, fig. on p. 94), three were described by Lu et al. (2017), and three others (undescribed and not illustrated) are preserved in private collections (VM, pers. obs.). These specimens have great importance for understanding the morphology of the family. Thus, the family is currently known from a total of 16 specimens belonging to nine species in seven genera (Table 1).

Here, we summarize all available data on Babinskaiidae, and analyse its morphological characters and phylogenetic relationships.

2. Material and methods

This study is based on three specimens from the Lower Cretaceous Baissa locality and the Crato Formation housed in different collections. The photographs of *Baisonelia vitimica* were taken by Alexander Khramov (PIN) using a Leica M165 stereomicroscope with an attached Leica DFC 425 digital camera; of *Neliana maculata* by SW using a Leica M165 stereomicroscope with an attached Leica DFC 495 digital camera and a Leica MZ12.5 stereomicroscope with an attached Nikon D300 camera, and of *Parababinskaia elegans* by M. Jared Thomas (INHSP) using a Canon 5D Mark III DSLR camera with Canon MP-E 65 mm 1–5× macro lens mounted on a Cognisys StackShot automated focus stacking rail. The photomicrograph shown in Fig. 4 was produced by M. Jared Thomas using a Zeiss SteREO Discovery.V8 zoom stereomicroscope. Line drawings were prepared by VM using Adobe Photoshop CS3.

The venational terminology in general follows Kukalová-Peck and Lawrence (2004) as modified by Yang et al. (2012, 2014). Terminology of wing spaces and details of venation (e.g., veinlets, traces) follows Oswald (1993). Terminology of genitalia follows Aspöck and Aspöck (2008).

Abbreviations: AA1–AA3, first to third anterior anal vein; CuA, anterior cubitus; CuA1, proximal-most branch of CuA; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; MA1, MP1, proximal-most branches of MA and MP, respectively. RA, anterior radius; RP, posterior sector; RP1, proximal-most branch of RP; ScA, subcosta anterior.

Institutional abbreviations: INHSP, Illinois Natural History Survey Paleontology Collection, Urbana-Champaign, Illinois, U.S.A.; PIN, Palaeontological Institute of the Russian Academy of Science, Moscow, Russia; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

3. Localities

The family Babinskaiidae is known from only three Cretaceous localities (or groups of localities): Baissa, the Crato Formation and Burmese amber.

The Baissa locality is situated in southern Siberia (western Transbaikalia), ca. 45 km WNW of Romanovka Village in Buryat Republic, Russia [53°17′58.37″N 112° 5′6.95″E]. This is a long (up to 1 km) river cliff on the left bank of the Vitim River ca. 10 km below the mouth of the Baissa River. The deposits belong to the Zaza Formation, the age of which is disputed. It is thought to be contemporaneous with the Yixian Formation of north-eastern China, with the age being Barreman/Aptian based on the flora (Vakhrameev and Kotova, 1977; Bugdaeva, 2010; Bugdaeva and Markevich, 2012). Other authors consider the Zaza Formation to be pre-Barremian (Zherikhin et al., 1999) or Hauterivian/early Barremian based on ostracods (Skoblo and Lyamina, 1986) and the Neuroptera assemblage (Makarkin et al., 2012). In this paper, the age of the Zaza Formation is tentatively considered as Barremian.

The Crato Formation is a well-known Lagerstätte famous for its Early Cretaceous biota located in north-eastern Brazil (see Martill et al., 2007, fig. 2.5). The majority of fossils are found in the finely laminated limestones of the basal Nova Olinda Member, which were deposited in a hypersaline lake or lagoon close to marine environments (Martill et al., 2007; Warren et al., 2017). The preserved plants and animals indicate the predominance of semi-arid to arid climatic conditions in the surrounding area (Menon and Martill, 2007; Mohr et al., 2007; Heimhofer et al., 2010). The age is generally accepted as late Aptian based on the flora and fauna (Martill and Heimhofer, 2007).

Burmese amber originates mainly from the Hukawng Valley in the state of Kachin in northern Myanmar. A map of this valley is given by Grimaldi et al (2002, fig. 1). The biological inclusions of Burmese amber represent a sample of a tropical forest community in equatorial southeastern Asia at ~12°N paleolatitude (Grimaldi et al., 2002; Poinar et al., 2008). The age is currently considered to be late Albian/early Cenomanian. The volcaniclastic matrix of the amber is estimated as ~98.79 ± 0.62 million years old, i.e., earliest Cenomanian (Shi et al., 2012), but the amber is considered to be slightly older, probably latest Albian, as some its pieces bear obvious features of redeposition (Ross, 2015; Grimaldi, 2016).

4. Systematic palaeontology

Order Neuroptera Linnaeus, 1758
Superfamily Myrmeleontoidea Latreille, 1802

Diagnosis. Large to medium-sized Neuroptera, with elongate wings; relatively narrow costal space; ScP and RA distally fused; ScP + RA entering margin after wing apex. Basal aligned crossveins between R, M, and M, Cu present in forewing. M forked very near wing base, and CuP fused with AA1 for some distance in hind wing.

Families included. Nymphidae (Middle Jurassic to Recent), †Palaeoleontidae (Barremian to Coniacian), †Araripeneuridae (Barremian to late Albian/earliest Cenomanian), †Babinskaiidae

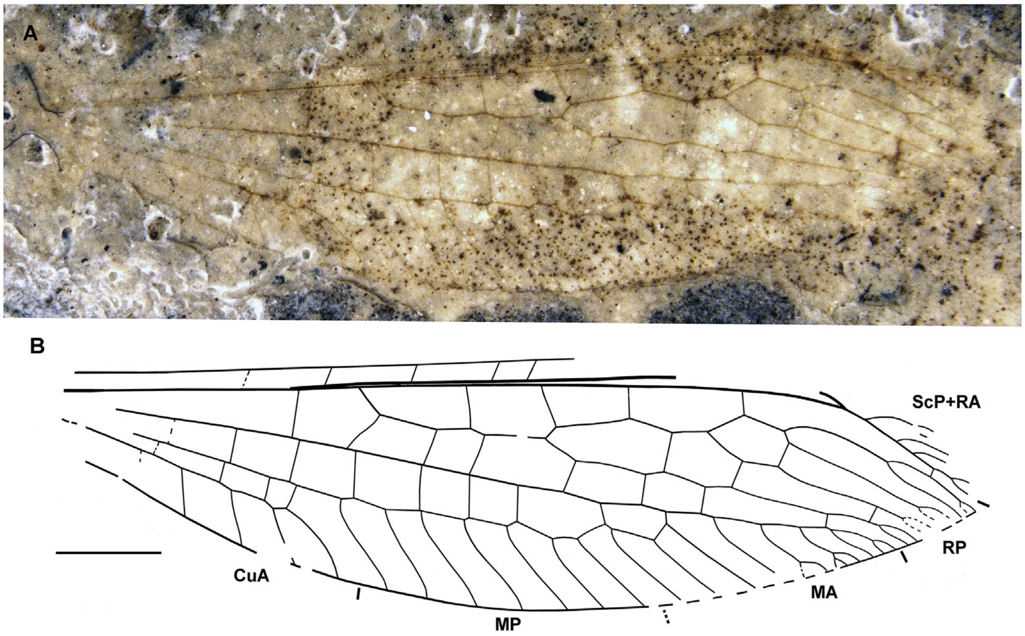


Fig. 1. *Baisonelia vitimica* Ponomarenko, 1992a, holotype PIN 3064/2420. A, specimen as preserved. B, hind wing venation (both converted to right dorsal view). Scale bar represents 1 mm (both to scale).

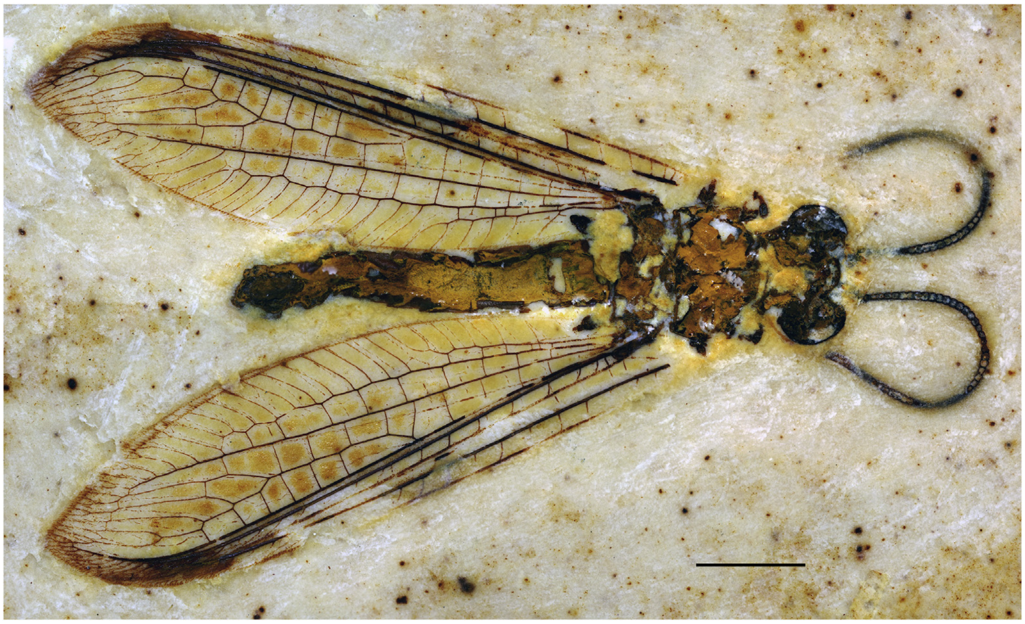


Fig. 2. *Parababinskaia elegans* gen. et sp. nov., holotype INHSP 1508; specimen as preserved (wetted with ethanol). Scale bar represents 2 mm.

(Barremian to late Albian/earliest Cenomanian), Nemopteridae (late Aptian to Recent), Myrmeleontidae (early Eocene to Recent), and Ascalaphidae (early Eocene to Recent).

Remarks. The aligned crossveins 1r-m and 1m-cu in the forewing is probably the only venational autapomorphy of the Myrmeleontoidea. This condition however, is not complete in Babinskaiidae, i.e., only 1m-cu is present, and 1r-m is lost (probably secondarily).

Epifamily Nymphidoidae Rambur, 1842, stat. nov.

Diagnosis. Myrmeleontoids with elongate, filiform antennae; trichosors present, and numerous along posterior margin of wings (i.e., several weak, setiferous thickenings between the tips of two veins); MP (or M) long, not fused with CuA in forewing.

Families included. Nymphidae and †Babinskaiidae.

Family Babinskaiidae Martins-Neto and Vulcano, 1989

Type genus: Babinskaia Martins-Neto and Vulcano, 1989a.

Revised diagnosis. Small myrmeleontoids (forewings 9–12.7 mm long) with the following combination of character states: antennae longer than half of forewing length, with elongate stout scapus. In both wings, several presectoral crossveins present; RP originating very far from wing base; multiple trichosors present along costal and hind margins. In the forewing, 1r-m lost; M single, pectinately

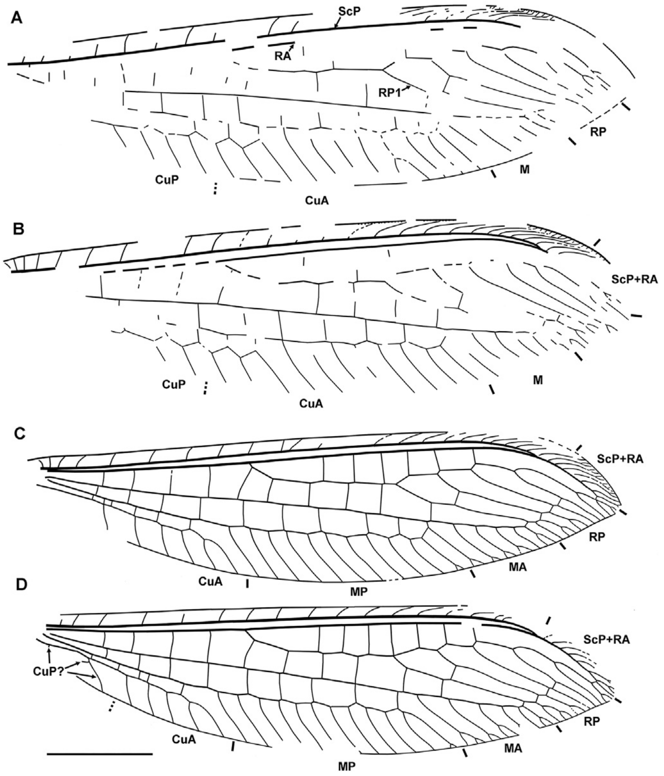


Fig. 3. *Parababinskaia elegans* gen. et sp. nov., wing venation of the holotype INHSP 1508. A, right forewing; B, left forewing; C, right hind wing; D, left hind wing (wings converted to standard view, with apex to the right). Scale bar represents 2 mm (all to scale).

branched distally; not fused with CuA. CuA very long, strongly pectinate; CuP pectinate or slightly pectinate; AA1 forked or simple; AA2, AA3 simple. In the hind wing, MA pectinate; MP strongly pectinate; CuA pectinate to slightly pectinate. CuP, AA1 simple distad fusion or entirely fused with one another in simple vein; AA2, AA3 reduced.

Genera included. Baisonelia Ponomarenko, 1992a from the Barremian Zaza Formation (Transbaikalia, Russia); *Babinskaia* Martins-Neto and Vulcano, 1989a, *Neliana* Martins-Neto, 1992, and *Parababinskaia* gen. nov. from the late Aptian Crato Formation (Brazil); *Burmobabinskaia* Lu et al., 2017, *Electrobabinskaia* Lu et al., 2017 and *Pseudobabinskaia* gen. nov. from the latest Albian/earliest Cenomanian Burmese amber.

Remarks. The reduction of AA2 and AA3 in the hind wing is a clear autapomorphy of the family, and the loss of the basal crossvein 1r-m in the forewing is a possible autapomorphy (see below for details).

Genus ***Baisonelia*** Ponomarenko, 1992

Type and only species: *Baisonelia vitimica* Ponomarenko, 1992a, by original designation.

Revised diagnosis. In hind wing, RP originating at level of termination of CuP [much distad in *Neliana*]; RP with four branches [three in *Pseudobabinskaia*; five or more in other genera (unknown in *Babinskaia*)]; CuA with four branches [one in *Burmobabinskaia*; two in *Neliana*; five in *Electrobabinskaia*, *Parababinskaia*]; three crossveins between stem of RP, M [two in *Neliana*, *Electrobabinskaia*; four-five in *Parababinskaia*]; one crossvein in radial space in outer gradate series [three in *Parababinskaia* and (probably) *Electrobabinskaia*; absent in other genera].

Remarks. The hind wing of *Babinskaia* is known fragmentarily, and the characters included in the diagnosis are unclear. Of other genera, the hind wing of *Baisonelia* is most similar to that of *Electrobabinskaia*; and may be distinguished from it (and other genera) by the combination of venation character states. The validity of the genus, however, should be confirmed by examination of additional characters as soon as a more complete specimen is available.

Baisonelia vitimica Ponomarenko, 1992

Fig. 1

1992a *Baisonelia vitimica* Ponomarenko, p. 48.

Material. Holotype PIN 3064/2420, deposited in PIN. A relatively well-preserved, almost complete hind wing.

Locality and horizon. Russia: Transbaikalia: Baissa locality (layer unknown). Lower Cretaceous: Barremian (Zaza Formation).

Redescription of the holotype. Hind wing elongate, ca. 9.2–9.4 mm long, ca. 2.5 mm wide (estimated). Trichosors not detected. Costal space narrow, with subcostal veinlets simple, straight, widely spaced and slightly oblique. Veinlets of ScP + RA poorly preserved, at least some of them probably forked. No subcostal crossveins detected. RA space broad basally, narrowed distad; with four long crossveins proximad fusion of ScP, RA, and one short distal crossvein distad fusion of ScP, RA. Hypostigmal cell long. RP originating approximately at 0.35 of wing length. Anterior trace of RP zigzagged, shallowly forked apically; with four branches, shallowly forked apically (RP4 simple). Four crossveins detected in radial space: one between RP1, anterior trace of RP; two between RP1, RP2; and one between RP2, RP3. In radiomedial space, at least one presectoral crossveins; three crossveins connecting stem of RP, M; and four crossveins connecting RP1, M. Origin of M not preserved, probably not fused with R. Basal forking of M into MA and MP not preserved, probably very near wing base judging from preserved venation. Anterior traces of MA nearly straight, shallowly forked distally; with six distal pectinate branches: MA1 deeply forked connecting with MA2 with crossvein; MA2, MA3, MA6 simple; MA4, MA5 shallowly forked. Anterior trace of MP straight basally, slightly zigzagged distally, with six pectinate branches not

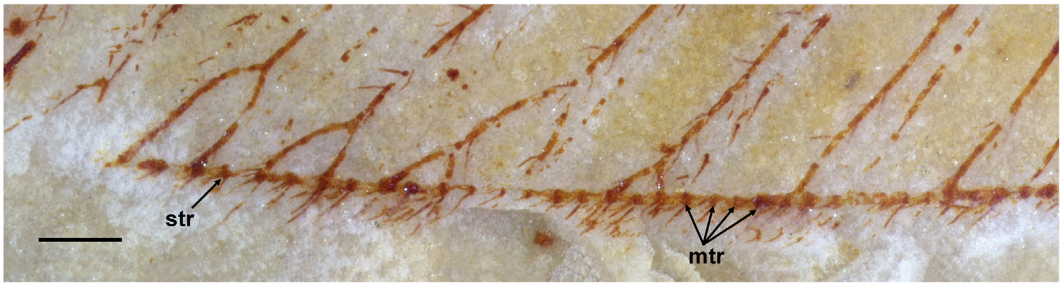


Fig. 4. *Parababinskaia elegans* gen. et sp. nov., holotype INHSP 1508. Posterior margin of the right hind wing showing single (str) and multiple trichosors (mtr). Scale bar represents 0.2 mm.

connected by crossveins. Several (eight detected) widely spaced crossveins in intramedial space. Origin of Cu and its division into CuA and CuP not preserved. CuA pectinate, with two four simple branches. At least four crossveins detected in cubitoanal space. CuP, anal veins not preserved.

Genus ***Parababinskaia*** gen. nov.
Type and only species: *Parababinskaia elegans* sp. nov.

Derivation of name. From the Greek *para*, beside, near, and *Babinskaia*, a genus-group name.
Diagnosis. In forewing, RP originating slightly distad termination of CuP [much more distad in *Neliana*]; four-five crossveins between stem of RP, M [three in *Babinskaia*; *Electrobabinskaia*, *Pseudobabinskaia*; two-three in *Neliana*; one in *Burmobabinskaia*]; six branches of RP [three-four in *Babinskaia*, *Pseudobabinskaia*; five in *Neliana*; eight in *Electrobabinskaia*]. In hind wing, RP originated slightly distad termination of CuP [much more distad in *Neliana*]; four-five crossveins between stem of RP, M [two in *Neliana*, *Electrobabinskaia*, *Pseudobabinskaia*; three in *Baisonelia*]; five branches of RP [three in *Pseudobabinskaia*; four in *Baisonelia*; eight in *Electrobabinskaia*]; three crossveins in radial space in outer gradate series [absent in *Neliana*, *Pseudobabinskaia*; one on *Baisonelia*]; CuA with five branches [one in *Burmobabinskaia*; two in *Neliana*; four in *Baisonelia*].
Remarks. The venation of the new genus is most similar to that of *Electrobabinskaia* and *Baisonelia*, and may be distinguished from these (and other genera) by its combination of wing character states (see above). Two other genera of Crato babinskaiids, *Babinskaia* and *Neliana*, differ from *Parababinskaia* gen. nov. by a more simple venation (i.e., fewer branches and crossveins).

Parababinskaia elegans sp. nov.
Figs. 2–4

Derivation of name. From the Latin *elegans*, elegant, graceful, fine.
Material. Holotype INHSP 1508. An almost complete specimen, with fore- and hind wings overlapping pairwise. The forewing venation is hardy visible, but the venation of the hind wings is well preserved.
Locality and horizon. Northeastern Brazil: Chapada do Araripe (precise locality unknown). Lower Cretaceous: upper Aptian (Crato Formation: Nova Olinda Member).
Description. Head transverse, with large eyes; slightly wider than mesothorax. Antennae filiform; scapus, pedicellus poorly visible; flagellum consists of nearly quadrate flagellomeres. Prothorax very short. Legs not preserved (only their basal portions visible). Abdomen completely, but very poorly preserved (ca. 7 mm long); details of terminal segments unclear (sex unknown).

Forewing elongate with sub-acute apex, ca. 12.0–12.3 mm long, 3.3 mm wide. Trichosors single along apical margin; multiple trichosors (up to five between veins) along costal (apically), posterior margins; no trichosors detected along proximal part of costal margin. Costal space narrow proximad fusion of ScP, RA, slightly dilated thereafter. Most subcostal veinlets simple, several distal ones forked once to twice near margin; relatively close spaced basally, rather widely spaced medially, close spaced and strongly curved distally. ScP + RA entering margin beyond wing apex; its branches poorly preserved. No subcostal crossveins detected. RP originating far from wing base, at 0.36 of wing length; its anterior trace zigzagged. RA space broad basally, narrow distally, with three preserved crossveins proximad fusion of ScP, RA (estimated total number of crossveins is four in right wing, and five in left); no preserved crossveins detected distad fusion of ScP, RA. RP with six branches, most of these forked; RR1 originating far from origin of RP; one long crossvein in radial space connecting RP1, RP2, and two preserved short crossveins forming outer series. In radiomedial space, six presectoral crossveins in right wing, three preserved crossveins in left wing; four preserved crossveins connecting stem of RP, M in right wing (total number probably five), three preserved crossveins in left wing (total number probably four); and two crossveins connecting RP1, M in right wings, three in right wing. M almost straight, with four-five pectinate branches distally. At least 10 crossveins between M, CuA. Anterior trace of CuA long, slightly zigzagged, almost parallel to M and hind margin, with 10 pectinate simple branches (except one, which is deeply forked in right wing); basal branches connected by two crossveins. At least three crossveins between CuA, CuP; distal crossvein together with those between branches of CuA form short gradate series. CuP with at least three pectinate branches. Anal veins not preserved.

Hind wing elongate with acute apex; 11.4 mm long, 2.7 mm wide. Trichosors as in forewing. Costal space narrow. Subcostal veinlets simple; relatively closely spaced basally, rather widely spaced medially, closely spaced and strongly curved distally. ScP + RA entering margin at or slightly beyond wing apex; its veinlets strongly curved, mostly shallowly forked. No subcostal crossveins detected. RA space broad basally, narrowed distad; with six long crossveins proximad fusion of ScP, RA in right wing, seven in left wing; and one short distal crossvein distad fusion of ScP, RA. Hypostigmal cell long. RP originating far from wing base, at 0.37 of wing length. Anterior trace of RP zigzagged, shallowly forked apically; with six branches in right wing, five branches in left wing; RP1 originating far from origin of RP, twice forked distally; RP2 once shallowly forked; other branches simple. Four crossveins in radial space: one long between RP1, RP2; two short between RP1, RP4 forming outer gradate series. In radiomedial space, four presectoral crossveins; five crossveins connecting stem of RP, M in right wing, four in left wing; and two crossveins connecting RP1, M in right wing, three in left wing. M forked very basally. Anterior trace of MA straight, shallowly forked distally; with five pectinate, shallowly forked branches, except distal-most which is simple. Anterior trace of MP slightly incurved, shallowly forked distally; with 10–11 pectinate, simple long branches, not connected by crossveins. Nine (left wing) to ten (right wing) crossveins in intramedial space. Five (left wing) to six (right wing) preserved crossveins in mediocubital space. CuA pectinate, with five simple branches. One incomplete crossvein detected in intracubital space. Only basal part of CuP preserved. Crossvein between CuA, CuP (icu) connects basal-most branches of CuA (left wing). Anal veins not preserved.

Genus ***Neliana*** Martins-Neto, 1992
1989b *Nelia* Martins-Neto and Vulcano, p. 316 [nomen praeoccupatum, non *Nelia* Hayward, 1953: 44 (Lepidoptera: Satyridae)].
1992 *Neliana* Martins-Neto, pp. 118 [nomen novum pro *Nelia* Martins-Neto and Vulcano, 1989b].
Type species: *Nelia maculata* Martins-Neto and Vulcano 1989b, by original designation.

Revised diagnosis. In both wings, RP originating far distal to termination of CuP; two crossveins between stem of RP, M; no crossveins in radial space in outer gradate series. In forewing, RP with five-six branches. In hind wing, RP with three to five branches; CuP with two pectinate branches.
Species included. Neliana maculata (Martins-Neto and Vulcano, 1989) and *N. impolluta* Martins-Neto, 1997 from the Crato Formation.
Remarks. The genus is clearly distinguished from other genera of the family by the very distal origin of RP.

Neliana maculata (Martins-Neto and Vulcano, 1989)
Figs. 5–8

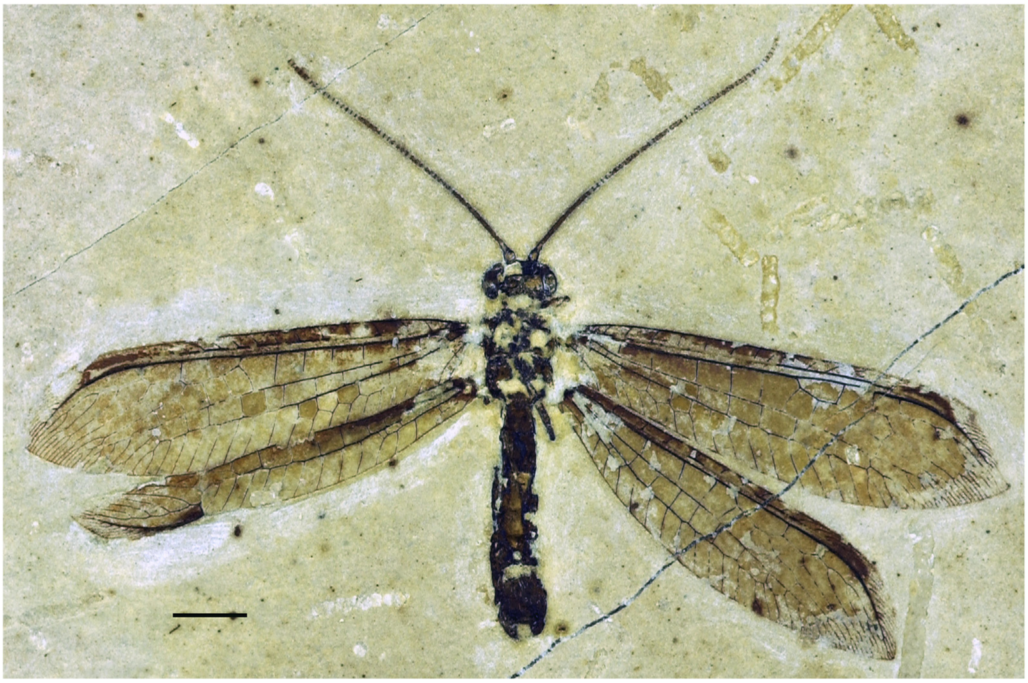


Fig. 5. *Neliana maculata* (Martins-Neto and Vulcano, 1989b); male specimen SMNS 66000/257 as preserved (in dry condition). Scale bar represents 2 mm.

1989b *Nelia maculata* Martins-Neto and Vulcano, p. 316;
2007 Chrysopidae: Martins-Neto et al., fig. 11-69;
2016a An undescribed species of Babinskaiidae: Makarkin, fig. 5d.

Material examined. Specimen SMNS 66000/257. A complete and well-preserved specimen exposed in ventral aspect with all wings outspread (right hind wing is longitudinally folded up).

Locality and horizon. Brazil: Chapada do Araripe (precise locality unknown). Early Cretaceous: upper Aptian (Crato Formation: Nova Olinda Member).

Diagnosis. RP in both wings with five–six branches [two-three branches in *N. impolluta*].

Description of the specimen SMNS 66000/257. Head transverse (in ventral view), 1 mm long, 2 mm wide; slightly wider that mesothorax. Eyes relatively large. Antennae 9 mm long (left antenna probably complete); scapus stout, elongate; pedicel much thinner than scapus, elongate; flagellum consists of 53 short flagellomeres. Prothorax very short. Only right metafemur completely preserved, 2 mm long. Abdomen ca. 6.5 mm long, visible in ventral view. Eighth sternite relatively narrow. Ninth sternite large, nearly

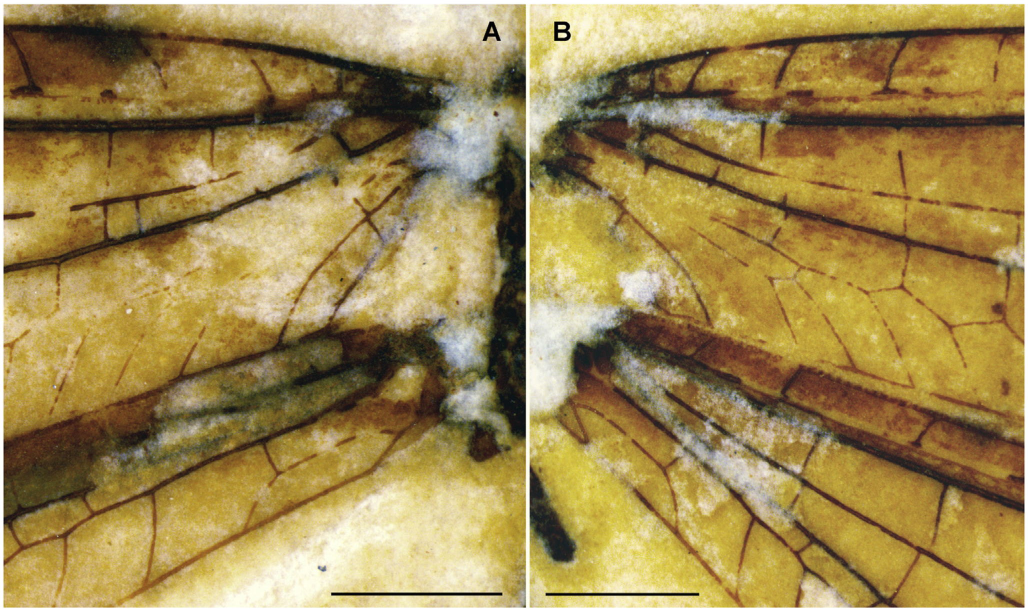


Fig. 6. *Neliana maculata* (Martins-Neto and Vulcano, 1989b), specimen SMNS 66000/257. Proximal part of wings (wetted with ethanol). A, right wings. B, left wings (the specimen is preserved in ventral aspect). Scale bars represent 1 mm.

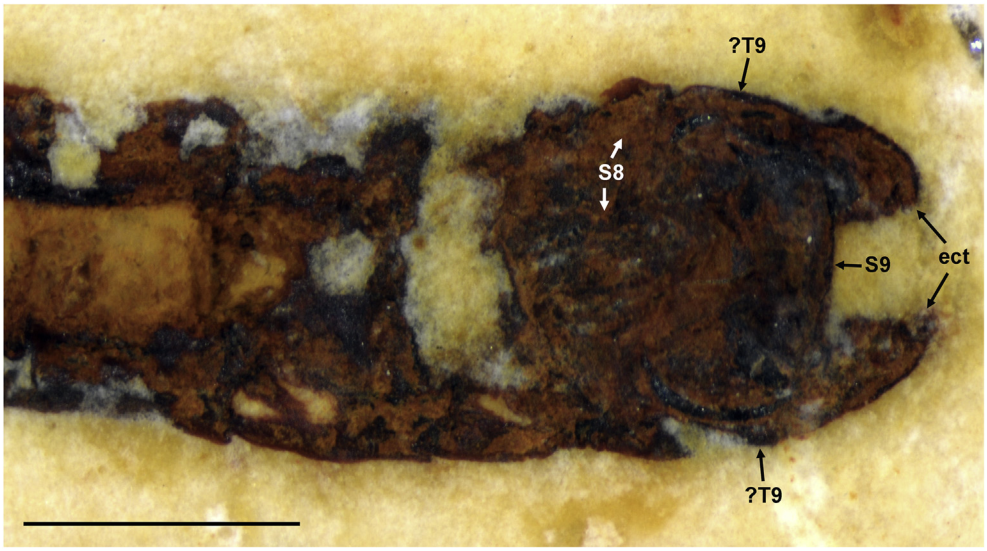


Fig. 7. *Neliana maculata* (Martins-Neto and Vulcano, 1989b), specimen SMNS 66000/257. Distal part of abdomen (wetted with ethanol), ventral view. ect, ectoptoct; S8, S9, 8th and 9th sternite; T9, 9th tergite. Scale bar represents 1 mm.

rounded in ventral view. Ectoprocts elongate, far extending beyond 9th sternite.

Forewing elongate with sub-acute apex, 12.7 mm long, 3.4 mm wide. Trichosors absent along proximal parts of costal, posterior margins; single along apical margin; multiple along distal parts of costal, posterior margins. Costal space relatively narrow proximad fusion of ScP, RA, dilated thereafter. Subcostal veinlets simple, widely spaced in proximal two-thirds; closely spaced, strongly curved with one-two short branches distally; stouter in pterostigmal region. ScP in pterostigmal region pale, poorly visible; probably fused with RA, but this fusion poorly visible. Presumed ScP + RA entering margin slightly after wing apex; its branches (eight-nine in number) mainly once forked; no crossveins between them detected. Subcostal space relatively broad; no crossveins detected. RA space broad basally, narrow distally; with three crossveins proximad fusion of ScP, RA, no crossveins detected distad fusion. RP originating very far from wing base, exactly at half of wing length; its anterior trace zigzagged, with five branches; RR1 originating relatively close to origin of RP, dichotomously forked distally; all other branches deeply forked (except one distal in right wing); only one long crossvein in radial space connecting RP1, RP2. In radiomedial space, five presectoral crossveins in left wing, six in right wing; two crossveins connecting stem of RP, M in left wing, three in right wing; and three crossveins connecting RP1, M. Anterior trace of M slightly arched, with three pectinate branches in left wing (proximal-most branch pectinate with two branches; other branches shallowly forked), four branches in right wing (all forked). Eleven-third crossveins between M, CuA. Anterior trace of CuA long, slightly zigzagged distally, almost parallel to hind margin, with 11–12 pectinate simple branches except distal-most, which is deeply forked; four basal-most branches connected by three crossveins forming gradate series. Three crossveins between CuA, CuP; distal crossvein continues gradate series between branches of CuA. CuP with one (left wing), two pectinate branches (right wing). AA1 deeply forked. One distal crossvein between CuP, AA1 connects CuP proximad forking, anterior branch of fork of AA1. AA2, AA3 rather long, simple. Nearly aligned crossveins between AA1, AA2, and AA2, AA3.

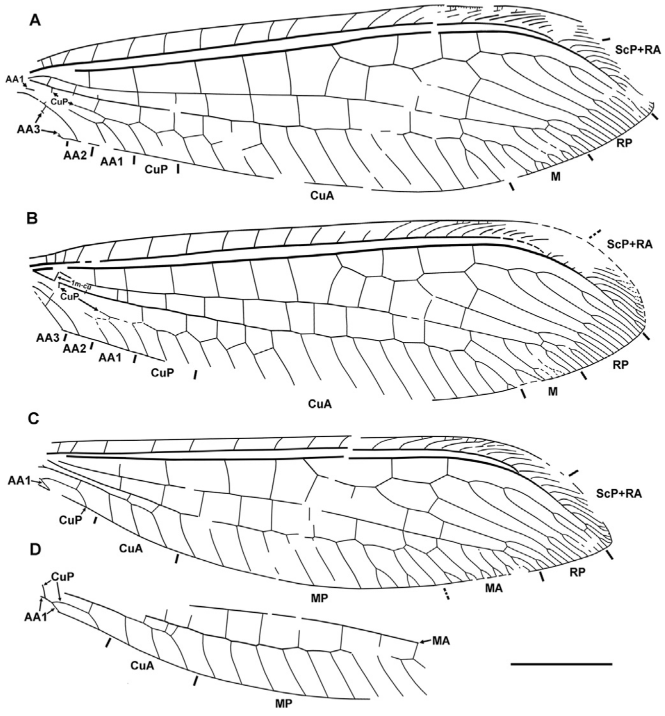


Fig. 8. *Neliana maculata* (Martins-Neto and Vulcano, 1989b), wing venation of the specimen SMNS 66000/257. A, left forewing; B, right forewing. C, left hind wing. D, right hind wing (wings converted to standard view, with apex to the right). Scale bar represents 2 mm (all to scale).

Hind wing elongate, with pointed apex, 11.7 mm long, 2.8 mm wide. Trichosors absent along proximal parts of costal, posterior margins; single along apical margin; multiple along distal parts of costal, posterior margins. Costal space narrow proximad fusion of ScP, RA, slightly dilated after. Subcostal veinlets simple, widely spaced in proximal two-thirds; closely spaced, strongly curved with one-two short branches distally. ScP poorly visible in pterostigmal region, probably fused with RA. Presumed ScP + RA entering wing margin slightly after apex. No subcostal crossveins detected. RA space in general as in forewing, with two crossveins proximad fusion of ScP, RA, one short distad fusion; hypostigmal cell long. RP originating very far from base, at 0.44 of wing length; its anterior trace zigzagged, rather deeply forked apically; with five pectinate branches; RP1 originating relatively close to origin of RP, twice forked distally; all other branches deeply forked (except one distal, which is simple); only one long crossvein in radial space connecting RP1, RP2. In radiomedial space nine crossveins, of these four presectoral; two connecting stem of RP, M, and three connecting RP1, M. Origin of M poorly preserved, forked into MA and MP probably very near wing base. Anterior trace of MA straight, with five pectinate branches (all shallowly forked); MA1, MA2 connect with crossvein. MP long, slightly incurved, somewhat zigzagged distally; with nine simple branches (except two forked distal in left wing), not connected by crossveins. In intramedial space at least eight crossveins, of these distal-most short. At least three crossveins between MP, CuA. CuA pectinate, with two simple, widely spaced branches. CuP short, simple; fused for short distance with AA1. One crossvein between CuA, CuP. AA1 very short, simple. AA2, AA3 not detected.

Remarks. A total of four specimens from the Crato Formation are assigned to this species, including the specimen described herein. The holotype is an almost complete specimen in dorso-lateral aspect from the vicinity of Santana do Cariri (Martins-Neto and Vulcano, 1989b). Two other specimens are an almost complete specimen from Mina Pedra Branca (assigned to this species by Martins-Neto, 1994), and an incomplete specimen from Mina Pedra Branca (assigned to this species by Martins-Neto, 1998).

The holotype is thought to have conspicuous colour pattern on the wings (see Martins-Neto, 1992, fig. 17A). However, this drawing shows that left and right wings have strongly dissimilar patterns. Wings of other specimens assigned to this species do not have such a colour pattern (see Martins-Neto, 1994, pl.1B, C; Martins-Neto, 1998, pl. 1A, B). The specimen SMNS 66000/257 also lacks a distinct pattern (Fig. 5). So, the colour pattern of the holotype may be false.

Genus ***Pseudobabinskaia*** *gen. nov.*
Type only species species: *Babinskaia martinsnetoi* Lu et al., 2017.

Derivation of name. From the Greek *pseudos*, false, and *Babinskaia*, a genus-group name.
Diagnosis. In both wings, RP originating slightly distal to termination of CuP; three crossveins between stem of RP, M; no crossveins in radial space in outer gradate series. In forewing, four branches of RP; branches of CuA short; AA1 simple. In hind wing, three branches of RP; branches of MP short; CuP with very three short pectinate branches; AA2, AA3 distally fused.

Pseudobabinskaia martinsnetoi (Lu et al., 2017), comb. nov.
Babinskaia martinsnetoi Lu et al., 2017, p. 15.

Material. Holotype PCXJ BA-0006, currently deposited in the Entomological Museum, China Agricultural University, Beijing, and will eventually be deposited in the Three Gorges Entomological Museum, Chongqing (according to Lu et al., 2017). A complete female specimen in amber.
Locality and horizon. Myanmar: Burmese amber (Hukawng Valley). Lower Cretaceous: upper Albian/Upper Cretaceous: lowest Cenomanian.
Remarks. The assignment of this species to the genus *Babinskaia* is erroneous. It differs from species of *Babinskaia* by the simple AA1 in the forewing (AA1 is deeply forked in *Babinskaia*; see Martins-Neto and Vulcano, 1989a, fig. 8B). In this respect, *Pseudobabinskaia* gen. nov. is similar to other Burmese amber babinskaiids in having the simple AA1, and *Babinskaia* is similar to *Neliana* in having the forked AA1 (Fig. 8A, C). Also, the branches of CuA in the forewing and the branches of MP in the hind wing are relatively short in *Pseudobabinskaia* gen. nov.; those in other genera are markedly longer (see Lu et al., 2017, fig. 1b). Finally, AA2 is distally fused with AA3 in the forewing of this species, whereas these veins (when preserved) in other genera are separate.

5. Discussion

5.1. Comparative characteristics of the wing venation of Babinskaiidae

The family Babinskaiidae is a rather homogeneous taxon, whose species differ mainly in small details of the venation (and by genitalia where these are known). The oldest known species, *Baisonelia vitimica* from the Barremian of Transbaikalian Russia, does not principally differ from the youngest known taxa, from the latest Albian/earliest Cenomanian Burmese amber.

5.1.1. Trichosors
In Babinskaiidae, trichosors are single along the apical margin and multiple along distal parts of the costal and posterior margins in the fore- and hind wings (Fig. 4; see Makarkin, 2017 for types of trichosors). Similar trichosors are present in Nymphidae – single along the apical margin, and multiple along the posterior margin (see Archibald et al., 2009, fig. 2; Shi et al., 2013, fig. 5). All other myrmeleontoid taxa lack trichosors (except for the genera *Cratosmylus* Myskowiak et al., 2015 and *Araripenymphes* Menon et al., 2005 from the Crato Formation whose systematic position is unclear (see below). The presence of trichosors is one of most striking autapomorphies of Neuroptera, and a plesiomorphic state within the order.

5.1.2. Distal ScP + RA
ScP + RA entering the margin after the wing apex as found in Babinskaiidae is characteristic of all Myrmeleontoidea. This condition occurs also in the chrysopoids, i.e., some Chrysopidae (e.g., the Mesozoic Limaiinae) and Ascalochrysidae. In Mesochrysopidae, ScP + RA enters the margin usually at the wing apex. Therefore, this character state is a putative synapomorphy of Myrmeleontoidea + Chrysopoidea (see Yang et al., 2012, fig. 32).

5.1.3. Origin of RP
The distal origin of RP from the wing base as found in Babinskaiidae also occurs in Nemopteridae (only forewings), and some Myrmeleontidae and Ascalaphidae. This is a clear apomorphic state in the order. Generally, the distal origin of RP is characteristic of the majority of Araripeneuridae, Myrmeleontidae, and Ascalaphidae. However, this condition in these groups may not be considered necessarily apomorphic within the order, as in most Permian Permithonidae RP clearly originates distally from the wing base (see e.g., Vilesov, 1995, fig. 2b; Novokshonov, 1996, fig. 5). RP originates near the wing base in Nymphidae and Palaeoleontidae. Again, this condition is not necessarily plesiomorphic in the order as it rarely occurs in Permian Neuroptera.

5.1.4. Presectoral crossveins
These crossveins connect R and M proximad the origin of RP and distal to the basal oblique crossvein 1r-m (the latter is absent in Babinskaiidae). In the Myrmeleontoidea, they are characteristic of both wings of Babinskaiidae, Myrmeleontidae and Ascalaphidae, and the forewings of Nemopteridae. Most Araripeneuridae lack these crossveins, which were nevertheless detected in a few species (e.g., Martins-Neto, 1994, fig. 2E; 2003, figs. 1B, 2D). Presectoral

crossveins are absent in Nymphidae and Palaeoleontidae due to the origin of RP close to the wing base. In other Neuroptera, several presectoral crossveins may only be found in Kalligrammatidae and Aetheogrammatidae, although RP usually originates close to the wing base in these families, which are generally characterized by numerous and closely spaced crossveins.

5.1.5. *Interrelation between M and CuA in the forewing*

The M of Babinskaiidae is single, not dividing into a long MA and MP. Martins-Neto (2003, 2005) believed that MP and CuA are fully fused in Babinskaiidae, like in higher Myrmeleontoidea (e.g., Myrmeleontidae, Ascalaphidae). However, the basal part of MP ('oblique vein') is not detectable in any species of Babinskaiidae. Moreover, the CuA space has a structure that is unlike that of the MP + CuA space in higher Myrmeleontoidea. So, there is no evidence for the fusion of M and CuA in Babinskaiidae.

In Nymphidae, M is deeply forked distal to the origin of RP in most extant species, but single (or shallowly forked) in many species in four genera (of seven): two species of *Nymphes* Leach, 1814, and all species of *Austronymphes* New, 1982, *Umbranymphes* New, 1988 and *Myiodactylus* Brauer, 1866 (New, 1982, 1988). The configuration of M in these species is generally similar to that of Babinskaiidae. Noteworthy, however, that M is deeply forked proximad the origin of RP in all known fossil species of Nymphidae. In no species of Nymphidae is M fused with CuA.

5.1.6. *CuA in the forewing*

The pectinate CuA in Babinskaiidae is most similar to that of Nymphidae, especially to that of the Early Cretaceous genus *Baissoleon* Makarkin, 1990, whose two species are relatively small in size (see Makarkin, 1990, fig. 1; Shi et al., 2015, fig. 11). In this genus, the branches of CuA are widely spaced and simple, and the proximal branches are connected by a crossvein, a configuration very similar to that found in all Crato genera of Babinskaiidae (see Figs. 3, 8; Martins-Neto and Vulcano, 1989a, figs. 8A, B). The branches of CuA in the Burmese amber genus *Electrobabinskaia* are longer, closely spaced and shallowly forked. This configuration is somewhat similar to that of some other Nymphidae (e.g., Shi et al., 2013, fig. 8). In other myrmeleontoids CuA is fused with MP.

5.1.7. *CuP in the forewing*

The configuration of CuP in the forewing of Babinskaiidae is hardly determined with certainty as its distal part is strongly zigzagged and continues in a gradate series between the branches of CuA. In general, this state is most similar to that of Nymphidae. CuP in *Babinskaia* and *Neliana* is pectinate, but with only one or two branches, a condition most similar to that of the Early Cretaceous nymphid genus *Baissoleon* (one branch). CuP in other babinskaiids is strongly pectinate (more than four branches), as in all nymphid species. The strongly pectinate CuP is also characteristic of most Osmylidae, Psychopsidae, and other Myrmeleontoidea. However, the configuration of CuP (or CuP + AA1) in these is dissimilar to that of Babinskaiidae in that CuP is not zigzagged and does not continue in a gradate series between the branches of CuA.

5.1.8. *M in the hind wing*

M dividing into MA and MP very close to the wing base is characteristic of all Myrmeleontoidea. A common basal stem of M is usually absent or very short. M is forked very proximally also in the osmylid clade (i.e., in Osmylidae, Saucrosmylidae, and Grammolingiidae), but a common basal stem of M is always rather long in Osmylidae.

5.1.9. *Interrelation between CuP and AA1 in the hind wing*

CuP is basally crossvein-like and then fused for some distance with AA1 in the hind wing in almost all Myrmeleontoidea. This is also true for those fossil species in which the basal part of the hind wing is well preserved. e.g., the nymphid *Sialium sinicus* Shi et al., 2015 (Shi et al., 2015, fig. 13c); the palaeoleontid *Baisopardus banksianus* Ponomarenko, 1992 (Ponomarenko, 1992a, fig. 5a); the araripeneurid *Burmaneura minuta* Huang et al., 2016 (Huang et al., 2016, fig. 3B). This interrelation between CuP and AA1 can also be seen in Babinskaiidae (Fig. 8D). In Burmese amber babinskiids, the distal parts of CuP and AA1 are entirely fused (Lu et al., 2017, figs. 1b, 3c, 5c). The only documented exception is some extant Palparinae (Myrmeleontidae), in which these veins are separate.

Similar interrelation between CuP and AA1 occurs in the chrysopid Mesochrysopidae and Ascalochrysidae (see Ponomarenko, 1992a, fig. 4b; Ren and Makarkin, 2009, fig. 3). Ren and Makarkin (2009) interpreted CuP being nearly completely reduced in these families (except a basal crossvein-like remnant). However, this may also be treated as the distal part of CuP entirely fused with AA1, as in the Burmese amber Babinskaiidae.

Moreover, CuP and AA1 are partially fused (or at least touch) in the hind wing of many Chrysopidae of different subfamilies (see for example Tjeder, 1966, figs. 784–786, 805; Adams, 1967, fig. 1). In particular, these veins are fused in *Leptochrysa prisca* Adams and Penny, 1992a (see Adams and Penny, 1992a, fig. 10; Adams and Penny, 1992b, fig. 11). This species is assumed to be a single extant representative of the mostly Mesozoic subfamily Limaiinae (Makarkin and Archibald, 2013). In other Chrysopidae, CuP and AA1 are connected by a very short crossvein.

The partial fusion of CuP and AA1 in the hind wing may be considered a putative synapomorphy of the clade Myrmeleontoidea + Mesochrysopidae + Ascalochrysidae (see Yang et al., 2012, fig. 32). In this case, the fully separate CuP and AA1 in Palparinae is probably a reversal, not a primary (plesiomorphic) state.

5.1.10. *Anal veins in the hind wing*

Three anal veins are plesiomorphically present in Neuroptera, but only one (short AA1 fused with CuP) is detected in Babinskaiidae. This condition is visible in the Burmese amber species (Lu et al., 2017, figs. 1B, 3B, 5C). The hind wing anal region in the examined specimen of *Neliana maculata* is most well preserved among impression fossil babinskaiids. In this specimen, an area posterior to AA1 is so small that the loss of AA2 and AA3 is the most probable assumption (Fig. 6A). The presence of AA1, which then is fused with CuP, is characteristic of all Myrmeleontoidea (see above). AA2 and AA3 are present in all Myrmeleontidae (see Riek, 1967, figs. 5B, D, E, F) and Nymphidae, including those Mesozoic species which have well-preserved basal parts of the hind wing (see Ponomarenko, 1992a, fig. 1b; Shi et al., 2015, fig. 13c). In Ascalaphidae, AA2 and AA3 are "more or less reduced and fused with one another" (Tjeder, 1992, p. 25). In Araripeneuridae, short AA2 and AA3 veins are detected in the Burmese amber *Burmaneura minuta* (Huang at al., 2016, fig. 4B). Anal veins are poorly preserved in all known Palaeoleontidae, but it appears that at least a short, simple AA2 is present (see Ponomarenko, 1992a, fig. 5a). The hind wings of Nemopteridae are strongly specialized, and their anal veins are not detectable.

Therefore, the reduction of AA2 and AA3 is a putative autapomorphy of Babinskaiidae. The same condition in some Ascalaphidae has certainly evolved independently, as their venation is most similar to that of Myrmeleontidae, which is distantly related to Babinskaiidae.

5.1.11. *Male genitalia*

The male terminalia of the examined Crato Formation *Neliana maculata* are rather plesiomorphic, with a large 9th sternite and well-developed ectoprocts (Fig. 7). These are probably similar to those of the Burmese amber *Burmobabinskaia tenuis* Lu et al., 2017 if seen in ventral view (Lu et al., 2017, figs. 2F, G). However, the 9th sternite of *Electrobabinskaia burmana* Lu et al., 2017 is smaller, but the ectoprocts are larger (Lu et al., 2017, figs. 4C, D). Inner genitalic structures are hard to interpret although Lu et al. (2017) found that those of *Electrobabinskaia* "show morphological similarities to that of Nymphidae in having paired, ventrally positioned gonocoxites 9 and a large, dorsally positioned arc (= gonocoxites 11)" (p. 22).

5.1.12. *Female genitalia*

The female terminalia are only known in the Burmese amber *Pseudobabinskaia martinsnetoi*. These are amazing in possessing a pair of finger-like gonocoxites 9, which are superficially very similar to gonocoxites 8 of Myrmeleontidae (see Lu et al., 2017, figs. 1C, D). It is unknown yet if this is an autapomorphy of the family or only of the genus. In any case, such structures of gonocoxites 9 do not occur in other Myrmeleontoidae.

5.2. *Systematic and phylogenetic position of Babinskaiidae*

The myrmeleontoid affinity of Babinskaiidae is based on the presence of a set of some character states in the venation, especially: (1) ScP + RA enters the margin after the wing apex in both wings, and (2) M is divided into MA and MP very close to the wing base. The venation of chrysopoids (i.e., Chrysopidae, †Mesochrysopidae, and †Ascalochrysidae), which possesses character state (1), and osmyloids (i.e., Osmylidae, †Saucrosmylidae, and †Grammolingiidae), which possesses also character state (2), strongly differs from Babinskaiidae in other aspects.

The superfamily Myrmeleontoidea includes seven families: Nymphidae, Myrmeleontidae, Ascalaphidae, Nemopteridae, †Palaeoleontidae, †Araripeneuridae, and †Babinskaiidae. The extant Myrmeleontoidea are considered to constitute a monophyletic clade by the majority of authors (e.g., Haring and Aspöck, 2004; Winterton et al., 2010; Beutel et al., 2010a,b; Wang et al., 2017). However, extinct families are rarely included in such phylogenies. When included, the Myrmeleontoidea turned out to be a non-monophyletic group. For example, according to Grimaldi and Engel (2005, fig. 9.4) the monophyletic Myrmeleontiformia contain also psychopsoid families, and the families of Myrmeleontoidea do not form a monophyletic clade.

According to the phylograms of Yang et al. (2012, fig. 32) and Makarkin et al (2013, fig. 7) the families of Myrmeleontoidea form a monophyletic clade together with those of Chrysopoidea. The monophyly of the clade Myrmeleontoidea + Chrysopoidea exclusive Chrysopidae (i.e., Mesochrysopidae and Ascalochrysidae) is supported by at least two synapomorphies: (1) the jugal lobe is reduced in the forewing (see Yang et al., 2012), and (2) CuP is basally crossvein-like, then partially fused with AA1 in the hind wing (see above analysis). We found that the monophyly of all Myrmeleontoidea, fossil and extant, is supported by at least one venational character state, i.e., aligned oblique basal crossveins 1r-m and 1m-cu. It is well developed in Myrmeleontidae, Ascalaphidae, many Nemopteridae (secondarily lost in Crocinae), those Araripeneuridae in which the basal part of the hind wing is well preserved (e.g., Ponomarenko, 1992b, fig. 8), Nymphidae (more primitive, see Riek, 1967, figs. 3B, D, F), and Palaeoleontidae (see Myskowiak and Nel, 2016, fig. 5; 1r-m is not clearly visible). In Babinskaiidae, 1r-m is probably reduced and 1m-cu is present (see Lu et al., 2017, figs. 1B, 5C). Chrysopoidea differ from Myrmeleontoidea by the relatively short and not strongly pectinately branched M in both wings, a possible synapomorphy of Chrysopoidea. Nevertheless, this group may be paraphyletic with respect to Myrmeleontoidea as this character state is weak and may be homoplasious.

The phylogenetic position of the family Babinskaiidae within Myrmeleontoidea was uncertain. A cladistic analysis of the phylogenetic relationships of the neuropteran genera of the Crato Formation revealed that the genera of Babinskaiidae are an adelphotaxon of the clade comprising genera of Ascalaphidae, Nemopteridae (s.l.), Myrmeleontidae, Palaeoleontidae and Araripeneuridae (Martins-Neto, 2003, fig. 9; Martins-Neto, 2005, fig. 4). According to Martins-Neto (2003, 2005) this placement is supported by two synapomorphies of Babinskaiidae: (1) the long forewing M + CuA ['MP + CuA1' of the author] reaches the apical margin, and (2) the forewing CuP is zigzag-like. Both these character states are not synapomorphies of the family (see above analysis), and so this phylogenetic position of Babinskaiidae is unsupported. Later, it was assumed that Babinskaiidae (and Araripeneuridae) "likely represent stem groups to the entire Nymphidae-Myrmeleontidae-Ascalaphidae clade." (Martins-Neto et al., 2007, p. 334). On the other hand, the family Babinskaiidae was assigned to the superfamily Nymphoidea in one of these papers (Martins-Neto, 2003, table 1).

Other authors believed that Babinskaiidae are most closely related to Ascalaphidae and Myrmeleontidae. These three families form a trichotomy (Grimaldi and Engel, 2005, fig. 9.4; Jepson and Penney, 2007, fig. 2), or the Babinskaiidae is considered as the sister group to the other two (Engel and Grimaldi, 2008, fig. 2). No arguments were provided to explain this phylogenetic position.

Finally, Lu et al. (2017) proposed "a thought-provoking hypothesis that Babinskaiidae might be closely related to Nemopteridae", and that "some nemopterid-like larvae in Burmese amber might be associated with babinskaiids" (p. 22). This hypothesis is based on the fact that the hind wings of *Burmobabinskaia* are strongly narrow, similar to the extremely long and narrow hind wings of Nemopteridae. The crocine-like larvae occurring in Burmese amber are very similar to those of Crocinae (Nemopteridae) in having a long cervix, but differ from the latter by the presence of 4–10 elongated teeth on the jaws. Unfortunately, no larvae were hitherto described in detail, although some are mentioned with photographs (Xia et al., 2015, figs. on pp. 99, 100). However, we believe that these larvae may belong to Araripeneuridae, which are most closely related to Nemopteridae (Makarkin et al. in preparation). The hind wings of some species of Araripeneuridae may also be narrow (see e.g., Martins-Neto and Vulcano, 1989a, fig. 6C; Martins-Neto, 2003, fig. 1B).

Our morphological analysis shows that the family is characterized by a mixture of character states. On the one hand, there are some plesiomorphic states at superfamily level, e.g., the presence of trichosors, and M and CuA fully separate. On the other, clearly apomorphic states are present, e.g., the distal origin of RP; the presence of several presectoral crossveins; the single M in the forewing; and the reduction of AA2 and AA3 in the hind wing. The latter is probably the only venational autapomorphy of the family.

Our data support the hypothesis that Babinskaiidae are most closely related to Nymphidae. These two myrmeleontoid families form an epifamily Nymphidoidae, whose MP (or M) is long, not fused with CuA, and trichosors are present. All other myrmeleontoids belong to another epifamily, Myrmeleontoidae, whose MP is crossvein-like, then fused with CuA, and trichosors are lost. A detailed review of the latter epifamily is beyond the scope of the current study. Unfortunately, the epifamily Nymphidoidae is defined by mainly plesiomorphic conditions (see diagnosis above), so this taxon may theoretically be paraphyletic. However, the presence of multiple trichosors along the posterior wing margin is apparently an apomorphic character state, but it is also found in some Chrysopidae and Mantispidae. It is most probable that the family Babinskaiidae evolved in the earliest Cretaceous as a side branch of Nymphidae from relatively small members, whose venation is similar to that of the Early Cretaceous genus *Baissoleon*.

Two enigmatic genera from the Crato Formation (*Cratosmylus* and *Araripenymphes*) also belong to Nymphidoidae based on their wing characters (see Menon et al., 2005; Myskowiak et al., 2015). The former genus was assigned to the monotypic subfamily Cratosmylinae in Osmylidae by Myskowiak et al. (2015), but subsequently was removed from this family by Winterton et al. (2017) who considered it to be more suitably placed in Nymphidae. However, we suppose that these two genera form a third family of Nymphidoidae, i.e., Cratosmylidae. Unfortunately, we could not examine any specimens of this group, and this assumption remains only our hypothesis.

6. Key to genera of Babinskaiidae

(Forewings of *Baisonelia* are unknown; hind wings of *Babinskaia* are fragmentary)

1. Hind wing strongly narrowed ....*Burmobabinskaia*
   Hind wing normal, ovate 2
2. RP originating much distal of termination of CuP in both wings..*Neliana*
   RP originating approximately at level of termination of CuP 3
3. Branches of MP slightly shorter than crossveins between MA, MP in hind wing ....*Pseudobabinskaia*
   Branches of MP much longer than crossveins between MA, MP in hind wing 4
4. Crossveins between branches of RP in outer gradate series absent at least in forewing .... *Babinskaia*
   Crossveins between branches of RP in outer gradate series present in both wings 5
5. Four-five crossveins between stem of RP, M in hind wing..*Parababinskaia*
   Two-three crossveins between stem of RP, M in hind wing......6
6. RP with four branches in hind wing ....*Baisonelia*
   RP with seven branches in hind wing ....*Electrobabinskaia*

7. Conclusions

The Babinskaiidae constitute a homogeneous taxon of small Cretaceous myrmeleontoids now comprising nine species in seven genera. The reduction of the veins AA2 and AA3 in the hind wing is its autapomorphy. Babinskaiidae are most closely related to Nymphidae, and have probably evolved as a side branch of the nymphid lineage. After examination of this family, we divide the superfamily Myrmeleontoidea into two epifamilies, i.e., Nymphidoidae (with Nymphidae and †Babinskaiidae), and Myrmeleontoidae consisting of five families (Myrmeleontidae, Ascalaphidae, Nemopteridae, †Palaeoleontidae, and †Araripeneuridae).

Acknowledgements

We thank M. Jared Thomas (INHSP) for help with photography of the holotype of *Parababinskaia elegans*; Alexander V. Khramov (PIN) for photographs of the holotype of *Baisonelia vitimica*; Günter Schweigert (SMNS) for loan of specimen of *Neliana maculata*; Dmitry E. Shcherbakov and Alexander P. Rasnitsyn (PIN) for information on the Baissa locality; and anonymous reviewers for providing valuable suggestions to improve this manuscript. The study is supported by Grant Nos. 16-04-00053 and 14-04-00649 of the Russian Foundation for Basic Research (to VM) and U.S. National Science Foundation (NSF) grant EF 1304622 (to SWH).

References

Adams, P.A., 1967. A review of the Mesochrysinae and Nothochrysinae (Neuroptera: Chrysopidae). Bulletin of the Museum of Comparative Zoology 135, 215–238.

Adams, P.A., Penny, N.D., 1992a. New genera of Nothochrysinae from South America (Neuroptera: Chrysopidae). Pan-Pacific Entomologist 68, 216–221.

Adams, P.A., Penny, N.D., 1992b. Review of the South American genera of Nothochrysinae (Insecta: Neuroptera: Chrysopidae). In: Canard, M., Aspöck, H., Mansell, M.W. (Eds.), Current Research in Neuropterology. Proceedings of the Fourth International Symposium on Neuropterology (24–27 June 1991, Bagnères-deLuchon, Haute-Garonne, France). Privately printed, Toulouse, France, pp. 35–41.

Archibald, S.B., Makarkin, V.N., Ansorge, J., 2009. New fossil species of Nymphidae (Neuroptera) from the Eocene of North America and Europe. Zootaxa 2157, 59–68.

Aspöck, U., Aspöck, H., 2008. Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). Systematic Entomology 33, 97–127.

Beutel, R.G., Friedrich, F., Aspöck, U., 2010a. The larval head of Nevrorthidae and the phylogeny of Neuroptera (Insecta). Zoological Journal of the Linnean Society 158, 533–562.

Beutel, R.G., Zimmermann, D., Krauss, M., Randolf, S., Wipfler, B., 2010b. Head morphology of *Osmylus fulvicephalus* (Osmylidae, Neuroptera) and its phylogenetic implications. Organisms Diversity & Evolution 10, 311–329.

Brauer, F., 1866. Zusätze und Berichtigungen zu Hagen's Hemerobidarum Synopsis Synonymica und Beschreibung einer neuen Nymphiden-gattung: *Myiodactylus osmyloides* aus Australien. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 16, 983–992.

Bugdaeva, E.V., 2010. New species of *Sphenobaiera* Florin (Ginkgoales) from the Lower Cretaceous of Transbaikalia. Paleontological Journal 44, 1240–1251.

Bugdaeva, E.V., Markevich, V.S., 2012. The age of Lycoptera beds (Jehol biota) in Transbaikalia (Russia), and correlation with Mongolia and China. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, pp. 453–464.

Carpenter, F.M., 1929. A Jurassic neuropteran from the lithographic limestone of Bavaria. Psyche 36, 190–194.

Engel, M.S., Grimaldi, D.A., 2008. Diverse Neuropterida in Cretaceous amber, with particular reference to the paleofauna of Myanmar (Insecta). Nova Supplementa Entomologica 20, 1–86.

Grimaldi, D.A., 2016. Diverse orthorrhaphan flies (Insecta: Diptera: Brachycera) in amber from the Cretaceous of Myanmar: Brachycera in Cretaceous amber, part VII. Bulletin of the American Museum of Natural History 408, 1–131.

Grimaldi, D.A., Engel, M.S., 2005. Evolution of the insects. Cambridge University Press, Cambridge, UK xv + 755 pp.

Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361, 1–72.

Haring, E., Aspöck, U., 2004. Phylogeny of the Neuropterida: a first molecular approach. Systematic Entomology 29, 415–430.

Hayward, K.J., 1953. Satíridos argentinos (Lep. Rhop. Satyridae) I. Los géneros (excluídos *Euptychia* y *Neomaniola*). Acta Zoologica Lilloana 13, 5–66.

Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S.P., Martill, D.M., Rios-Netto, A.M., 2010. Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous, Araripe Basin, north-eastern Brazil). Sedimentology 57, 677–694.

Huang, D.Y., Azar, D., Engel, M.S., Garrouste, R., Cai, C.Y., Nel, A., 2016. The first araripeneurine antlion in Burmese amber (Neuroptera: Myrmeleontidae). Cretaceous Research 63, 1–6.

Jepson, J.E., Penney, D., 2007. Neuropteran (Insecta) palaeodiversity with predictions for the Cretaceous fauna of the Wealden. Palaeogeography, Palaeoclimatology, Palaeoecology 248, 109–118.

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.

Latreille, P.A., 1802. Histoire naturelle, générale et particulière de Crustacés et des Insectes. Vol. 3. Familles naturelles des genres. F. Dufart, Paris, 467 pp.

Leach, W.E., 1814. Zoological miscellany; being descriptions of new, or interesting animals, vol. 1. London.

Linnaeus, C., 1758. Systema natura per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, tenth ed., vol. 1. Salvii, Holmiae. 824 pp.

Lu, X.M., Zhang, W.W., Liu, X.Y., 2017. Discovery of the family Babinskaiidae (Insecta: Neuroptera) from the mid Cretaceous amber of Myanmar. Cretaceous Research 71, 14–23.

Makarkin, V.N., 1990. *Baissoleon cretaceus* gen. and sp. nov. Fossil Neuroptera from the Lower Cretaceous of Baisa, East Siberia. 2. Nymphitidae. Annales de la Société Entomologique de France (N.F.) 26, 125–126.

Makarkin, V.N., 2016a. The amazing diversity of Cretaceous Neuroptera. In: A.I. Kurenstov's Annual Memorial Meetings. Issue 27. Dalnauka, Vladivostok, pp. 27–47 (in Russian, English summary).

Makarkin, V.N., 2016b. The neuropteran assemblage (Insecta) of the mid-Cretaceous Burmese amber confirms transitional character of its biota. In: Dzyuba, O.S., Pestchevitskaya, E.B., Shurygin, B.N. (Eds.), Cretaceous Ecosystems and Their Responses to Paleoenvironmental Changes in Asia and the Western Pacific. Short papers for the Fourth International Symposium of International

Geoscience Programme IGCP Project 608. August 15–20, 2016, Novosibirsk, Russia. Trofimuk Institute of Petroleum Geology and Geophysics of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, pp. 27–29.

Makarkin, V.N., 2017. New taxa of unusual Dilaridae (Neuroptera) with siphonate mouthparts from the mid-Cretaceous Burmese amber. Cretaceous Research 74, 11–22.

Makarkin, V.N., Archibald, S.B., 2013. A diverse new assemblage of green lacewings (Insecta: Neuroptera: Chrysopidae) from the Early Eocene Okanagan Highlands, western North America. Journal of Paleontology 87, 123–146.

Makarkin, V.N., Yang, Q., Peng, Y.Y., Ren, D., 2012. A comparative overview of the neuropteran assemblage of the Early Cretaceous Yixian Formation (China), with description of a new genus of Psychopsidae (Insecta: Neuroptera). Cretaceous Research 35, 57–68.

Makarkin, V.N., Yang, Q., Shi, C.F., Ren, D., 2013. The presence of the recurrent veinlet in the Middle Jurassic Nymphidae (Neuroptera) from China: a unique condition in Myrmeleontoidea. ZooKeys 325, 1–20.

Martill, D.M., Heimhofer, U., 2007. Stratigraphy of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil. Window into an Ancient World. Cambridge University Press, Cambridge, UK, pp. 25–43.

Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), 2007. The Crato Fossil Beds of Brazil. Window into an Ancient World. Cambridge University Press, Cambridge, UK, 624 pp.

Martins-Neto, R.G., 1992. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior) Bacia do Araripe, Nordeste do Brasil. V – Aspectos filogenéticos, paleoecológicos, paleobiogeográficos e descrição de novos taxa. Anais da Academia Brasileira de Ciencias 64, 117–148.

Martins-Neto, R.G., 1994. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil – IX – Primeiros resultados da composição da fauna e descrição de novos táxons. Acta Geologica Leopoldensia 17 (39/1), 269–288.

Martins-Neto, R.G., 1997. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. X – Descrição de novos táxons (Chrysopidae, Babinskaiidae, Myrmeleontidae, Ascalaphidae e Psychopsidae). Revista Uniersidade de Guarulhos, Série Ciências Exatas e Tecnológicas 2 (4), 68–83.

Martins-Neto, R.G., 1998. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. XI – Descrição de novos táxons de Myrmeleontidae (Paleoleontinae e Pseudonymphinae). Revista Universidade de Guarulhos, Série Ciências Biológicas e da Saúde 3 (5), 38–42.

Martins-Neto, R.G., 2003. The Santana Formation Paleoentomofauna reviewed. Part I – Neuropteroida (Neuroptera and Raphidioptera): systematic and phylogeny, with description of new taxa. Acta Geologica Leopoldensia (R.S.) 25 (55) (for 2002), 35–66.

Martins-Neto, R.G., 2005. New Neuroptera from Crato Formation, Lower Cretaceous, Araripe Basin, Northeast Brazil. GAEA 1, 5–10.

Martins-Neto, R.G., Heads, S.W., Bechly, G., 2007. Neuropterida: snakeflies, dobsonflies, and lacewings. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil. Window into an Ancient World. Cambridge University Press, Cambridge, UK, pp. 328–340.

Martins-Neto, R.G., Vulcano, M.A., 1989a. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), bacia do Araripe, nordeste do Brasil. II. Superfamília Myrmeleontoidea. Revista Brasileira de Entomologia 33, 367–402.

Martins-Neto, R.G., Vulcano, M.A., 1989b. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. IV – Complemento às partes I e II, com descrição de novos taxa. Anais da Academia Brasileira de Ciencias 61, 311–318.

Menon, F., Martill, D.M., 2007. Taphonomy and preservation of Crato Formation arthropods. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil. Window into an Ancient World. Cambridge University Press, Cambridge, UK, pp. 79–96.

Menon, F., Martins-Neto, R.G., Martill, D.M., 2005. A new Lower Cretaceous nymphid (Insecta, Neuroptera, Nymphidae) from the Crato Formation of Brazil. GAEA 1, 11–15.

Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., Loveridge, R.F., 2007. The macrophyte flora of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil. Window into an Ancient World. Cambridge University Press, Cambridge, UK, pp. 537–565.

Myskowiak, J., Nel, A., 2016. New antlion species (Insecta, Neuroptera, Palaeoleontidae) from the Lower Cretaceous Crato Formation in northeastern Brazil. Cretaceous Research 59, 278–284.

Myskowiak, J., Escuillié, F., Nel, A., 2015. A new Osmylidae (Insecta, Neuroptera) from the Lower Cretaceous Crato Formation in Brazil. Cretaceous Research 54, 27–33.

New, T.R., 1982. A revision of the Australian Nymphidae (Insecta: Neuroptera). Australian Journal of Zoology 29 (for 1981), 707–750.

New, T.R., 1988. Nymphidae (Insecta: Neuroptera) from New Guinea. Invertebrate Taxonomy 1 (for 1987), 807–815.

Novokshonov, V.G., 1996. The systematic position of some Upper Permian lacewings (Insecta; Myrmeleontida=Neuroptera). Paleontologicheskii Zhurnal 1996 (1), 39–47 (in Russian; English translation: Paleontological Journal 30, 38–45).

Oswald, J.D., 1993. Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). Journal of New York Entomological Society 101, 143–299.

Poinar Jr., G.O., Buckley, R., Brown, A.E., 2008. The secrets of Burmite amber. MAPS Digest 20, 20–29.

Ponomarenko, A.G., 1992a. Neuroptera (Insecta) from the Lower Cretaceous of Transbaikalia. Paleontologicheskii Zhurnal 1992 (3), 43–50 (in Russian; English translation: Paleontological Journal 26, 56–66).

Ponomarenko, A.G., 1992b. New lacewings (Insecta, Neuroptera) from the Mesozoic of Mongolia. In: Grunt, T.A. (Ed.), New taxa of fossil invertebrates of Mongolia. Transactions of the Joint Russian-Mongolian Paleontological Expedition, vol. 41. Nauka Press, Moscow, pp. 101–111 (in Russian).

Rambur, J.P., 1842. Histoire Naturelle des Insectes, Névroptères. Fain et Thunot, Paris. [xviii] + 534 pp.

Ren, D., Makarkin, V.N., 2009. Ascalochrysidae – a new lacewing family from the Mesozoic of China (Insecta: Neuroptera: Chrysopoidea). Cretaceous Research 30, 1217–1222.

Riek, E.F., 1967. Structures of unknown, possibly stridulatory, function of the wings and body of Neuroptera; with an appendix on other endopterygote orders. Australian Journal of Zoology 15, 337–348.

Ross, A.J., 2015. Insects in Burmese amber. In: Schmitt, T., Blank, S.M., Kohler, A., Kramp, K., Weyer, J. (Eds.), Entomologentagung 02.–05.03.2015 Frankfurt/M. Programm und Abstracts. Frankfurt/Main, p. 72.

Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L., Li, X.H., 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. Cretaceous Research 37, 155–163.

Shi, C.F., Makarkin, V.N., Yang, Q., Archibald, S.B., Ren, D., 2013. New species of *Nymphites* Haase (Neuroptera: Nymphidae) from the Middle Jurassic of China, with a redescription of the type species of the genus. Zootaxa 3700 (3), 393–410.

Shi, C.F., Winterton, S.L., Ren, D., 2015. Phylogeny of split-footed lacewings (Neuroptera, Nymphidae), with descriptions of new Cretaceous fossil species from China. Cladistics 31, 455–490.

Skoblo, V.M., Lyamina, N.A., 1986. Biostratigraphic correlation of the Jurassic and Cretaceous continental deposits of western Transbaikalia and some other regions of Asia, USSR, and Mongolia. In: Yanshin, A.L., Dagis, A.S. (Eds.), Biostratigraphy of the Mesozoic deposits of Siberia and the Russian Far East. Nauka, Novosibirsk, pp. 144–150 (In Russian).

Tjeder, B., 1966. Neuroptera-Planipennia. The Lace-wings of Southern Africa. 5. Family Chrysopidae. In: Hanström, B., Brinck, P., Rudebec, G. (Eds.), South African Animal Life, vol. 12. Swedish Natural Science Research Council, Stockholm, pp. 228–534.

Tjeder, B., 1992. The Ascalaphidae of the Afrotropical Region (Neuroptera). 1. External morphology and bionomics of the family Ascalaphidae, and taxonomy of the subfamily Haplogleniinae including the tribes Proctolyrini n. tribe, Melambrotini n. tribe, Campylophlebini n. tribe, Tmesibasini n. tribe, Allocormodini n. tribe, and Ululomyiini n. tribe of Ascalaphidae. Entomologica Scandinavica Supplement 41, 3–169.

Vakhrameev, V.A., Kotova, I.Z., 1977. Early angiosperms and associated plants from the Lower Cretaceous deposits of Transbaikalia. Paleontologicheskii Zhurnal 1977 (4), 101–109 (In Russian).

Vilesov, A.P., 1995. Permian lacewings (Insecta: Myrmeleontida) from the Chekarda locality (Urals). Paleontologicheskii Zhurnal 1995 (2), 95–105 (In Russian; English translation: Paleontological Journal 29, 115–129).

Wang, Y.Y., Liu, X.Y., Garzón-Orduña, I.J., Winterton, S.L., Yan, Y., Aspöck, U., Aspöck, H., Yang, D., 2017. Mitochondrial phylogenomics illuminates the evolutionary history of Neuropterida. Cladistics. http://dx.doi.org/10.1111/cla.12186 (in press).

Warren, L.W., Varejão, F.V., Quaglio, F., Simões, M.G., Fürsich, F.T., Poiré, D.G., Catto, B., Assine, M.L., 2017. Stromatolites from the Aptian Crato Formation, a hypersaline lake system in the Araripe Basin, northeastern Brazil. Facies 63, 3. http://dx.doi.org/10.1007/s10347-016-0484-6.

Winterton, S.L., Hardy, N.B., Wiegmann, B.M., 2010. On wings of lace: phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. Systematic Entomology 25, 349–378.

Winterton, S.L., Zhao, J., Garzón-Orduña, I.J., Wang, Y.J., Liu, Z.Q., 2017. The phylogeny of lance lacewings (Neuroptera: Osmylidae). Systematic Entomology 42, 555–574.

Xia, F.Y., Yang, G.D., Zhang, Q.Q., Shi, G.L., Wang, B., 2015. Amber: Lives Through Time and Space. Science Press, Beiping, 197 pp. (in Chinese).

Yang, Q., Makarkin, V.N., Winterton, S.L., Khramov, A.V., Ren, D., 2012. A remarkable new family of Jurassic insects (Neuroptera) with primitive wing venation and its phylogenetic position in Neuropterida. PLoS One 7 (9), e44762.

Yang, Q., Makarkin, V.N., Ren, D., 2014. Two new species of *Kalligramma* Walther (Neuroptera: Kalligrammatidae) from the Middle Jurassic of China. Annals of the Entomological Society of America 107, 917–925.

Zherikhin, V.V., Mostovski, M.B., Vrsansky, P., Blagoderov, V.A., Lukashevich, E.D., 1999. The unique Lower Cretaceous locality Baissa and other contemporaneous fossil insect sites in North and West Transbaikalia. In: Proceedings of the First Palaeoentomological Conference, Moscow 1998. AMBA projects AM/PFICM98/1.99, Bratislava, pp. 185–191.