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The first fossil species and genus of Palparinae (Neuroptera: Myrmeleontidae) from the early Eocene Green River Formation

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Articles

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Abstract

Protopalpares lindgrenae new genus new species (Neuroptera: Myrmeleontidae) is described from the Fossil Butte Member of the early Eocene Green River Formation (Wyoming, USA). This is the first Neuroptera species from the Fossil Butte Member, and the first fossil Palparinae. It is assigned to this subfamily based on the synapomorphy proposed here that the forewing posterior branch of RP1 and the stem of MP+CuA1 curve toward each other and are connected by two aligned crossveins at their closest. The venation of *Protopalpares* is most similar within the family to that of the Early Cretaceous Palaeonleontidae, indicating that Palparinae and Palaeonleontidae are likely closely related.

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Non-technical Summary

We describe the first fossil antlion (lacewing order Neuroptera, family Myrmeleontidae) from the Fossil Butte Member of the early Eocene Green River Formation of Wyoming, USA, and name the new genus and species *Protopalpares lindgrenae* based on it. It is the first reported fossil of the modern antlion subfamily Palparinae. Analysis of its wing venation indicates that Palparinae is closely related to the Cretaceous lacewing family Palaeonleontidae.

Introduction

The Myrmeleontidae (antlions) is the most speciose family of Neuroptera today, with ~ 1700 species (Oswald and Machado, 2018) distributed nearly worldwide, more diverse in warm, arid regions. Adults are typically relatively large, including the largest living neuropterans, with a wingspan to 170 mm in some Palparinae (Hevin et al., 2023). Many of their predatory larvae are remarkable for constructing conical pitfall traps in sand to capture arthropods walking on the ground (Mansell, 1999).

Our current understanding of their Mesozoic history is confusing and contradictory. They are speciose and diverse in the Cretaceous, with 58 generally accepted species described based on adults, none in extant subfamilies (see list of species not belonging to Palaeonleontidae by Lu et al., 2022, and Bueno et al., 2025a, b; Lu et al., 2026; species of Palaeonleontidae are not summarized in any single work, so see Menon and Makarkin, 2008; Millet and Nel, 2010; Shi et al., 2012; Myskowiak and Nel, 2016). The oldest myrmeleontoid species are from the Barremian/Aptian Yixian Formation in China (*Choromyrmeleon othneius* Ren and Guo, 1996; *C. aspoeckorum* Ren and Engel, 2008) and the probably Barremian/Aptian Bon-Tsagaan locality in Mongolia (*Baissopardus banksianus* Ponomarenko, 1992). These genera are currently considered to belong to Myrmeleontidae subfamily incertae sedis (see Lu and Liu, 2022; Bueno et al., 2026) and Palaeonleontidae (see Myskowiak and Nel, 2016), respectively.

Three myrmeleontoid family-level taxa have been proposed for these genera (Araripeneuridae/-nae, Palaeonleontidae/-nae, and Pseudonymphinae/-dae), but these are not universally recognized. Although Araripeneuridae and Palaeonleontidae are often treated as subfamilies of Myrmeleontidae (e.g., Stange, 2004; Machado et al., 2019; Bueno et al., 2025a, b), they are quite distinct and are better considered as separate families (see e.g., Makarkin et al., 2018). We consider Pseudonymphinae (as defined by Makarkin et al., 2018) to be paraphyletic, with genera probably belonging to stem Myrmeleontidae sensu lato within it. However, some mid-Cretaceous genera (see Huang et al., 2016; Lu et al., 2019, 2026; Lu and Liu, 2022) appear more closely related to extant Myrmeleontidae than to other Cretaceous taxa and are currently treated as Myrmeleontidae subfamily incertae sedis (Lu et al., 2026). In general, the systematics of Cretaceous antlions needs revision.

Only three species of Myrmeleontidae are confidently known from the Cenozoic, belonging to one and possibly two modern subfamilies: *Epignopholeon sophiae* Makarkin, 2017

(Myrmeleontinae: ?Gnopholeontini) from the early Eocene Green River Formation, Colorado, USA; *Dendroleon septemmontanus* Statz, 1936 (?Dendroleontinae) from late Oligocene Rott (Germany), and *Porrerus dominicanus* Poinar and Stange, 1996 (Myrmeleontinae: Myrmeleontini: Porerenina) from early/middle Miocene Dominican amber (Poinar and Stange, 1996; Engel and Grimaldi, 2007; Makarkin, 2017).

The modern subfamily Palparinae has no reported fossil occurrences. It has >140 species today distributed in subtropical and tropical regions of the Old World (mainly in Africa), and rarely in South America. It has traditionally been divided into four tribes (Stange, 2004), i.e., Dimarini with *Echthromyrmex* McLachlan, 1867 (southern Asia), *Dimares* Hagen, 1866 (South America), *Millerleon* Stange, 1989 (South America); Palparidiini wth *Palparidius* Péringuey, 1910 (South Africa); Pseudimarini with *Pseudimares* Kimmins, 1933 (Morocco and Iran), and Palparini (15 genera distributed in Africa and southern Eurasia). The genus *Echthromyrmex* has often been treated as constituting the monotypic tribe Echthromyrmecini (e.g., Markl, 1954; Hölzel, 1986) or even the subfamily Echthromyrmecinae (Krivokhatsky, 1998).

However, in recent years the taxonomy of extant Myrmeleontidae has been significantly revised. The morphological analysis of Badano et al. (2017) supported two tribes of Palparinae: Stilbopterygini (subtribes Stilbopterygina and Pseudimarina) and Palparini (subtribes Palparina, Palparidiina, Dimarina and Echthromyrmecina). The phylogenomic analysis of Machado et al. (2019) synonymized Ascalaphidae with Myrmeleontidae, and eliminated Palparinae, considering its genera as belonging to two tribes (Palparini and Dimarini) in Ascalaphinae, and *Pseudimares* as Ascalaphinae incertae sedis. The molecular analysis of Hévin et al. (2023) subsequently restored the Palparinae, composed of Palpirini, Palparidiini, and Pseudimarini (genera of Dimarini were not analyzed). We accept the synonymization of Ascalaphidae with Myrmeleontidae proposed by Machado et al. (2019), but consider Ascalaphinae to consist of the tribes Stilbopterygini, Albardiini, Ululodini, Haploglenini, and Ascalaphini, without genera of the Palparinae.

Here, we describe the first fossil species of Palparinae and the first neuropteran from the Fossil Butte Member of the early Eocene Green River Formation (Wyoming, USA) and compare its characters with those of the Cretaceous Palaeonleontidae.

Materials and methods

Terminology of wing venation follows Breitkreuz et al. (2017) except treatment of CuA, which we and other authors (see e.g., Lu et al., 2026) follow Tillyard (1915): the proximalmost branch of CuA is CuA2 (Tillyard's 'Cu2'); other branches of CuA considered to be fused with MP are MP+CuA1 (Tillyard's 'Cu1+M2'). See captions of Figures 3–5 for abbreviations used in the text. Contrary character states of taxa compared in diagnoses are provided in brackets.

We follow the traditional understanding of Palparinae systematics of Stange (2004) above the tribal level. Relationships are less confident at the tribe level and below.

Locality information. The Green River Formation consists of highly fossiliferous lacustrine shale deposited between ~ 53.5 and 48.5 Ma (Smith et al., 2003) in a large lake system of Lake Gosiute and Fossil Lake in southwestern Wyoming and Lake Uinta in northeast Utah and northwestern Colorado (see summaries of its geology and paleontology by Grande, 1984, 1994, 2013). This was during the Early Eocene Climatic Optimum, the globally warmest sustained temperatures of the Cenozoic (e.g., Inglis et al., 2020). Analysis of leaf physiognomy gives Fossil Butte mean annual temperature estimates from 18.3°C to 19.6°C (with 4 °C standard errors) at its Little Mountain locality (Wilf, 2000, Fricke and Wing, 2004).

The Fossil Butte Member is famous for its rich vertebrate assemblage of reptiles, amphibians, birds, mammals, and diverse and abundant fish (Grande references above). The specimen was collected in the Fossil Butte Member ~ 6 m below the K-spar tuff in the 18-in (45.7-cm) layer, 17.7 km west of Kemmerer, Lincoln County, Wyoming, USA, in Clear Creek Valley. The K-spar tuff near the top of the Fossil Butte Member is dated mid-Ypresian, 51.97 ± 0.09 Ma (Smith et al., 2010).

Samuel Scudder (1878, 1890) described 191 species of Green River insects in the late nineteenth century, mostly from Grande's (1984, fig I.4) Lake Gosiute locality G-1 and a lesser number from Fossil Lake locality F-1 and 53 from Scudder's White River locality in Utah near the Colorado border, apparently the Lake Uinta U-4 locality of Grande. Other authors, notably Cockerell in the early twentieth century (e.g., Cockerell, 1925), also described insects from the Lake Uinta Parachute Creek Member of the Piceance Basin in Colorado. In recent years, there has been an increase in works published on insects of the Parachute Creek Member (e.g., Makarkin, 2017; Archibald and Makarkin, 2021), Lake Gosiute Laney Member (Archibald et al., 2011), and Fossil Butte Member (e.g., Archibald et al., 2021, Bechly et al., 2020). Previously, Neuroptera (and Raphidioptera) have only been reported from the Parachute Creek Member.

Repositories and institutional abbreviations. The type specimen is deposited in the collection of Fossil Butte National Monument, Kemmerer, Wyoming, USA (FOBU). Other repositories cited in the text are Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN), and the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS).

Systematic paleontology

Order **Neuroptera** Linnaeus, 1758
Family **Myrmeleontidae** Latreille, 1802
Subfamily **Palparinae** Banks, 1911
Genus ***Protopalpares*** new genus

Type species. Protopalpares lindgrenae new genus, new species.

Diagnosis. As for the type species by monotypy.

Etymology. The generic name is formed from the Greek *protou*, 'before' or 'in former times,' and the genus-group name *Palpares* Rambur, 1842. Gender masculine.

Remarks. All wings most likely belong to the same specimen, although both forewings and both hind wings are preserved with their apex to the left; we assume that one of each has been folded over (Figs. 1, 2).

Protopalpares lindgrenae new genus new species
Figures 1–4

Holotype. FOBU 13564, two isolated pairs of wings most likely belonging to the same specimen: one pair (positioned as right wings)

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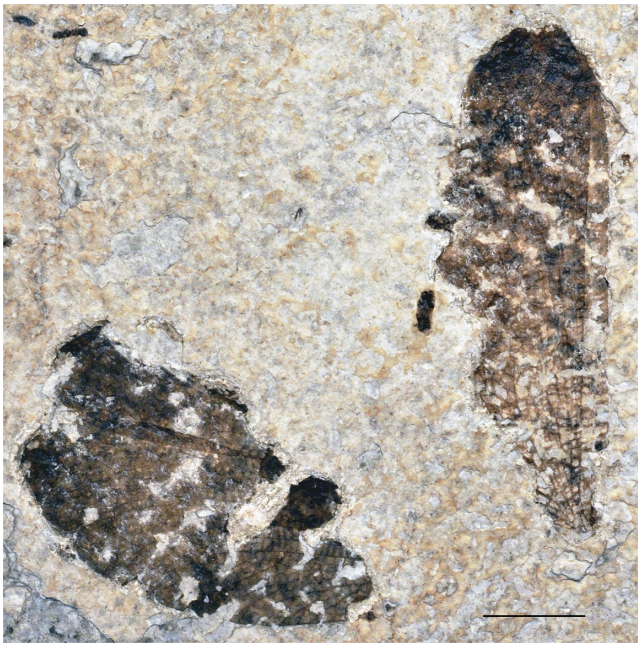

Figure 1. *Protopalpares lindgrenae* n. gen. n. sp., holotype FOBU 13564 as preserved before preparation. Scale bar = 10 mm.

is nearly complete but poorly preserved, especially distally; the other pair (positioned as left wings) are distal portions of wings in relatively good condition.

Diagnosis. Distinguished from other species of Palparinae by the following forewing character states: one presectorial crossvein (between R and M proximad the origin of RP) [more than one in other genera]; posterior branch of CuA (CuA2) long, with its anterior trace pectinately forked (shorter, often with its posterior trace pectinately forked in other genera); branches of MP+CuA1 widely spaced with crossveins between them connecting with numerous additional crossveins [see Materials and Methods: "Contrary character states of taxa compared in diagnoses are provided in brackets." more closely spaced with no or few additional crossveins in other genera].

Occurrence. Ypresian, as above in locality information.

Description. Forewing ~ 52 mm long, 17.2 mm wide. Costal space relatively narrow, slightly dilated toward wing apex. Preserved subcostal veinlets simple proximally; some forked distally; rather closely spaced. Subcostal space very narrow. Sc, RA fused distally. Sc+RA terminated well posterior to wing apex; with long, dichotomously forked branches; several irregularly spaced crossveins detected between them. RA space narrow, with preserved crossveins rather densely spaced; hypostigmal cell long. RP originating near wing base, with eight branches. RP1 originating relatively close to origin of RP, deeply, profusely dichotomously forked; RP2, RP3 much less deeply dichotomously forked; other RP branches relatively shallowly forked one to three times. Discernible crossveins between RP branches very rarely connecting with other crossveins. One presectorial (between R, M before RP) and basal aligned oblique crossveins 1r-m and 1m-cu rather well discernible. Fork of M indiscernible. MA smoothly curved backward, distally forked once. Basal part of MP indiscernible. Cu forked very close to wing base (poorly preserved). CuA forked slightly distad origin of RP1. Anterior branch of CuA (CuA1) fused with MP; MP+CuA1 pectinately forked, with four widely spaced branches (three proximal ones dichotomously forked; distalmost forked twice); many crossveins between these branches connect with additional crossveins (as in extant Acanthaclinini). Proximal branch of CuA (CuA2) long, with four long branches (one deeply dichotomously forked; others forked once); crossveins between them connect with few other crossveins. CuP and A1 fragmentarily preserved; their fusion not preserved. A2 deeply forked once. A3 short, pectinately forked, with two simple branches.

Hind wing ~ 50 mm long, 16 mm wide as preserved (very slightly wider when complete). Costal space relatively narrow, dilated apically. Subcostal veinlets simple for most part; forked once in distal part; rather closely spaced. Subcostal space very narrow. Sc, RA probably fused distally (poorly preserved). Sc+RA terminating on margin well posterior to, beyond wing apex, with long, dichotomously forked veinlets; few crossveins detected between them. RA space with preserved crossveins rather dense. RP originating near wing base; anterior trace forked once distally, apparently with seven branches, all poorly and incompletely preserved except distal branch, which is forked once. RP1 originating relatively close to origin of RP. Crossveins between branches of RP poorly preserved; few preserved crossveins connecting by additional crossveins. No presectorial crossveins detected. M forked near wing base. MP long, its anterior trace slightly sinuous in proximal half; pectinately forked distally (two branches discernible); apical part poorly discernible. CuA long, its anterior trace slightly sinuous, with at least seven pectinate branches (one preserved branch dichotomously forked); few crossveins clearly discernible. CuP very poorly discernible. A1 incompletely preserved, connecting with CuP by relatively long crossvein.

Etymology. The specific epithet *lindgrenae* is a patronym formed from the surname of fossil preparator Elizabeth Lindgren, honoring her support and love of her husband Anthony Lindgren, who found the holotype and donated it to Fossil Butte National Monument.

Remarks. The holotype of the new species is rather poorly and fragmentarily preserved, and attempts to expose more of it were unsuccessful.

Subfamily and tribe affinities of the new genus

The venation of *Protopalpares* is generally similar to that of Palparinae. In Myrmeleontidae, the long and slightly sinuous CuA in the hind wing as found in this genus is present only in five genera of three tribes of Palparinae: Dimarini (*Echthromyrmex*, *Dimares*, and *Millerleon*), Palparidiini (*Palparidius*), and Pseudimarini (*Pseudimares*) (see Péringuey, 1910, pl. 8, fig. 5; Kimmins, 1933, pl. 6; Markl, 1954, fig. 62; Stange, 1989, figs. 6–10; 2010, fig. 1; Khrivokhatsky, 1998, fig. 6; Aspöck and Aspöck, 2009, fig. 8; Tauber et al., 2019, fig. 89).

A similarly long, sinuous CuA in the hind wing is also characteristic of some Ascalaphinae (i.e., Stilbopterygini, Albardiini, and Ululodini, including one fossil species from the middle Eocene Kishenehn Formation, Montana, USA: Jepson and Makarkin, 2023), and all Palaeoleontidae (see e.g., Ponomarenko, 1992, fig. 5; Heads et al., 2005, fig. 1; Shi et al., 2012, figs. 2E, F). However, in all ascalaphines, RP originates far from the wing base, there is a short, dark pterostigma (with all pterostigmal veinlets simple), and Sc+RA curves immediately after the fusion of Sc and RA and runs in a straight line. In *Protopalpares*, these characters are different. In all Palaeoleontidae, RP originates very close to the wing base and presectorial crossveins are absent.

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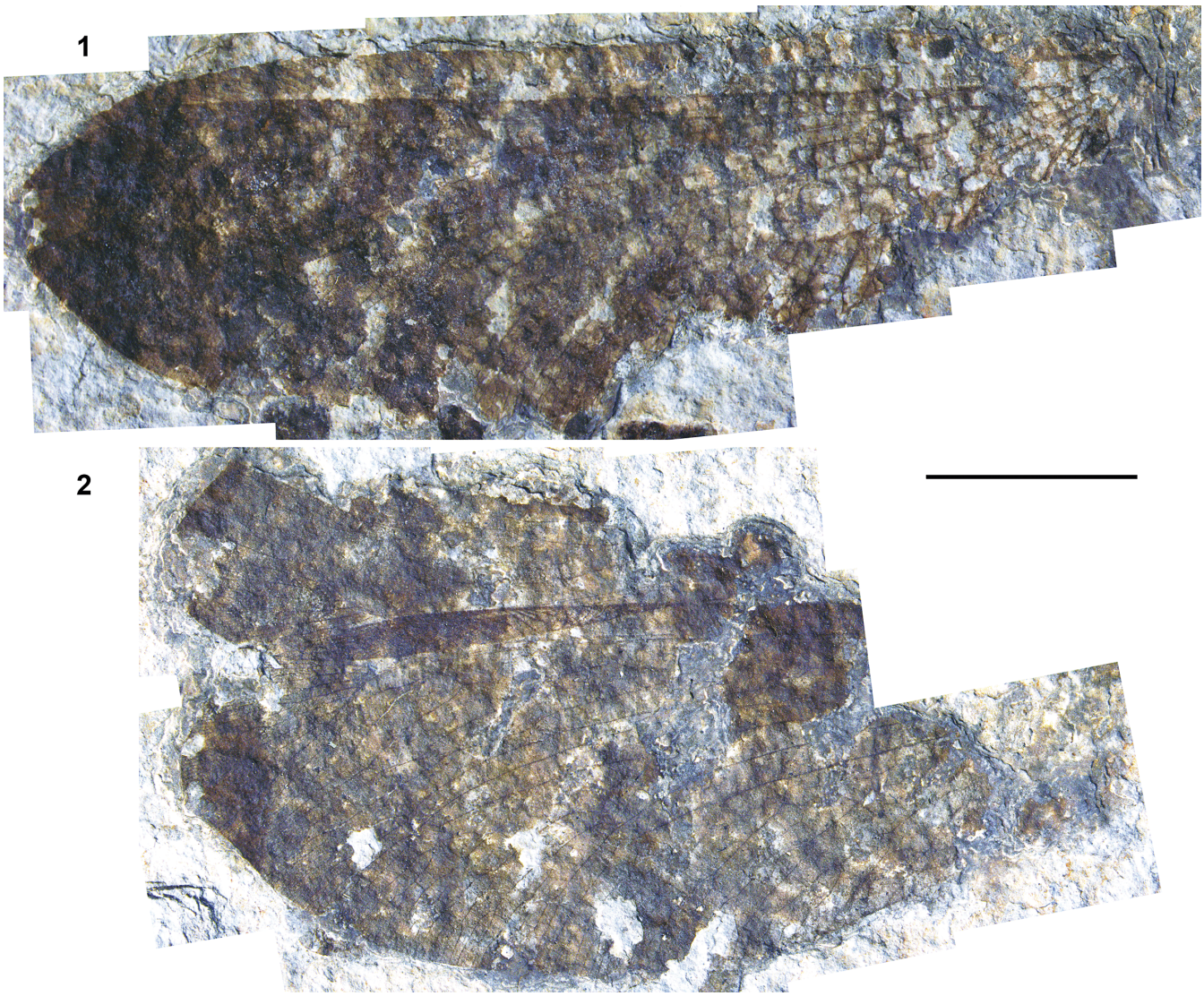

Figure 2. *Protopalpares lindgrenae* n. gen. n. sp., holotype FOBU 13564 after preparation. (**1**) Both positioned as right wings. (**2**) Both positioned as left wings. Scale bar = 10 mm.

This form of hind wing CuA is probably plesimorphic. We did, however, find a character state of *Protopalpares* venation that we consider apomorphic. The forewing posterior branch of RP1 and the stem of MP+CuA1 curve toward each other and are connected by two aligned crossveins where they are closest (Fig. 4). This character state is similar to that in most extant Palparinae of three tribes: Palparidini (e.g., *Palparidius capicola* Péringuey, 1910); Palparini (e.g., *Palpares hispanus* Koçak, 1976; *Pamares damarus* Mansell, 1990); and Dimarini—e.g., *Dimares elegans* (Perty, 1833 [1830–1834]), *Echthromyrmex orientalis* McLachlan, 1873—(Mansell, 1990, fig. 43; Krivokhatsky, 1998, fig. 6; Stange, 2010, fig. 1; Khabiev and Krivokhatsky, 2014, fig. 6; Tauber et al., 2019, fig. 89). There are no such curvatures in other Myrmeleontidae s.l. (including Cretaceous taxa), and we consider this to be a synapomorphy of Palparinae.

Thus, it is certain that *Protopalpares* belongs to Palparinae, but what tribe it belongs to remains unresolved due to the incomplete preservation of the specimen. The new genus definitely does not belong to Palparini, in which the hind wing CuA is strongly curved at its junction with the posterior branch of M (e.g., Mansell, 1990, fig. 43; 1992, figs. 1–5; 2018, figs. 2, 3; Krivokhatsky, 1998, fig. 4; Michel, 1999, figs. 13, 14; Hassan et al., 2023, figs. 1, 2, 6, 9, 12, 13).

All three tribes with a long and slightly sinuous CuA in the hind wing (Dimarini, Palparidiini, and Pseudimarini) have rather similar venation. However, the configuration of the forewing CuA (see below) and the presence of numerous crossveins connecting crossveins in the MP+CuA1 space of *Protopalpares* indicate that this genus might not belong to any of these tribes.

Palparinae and Palaeonleontidae

The myrmeleontid subfamily Palparinae is clearly similar to Palaeonleontidae by wing shape, size, and venation. The wings of all other Cretaceous myrmeleontoids have less dense venation (sometimes much less). Nine genera (15 species) of Palaeonleontidae are known from the Barremian/Aptian of Baissa (Russia: Transbaikalia) and Yixian Formation (China); the late Aptian Crato Formation (Brazil); the Albian/Cenomanian of Redmond (Canada); the Turonian of the Ora Formation (Israel); and the Coniacian of Antibes (Russia: southern Siberia) (Rice, 1969;

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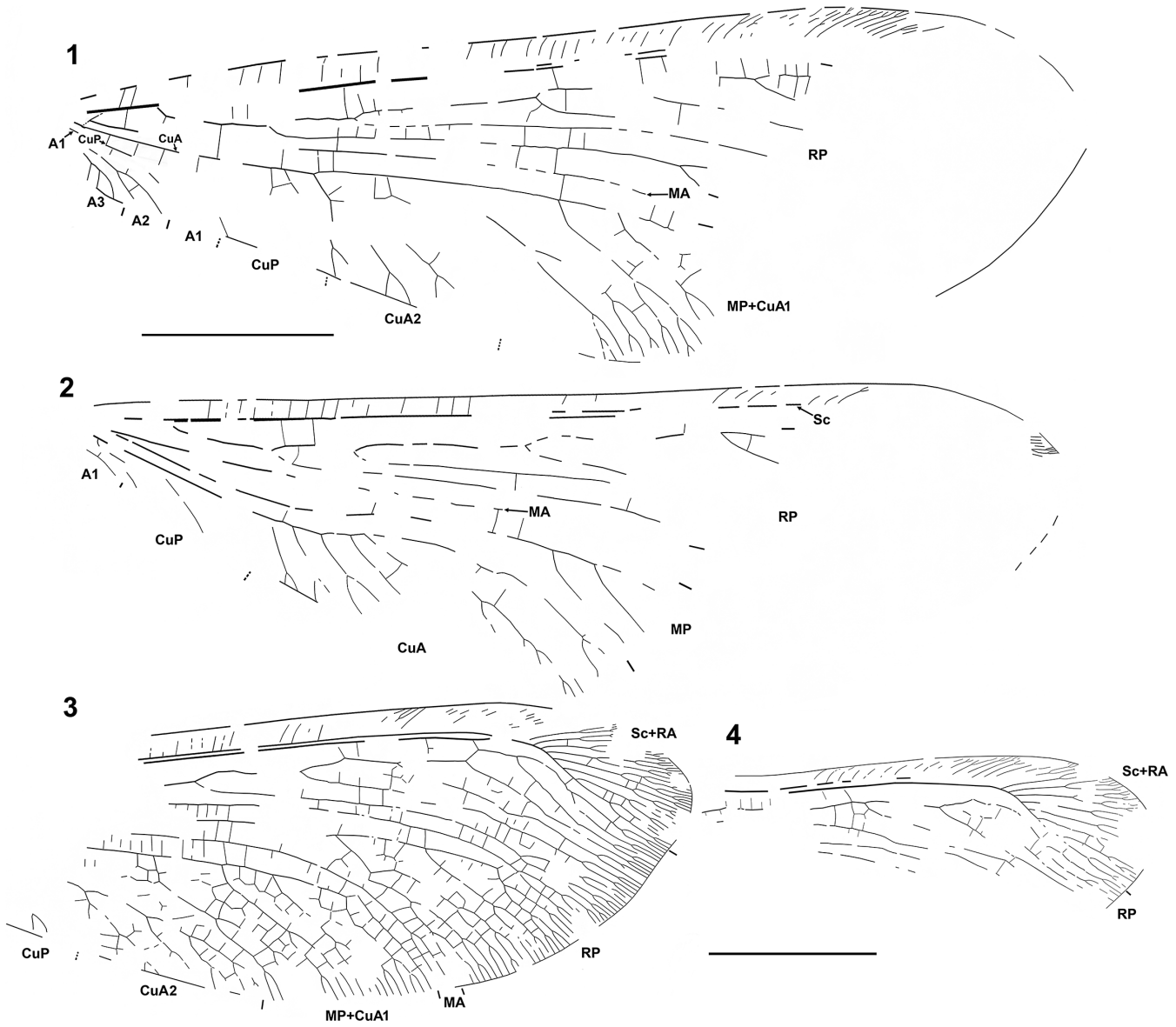

Figure 3. Wing venation of *Protopalpares lindgrenae* n. gen. n. sp., holotype FOBU 13564 (all shown in standard right view). (**1**) Conditionally right forewing. (**2**) Conditionally right hind wing. (**3**) Conditionally left forewing. (**4**) Conditionally left hind wing. A1–A3, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; MA, anterior media; MP, posterior media; RA, anterior radius; RP, posterior radius; Sc, subcosta. Scale bar = 10 mm.

Makarkin, 1990; Martins-Neto, 1992, 1997, 1998; Ponomarenko, 1992; Dobruskina et al., 1997; Martins-Neto and Vulcano, 1997; Heads et al., 2005; Menon and Makarkin, 2008; Martins-Neto and Rodrigues, 2010; Millet and Nel, 2010; Shi et al., 2012; Myskowiak and Nel, 2016).

Palaeonleontidae is usually treated as a family (e.g., Dobruskina et al., 1997; Heads et al., 2005; Menon and Makarkin, 2008; Michel et al., 2017; Lu et al., 2021, 2022; Bueno et al., 2025a, b) and rarely as a primitive subfamily of Myrmeleontidae (e.g., Martins-Neto, 1997; Stange, 2004; Ren and Engel, 2008; Machado et al., 2019). The venation of its oldest (Early Cretaceous) genera (e.g., *Baisopardus* Ponomarenko, 1992; *Parapalaeoleon* Menon and Makarkin, 2008; *Guyiling* Shi et al., 2012) are more similar to Palparinae than to the youngest (Late Cretaceous) genera (*Metahemerobius* Makarkin, 1990; *Samsonileon* Ponomarenko in Dobruskina et al., 1997), which are clearly more derived (see Makarkin, 1990, fig. 5; Dobruskina et al., 1997, fig. 4).

The genus *Guyiling* was described as Myrmeleontiformia insertae sedis (Shi et al., 2012) but was later classified as belonging to the Palaeonlentidae (e.g., Myskowiak and Nel, 2016; Lu et al., 2021, 2022). We agree with this assignment, because the only species of this genus has venation similar to that of other members of the family, especially to *Parapalaeoleon*, although its antennae are slightly dilated distally.

In addition to the general similarity of venation in these groups, A1 and CuP are separated along their entire length in both Palaeonleontidae and most Palparinae (except Dimarini) (a plesiomorphic character state). In other extant Myrmeleontidae, CuP is short and ends in a fusion with A1; all Cretaceous taxa of antlions also have this plesiomorphic state.

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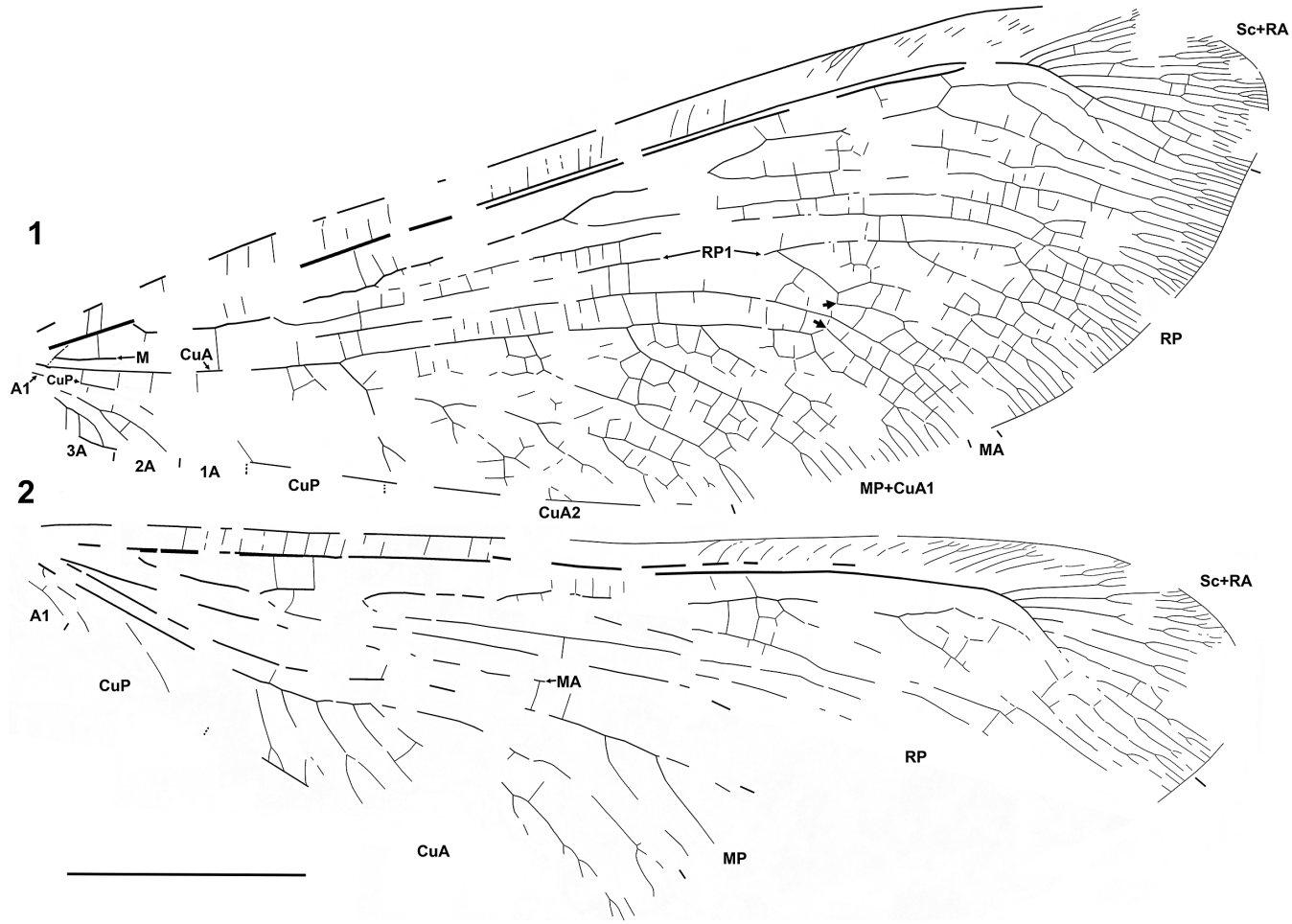

Figure 4. Preserved venation of *Protopalpares lindgrenae* n. gen. n. sp. based on all wings. (**1**) Forewing. (**2**) Hind wing. Thick arrows show the curvatures of the forewing RP1 (proximalmost branch of RP) and MP+CuA1. 1A–A3, first to third anal veins; M, media; other abbreviations as in Figure 3. Scale bar = 10 mm.

Within the Palparinae, the venation of *Protopalpares* is most similar to that of the Early Cretaceous genera of Palaeonleontidae (cf. Figs. 4, 5). First, the forewing configuration of CuA2 as found in the new genus is similar to that of most Palaeonleontidae, being clearly pectinate (see e.g., Menon and Makarkin, 2008, fig. 4B; Martins-Neto and Rodrigues, 2010, fig. 3A; Shi et al., 2012, fig. 2C, D). In other Palparinae, the forewing CuA2 is never so long and clearly pectinate.

However, it is unclear yet if this condition is plesiomorphic or apomorphic in Myrmeleontoidea. In all Cretaceous genera of Araripeneuridae (including the oldest), CuA2 is deeply bifurcate and rarely shallowly forked (see e.g., Makarkin et al., 2018, figs. 2, 4, 5; Bueno et al., 2026, fig. 1). But in a few Cretaceous genera of unclear subfamily position, CuA2 is clearly pectinate, e.g., *Blittersdorffia* Martins-Neto and Vulcano, 1989 from the late Aptian Crato Formation, and *Babinoleon* Lu et al., 2026 from mid-Cretacious Kachin amber (Bueno et al., 2025b, figs. 14, 15; Lu et al., 2026, fig. 2). In some extant and Cenozoic Ascalaphinae (especially Stilbopterygini) and other Myrmeleontidae (including *Epignopholeon sophiae* from the Green River Formation), CuA2 is also clearly pectinate (see e.g., Kimmins, 1940, fig. 3; Makarkin, 2017, figs. 5A, B; designated as CuA1).

Secondly, RP originates more proximally in *Protopalpares* than in other Palparinae, with only one presectrial crossvein (between R and M proximad the origin of RP).

In general, the venation of Palaeonleontidae differs from that of Myrmeleontidae s. str. (without the vast majority of Cretaceous genera) only by RP originating very close to the wing base, leaving no room for presectrial crossveins; by the absence of a long hypostigmal cell (between RA and RP below the pterostigmal area); and the presence of a medial flexion fold/line.

All of these character states are plesiomorphic. The origin of RP very close to the wing base is never found in other Myrmeleontidae s.l. (i.e., including all Cretaceous taxa), but is shared with Nymphidae, the only group of Myrmeleontoidea known in the Jurassic. Also, in the Myrmeleontoidea, the medial flexion fold/line occurs only in Palaeonleontidae (see Fig. 5.1; Menon and Makarkin, 2008); it is not detected even in Nymphidae. But in other Neuroptera, this is detected in the basal Jurassic Kalligrammatidae and Parakseneuridae, and in the Hemerobiidae (Yang et al., 2012, fig. 13; Makarkin and Perkovsky, 2020, fig. 2A).

All extant and Cenozoic taxa of Myrmeleontidae (including the new genus) have presectrial crossveins. The absence of these crossveins is characteristic of the vast majority of Cretaceous taxa, including all Palaeonleontidae and most Araripeneuridae.

A long hypostigmatic cell is characteristic of Myrmeleontidae s.l., i.e., including Araripeneurinae (Stange, 2004), but also Nymphidae, some Nemopteridae, and Mesochrysopidae. Its absence occurs not only in Palaeonleontidae, but also in Ascalaphinae, most

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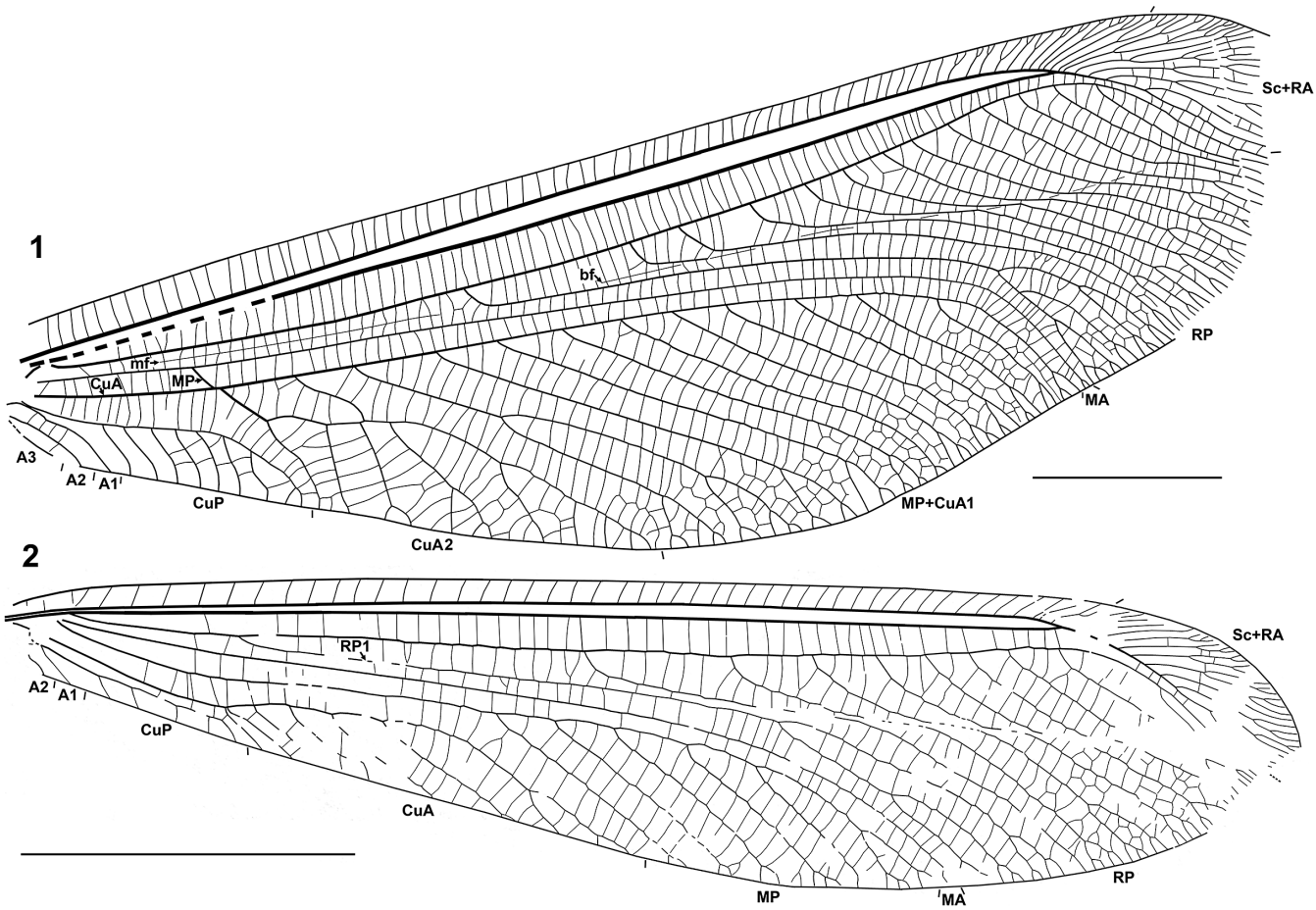

Figure 5. Well-preserved wings of the Early Cretaceous Palaeoleontidae. (**1**) Forewing of *Parapalaeoleon magnus* Menon and Makarkin, 2008 (holotype SMNS 66000/268) from the Crato Formation, Brazil (redrawn from Menon and Makarkin, 2008, with insufficient changes based on photographs). (2) Hind wing of *Baisopardus banksianus* Ponomarenko, 1992 (holotype PIN 1989/51) from Baissa, Transbaikalian Russia (original drawing based on photographs by A. Khramov). bf, anterior Banksian flexion fold/line; mf, medial (radiomedial) flexion fold/line; other abbreviations as in Figure 3. Scale bars = 10 mm.

Mesochrysopidae, and some Nemopteridae. We assume that this characteristic is of little significance.

The anterior Banksian flexion fold/line is absent in Palparinae, but present in most Palaeoleontidae, with the exception of the Coniacian *Metahemerobius kalligrammus* Makarkin, 1990, the Aptian *Araripeleon alphonsei* Millet and Nel, 2010, and an undescribed species from the Crato Formation (unpublished data, Makarkin, 2018). In other Myrmeleontidae this fold is often present (e.g., Zheng et al., 2025, fig. 12A).

The discovery of *Protopalpares* supports Palparinae as more similar to Palaeonleontidae. Given this, should Palaeonleontidae be considered a subfamily of Myrmeleontidae?

Palaeonleontidae species do not have diagnostic features of Myrmeleontidae, even considering Myrmeleontidae s.l. (i.e., with Cretaceous taxa and including Ascalaphidae). Unfortunately, recent studies of the phylogenetic relationships within Myrmeleontoidea based on molecular data usually do not recognize synaphomorphies or other morphological characteristics of Myrmeleontidae (e.g., Haring and Aspöck, 2004; Winterton et al., 2010, 2018; Wang et al., 2017; Machado et al., 2019; Vasilikopoulos et al., 2020).

Lu et al. (2026) stated that the monophyly of Myrmeleontidae s.l. (i.e., including Ascalaphidae) is supported by: (1) antennae strongly dilated distally; (2) RP originating distad the wing base, and (3) elongated tibial spurs. Previously, Stange (1994) identified as synapomophies of Myrmeleontidae s.l.: (4) the presence of the pilula axillaris ('Eltringham's organ': a projection at the base of hind wings in males) as an autapomorphy of Myrmeleontidae (including Stilbopteryginae); and (5) the absence of the basal subcostal crossvein in both wings.

Palaeonleontidae does not conform to any of (1–4) and possibly (5): (1) the antennae are not dilated distally (except in *Guyiling*, in which they are slightly dilated); (2) RP originates very close to the wing base; (3) tibial spurs are relatively short and straight in the Cretaceous *Parapalaeoleon magnus* Menon and Makarkin, 2008 and *Guyiling jianboni* Shi *et al.*, 2012 (Menon and Makarkin, 2008, fig. 4A; Shi et al., 2012, fig. 2B). These are quite similar to those of Ascalaphinae (see e.g., Tjeder, 1992, fig. 32). In most extant Myrmeleontidae, the spurs are longer and usually curved (see e.g., Vshivkova and Makarkin, 2010, fig. 40). Such spurs were also detected in the mid-Cretaceous *Babinoleon jinmingae* Lu et al., 2026; *Nanoleon wangae* Hu, Lu, and Liu in Lu et al., 2019; *Xiaoleon amoena* Lu and Liu, 2022 (Lu and Liu, 2022, fig. 1C; Lu et al., 2019; fig. 9B; 2026, fig. 1D). Thus, the shape of the tibial spurs in Palaeoleontidae is more plesiomorphic than in most Myrmeleontidae. Their presence is generally normal in all Neuroptera, but are usually short. (4) A pilula axillaris is not detected; and (5) the absence of the basal subcostal crossvein is difficult to establish with certainty due to preservation, but numerous

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subcostal crossveins are present at least in *Metahemerobius* (Makarkin, 1990, fig. 5).

There are other character states considered diagnostic by Aspöck et al. (2001), Zimmermann et al. (2011), and Randolf et al. (2014), but these are difficult identify in fossils. For example, tergite 9 divided ventrolaterally, closed anterior tentorial pits, and the anterior tentorial arms as flat tubes were considered by these authors to be synapomorphies of Myrmeleontidae+Ascalaphidae.

Therefore, we agree that the genera of Palaeonleontidae constitute a distinct family, although they do not possess any known synapomorphies. However, judging by their strong similarity to Palparinae, it can be assumed that Palparinae had a close relationship with Early Cretaceous Palaeonleontidae.

Conclusions

The discovery of the first fossil Palparinae is important because its venation is most similar to that of the Early Cretaceous Palaeonleontidae, indicating that they are likely closely related. The presence of two genera belonging to completely different lineages of Myrmeleontidae (*Epignopholeon* Makarkin, 2017 and *Protopalpares*, of Myrmeleontinae and Palparinae, respectively) in the early Eocene Green River Formation supports the idea that the family diversified deep in the Cretaceous (e.g., Hevin et al., 2023).

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