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Oldest new genus of Myrmeleontidae (Neuroptera) from the Eocene Green River Formation

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Abstract

Epignopholeon sophiae **gen. et sp. nov.** (Neuroptera: Myrmeleontidae) is described from the early Eocene of the Green River Formation (Colorado, U.S.A.). It represents the oldest confident record of the family. The new genus is remarkable in that tergite 7 of the female is much shorter than its long sternite 7. The preserved wing venation shows that the genus belongs to the subfamily Myrmeleontinae, and most probably to the tribe Gnopholeontini. The discovery of this species is consistent with estimations of relatively dry and warm conditions during deposition of the upper Parachute Creek Member of the Green River Formation.

Key words: Myrmeleontinae, Gnopholeontini, Green River Formation, Eocene

Introduction

The family Myrmeleontidae (antlions) is the most speciose extant neuropteran group, comprising about 1800 valid species (Oswald 2017). Some antlions are among the largest extant neuropterans, with forewings up to 80 mm long (e.g., Mansell 1996a; Ábrahám 2012). Their larvae are predaceous, many of which construct pitfall traps in sand to capture arthropods walking on the ground (New 1986). Antlions are distributed nearly worldwide, but prefer warm, arid regions.

In contrast with the high diversity of extant Myrmeleontidae, their fossils are extremely rare. Hitherto, only two species have been described: *Dendroleon septemmontanus* Statz, 1936 from the late Oligocene of Rott (Germany), known from only the distal part of a forewing, and *Porrerus dominicanus* Poinar & Stange, 1996, from the early/middle Miocene of Dominican amber, which is represented by five adult specimens (Poinar & Stange 1996; Scheven 2004; Engel & Grimaldi 2007). Both species were assigned to extant genera, although the generic attribution of the former species should be considered as preliminary.

The myrmeleontid affinity of *Myrmeleon reticulatus* Charpentier, 1843 from the Miocene Radoboj locality (Croatia) is quite doubtful, judging from the published figure (see Charpentier 1843: Pl. 22, Fig. 2). *Myrmeleon brevipennis* Charpentier, 1843 from the same locality was also cited as a myrmeleontid by Stange (2004). However, this insect has been long recognized as the gryllacridid orthopteran *Gryllacris brevipennis* (see e.g., Handlirsch 1907, p. 684).

Three myrmeleontid larvae are known from Dominican amber (see Poinar & Poinar 1999; Scheven 2004; Engel & Grimaldi 2007). A myrmeleontoid larva was reported from the Parachute Creek Member of the Green River Formation (Dayvault *et al.* 1995: Fig. 26), but its precise family affinity is unclear (Myrmeleontidae or Ascalaphidae) due to a poor preservation.

Some Cretaceous myrmeleontoids (e.g., Palaeoleontidae, Araripeneuridae, and some other genera of uncertain families affinities) have sometimes been considered members of the Myrmeleontidae (e.g., Stange 2004; Engel & Grimaldi 2007; Engel & Grimaldi 2008). However, it is currently generally thought that there are no known Cretaceous taxa unambiguously belonging to the family (e.g., Makarkin *et al.* 2013; Makarkin 2016; Michel *et al.* 2017).

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Therefore, the discovery of this new species from the early Eocene Green River Formation, which can be confidently assigned to the Myrmeleontidae, is very important, as it represents the oldest record of the family.

Material and methods

The specimen examined here was found in the upper-most part of the Parachute Creek Member of the Green River Formation (D. Kohls, pers. comm.). This formation is considered to span from 53.5 to 48.5 Ma based on ^{40}Ar/^{39}Ar dating (Smith *et al*. 2003, 2008). The Parachute Creek Member accumulated during ca. 2.5 million years of the Ypresian, from 51.3 to 48.5 Ma, and therefore the geological age of this specimen is most likely close to ca. 48.5 Ma, i.e., late Ypresian according to the scale of Cohen *et al*. (2013).

Photographs were taken by David Zelagin using a Canon 5D Mark II camera and a Canon 65 MP-E macro lens. The specimen was wetted with ethanol to increase colour contrast. Helicon Focus v 5.3 was used to stack the images for increased focal depth. Line drawings were prepared by the author using Adobe Photoshop CS3 based on high resolution photographs.

Venational terminology in general follows Kukalová-Peck & 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). The posteriorly directed branches of pectinately-branched veins (i.e., RP, MP in the hind wing, MP+CuA and CuA in the forewing) are designated successively from the anterior traces of those veins, starting from the wing base: e.g., vein RP1 is the proximal-most branch of the anterior trace of RP; vein RP2 is the second branch of the anterior trace of RP; vein CuA1 is the proximal-most branch of the anterior trace of CuA (see Fig. 5). Terminology of genitalia follows Aspöck & Aspöck (2008).

Abbreviations: AA1, first branch of Anterior Analis; CuA, Anterior Cubitus; CuA1, proximal-most branch of CuA; CuP, Posterior Cubitus; MA and MP, anterior and posterior branches of Media; MP1, proximal-most branch of MP; RA, Anterior Radius; RP, Posterior Radius; RP1, proximal-most branch of RP; ScP, Posterior Subcosta.
Institutional abbreviations: UCM, Museum of Natural History of the University of Colorado, Boulder, U.S.A.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Myrmeleontidae Latreille, 1802

Subfamily Myrmeleontinae Latreille, 1802

Tribe ?Gnopholeontini Stange, 1994

Genus *Epignopholeon* gen. nov.

Type and only species. *Epignopholeon sophiae* sp. nov.

Diagnosis. May be distinguished from other genera of Myrmeleontidae by a combination of the following character states: Tergite 7 of female much (almost twice) shorter that sternite 7; digging (fossorial) setae on ectoproct present; gonocoxites 9 probably present, bearing presumed digging setae; RP originates far from wing base (at 0.36 of wing length in forewing; 0.34 in hind wing), slightly proximad origin of CuA1 (forewing) and origin of MP1 (hind wing); CuP (or CuP+AA1) in forewing, and CuA in hind wing distant from, and nearly parallel to posterior wing margin.

Etymology. From the Greek *epi*, near, and *Gnopholeon*, a genus-group name, referring to the assumed tribal affinity of the genus. Gender masculine.

Remarks. The boundaries of some terminal abdominal segments and their appendages are poorly or not discernible. The occurrence of these (i.e., the process of sternite 8, and gonocoxites 8 and 9) is only assumed judging by the presence of their presumed setae.

***Epignopholeon sophiae* sp. nov.**

Figs 1–5

Holotype. UCM 88421a,b (part, counterpart), collected in 2010 by David Kohls, and deposited in the collections of UCM. An incomplete female specimen, with three preserved wings (two forewings, one hind wing).

Type locality and horizon. UCM locality 2009063 (Claudia's Place), situated between East Fork and Middle Fork of Parachute Creek; Garfield County, Colorado, U.S.A. Parachute Creek Member of the Green River Formation; early Eocene (late Ypresian).

Etymology. From the first name of Sophia Elizabeth Kohls, grand-daughter of the collector of the specimen.

Description. Female. Length of body ca. 16 mm.

Head poorly preserved except for large eyes (ca. 1 mm in diameter); vertex slightly elevated; mouthparts not preserved; antennae ca. 5 mm long, dilated apically.

Thorax poorly preserved; prothorax probably short; mesothorax large.

Legs fragmentarily preserved. Forelegs: protibia covered with fine short setae, few strong acute setae. Midlegs: mesofemur moderately stout, with several long strong setae; mesotibia densely covered with fine short setae, several long strong setae. Hind legs: metafemur covered with fine short setae, apparently with few long strong setae; metatibia densely covered with fine short setae, several long strong setae; tibial spurs not detected. Tarsus of all legs poorly preserved, probably similarly constructed; at least four proximal tarsomeres short, covered with fine dense setae, ventrally apparently with pair of rather long, strong setae.

Abdomen complete, but rather poorly preserved. Basal segments poorly or not preserved. Tergites 4–6 longer than others, covered with fine, rather short setae. Sternites 4–6 long, but very poorly preserved. Tergite 7 short, much shorter than sternite 7, covered with fine, rather short setae. Sternite 7 very long, covered with rare, rather strong, elongated setae (Fig. 3B, sS7). Tergite 8 poorly preserved, short. Boundaries of process of sternite 8 (according of Badano *et al*. 2017a; = anterior gonapophyses of Stange 1994) not discernible, but its presumed four-five setae strong, elongated (Fig. 3B, spS8). Boundaries of gonocoxites 8 (= posterior gonapophyses of Stange, 1994) not discernible; their setae fine, dense, very long (Fig. 3B, sgx8). Tergite 9 very poorly preserved; its boundaries not discernible. Boundaries of ectoproct not discernible; its distal setae dense, rather strong, elongated; three digging (fossorial) setae very stout, blunt-pointed, directed upwards (Fig. 3B, dse). Boundaries of gonocoxites 9 (= lateral gonapophyses of authors) not discernible, but their presumed setae long, fine; among these several strong, elongate pointed digging setae.

Forewing narrow, dilated in distal part; ca. 19.7 mm long, 4.5 mm wide at its widest. Costal space very narrow basally, gradually dilated towards apex, strongly dilated after fusion of ScP and RA. Subcostal veinlets widely spaced proximally becoming increasingly closely spaced towards pterostigma; all veinlets simple proximad pterostigma (left wing) or two distal veinlets proximad pterostigma forked (right wing); all subcostal veinlets once forked within pterostigma. Proximal part of pterostigma dark brown. ScP and RA fused; ScP+RA entering margin well beyond wing apex. All veinlets of ScP+RA forked at least twice; five (right wing) to seven (left wing) crossveins between veinlets of ScP+RA detected, forming gradate series; some of them narrowly margined with dark brown. Subcostal space poorly preserved, narrow, without crossveins. One presectoral crossvein detected, other possible. In RA space (between RA and RP), six crossveins proximad fusion of ScP and RA (right wing); no crossveins detected distad this fusion, although one may be present within rather large dark spot; hypostigmal cell long. Origin of RP far from wing base (ca. at 0.36 of wing length). Pectinate RP with eight branches; RP1 originates rather far from origin of RP (four crossveins between RP and M/MA proximad origin of RP1), rather deeply dichotomously branched; RP2–RP3 once to twice forked; RP4–RP8 poorly preserved. Crossveins between branches of RP not numerous, most of them arranged in two gradate series. Distal gradate series consists of eight crossveins, all markedly margined with dark brown. Five crossveins between RP1 and MA detected. M forking into MA and MP markedly distad origin of CuA1. MA with few distal branches, forked twice. Basally, MP appears as oblique crossvein then fused with CuA. Eight crossveins detected between MA and anterior trace of MP+CuA. CuA forked slightly distad origin of RP; distal part of CuA1 strongly arched, with three branches, connected by three crossveins. Two-three long crossveins between anterior trace of MP+CuA and CuA1. MP+CuA pectinate, with five branches, forked once to twice, connected by one to three crossveins (distal-most branch simple). Intracubital space slightly divergent distally. Two crossveins between CuA1 and CuP+AA1 (or CuP). CuP+AA1 (or CuP) distant from and nearly parallel to posterior margin, reaching it distad origin of CuA1, with several simple branches (six detected). Color pattern: transverse spot at pterostigma; all distal gradate series between branches of RP, several gradate series between veinlets of ScP+RA markedly margined with dark brown; rather large spot in distal part of RA space; elongated spot at crossvein between CuA1 and CuP+AA1, adjoining part of CuA1.

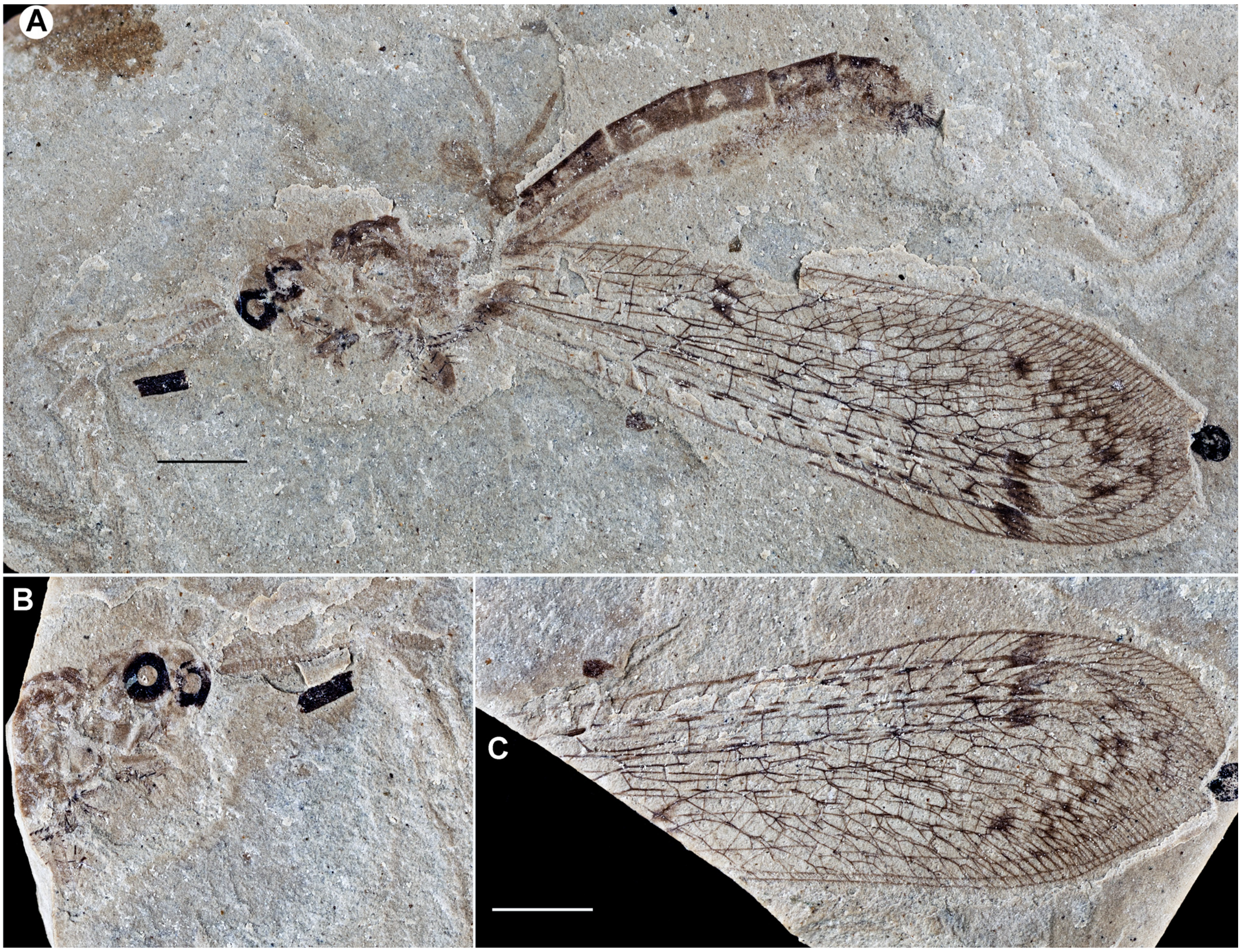

FIGURE 1. *Epignopholeon sophiae* **gen. et sp. nov.**, holotype UCM 88421, specimen as preserved (dry). A, part. B, C, counterpart. Scale bars are 2 mm (B, C to scale).

Hind wing very narrow, ca. 18.0 mm long, 3.5 mm wide as preserved (actual width slightly greater as wing crumpled). Costal space very narrow basally, gradually slightly dilated towards apex, strongly dilated after fusion ScP and RA. Subcostal veinlets widely spaced proximally becoming increasingly more closely spaced towards pterostigma; all veinlets simple proximad pterostigma, once forked within pterostigma. Proximal part of pterostigma dark brown. ScP and RA fused; ScP+RA entering margin well beyond wing apex. All veinlets of ScP+RA once to twice forked; two crossveins between veinlets of ScP+RA detected, forming gradate series. Subcostal space poorly preserved, narrow, without crossveins. No presectoral crossveins detected. In RA space, five crossveins proximad fusion of ScP and RA detected; one distad fusion; hypostigmal cell long. RP originates far from wing base (ca. at 0.34 of wing length). Pectinate RP with eight branches; RP1 originates rather far from origin of RP (three crossveins between anterior traces of RP and MA proximad origin of RP1), rather deeply dichotomously branched (primary fork at fuscous spot); RP2–RP4 once forked; RP5–RP8 simple. Few crossveins between branches of RP detected, all not margined with dark brown. Six crossveins between RP1 and anterior trace of MA. Fork of M not detected, probably near wing base; MA with one, rather long terminal fork. MP strongly pectinate; with 11 branches, once forked (when preserved) except two simple distal-most branches; connected by one crossvein (four crossveins detected). Origin of MP1 slightly distad origin of RP. CuA poorly preserved; its distal part distant from, parallel to posterior margin; distal branches probably widely spaced, simple. CuP and anal veins not preserved. Color pattern: transverse spot at pterostigma, and rounded spot at primary forks of RP1 and MA.

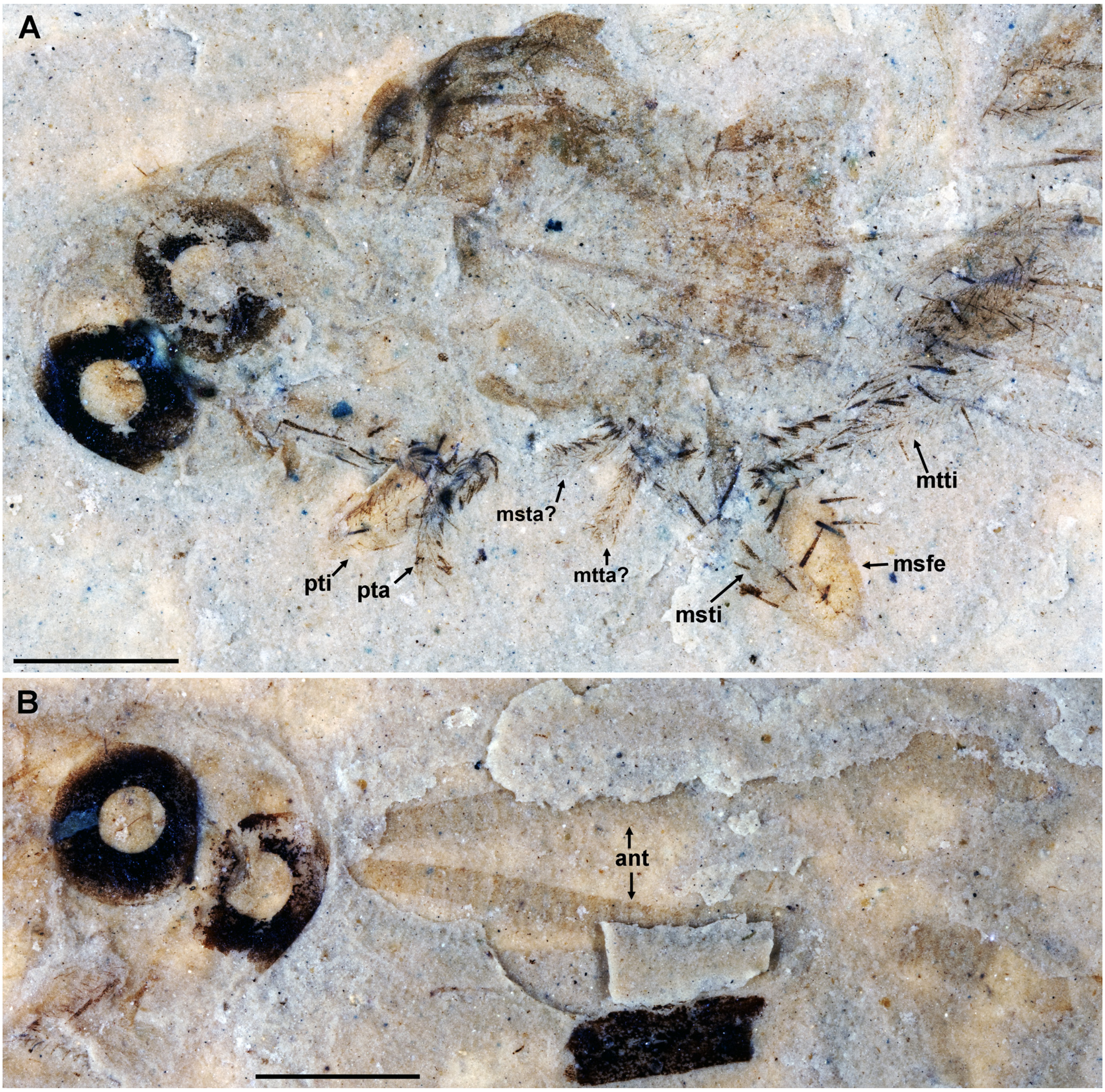

FIGURE 2. Head and thorax of *Epignopholeon sophiae* **gen. et sp. nov.**, holotype UCM 88421 (wetted with ethanol). A, head and thorax of the part. B, head of the counterpart. ant, antennae; msfe, mesofemur; msta, mesotarsus; msti, mesotibia; mtta, metatarsus; mtti, metatibia; pta, protarsus; pti, protibia. Scale bars are 1 mm.

Systematic position of *Epignopholeon* gen. nov.

By the preserved venation of its only known species, this genus can be assigned to the subfamily Myrmeleontinae *sensu* Stange (2004) with confidence. The relative short CuA of the hind wing is especially characteristic of this subfamily. This vein is very long (entering the margin nearly at or after wing mid-point) or fused distally with MP1 in other subfamilies (i.e., Palparinae and Stilbopteryginae). Stange (2004) divided Myrmeleontinae into ten tribes: the Acanthaclisini, Brachynemurini, Dendroleontini, Gnopholeontini, Lemolemini, Maulini, Myrmecaelurini, Myrmeleontini, Nemoleontini, and Nesoleontini. Of these, the Acanthaclisini may be excluded from further consideration, as all of its species have strongly different venation (see e.g., Esben-Petersen 1928b: Fig. 2; Hölzel 1972: Figs 5, 15; New 1985c: Figs 1486, 1549, 1594, 1600; Krivokhatsky 1998b: Fig. 5). This group is often treated as a subfamily (e.g., Krivokhatsky 1998b, 2011; Michel *et al.* 2017). According to the alternative classification of Krivokhatsky (1998b, 2011), the family is divided into eleven subfamilies, seven of which (Myrmeleontinae, Dendroleontinae, Nemoleontinae, Glenurinae, Brachynemurinae, Myrmecaelurinae, and Acanthaclisinae), combined, are identical to the subfamily Myrmeleontinae *sensu* Stange (2004).

The preservation of the specimen is insufficient to assign *Epignopholeon* **gen. nov.** to any of the nine tribes of Myrmeleontinae *sensu* Stange (2004) based on the diagnoses of Stange (1994, 2004, 2008) and Miller & Stange (2009), as most of the important characters used in these are not preserved in this fossil (e.g., of the basal parts of the wings, the male genitalia, and the female terminalia appendages). Given these difficulties, here, I compared characters of the wings in these tribes to discern their diagnostic differences, and so evaluated the tribal affinity of *Epignopholeon sophiae* **sp. nov.** by this means. I used all available literature (see Oswald 2016), especially those works that contain drawings and photographs of the wings, and studied available specimens of extant antlions. Below, the references regarding characteristics of the tribal venation are mainly omitted due to their large amount.

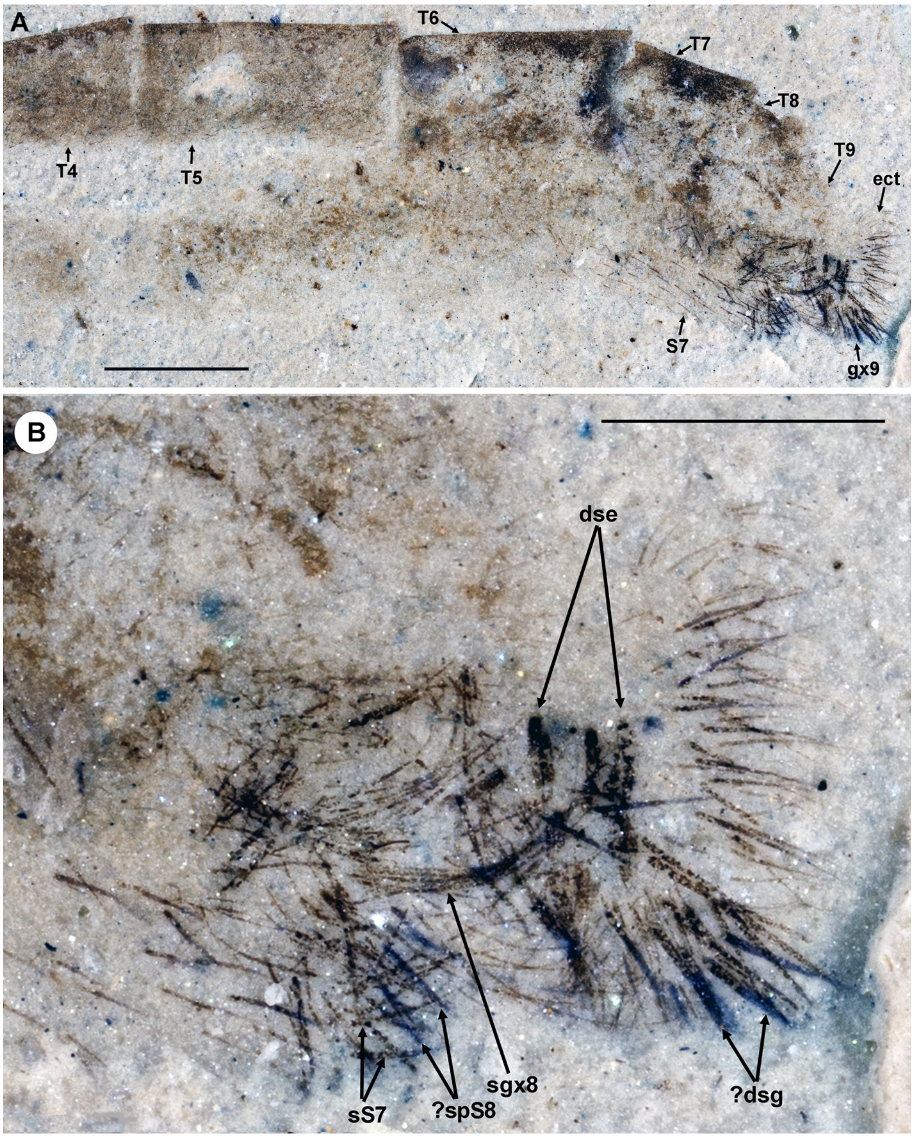

FIGURE 3. Abdomen of *Epignopholeon sophiae* **gen. et sp. nov.**, holotype UCM 88421 (wetted with ethanol). A, distal segments (lateral view). B, setation of terminal segments. dse, digging setae of ectoproct; dsg, digging setae of gonocoxites 9; ect, ectoproct; gx9, gonocoxite 9; sgx8, fine long setae of gonocoxites 8; sS7, terminal setae of sternite 7; spS8, strong setae of process of sternite 8; S7, 7th sternite; T4–T9, 4th to 9th tergites. Scale bars are 1 mm (A), 0.5 mm (B).

The tribe **Myrmecaelurini** has about 150 valid species in 16–17 genera distributed in the Eastern Hemisphere (i.e., Africa, Europe and Asia). Myrmecaelurini *sensu* Stange (2004) includes the tribe Gepini, with four genera, which were recently confirmed as valid (Michel *et al*. 2017). However, the venation of Gepini and Myrmecaelurini s.str. is not fundamentally different, and therefore the tribe is considered herein *sensu* Stange (2004). It includes species with relatively broad wings. In the vast majority of its species, RP originates [1] distad (often far distad) the origin of CuA1 in the forewing, and [2] distad the origin of MP1 in the hind wing. RP very rarely originates opposite the origin of CuA1 in the forewing (i.e., in the genus *Afghanoleon* Hölzel, 1972 and *Lopezus* Navás, 1913). The only species of this tribe in which RP originates proximad the origin of CuA1 in the forewing and the origin of MP1 in the hind wing is *Nannoleon michaelseni* Esben-Petersen, 1928a. However, the origin of the forewing CuA1 is placed in a very distal position. All species of this tribe are characterized by [3] CuP+AA1 in the forewing (and often CuA in the hind wing) being straight, inclined to the posterior margin (i.e., the distal branches are much shorter than the proximal ones).

The range of the tribe **Nesoleontini** (about 80 species) is similar to that of Myrmecaelurini. The venation of all of its species is similar to that of Myrmecaelurini, with RP originating distad the origins of CuA1 and MP1 in the fore- and hind wing respectively, and with a similar configuration of CuP+AA1 in the forewing.

The tribe **Maulini** has two known species, and is distributed in sub-Saharan Africa. In both species, RP originates far proximad the origin of MP1 in the hind wing, and an anterior Banksian line is present in both wings (Esben-Petersen 1928a: Fig. 1; Markl 1954: Fig. 66).

The tribe **Nemoleontini** is the most speciose in the family, comprising ca. 650 species, which are distributed nearly worldwide. In all of species, [1] RP in the hind wing originates in a basal position (markedly proximad the origin of MP1); [2] RP in the forewing originates markedly distad the origin of CuA1 in the vast majority of species; and [3] in the majority of species the configuration of CuP+AA1 is similar to that found in the Myrmecaelurini. Also, [4] many species have a very long CuP in the forewing, which terminates at the posterior margin much distad the origin of CuA1. The venation of proximal parts of the wings typical of the tribe was illustrated by Michel & Akoudjin (2012: Figs 2, 3) and Badano *et al*. (2017a: Fig. 5). In this tribe, the venation of some species of *Mesonemurus* Navás, 1920 is most similar to that of the new genus, in which the forewing RP originates only slightly distad the origin of CuA1 (but its CuP+AA1 is similar to that of other genera of Nemoleontini, and dissimilar to that of the new genus).

Therefore, the new genus is probably distantly related to these four tribes.

The tribe **Myrmeleontini** comprises about 200 species, distributed worldwide. Most have [1] numerous crossveins in areas between RP and CuA1; [2] RP originates distad the origin of CuA1 in the forewing and [3] the origin of MP1 in the hind wing; and [4] CuP+AA1 in the forewing is inclined to the posterior margin. Also, many species are characterized by [5] the presence of a posterior Banksian line (e.g., New 1985a: Fig. 83). The general venation of all species of this tribe is therefore very dissimilar to that the new genus.

The tribe **Lemolemini** with about 15 species is distributed in South America and the Galapagos Islands. Its venation (documented only in a few species) is similar to that of the Gnopholeontini (see e.g., Stange 1969: Fig. 15), but the tribe is characterized by the female ectoproct lacking digging setae (Stange 1994). These setae are distinct in the new genus (Fig. 3B, dse).

The tribe **Brachynemurini** is distributed in the Americas, and includes about 180 species. Its venation is roughly similar to that of *Epignopholeon* **gen. nov.** In particular, [1] RP originates proximad the origin of CuA1 in the forewing and [2] proximad or opposite the origin of MP1 in the hind wing in most of its species. Within this tribe, the venation of the new species is most similar to that of *Dejuna* Navás, 1924 from Mesoamerica, and *Stangeleon* Miller, 2008 from Venezuela (see Stange 1970: Figs 189, 190; Miller 2008: Fig. 1). However, neither of these have the particular combination of character states observed in the new genus. Also, many species of these genera have a distinct anterior Bansksian line, rather dense crossvenation and closely spaced subcostal veinlets, contrary to the condition found in *Epignopholeon* **gen. nov.**

The tribe **Dendroleontini** is rather speciose (about 190 valid species) and widely distributed in the Eastern Hemisphere, but is represented by only three species of *Dendroleon* Brauer, 1866 in North America (Stange 2008). It is characterized in particular by [1] CuP+AA1 in the forewing running in an even curve from, or nearly parallel to, the base to the hind margin (i.e., its distal branches are not particularly shorter than its basal, or the basal and distal branches are approximately same length as in *Epignopholeon* **gen. nov**.), and [2] the proximal origin of RP, e.g., RP in the hind wing usually originates at 0.10–0.20 of wing length. In some Australian genera, however, RP originates more distally, e.g., at 0.25 of wing length in *Csiroleon tumidipalpus* New, 1985b to 0.30 in *Parvoleon minimus* New, 1985b (see New 1985b: Figs 898, 1026, 1034). Character state [1] is characteristic of the vast majority of Dendroleontini species, with few exceptions.

Furthermore, most genera of this tribe are characterized by RP originates proximad [3] the origin of CuA1 in the forewing, and [4] the origin of MP1 in the hind wing. This is characteristic of the genera *Dendroleon* (see New 1985b; Wan *et al.* 2004; Stange 2008; Zhan *et al*. 2012), *Bankisus* Navás, 1912a (see Mansell 1985; Ábrahám 2009; Zhan & Wang 2012), *Gatzara* Navás, 1915 (see Wang *et al.* 2012), *Layahima* Navás, 1912b (see Wan *et al.* 2006), *Tricholeon* Esben-Petersen, 1925 (see Mansell 1988), *Froggattisca* Esben-Petersen, 1915, *Mossega* Navás, 1914 (see New 1985b), and some other genera containing few species. In many species of the speciose Australian genera *Glenoleon* Banks, 1913 and *Austrogymnocnemia* Esben-Petersen, 1917, and the Asian genus *Epacanthaclisis* Okamoto, 1910, RP originates only slightly proximad these origins in both wings (as in *Epignopholeon* **gen. nov**.) or at nearly the same level in the forewing (see New, 1985b; Krivokhatsky 1998a; Ao *et al*. 2010).

The monotypic African genus *Omoleon* Navás, 1936, also belonging to the Dendroleontini, has relatively narrow wings and rather similar venation of the forewing as in *Epignopholeon* **gen. nov**., in particular, RP originates relatively distally, at 0.30 of wing length. But its hind wing RP originates at 0.20 of wing length, and the subcostal veinlets are closely spaced in both wings (see Dobosz & Ábraham 2014: Fig. 1).

Furthermore, some females of Australian Dendroleontini have sternite 7 markedly longer than tergite 7 (e.g., *Austrogymnocnemia* Esben-Petersen, 1917: New 1985b: Figs 485, 521, 531; *Glenoleon* Banks, 1913: New 1985b: Figs 654, 698, 705), but not to such an extreme extent as in the new species.

Therefore, the wing venation and relevant female abdominal characters of *Epignopholeon* **gen. nov**. are somewhat similar to those of some extant genera of Dendroleontini.

The tribe **Gnopholeontini** is distributed in North America (southwestern USA and Mexico), and comprises 10 small species in four genera, with body lengths ranging from 10 to 22 mm (Stange 1994; Miller & Stange 2009). The wing venation patters of *Gnopholeon* Stange, 1970 and *Tyttholeon* Adams, 1957 are most similar to that of *Epignopholeon* **gen. nov.** (see e.g., Stange 1970: Figs 226, 228, 231; 1994: Fig. 15). In particular, these genera share [1] widely spaced subcostal veinlets; [2] a distal origin of RP in both wings (e.g., at 0.26–0.33 of hind wing length in *Gnopholeon*, 0.34 in both *Tyttholeon* and *Epignopholeon* **gen. nov.**); and [3] RP originates slightly proximad the origin of CuA1 in the forewing and [4] the origin of MP1 in the hind wing. [5] The forewing CuP+AA1 in *Gnopholeon* and *Tyttholeon* is somewhat inclined to the posterior margin, distinguishing them from *Epignopholeon* **gen. nov.** However, the forewing CuP+AA1 is also parallel to the posterior margin in the monotypic genus *Menkeleon* Stange, 1970 (see Stange 1970: Fig. 230). Therefore, the venation of the new genus is most similar to that of species of this tribe.

In summary, the combination of character states displayed by *Epignopholeon* **gen. nov.** is more similar to that of Gnopholeontini, Dendroleontini, and Brachynemurini than to any other tribe of the Myrmeleontinae *sensu* Stange (2004). While *Dejuna* and *Stangeleon* share a rather similar venation with the new genus, Brachynemurini is the least possibility of these. A Dendroleontini affinity is supported by CuP+AA1 running nearly parallel to the posterior margin of the forewing in most species, and sternite 7 markedly longer than tergite 7 in some species. But in all extant Dendroleontini, the hind wing RP originates in a proximal position. Finally, the distal origination of RP and widely spaced subcostal veinlets in both wings, RP originating slightly proximad the origin of CuA1 in the forewing, and the origin of MP1 in the hind indicate that Gnopholeontini is the most probable tribal affinity of *Epignopholeon* **gen. nov.**

The phylogenetic context

The phylogenetic position of Gnopholeontini is unclear. It was considered as sister to Lemolenini by Krivokhatsky (1998b: Fig. 3; 2011: Fig. 65) in his subfamily Brachynemurinae, and as the sister group of Dendroleontini by Stange (1994: Fig. 2). In general, Stange (1994) presumed a close relationship of Dendroleontini and Gnopholeontini, supported by a single synapomorphy: the 'gonapophyseal plate' (i.e., "an asetose sclerite which forms part of the floor of the genital chamber and apparently articulates with the posterior gonapophyses": Stange 1994, p. 69, = gonapophyses 8 of Aspöck & Aspöck 2008) is wider than the width of gonocoxite 8 (= posterior gonapophysis of Stange 1994). This character is not detectable in *Epignopholeon* **gen. nov.**

According to the cladogram of Michel *et al.* (2017) based on molecular data, the Dendroleontini and Brachynemurini are sister taxa. However, no genera of Gnopholeontini and Lemolemini (which together with Brachynemurini *sensu* Stange 2004 constitute Brachynemurini *sensu* Stange 1970) were included in that study, leaving the relationships among these tribes unresolved.

Larvae of neither Dendroleontini nor Gnopholeontini live in sand except for those of *Tyttholeon*, which, however, are not pit-building (Mansell 1999; Miller & Stange 2009). Mansell (1996b, 1999) believed that both tribes represent ancient lineages of Myrmeleontidae based on this presumably plesiomorphic larval habit. However, at least the tribe Dendroleontini has been recovered as a rather distant branch from the base of the Myrmeleontidae in recent phylogenetic analyses (i.e., Badano *et al*. 2017b; Michel *et al*. 2017).

If *Epignopholeon* **gen. nov.** indeed belongs to Gnopholeontini, this means that representatives of the tribe lived in North America at least since the early Eocene. However, given a presumably close relationship of Gnopholeontini with Dendroleontini and given the incomplete preservation of this fossil, it might also be assumed that the new genus belongs to the stem group of Dendroleontini + Gnopholeontini. Also, some possibility remains that it belongs to either the Dendroleontini or the Brachynemurini. In any case, the discovery of this genus is important despite the poor preservation of some of its characters which leaves some doubt as to its placement.

FIGURE 4. Wings of *Epignopholeon sophiae* **gen. et sp. nov.**, holotype UCM 88421 (wetted with ethanol). Scale bar is 1 mm.

The paleoenvironmental applications

The deposition of evaporites throughout the Parachute Creek Member (see Smith *et al*. 2008) and the members of its Neuroptera assemblage, including a relative abundance of Ascalaphidae (five undescribed specimens of at least three species: pers. obs.), imply relatively dry and warm conditions during the interval of its upper portion (or at least the existence of intermittent dry periods: Wilf *et al*. 1998). The presence of this antlion is consistent with this model. *Xenoberotha angustialata* Makarkin, 2017 (Berothidae) was the only species of Neuroptera described from that locality and generally from the Green River Formation. A larva of "Myrmeleontidae or perhaps Ascalaphidae" (Dayvault *et al*. 1995, p. 106, Figs. 26) and an adult of presumable Nemopteridae (erroneously determined as a "crane fly, probably of family Ptychopteridae": Dayvault *et al*. 1995, p. 105, Figs. 30) were reported but not described from the upper Parachute Creek Member. The undescribed material in collections from these layers also includes Hemerobiidae (three specimens), Myrmeleontidae (an apical fragment of a wing not conspecific with *Epignopholeon* **gen. nov.**), and Osmylidae (one specimen). Of these, only the occurrence of Osmylidae would be consistent with a relatively humid environment. However, these conditions might be locally present in microclimates of riparian forests along rivers and coastal forests near lakes. So, the general Neuroptera assemblage supports MacGinitie's (1969, p. 2) environmental interpretation based on the flora of the upper Parachute Creek Member and the lower Evacuation Creek Member: "the closest resemblances in environment and composition are found in the savanna-woodland floras along the equatorward border of the dry tropics, east of Mazatlan, Mexico, and in the area of Santiago, Argentina, and the region around Monterrey, Mexico".

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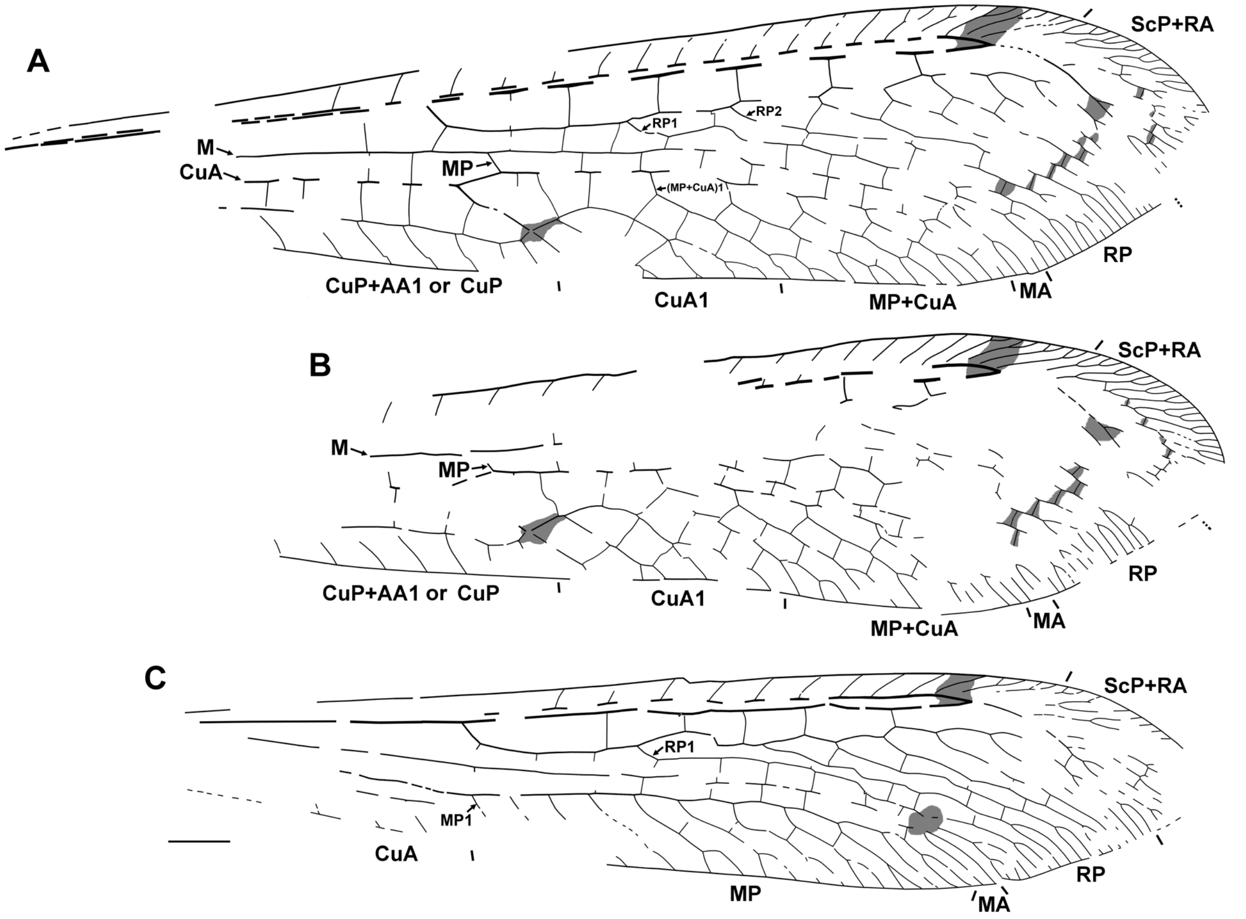

FIGURE 5. Wing venation of *Epignopholeon sophiae* **gen. et sp. nov.**, holotype UCM 88421. A, right forewing; B, left forewing (converted to standard view, with apex to the right); C, right hind wing. Scale bar is 1 mm (all to scale).

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