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## A hangingfly (Mecoptera, Bittacidae) from the late Oligocene Fossilagerstätte Enspel, Westerwald (SW Germany)

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### Abstract

A hangingfly (Mecoptera, Bittacidae) is described from bituminous shales of the late Oligocene crater-lake of Enspel, Germany. It is attributed to a new species, *Eremobittacus opeth* sp. nov., and constitutes the first post-Eocene record of fossil hangingflies from Germany. The genus *Eremobittacus* was hitherto exclusively known from Mexico. Its presence in the Oligocene of Germany is a further case of insect dispersion between North America and Europe, via the Beringian, the Thulean, or the De Geer routes during the Paleogene.

**Keywords:** Insecta, Mecoptera, Bittacidae, *Eremobittacus*, Oligocene, Enspel

### Introduction

Hangingflies (Bittacidae) are a species-rich but little-known family in the order Mecoptera. The family comprises about 270 extant species mainly distributed in subtropical and tropical regions (Krzemiński, 2007). The oldest known stem representative of the Bittacidae is *Archebittacus exilis* Riek, 1955 from the Upper Triassic of Australia (Riek, 1955; Lambkin, 2017), whereas the generic diversity of the family was greatest in the Jurassic (Novokshonov, 2002). The worldwide distributed *Bittacus* is the most diverse genus in Bittacidae comprising about 150 extant species (Bicha, 2018). In contrast, the fossil record of hangingflies is comparatively meager and Oligocene records are hitherto restricted to *Bittacus biamensis* Novokshonov, 1993 from Russia, *Bittacus veterinus* (Cockerell, 1921), and an unnamed species *Bittacus* sp. A (*sensu* Jarzembowski, 1980), both from the late Eocene/early Oligocene of the Isle of Wight (Krzemiński, 2007).

Here, we describe the first hangingfly fossil in the closely related extant genus *Eremobittacus* Byers, 1997 from the late Oligocene Fossilagerstätte Enspel, the first post-Eocene record of fossil hangingflies from Germany.

### Material and methods

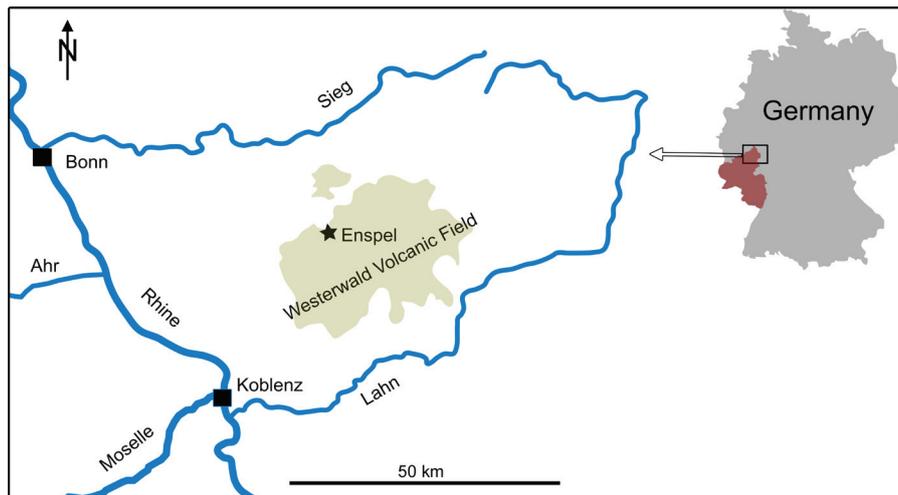
#### Material

The fossil described herein originates from bituminous black shales deposited in an ancient crater lake near Enspel, Westerwald, SW Germany (Fig. 1). It was found in the year 2006 at excavation site G23, layer S16, for numbering of layers and position in the lithologic log see Schindler & Wuttke (2015: fig. 1) and Uhl & Poschmann (2018: fig. 2). The Enspel-Fossilagerstätte is a particularly diverse locality for biota of the terrestrial late Oligocene of Central Europe (for an overview see Poschmann *et al.*, 2010).

#### Methods

The fossil was photographed while it was immersed in water using a Canon EOS 600D SLR camera equipped with a Canon EFS 60 mm or, in case higher magnifications were employed, a Canon MP-E 65 mm macro lens. In order to enhance depth of field, multiple images with differing focal planes were stacked into a composite with the free software CombineZM (by Alan Hadley). Photographs were processed and arranged into figures using Affinity Photo. Drawings are meant to explain the visible structures and are not reconstructions.

We follow the wing venation terminology of Schubnel *et al.* (2020), because it considers the presence of a PCu vein in the wings of the Mecoptera.



**FIGURE 1.** Approximate geographical position of the Enspel site. State of Rhineland-Palatinate shown in red.

### Abbreviations

A, anal vein; An, antenna; Av, anal crossvein; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; Cuv, cubital crossvein; Fe, Femur; FM, first fork of media; FRs, first fork of radial sector; H, head with proboscis; M, media; MA, media anterior; MP, media posterior; OM, origin of media; ORs, origin of radial sector; PCu, postcubital crossvein; Pcv1 and Pcv2, pterostigmal crossveins; Pt, pterostigma; R, radius; RA, radius anterior; RP, radius posterior; ScP, subcosta; Scv, subcostal crossvein; T, tarsomere; Ti, tibia.

### Systematic palaeontology

**Order Mecoptera Packard, 1886**

**Infraorder Raptipedia Willmann, 1987**

**Family Bittacidae Handlirsch, 1906**

**Genus *Eremobittacus* Byers, 1997**

**Type species.** *Eremobittacus spinulatus* Byers, 1997 (extant).

**Other species.** *Eremobittacus sodalium* Byers, 2011 (extant), *Eremobittacus opeth* **sp. nov.** (late Oligocene).

***Eremobittacus opeth* sp. nov.**

(Figs 2–6)

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**Type material.** Holotype NHMMZ PE 2006/5031-LS a, b, part and counterpart, preserved in bituminous black pelites from Enspel (Germany). Deposited in the Landessammlung für Naturkunde Rheinland-Pfalz at the Naturhistorisches Museum Mainz, Germany (NHMMZ).

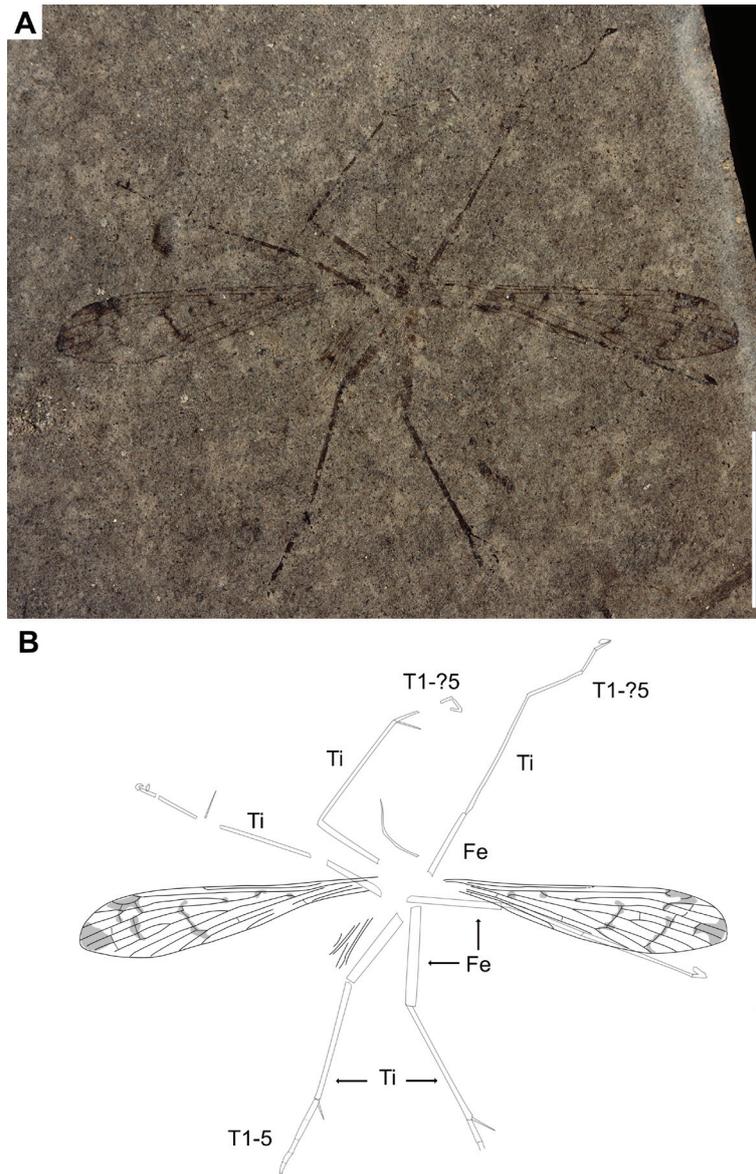
**Etymology.** Named for the Swedish metal/hardrock band Opeth.

**Diagnosis.** A species of *Eremobittacus* with clouded (colored) areas in forewing very similar to those of *Eremobittacus spinulatus* except for the presence of hyaline zone between CuA and posterior wing margin vs. colored; hind basitarsomere about as long as tibia spurs and shorter than second plus third, as in *E. spinulatus*.

**Type locality and horizon.** Enspel, Westerwald, SW Germany; Laminites of the uppermost Enspel Formation (Schäfer *et al.*, 2011; Schindler & Wuttke, 2015; lithozone C/D *sensu* Felder *et al.*, 1998); Late Oligocene, 24.9–24.5 Ma; Mammal Paleogene zone MP 28 (Storch *et al.*, 1996; Mertz *et al.*, 2007).

**Description.** The fossil is a rather complete compression, except for lacking details of hind wings and of abdomen. Clouded (colored) areas in forewing consisting of small maculae at OM, ORs, and FRs, transverse stripes covering crossveins at origins of RP3–RP4 fork to MP1–MP2 fork, below Pt in area between RP3 and MP2, and larger colored patches at Pt and in apical part of wing, but not in area between CuA and posterior wing margin. Forewings petiolate, slender in basal one-third, with rather straight anterior margin, about 18 mm long and 3.9 mm wide; subcostal area between C and ScP up to 0.21 mm wide, narrower than that between ScP and R/RA (0.24 mm wide); base to OM (divergence of M from M+CuA) at 28 % of total length in forewing; Sc joining C well beyond FRs in forewing; two Pcv; vein CuP ending far beyond FM in forewing; vein PCu ending far beyond OM in forewing; A ending well basad OM in forewing; crossveins of second and third ranks between RP4 and MP2 well aligned.

Legs uniform dark-brown, quite elongate; fore and mid femora thin; hind femora widened in basal two-thirds; tibiae distinctly longer than respective femora; apical



**FIGURE 2.** *Eremobittacus opeth* sp. nov., holotype, part NHMMZ PE 2006/5031-LSa. **A**, Photograph. **B**, Sketch drawing. Scale bars = 10 mm.

spurs of hind tibia very long, as long as basitarsomere; hind basitarsus approximately 1.7 times the length of the fourth tarsomere, distinctly shorter than the second and third together (Fig. 6).

## Discussion

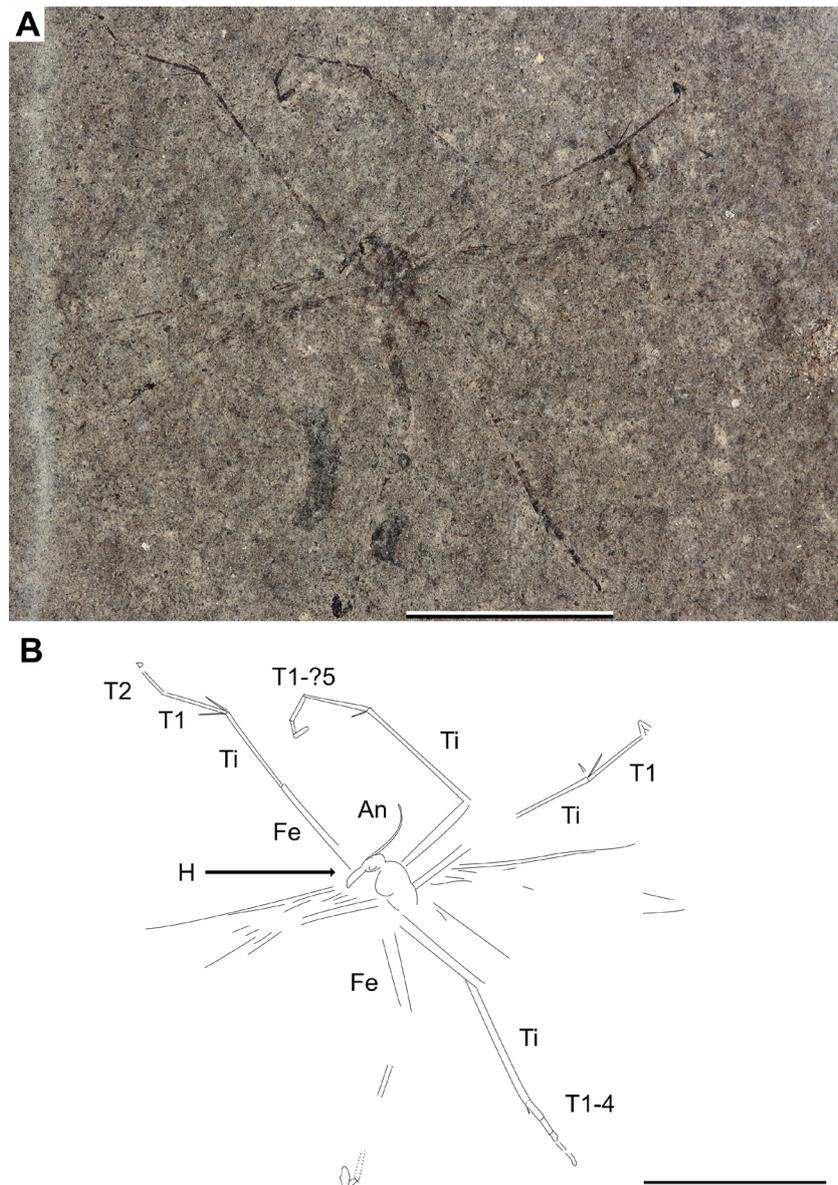
### *Comparison with other fossil and extant bittacid genera*

The new hangingfly fossil can be attributed to the Bittacidae because of the petiolate wings due to the narrow postcubital-anal area, and by the single claw on the legs. The Mesozoic Neorthophlebiidae have also petiolate wings and are considered by Willmann (1989) as a closely related (stem group?) to the Bittacidae. They

differ from the latter family in the forewing vein M with more than four branches, vs. four or less in Bittacidae (see also Ansorge, 1993). Willmann (1989) also put the Jurassic–Eocene Cimbrophlebiidae in the Raptipedia together with the Bittacidae and the Neorthophlebiidae, but they strongly differ from the new fossil and the Bittacidae in the anal vein having numerous posterior branches (Willmann, 1977; Bechly & Schweigert, 2000).

Here we compare the new fossil with all genera currently attributed to the Bittacidae, because even the Mesozoic fossils bear some similarity to extant taxa, especially in wing venation.

Novokshonov (1993a, b) considered the Neorthophlebiidae as a subfamily of the Bittacidae, and included in the Neorthophlebiinae several genera with only four

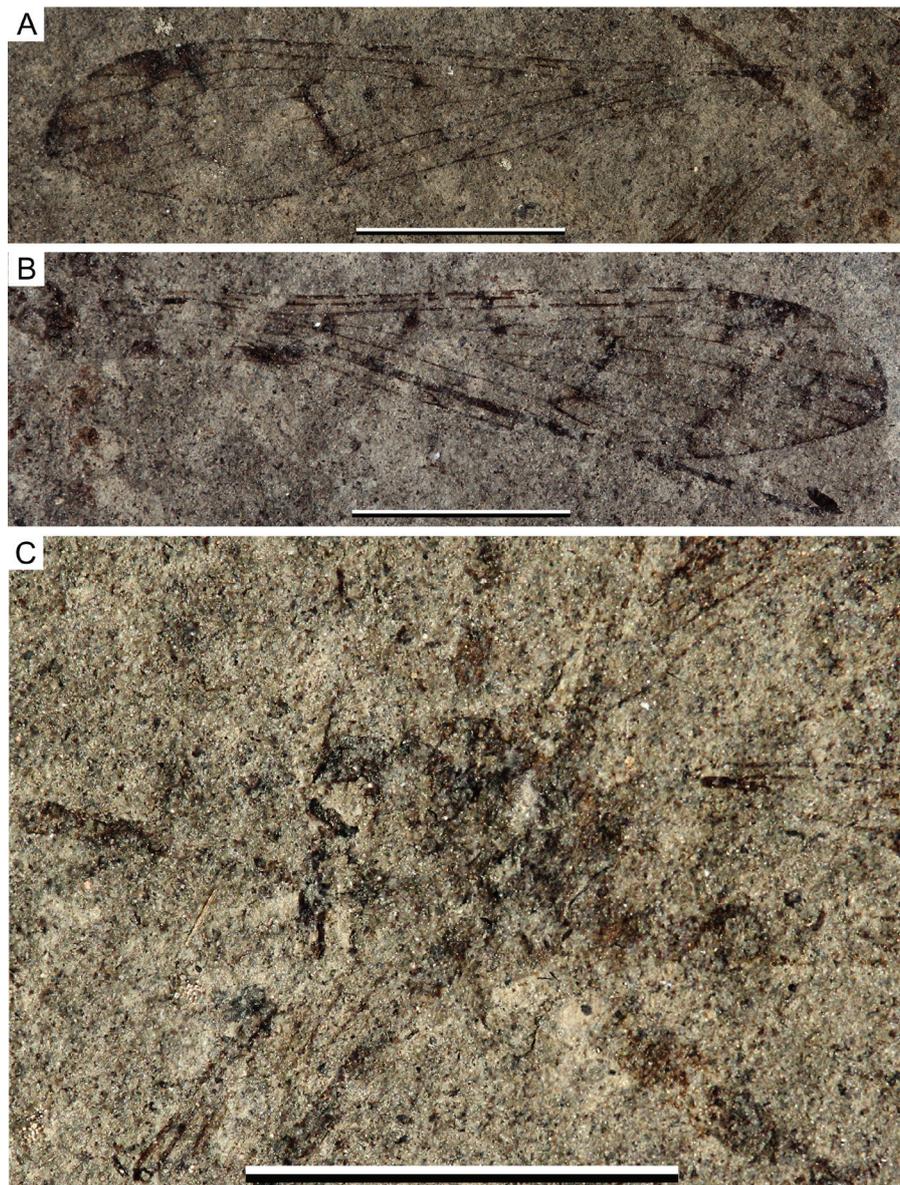


**FIGURE 3.** *Eremobittacus opeth* sp. nov., holotype, counterpart NHMMZ PE 2006/5031-LSb. **A**, Photograph. **B**, Sketch drawing. Scale bars = 10 mm.

branches of M. Among these, the genera *Antiquanabittacus* Petrulevičius & Jarzembowski, 2004, *Archebittacus* Riek, 1955, *Asiobittacus* Novokshonov, 1993, *Baissobittacus* Novokshonov, 1997a, *Composibittacus* Liu *et al.*, 2016, *Cretobittacus* Novokshonov, 1993, *Decoribittacus* Li & Ren, 2009, *Haplobittacus* Bode, 1953, *Karattacus* Novokshonov, 1997a, *Megabittacus* Ren, 1997, *Microbittacus* Novokshonov, 1993, *Mongolbittacus* Petrulevičius *et al.*, 2007, *Orobittacus* Villegas & Byers, 1981, *Orthobittacus* Willmann, 1989, *Plesiobittacus* Novokshonov, 1997b, *Pleobittacus* Bode, 1953, *Preanabittacus* Novokshonov, 1993, *Probittacus* Martynov, 1927, *Scharabittacus* Novokshonov, 1993, and *Sibirobittacus* Sukatcheva, 1990 differ from NHMMZ PE 2006/5031-LS in the crossveins between the base of

MP1 and MA and between MA and RP4 being not well aligned and/or much more oblique ('Kreuz der Bittaciden' absent or strongly oblique) (Bode, 1953; Sukatcheva, 1990; Novokshonov, 1993a, b, 1997a, b; Ren, 1997; Petrulevičius *et al.*, 2007; Li & Ren, 2009; Yang *et al.*, 2012a, b; Liu *et al.*, 2016; Kopeć *et al.*, 2016; Lambkin, 2017).

The genera *Prohylobittacus* Novokshonov, 1993, *Exilibittacus* Yang *et al.*, 2012, *Jurahylobittacus* Li *et al.*, 2008, and *Formosibittacus* Li *et al.*, 2008 have the 'Kreuz der Bittaciden' more similar to that of NHMMZ PE 2006/5031-LS, but all differ from the latter in the wing being much more rounded apically and the base of RP is much closer to the point of separation between M and CuA (Li *et al.*, 2008; Yang *et al.*, 2012b). The Jurassic

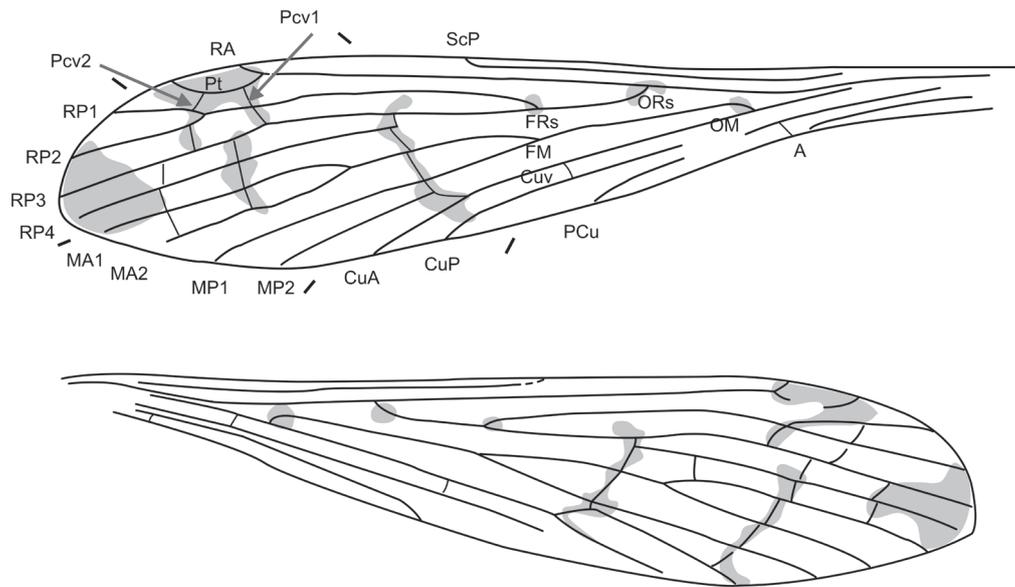


**FIGURE 4.** *Eremobittacus opeth* sp. nov., holotype NHMMZ PE 2006/5031-LS. **A, B,** Forewings from part. **A,** Left forewing. **B,** Right forewing. **C,** Detail of counterpart showing head with proboscis and thoracic region. Scale bars = 5 mm.

*Liaobittacus* Ren, 1993 also differs from NHMMZ PE 2006/5031-LS in the same second character plus the first fork of RP being opposite that of M (Ren, 1993). The mid-Cretaceous genus *Burmobittacus* Zhao *et al.*, 2017 has much narrower wings than NHMMZ PE 2006/5031-LS and a different pattern of pterostigma (Zhao *et al.*, 2017). *Austrobittacus* Riek, 1954 is mainly diagnosed based on features of the hind wing and thus difficult to compare to our fossil, but the type species *A. anomalus* Riek, 1954 differs from NHMMZ PE 2006/5031-LS in a shorter PCu [A1 *sensu* Riek, 1954], which is only half the length of CuP (Riek, 1954).

The extant genera *Pazius* Navás, 1913, *Tythobittacus* Smithers, 1973, and *Symbittacus* Byers, 1986 have very narrow wings with the base of RP very far from the point

of separation of M with CuA (Smithers, 1973; Byers, 1986; Lima & Dias, 2016; Kopeć *et al.*, 2016). *Anomalobittacus* Kimmins, 1928 has only vestigial wings (Kimmins, 1928). *Anabittacus* Kimmins, 1929 has no crossveins between RA and RP at pterostigma level, the median vein is only trifurcate and RP bifurcate (Kimmins, 1929; Byers, 1965; Machado *et al.*, 2009). *Apterobittacus* MacLachlan, 1893 has no wings (Carpenter, 1931). *Austrobittacus* Riek, 1955 and *Kalobittacus* Esben-Petersen, 1914 have a very long forewing stem of M basal to its fusion with CuA (Riek, 1954). *Kalobittacus* has also a shortened PCu, as for *Nannobittacus* Esben-Petersen, 1927 and *Issikiella* Byers, 1972 (Esben-Petersen, 1927; Byers, 1965, 1972, 1997; Machado *et al.*, 2009). *Edriobittacus* Byers, 1974 has the vein PCu very short, extending only slightly



**FIGURE 5.** *Eremobittacus opeth* sp. nov., holotype, part NHMMZ PE 2006/5031-LSa. Sketch drawings of left (labelled) and right forewings, respectively. Scale bar = 10 mm.

beyond the level of the base of M in the forewing (Byers, 1974). *Thyridates* Navás, 1908 is supposed to have vein RP1+2 forking from RP forming nearly a right angle (Petrulevičius, 2003), but Machado *et al.* (2009) indicated that this character is unstable among the species currently in this genus and also in some *Bittacus* spp. Thus, they synonymized *Thyridates* with *Bittacus*. Machado *et al.* (2009) also synonymized *Neobittacus* Penny, 1977 with *Bittacus*.

The type species of the Nearctic genus *Eremobittacus* Byers, 1997 (*E. spinulatus* Byers, 1997) has a venation very close to those of the representatives of *Bittacus* Latreille, 1805, *Harpobittacus* Gerstaecker, 1885, and *Bicaubittacus* Tan & Hua, 2009, except for the well aligned crossveins of second and third ranks between RP4 and MP2 (Lambkin, 1994; Byers, 1997; Tan & Hua, 2009a; Machado *et al.*, 2009: 34; Jácome, 2020). The situation in *Eremobittacus* is exactly what is observed in NHMMZ PE 2006/5031-LS, at least in the right wing where those crossveins are preserved (Fig. 5). Nevertheless, some *Bittacus* species (e.g., *B. mexicanus* Klug, 1836 or *B. spinulatus* Byers, 1997) have also the crossveins of second and third ranks between RP4 and MP2 better aligned than in others species, but less than in *Eremobittacus* and NHMMZ PE 2006/5031-LS. Also, *Eremobittacus spinulatus* and NHMMZ PE 2006/5031-LS share the presence of dark spots on these crossveins, unlike the majority of *Bittacus* species, even if *B. strigosus* also has these crossveins darkened. *Eremobittacus*, numerous *Bittacus* species,

and NHMMZ PE 2006/5031-LS also share the presence of two pterostigmal crossveins. The second species of *Eremobittacus*, *E. sodalium* Byers, 2011 has the crossveins between branches of R and M not transversely aligned as in *E. spinulatus* and not bordered by darker membrane. Therefore, these characters alone are not sufficient to discriminate the two genera *Eremobittacus* and *Bittacus*.

The genus *Eremobittacus* is better characterized by the hind basitarsus being shorter than the second and third together, while in *Bittacus*, the hind basitarsus is longer than the second and third together (Willmann, 1986: fig. 5; Byers, 1997; Jácome, 2020: fig. 14). NHMMZ PE 2006/5031-LS most closely approximates the situation in *Eremobittacus* with the basitarsomere shorter than the second + third, and the fourth tarsomere slightly wider than the others, but less than in *E. spinulatus*. Thus, we prefer to attribute the new fossil to *Eremobittacus*.

NHMMZ PE 2006/5031-LS differs from *E. sodalium* in the pattern of the crossveins between R and M, and in the hind tibia spurs being as long as the basitarsomere vs. longer (Byers, 2011).

The Australian genus *Harpobittacus* also has short hind basitarsi, but still longer than the fourth tarsomeres, in males at most 1.5× length of fourth tarsomeres, in females at most 1.7× (Lambkin, 1994), which closely corresponds to the ratios in the new fossil. But *Harpobittacus* has the crossveins of second and third ranks between RP4 and MP2 not aligned.

*Afrobittacus* Londt, 1994 is characterized by the hind wing PCu basally fused with CuP for a long distance, a character difficult to evaluate in NHMMZ PE 2006/5031-LS, but its hind tarsomeres are similar to those of *Bittacus* (Londt, 1994). *Terrobittacus* Tan & Hua, 2009 has also the crossveins of second (and sometimes third) rank(s) between RP4 and MP2 as well aligned as in NHMMZ PE 2006/5031-LS, but it differs in the presence of only one pterostigmal crossvein Pcv (Tan & Hua, 2009b). This character seems to be rather weak as some *Bittacus* sp. have the two Pcv veins strongly approximate (e.g., *B. pinguipalpis* Wood, 1933) (Wood, 1933). *Terrobittacus* would share with NHMMZ PE 2006/5031-LS the presence of dark spots on the crossveins of second and third ranks between RP4 and MP, but it shares with *Bittacus* the hind basitarsus longer than second and third together.

*Hylobittacus* Byers, 1979 also differs from NHMMZ PE 2006/5031-LS in the presence of only one pterostigmal crossvein Pcv, elongate hind basitarsomere, and crossveins of second and third ranks between RP4 and MP not aligned (Byers, 1979).

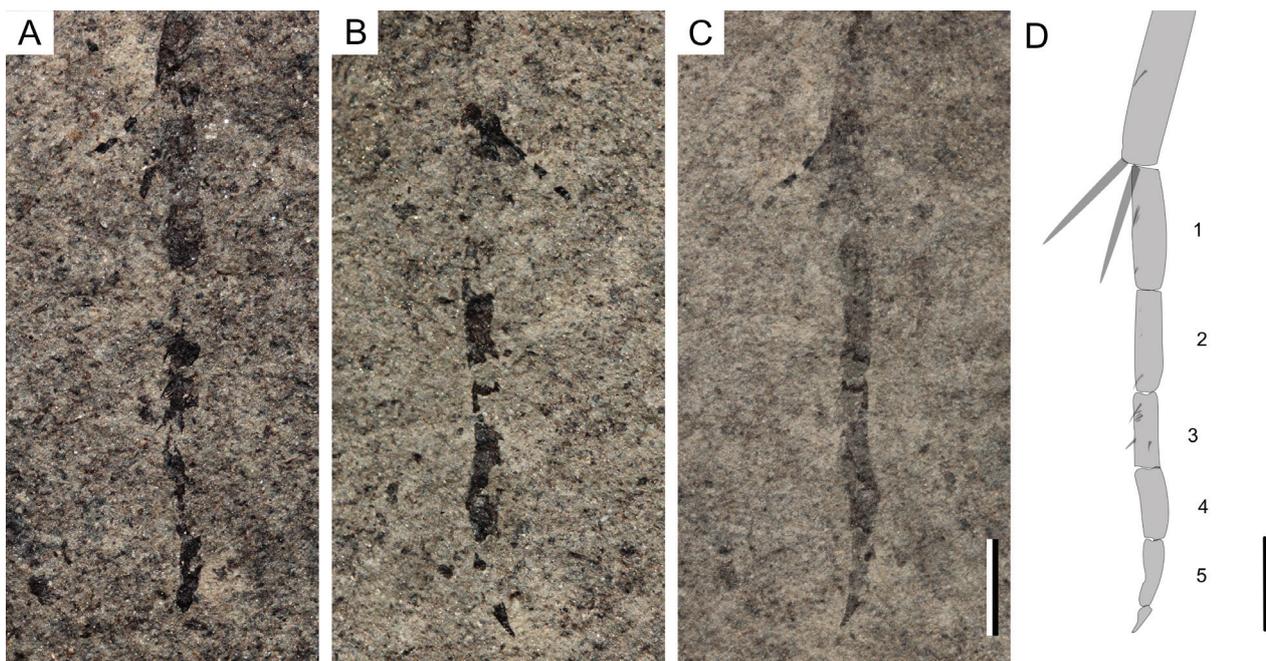
The genus *Palaeobittacus* Carpenter, 1928 (*P. eocenicus* Carpenter, 1928, Eocene, Piceance Creek, Green River, Colorado, USA) also shares with NHMMZ PE 2006/5031-LS the crossveins of second (and sometimes third) rank(s) between RP4 and MP2 well aligned. *Palaeobittacus eocenicus* differs from NHMMZ PE 2006/5031-LS in the hyaline wings and the fork between RP3 and RP4 much more basal than that between MA1 and MA2 (Carpenter, 1928), but these last characters are at most a species difference. Carpenter (1928) indicated nothing about the leg structures of *P. eocenicus*, thus it is

hard to compare with *Eremobittacus*, even if it could be closely related or even belong to it.

#### Comparison with the fossil representatives of the crown group Bittacidae

The mid-Cretaceous *Bittacus lepiduscretaceus* Li *et al.*, 2018 shares with NHMMZ PE 2006/5031-LS the crossveins of second rank between RP4 and MP2 well aligned, but it has no crossveins of the third row. Also, it has a very narrow area between PCu and the posterior wing margin, and has hyaline wings (Li *et al.*, 2018). Note that these authors did not discuss its possible relationships with *Eremobittacus*, *Terrobittacus*, or *Palaeobittacus*. Its attribution to the extant genus *Bittacus* is questionable.

The late Paleocene *Bittacus novokschonovi* (Petrulevičius, 2003) differs from NHMMZ PE 2006/5031-LS in the non-aligned crossveins of second rank between RP4 and MP2, and the vein PCu reaching the level of fork of M (Petrulevičius, 2003). The Eocene Baltic amber species *Hylobittacus antiquus* (Pictet, 1854), *Hylobittacus fossilis* (Carpenter, 1954), *Hylobittacus minimus* (Carpenter, 1954), and *Hylobittacus picteti* Krzemiński, 2007 have the wings uniformly light brown and only one crossvein Pcv. *Hylobittacus antiquus* has the crossveins of second rank between RP4 and MP2 better aligned than in the other Baltic amber species, but less than in NHMMZ PE 2006/5031-LS. *Bittacus succinus* Carpenter, 1954 shares with NHMMZ PE 2006/5031-LS the two crossveins Pcv1 and Pcv2. It also has ‘nebulous’ dark areas in the distal part of the wings, but its crossveins of the second rank between RP4 and MP2 are not aligned, and its ratio wing length/wing width is 3.4, vs.



**FIGURE 6.** *Eremobittacus opeth* sp. nov., holotype NHMMZ PE 2006/5031-LS. Hind tarsus. **A**, Counterpart. **B**, Part. **C**, Combination of part and counterpart. **D**, Sketch drawing. Scale bars = 1 mm.

4.7 in NHMMZ PE 2006/5031-LS (Carpenter, 1954; Krzemiński, 2007). The Oligocene *Bittacus biamensis* Novokshonov, 1993b also has its crossveins of the second rank between RP4 and MP2 not aligned. NHMMZ PE 2006/5031-LS also differs from this species in the narrower wing (length/width ratio 4.7 vs. 4.0 in *Bittacus biamensis*). The Eocene Green River *Bittacus egestionis* Carpenter, 1955 differs from NHMMZ PE 2006/5031-LS in the non-aligned crossveins of second rank between RP4 and MP2 (Carpenter, 1955).

#### *Paleobiogeographic and palaeoecologic discussion*

The attribution of the new German fossil to *Eremobittacus*, nowadays strictly Nearctic (Mexico), is in accordance with the hypotheses proposed by Byers (1988) in faunistic transfers between North America and Eurasia during the Cenozoic. Also, it is not so surprising as some other Oligocene Palearctic insects belonging to extant Nearctic genera have already been recorded, e.g., the aeshnid genus *Epiaeschna* (Nel & Petrulevičius, 2010), which is also known from Enspel (Nel *et al.*, 2020). There were numerous opportunities for dispersal via several land bridges between North America and Eurasia during the Cenozoic, either via the Beringian, the Thulean, or the De Geer routes (Brikiatis, 2014). The presence of *Palaeobittacus eocenicus* that shows at least strong similarities with *Eremobittacus* in the Green River formation could also support a more northern extension of the latter genus during the early Cenozoic, rendering a potentially possible dispersal via these quite northern routes. This situation may be comparable to that of the extant Antillean genus *Teredon* and the Eocene Green River *Eoteredon* (in Siricidae) (Archibald *et al.*, 2021).

Extant Bittacidae are cosmopolitan, but show a preference for the tropical southern hemisphere. Adult hangingflies have a peculiar morphology related to their essentially predaceous lifestyles. They mainly prey on other flying insects such as dipterans, hymenopterans, trichopterans, small lepidopterans, but also on spiders (Willmann, 1986). Some can be kleptoparasites (Jennings & Sferra, 2002). Prey is caught chiefly with the hind legs while foraging actively in the vegetation. Also, if a prey item approaches the resting hangingfly attached with its forelegs to vegetation (hence the name), it may be grabbed with the raptorial hind legs folding the fifth tarsomere back tightly against the fourth. In *Bittacus* species, it is mainly the males that show this behaviour while females largely rely on nuptial gifts offered by the males during courtship and copulation (e.g., Willmann, 1986; Chen *et al.*, 2013).

Generally, Mecoptera are quite rare in the Western European Oligocene lacustrine outcrops. We never found any in the very abundant collections done at Céreste or Aix-en-Provence. The specimen described herein is the

only known Bittacidae from Enspel. Although we cannot exclude the possibility that further hangingflies remain unrecognized among the more than 12,000 arthropod finds from this locality, these insects are clearly exceedingly rare at Enspel. The same is true, for example, with respect to cockroaches (Vršanský *et al.*, 2021), whereas winged specimens of ants, bionid flies, and weevils are the most abundant insects at Enspel (Wedmann *et al.*, 2010; Legalov & Poschmann, 2020; Jessen, 2020; Skartveit & Wedmann, 2021). Both nymphs and adults of Odonata are moderately rare at Enspel, but show a diversity that can be considered typical for Cenozoic lakes (Brockhaus *et al.*, 2020; Nel *et al.*, 2020). The contrasting abundance of the various insect groups reflect a mixture of palaeoecologic and taphonomic factors acting in concert. In the case of the hangingflies, it may be significant that these are predatory insects that preferentially fly close to the ground while foraging for prey (Willmann, 1986). Thus, the chances of being drifted to the open space above the lake are few and the lake margin vegetation may then have acted as a taphonomic filter, as it has been discussed with respect to water-dwelling palaeobatrachid frogs (Wuttke & Poschmann, 2010) and cockroaches (Vršanský *et al.*, 2021) from Enspel.

Extant hangingflies prefer shady environments with high moisture levels. The habitat of *Eremobittacus opeth* **sp. nov.** was probably the riparian forest and adjacent areas in the immediate vicinity of palaeolake Enspel (*cf.*, Köhler & Uhl, 2014). Here, these insects found ideal living conditions, even more so as the late Oligocene subtropical climate at Enspel was much warmer than it is nowadays, with a mean annual temperature of 15°C–17°C vs. about 9°C today (Uhl & Herrmann, 2010).

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