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A new hangingfly species (Mecoptera: Bittacidae) from the Paleocene Paskapoo Formation (Canada)

CORENTIN JOUAULT[1, 2, 3, 4, *], BAPTISTE COUTRET[4], KURT O. KONHAUSER[4] & ANDRÉ NEL[1]
[1]*Institut de Systématique, Évolution, Biodiversité (ISYEB), UMR 7205, Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 75005 Paris, France*
[2]*Géosciences Rennes (UMR 6118), Université de Rennes, CNRS, F-35000 Rennes, France*
[3]*Institut des Sciences de l'Évolution (UMR 5554), Université de Montpellier, CNRS, F-34095 Montpellier, France*
[4]*Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, AB, T6G 2E3, Canada*
jouaultc0@gmail.com; https://orcid.org/0000-0002-3680-5172
baptiste.coutret@gmail.com; https://orcid.org/0000-0002-0893-0638
kurtk@ualberta.ca; https://orcid.org/0000-0001-7722-7068
anel@mnhn.fr; https://orcid.org/0000-0002-4241-7651
**Corresponding author*

Abstract

The order Mecoptera, commonly known as scorpionflies, has a long and fascinating evolutionary history that spans over 270 million years, if we consider its stem group. Despite their well-documented fossil record during the Mesozoic, many aspects of their diversity and evolution remain poorly understood. In this study, we increase the fossil record of Mecoptera by describing a new taxon from the Paleocene Paskapoo Formation (Alberta, Canada). This specimen is described as *Bittacus*? *paskapooensis* **sp. nov.** (Raptipedia: Bittacidae) but is assigned with caution to *Bittacus* due to the lack of apomorphic wing venation characters for this genus.

Keywords: Alberta, Bittacidae, Cenozoic, new taxon, open nomenclature

Introduction

The order Mecoptera comprises approximately 750 extant species, distributed among more than 35 genera and nine families (Bicha, 2018), and it is considered one of the minor orders of insects (*i.e.*, in terms of the number of extant species). They include the families Apteropanorpidae, Bittacidae (or hangingflies), Boreidae (or snow scorpionflies), Choristidae, Eomeropidae, Meropeidae (or earwigflies), Nannochoristidae, Panorpidae, Panorpodidae, *plus* a series of fossil families in their stem group. The Mecoptera are also abundant in the fossil record, but their diversity dynamics are poorly known (Aristov *et al.*, 2013; Jouault *et al.*, 2022a). It is assumed that their extant families show no burst of diversification in genus or species number (*e.g.*, Bittacidae today comprise about 16 genera and more than 210 extant species: Bicha, 2018). Their antiquity suggests that these insects managed to survive and adapt throughout mass extinctions (*i.e.*, the latest Permian, the Triassic–Jurassic, and the Cretaceous–Paleogene extinction events: Raup & Sepkoski, 1982). However, other extinctions have been evidenced by the fossil record of the order. For instance, the Late Cretaceous encompasses the extinction of the long-proboscid mecopterans (*e.g.*, Ren *et al.*, 2009; Labandeira, 2010; Peñalver *et al.*, 2015; Lin *et al.*, 2016, 2019; Peris & Condamine, 2023). The magnitude of this extinction is shrouded by a dearth of fossil evidence during the Late Cretaceous and the Paleocene, a well-known gap in the fossil record of insects (Schachat & Labandeira, 2021). It is, therefore, extremely important to document the occurrences of mecopterans during these epochs to refine the magnitude and timing of this decline.

Interestingly, the Mecoptera are thought to decline during a transitional period in flora assemblages—the transition between ecosystems dominated by the gymnosperms to ecosystems dominated by the angiosperms—called the Angiosperm Terrestrial Revolution (ATR, 100–50 Ma, Benton *et al.*, 2022). The ATR is marked by the rapid diversification of the angiosperms during the Cretaceous, which likely participated in the decline of conifers (Condamine *et al.*, 2020). The diversification and rapid radiation of the angiosperms are assumed to have led to the rise of mutualistic relationships (pollination, herbivory) with insects, and are often considered as the trigger for the diversification of the 'big five' insect clades *i.e.*, Coleoptera,

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Diptera, Hemiptera, Hymenoptera, Lepidoptera (*e.g.*, Farrell, 1998; Espeland *et al.*, 2018; Kawahara *et al.*, 2019, 2023; McKenna *et al.*, 2019). If this event indeed played a key role in the diversification of some insect clades, it may also have generated perturbations in the ecosystems that led to the decline of other lineages (*e.g.*, Sinitshenkova, 2003; Jouault *et al.*, 2022b). In the case of mecopterans, the reduction and replacement of their former ecological niches (*i.e.*, gymnosperms) by new plants and the diversification of insect orders that probably outcompeted them in mutualistic relationships are factors that likely were responsible for their decline. Today, this past decline is illustrated by some extant families with a relic diversity (Bicha, 2018: table 23.1), and others maintaining, without increasing their diversity (*e.g.*, the family Bittacidae). However, the paucity of the fossil record of the Mecoptera during the ATR complicates our understanding of the effect of this event on their past diversity. Herein, we describe a new species of Mecoptera belonging to the family Bittacidae, commonly called hangingfly, from the Paleocene of Canada, which increases the diversity of the clade during this epoch.

Material and methods

Specimen origin, examination, and illustration

The Paskapoo Formation (Red Deer, Alberta) is a Paleocene unit from the extreme West of the Western Canada Sedimentary Basin (Glass, 1997). The Paskapoo Formation is renowned for its abundant and well-preserved paleofauna and paleoflora and is mostly composed of interbedded mudstone and sandstone, with subordinate pebble-conglomerate (Glass, 1997; Hoffman & Stockey, 2000). This formation was deposited by low-energy fluvial systems under humid conditions, with associated overbank environments including ponds and oxbow lakes (Hoffman & Stockey, 2000). The Paskapoo Formation is widespread in western Alberta, outcropping from Calgary in the south to the Hinton area northwest of Edmonton.

The Tiffanian Joffre locality, near Red Deer (Hoffman & Stockey, 2000: fig. 1), has yielded extremely well-preserved fossil material such as plants, mammals, fishes, and insects (Fox, 1990; Wilson, 1996a, b; Wighton & Wilson, 1986; Jouault *et al.*, 2023). The strata were dated by biostratigraphy to the middle Paleocene (Tiffanian) age using faunal remains (Fox, 1990, 1991), palynological data (Demchuk & Hills, 1991), and magnetostratigraphy (Lerbekmo *et al.*, 1992). It is currently accepted that the age of the locality is *ca*. 58–60 Ma (Ti_3 zone: Fox, 1990; 26r reverse polarity zone: Lerbekmo *et al.*, 1992; P4 palynostratigraphic zonation: Demchuk, 1987, 1990).

The holotype of *Bittacus*? *paskapooensis* **sp. nov.** was collected by Mrs. Betty A. Speirs in 1989 and is currently housed in the Fossil Insect Collection (E.H. Strickland Entomological Museum) of the University of Alberta (Edmonton, UAFIC). The specimen was studied using a stereomicroscope Olympus SZX16. Photographs were taken with a Nikon D90 with an attached 60 mm lens or with a Tagarno Digital Microscope. All the final images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software.

Abbreviations

We follow the wing venation terminology of Poschmann & Nel (2022) and we consider the PCu vein present in the wings of the Mecoptera (Schubnel *et al.*, 2020). C, costa; CuA, anterior cubitus; CuP, posterior cubitus; Cuv, cubital crossvein; FM, first fork of media; FRp, first fork of radius posterior; M, media; MA, media anterior; MP, media posterior; OM, origin of media; ORp, origin of radius posterior; PCu, postcubital crossvein; Pcv1 and Pcv2, pterostigmal crossveins; Pt, pterostigma; R, radius; RA, radius anterior; RP, radius posterior; Sc, subcosta; Scv, subcostal crossvein; T, tarsomere.

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Systematic palaeontology

Order Mecoptera Packard, 1886
Infraorder Raptipedia Willmann, 1987
Family Bittacidae Handlirsch, 1906
Genus *Bittacus* Latreille, 1805

***Bittacus*? *paskapooensis* Jouault & Nel sp. nov.**
(Figs. 1, 2)
urn:lsid:zoobank.org:act:D0E5BE63-E3BE-4E64-A313-A128CBE2214F

Type material. Holotype UAFIC 6724/6725, part and counterpart, housed in the E.H. Strickland Entomological Museum at the University of Alberta (Edmonton, Canada).

Etymology. The species name refers to the originating Formation of the specimen.

Diagnosis. Wings without distinctive coloration patterns. Fore wing with Sc ending slightly distad FRp; pterostigma short and fully enclosed; two pcv crossveins present; Pcv1 aligned with crossvein between RP_{1+2} stem

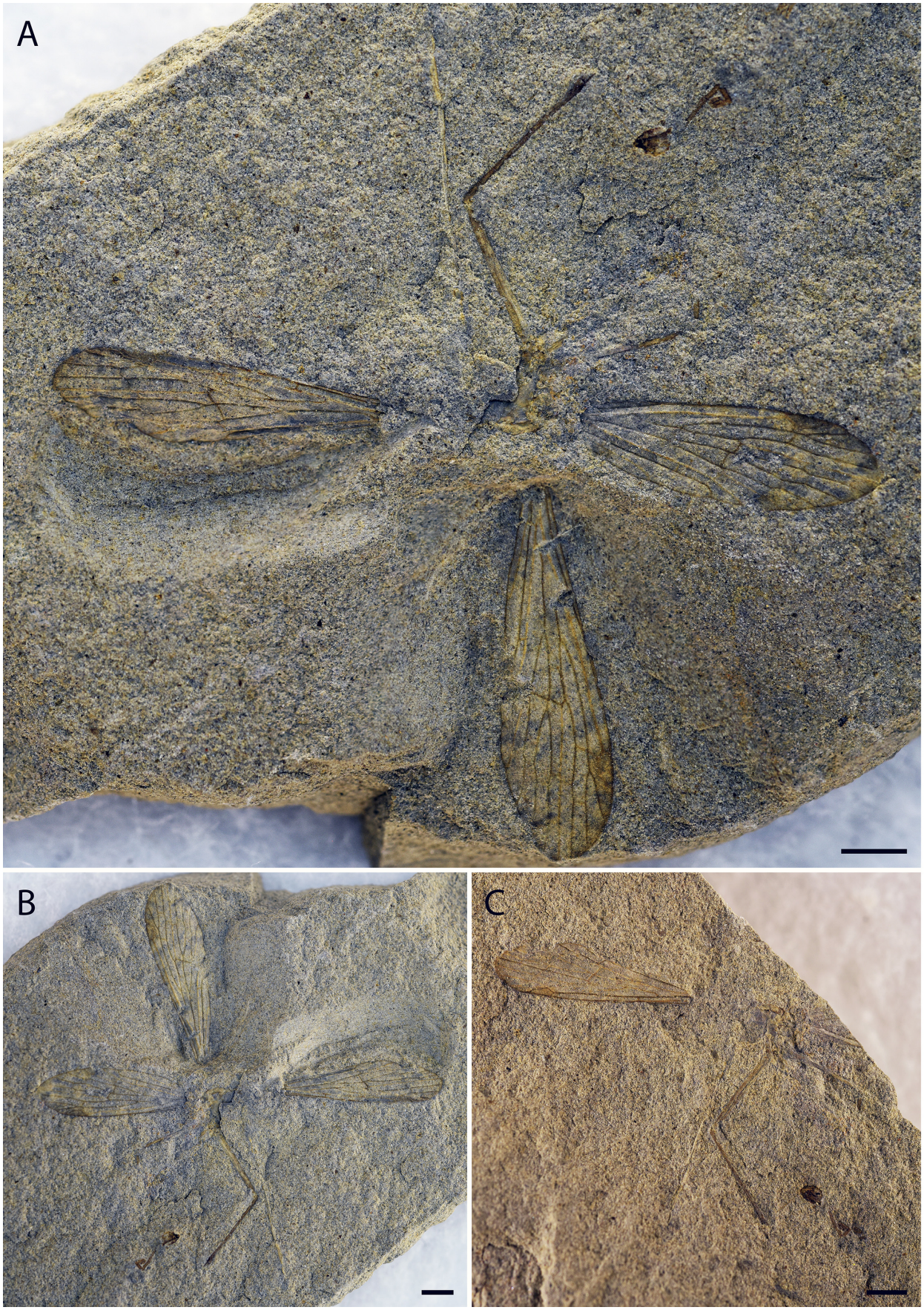

FIGURE 1. *Bittacus*? *paskapooensis* **sp. nov.**, holotype UAFIC 6724/6725, Paskapoo Formation, Alberta, Canada. **A**, Part. **B**, Part under different illumination. **C**, Counterpart. Scale bars = 2 mm.

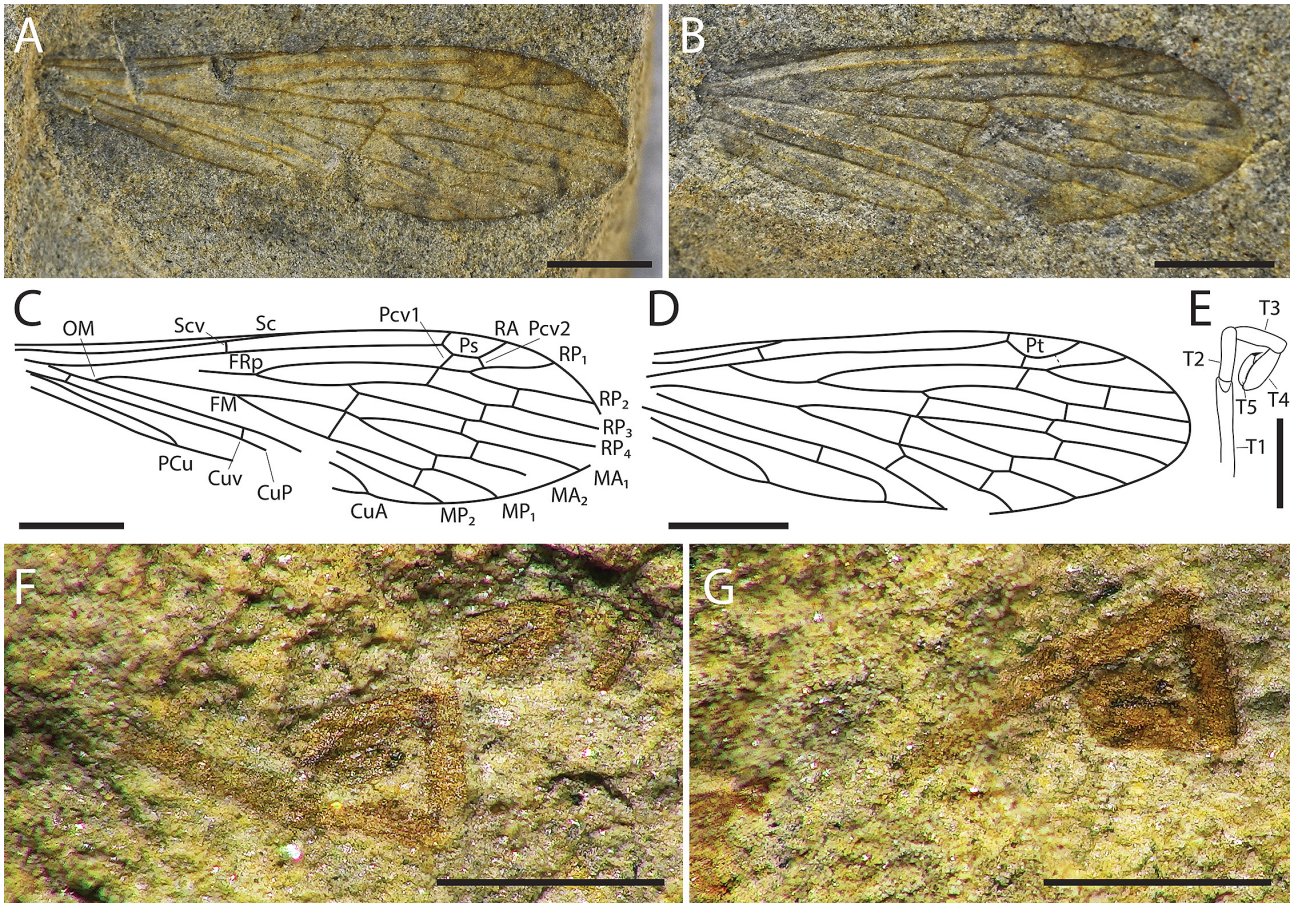

FIGURE 2. *Bittacus*? *paskapooensis* **sp. nov.**, holotype UAFIC 6724/6725, Paskapoo Formation, Alberta, Canada. **A**, Fore wing. **B**, Hind wing. **C**, Interpretative drawing of fore wing venation with names of veins labeled. **D**, Interpretative drawing of hind wing venation with names of veins labeled. **E**, Interpretative drawing of preserved tarsus with tarsomeres labeled. **F**, Preserved tarsus of counterpart. **G**, Preserved tarsus of part. Scale bars = 2 mm (**A**–**D**); 1 mm (**E**–**G**).

and RP_3; Scv located between ORp and FRp; FRp slightly distad FM; RP and M respectively with four branches; one row of crossveins in distal part of wing. Hind wing with Sc ending between ORp and FRp; 'bittacid cross' veins not aligned; Pcv1 not aligned with crossvein between RP_{1+2} stem and RP_3.

Type locality and horizon. Paskapoo Formation, Paleocene (Tiffanian), Joffre Gas Plant near Red Deer, Alberta, Canada.

Description. Head not preserved. Thorax with elongated and slender legs. Preserved leg with femur *ca*. 4.62 mm long and *ca*. 0.41 mm wide; tibia with at least one distal spur, *ca*. 5.17 mm long and *ca*. 0.16 mm wide. Preserved tarsus with tarsomeres (T) respective length (in mm): TI 1.18, TII 0.62, TIII 0.60, TIV 0.57, TV 0.42; TII to IV about same length, TV slightly shorter and prehensile; TIII and TIV slightly constricted in distal third; small teeth present along ventral margin of TIV and TV; no additional spine or spur visible on TIV (maybe not preserved).

Fore wing narrow with apex rounded; pterostigma infuscated; preserved part *ca*. 11.55 mm long, *ca*. 3.36 mm wide; Sc reaching C slightly distad FRp; Scv located slightly anteriad FRp; subcostal space slightly widening distad Scv (C2 cell); RA long and nearly straight before pterostigma; pterostigma short, longer than wide, fully enclosed; two Pcv crossveins present between RA and RP, first one between RA and stem of RP_{1+2}, second one between RA and RP_1; origin of RP between OM and Scv, likely closer to Scv than to OM; RP with four branches; FRp slightly distad FM; fork of RP_{1+2} well distad fork of RP_{3+4} but anteriad to pterostigma end; one crossvein present between RP_{1+2} and RP_3, one crossvein present between RP_2 and RP_3; RP_1 curved toward anterior wing margin; RP_2 nearly straight; RP_{3+4} fork located slightly anteriad middle of distance between FRp and RP_{1+2} fork; RP_3 long slightly zigzagged (due to crossvenation); one crossvein present between RP_3 and RP_4; RP_4 nearly straight; crossveins 1rp4-ma and ma-mp nearly aligned ('bittacid cross'); 2rp4-ma1 slightly anteriad rp3-rp4; MA_{1+2} fork distad RP_3+RP_4 fork; ma1-ma2 slightly distad 2rp4-ma1; ma2-mp1 anteriad ma1-ma2; mp1-mp2

slightly anteriad ma2-mp1; CuA long nearly straight, abruptly bending distally towards posterior wing margin; CuP parallel to CuA; one crossvein present between stem of M+CuA and CuP, located anteriad OM; Cuv crossvein aligned with FRp; PCu long, ending into posterior wing margin slightly before level of Scv.

Hind wing slightly broader than forewing, apex rounded, no coloration pattern (except infuscated pterostigma); preserved part *ca*. 9.25 mm long, *ca*. 3.05 mm wide; wing venation similar to forewing except Sc reaching C anteriad FRp; 'bittacid cross' veins not aligned.

Abdomen not preserved.

Remarks. The description of extant species of Bittacidae relies mostly on the genitalia configuration, but in fossil specimens this part of the body is rarely preserved. Consequently, the delimitation and the diagnosis of fossil species are mainly based on wing venation characters, which complicates the comparison between fossil and extant species (Jouault *et al*., 2021).

Several extant species of the genus *Bittacus* have distinctive coloration patterns on the wing and their presence, or their absence, is often considered diagnostic (*e.g*., Chen *et al*., 2013; Machado, 2019; Zhang *et al*., 2020). The ending position of Sc is often used to separate fossil Bittacidae *(e.g*., Krzemiński, 2007; Li *et al*., 2018). The length and shape of the pterostigma are not often used to distinguish fossil *Bittacus* spp. but regarding recent descriptions (*e.g*., Machado, 2019), these characters may become useful when additional fossil species will be described. The crossvein Scv is most of the time located between ORp and FRp but some species of *Bittacus* have this crossvein located distad FRp (*e.g*., *Bittacus vazdemelloi* Machado, 2019, and most South American species). The differences of coloration virtually present on the wing of the specimen are impossible to separate from the differences of coloration present on the rest of the matrix. Therefore, we consider that the new species is not characterized by a distinctive coloration pattern.

The vein Pcv2 in the hind wing is evidenced by a feeble imprint in the clay matrix but it is less sclerotized than the Pcv1. This condition is found in numerous extant species of the genus *Bittacus* (*e.g*., Zhang *et al*., 2020).

Discussion

Systematic placement

The new fossil can be attributed to the family Bittacidae because of its petiolate wings and its tarsi bearing a single claw (*e.g*., Petrulevičius *et al*., 2007; Poschmann & Nel, 2022). Note that the fossil also possesses the typical configuration of the tarsi found in extant Bittacidae, *i.e*., the fifth tarsomere is folded against the fourth (Fig. 2F, G).

The Bittacidae are grouped with the Cimbrophlebiidae into the infraorder Raptipedia and sometimes with the Neorthophlebiidae (*e.g*., Kopeć *et al*., 2018). However, the familial rank of the Neorthophlebiidae is not always followed in the literature as some authors considered this clade to be a subfamily of Bittacidae (Ansorge, 1996), or a synonym of Bittacidae (Novokschonov, 1993b; see discussion in Bechly & Schweigert, 2000). This difference in systematic treatment stems from phylogenetic consideration. In fact, this clade is either considered to be closely related to the Bittacidae (maybe representing their stem group) or to be a constitutive subfamily of the Bittacidae (Willmann, 1989). Nevertheless, the new fossil cannot be attributed to this clade because its fore wing has only four branches of M, *vs.* more than four branches in the Neorthophlebiidae (Fig. 2; see also Ansorge, 1993). Additionally, the "Neorthophlebiidae" are mainly a group (or grade) from the Jurassic Period and are absent from the Cenozoic Era.

The representatives of the family Cimbrophlebiidae have wing venations that strongly differ from the new fossil and from the Bittacidae. In fact, the narrow anal area of the new specimen (*i.e*., without numerous posterior branches of the anal veins) precludes its placement in the Cimbrophlebiidae. The latter family is virtually supported by the branching of the anal veins (AA2 *sensu* Bechly & Schweigert, 2000) and by the long and closely parallel course of CuA and CuP (Bechly & Schweigert, 2000: p. 6). This particular configuration is exacerbated in *Cimbrophlebia bittaciformis* Willmann, 1977 in which more than six posterior branches of A1 (A2 *sensu* Willmann, 1977) are found (Willmann, 1977: fig. 2).

Comparison with other Bittacidae

The new specimen differs from the genera *Antiquanabittacus* Petrulevičius & Jarzembowski, 2004, *Archebittacus* Riek, 1955, *Asiobittacus* Novokshonov, 1993, *Baissobittacus* Novokshonov, 1997, *Composibittacus* Liu *et al*., 2016, *Cretobittacus* Novokshonov, 1993, *Decoribittacus* Li & Ren, 2009, *Haplobittacus* Bode, 1953, *Karattacus* Novokshonov, 1997, *Megabittacus* Ren, 1997, *Microbittacus* Novokshonov, 1993, *Mongolbittacus* Petrulevičius *et al*., 2007, *Orobittacus* Villegas & Byers, 1981, *Orthobittacus* Willmann, 1989, *Plesiobittacus* Novokshonov, 1997, *Pleobittacus* Bode, 1953, *Preanabittacus* Novokshonov, 1993, *Probittacus* Martynov, 1927, *Scharabittacus* Novokshonov, 1993, and *Sibirobittacus* Sukatcheva, 1990, *inter alia*, because the crossveins ma-mp and 1rp4-ma are well aligned and both only slightly oblique (Bode, 1953; Sukatcheva, 1990; Novokshonov, 1993a, b, 1997a, b; Ren, 1997; Petrulevičius *et al*., 2007; Li & Ren, 2009; Yang *et al*.,

2012; Liu *et al*., 2016; Kopeć *et al*., 2016; Lambkin, 2017). Note that this character is not the only difference between the above-listed genera and the new specimen. Some also differ owing to the number of M branches, or other wing venation characters. The configuration of the ma-mp and 1rp4-ma is referred to as 'bittacid cross' by numerous authors and was originally assumed to be a distinctive character of the Bittacidae.

The wing venation of the new fossil strongly differs from the fossil genera *Prohylobittacus* Novokshonov, 1993, *Jurahylobittacus* Li *et al*., 2008, and *Formosibittacus* Li *et al*., 2008 because the base of RP is located far after the point of origin of M but also because it possesses a reduced number of rows of crossveins in the distal part of the wings (Novokshonov, 1993b; Li *et al*., 2008). The new specimen also differs from the genus *Exilibittacus* Yang et *al*., 2012 due to its pterostigma being fully enclosed (*vs*. basally open in *Exilibittacus*), the presence of distinct Pcv1 and Pcv2 crossveins (*vs*. only Pcv2 present), and its fork of R located slightly distad the fork of M (*vs*. anteriad the fork of M) (Yang *et al*., 2012). The new fossil also cannot be attributed to the genus *Liaobittacus* because of its reduced crossvenation (*vs*. with numerous crossveins in *Liaobittacus*), the crossveins forming the 'bittacid cross' well-aligned (*vs*. not aligned), and the FRp and FM being nearly aligned (*vs*. FRp strongly anteriad FM) (Ren, 1993: fig. 1d).

The age of the new fossil is closer to that of the mid-Cretaceous genus *Burmobittacus* Zhao *et al*., 2017 but it strongly differs, at least, because of the shape of their wings (elongate and narrow in *Burmobittacus vs.* shorter and broader in the new fossil), the shape of the pterostigma (only one Pcv crossvein is present in *Burmobittacus vs*. two in the new fossil), and the position of FRp and FM (FM far distad FRp in *Burmobittacus vs*. close in the new fossil) (Zhao *et al*., 2017: fig. 2).

The illustrations provided for the description of the extant genus *Austrobittacus* Riek, 1954 are reduced to the bases of the fore- and hind wings (Riek, 1954: figs 3–4), which complicates the comparison with the new fossil. Nevertheless, the new fossil differs from the latter genus because of its fore wing with Cuv slightly distad FM (*vs*. anteriad FM in *Austrobittacus*), and because of the presence of three rows of crossveins between branches of M in the latter (Byers, 1991: fig. 37.5.C).

The extant genera *Pazius* Navás, 1913, *Tytthobittacus* Smithers, 1973, and *Symbittacus* Byers, 1986 have very narrow wings while comparatively broader in the new specimen (Smithers, 1973; Byers, 1986; Lima & Dias, 2016; Kopeć *et al*., 2016). The genera *Symbittacus*, *Edriobittacus* Byers, 1974, and *Tytthobittacus* also have a very short stem of RP_{3+4}, unlike in the new fossil (Lambkin, 1993).

Males of the extant genus *Anomalobittacus* Kimmins, 1928 have only vestigial wings (Kimmins, 1928). The females of *Anomalobittacus gracilipes* have a morphology similar to that of the male 'General description agrees with that of the male' (Londt, 1972: p. 315). Therefore, we consider that both sexes have vestigial wings.

The genus *Apterobittacus* MacLachlan, 1893 is apterous (Carpenter, 1931). The extant genus *Anabittacus* Kimmins, 1929 has the crossveins forming the 'bittacid cross' not aligned (*vs*. aligned in the new genus), and no Pcv crossvein between RA and RP (*vs*. Pcv1 and Pcv2 present) (Kimmins, 1929; Byers, 1965; Penny & Byers, 1979). *Anabittacus* also differs from the new specimen in having the FRp located in the basal half of the wing considerably basad FM (a putative synapomorphy shared with *Jichoristella* Ren, 1995) (Bashkuev, 2023). In the new specimen, the FRp is located distad FM and in the second half of the wing (Fig. 2).

The extant genera *Austrobittacus* Riek, 1955 and *Kalobittacus* Esben-Petersen, 1914 further differ from the new fossil because of their fore wings with a long stem of CuA+M before OM (*vs*. short) (Riek, 1954: figs. 3–5). *Nannobittacus* Esben-Petersen, 1927 and *Issikiella* Byers, 1972 have only one Pcv crossvein, the vein MA_{1+2} more arcuate at base unlike the new fossil, MA_1 and MA_2 strongly zigzagged (*vs*. nearly straight in the new fossil), and extremely petiolate wings, with a very short PCu while the wings of the new fossils appear to be less petiolate and the PCu is conspicuously longer (Esben-Petersen, 1927; Byers, 1965, 1972, 1997; Penny & Byers, 1979; Machado *et al*., 2018, 2022). The genus *Edriobittacus* has a very short vein PCu, extending only slightly beyond the level of the base of M in the fore wing (Byers, 1974). Affinities with the genus *Hylobittacus* Byers, 1979 are ruled out because of the presence of two Pcv crossveins (*vs*. only one in *Hylobittacus*) (Byers, 1979; Tan & Hua, 2009a).

The genus *Afrobittacus* Londt, 1994 is characterized by the hind wing PCu basally fused with CuP for a long distance (a character shared with *Tytthobittacus*), this configuration does not seem to be present in the new fossil (see Londt, 1994: fig. 4). Affinities with the genus *Terrobittacus* Tan & Hua, 2009 are excluded because the new fossil possesses two Pcv crossveins (*vs*. one in *Terrobittacus*) (Tan & Hua, 2009b).

The type species of the Nearctic genus *Eremobittacus* Byers, 1997 (*E. spinulatus* Byers, 1997) has well-aligned crossveins of second and third ranks between RP_3 and MP_4 (*vs*. only one row of crossvein present in the new genus) but this condition is variable within the genus (Byers, 1997, 2011; Villagomez *et al*., 2015). The main difference between *Eremobittacus* and *Bittacus* is the length of the hind basitarsus, *viz*. 'basitarsi of the hind legs in *Bittacus* are far longer than TII and TIII together, but they are approximately equal in length to TII and TIII in *Eremobittacus*' (Byers, 2011: 9). In the preserved leg

of the new fossil, the basitarsus is 1.18 mm long while TII + TIII make 1.22 mm long together, which would better fit with *Eremobittacus*. However, it is nearly impossible to determine if this leg is a hind leg or not, and if the basitarsus is complete.

Some species of *Eremobittacus*, *Terrobittacus*, and *Bittacus* share the presence of dark spots on or close to the crossveins or close to the fork of main veins, yet no coloration pattern is found on the new fossil. The wing venations of the genera *Eremobittacus*, *Bittacus*, *Harpobittacus* Gerstaecker, 1885, and *Bicaubittacus* Tan & Hua, 2009 are extremely similar and, in general, these genera cannot be separated based on the wing venation only (*e.g*., Lambkin, 1994; Tan & Hua, 2009a,b; Villagomez *et al*., 2015; Zhang *et al*., 2020). They are differentiated using the leg morphology (*i.e*., shape of the femur, relative lengths of tarsomeres). Unfortunately, we cannot confidently consider the preserved tarsus as that of the hind tarsus (Figs. 1, 2). Nonetheless, most of these genera have several rows of crossveins in the apical part of the wing while the new specimen only has one row of crossvein distally (except *Bittacus* with a variable number of crossveins and fossil species with only one row of them). This character is considered sufficient to preclude affinities with *Eremobittacus* and *Harpobittacus*. Therefore, the new specimen is assigned to the genus *Bittacus* but with uncertainty. To express uncertainty in fossil classification and placement a question mark is added after the genus name (Matthews, 1973).

The new fossil differs from the extinct species *Palaeobittacus eocenicus* Carpenter, 1928 owing to the FRp slightly distad FM (*vs*. FRp strongly anteriad FM in *P. eocenicus*), and the fork of RP_{3+4} located halfway between FRp and Pcv1 (*vs*. distinctly closer to Pcv1 than to FRp) (Carpenter, 1928).

Comparison with the fossil representatives of the crown group Bittacidae

The new fossil differs from *Bittacus biamensis* Novokshonov, 1993, at least, because of wings with only one row of crossveins (*vs*. two in *B. biamensis*) (Novokshonov, 1993b). The species *Bittacus egestionis* Carpenter, 1955 differs from the new specimen (Carpenter, 1955) because of the number of crossveins between the main R and M veins (*i.e*., no crossvein aligned with Pcv1 *vs*. one present and aligned in the new fossil), only one crossvein present between RP_4 and MA_1 (*vs*. two present) but also because of their different age (Bridgerian: Eocene *vs*. Tiffanian: Paleocene). The species *Bittacus succinus* Carpenter, 1954 has the typical crossvenation of the genus with numerous rows of crossveins, while the new fossil has only one row of crossveins (Carpenter, 1954). The species *Bittacus veternus* (Cockerell, 1921) was described from the latest Eocene Bouldnor Formation in the United Kingdom and initially placed within the Panorpidae (Cockerell, 1921). The holotype used to describe this species is extremely fragmentary; but it differs from the new fossil, at least, because of the lack of Pcv2 (*vs*. present in the new fossil) but also because it has two rows of crossveins in the distal part of the wing (*vs*. only one) (Cockerell, 1921; Jarzembowski, 1980).

Bittacus lepiduscretaceus Li *et al*., 2018, recently described from the mid-Cretaceous Kachin amber, shares with the new fossil the presence of only one row of crossveins between RP and M veins. This character may question affinities with the genus *Bittacus.* The study of a male specimen from the same deposit strongly resembling this species shows that the genitalia are very different from those of the genus *Bittacus* (A.S. Bashkuev, pers. comm.). Therefore, the placement of this species in the *Bittacus* appears to be doubtful. On the other hand, the hind tarsi configuration agrees with the configuration of *Bittacus* species *i.e*., hind basitarsus considerably longer than the 4th tarsomere (Tan *et al*., 2009a). Nevertheless, the new fossil differs from this species because its wings are less spatulate, its hind wing with two Pcv crossveins (*vs*. one in *Bittacus lepiduscretaceus*), and the Scv well distad the origin of RP (*vs*. nearly aligned) (Li *et al*., 2018). Therefore, this species should be revised.

The synonymization of the genus *Thyridates* under *Bittacus* (Machado *et al*., 2009) led to the transfer of the fossil species *Thyridates novokschonovi* Petrulevičius, 2003 to the genus *Bittacus* (Petrulevičius, 2003). Nevertheless, the new fossil differs from *B. novokschonovi* because of its comparatively short pterostigma (*vs*. long in *B. novokschonovi*), FRp distad Scv crossvein (*vs*. anteriad), and the presence of crossvein in the distal part of the wing between R and M branches (*vs*. apparently absent) (Petrulevičius, 2003).

The new fossil differs from *Eremobittacus opeth* Poschmann & Nel, 2022 for all the reasons used to exclude affinities with the genus *Eremobittacus* and detailed above (Poschmann & Nel, 2022).

The genus *Hylobittacus* is known from four fossil species all recently revised by Krzemiński (2007). *Hylobittacus antiquus* Pictet & Hagen, 1856 differs from the new fossil because it has a very long Sc, ending distally far beyond the fork of RP (*vs*. ending close to FRp in the new fossil) and numerous crossveins in the distal part of the wing (Pictet & Hagen, 1856; Krzemiński, 2007). *Hylobittacus fossilis* (Carpenter, 1954) is easily distinguished from the new fossil because of the presence of only one Pcv crossvein between the pterostigma and RP (*vs*. two in the new fossil), and Sc short, ending well before FRp (*vs*. distad FRp) (Carpenter, 1954; Krzemiński, 2007).

The new fossil cannot be attributed to the species *Hylobittacus minimus* (Carpenter, 1954) because of

its Sc ending distad FRp (*vs*. at the level of FRp in *H. minimus*), and the presence of two Pcv crossveins under the pterostigma (*vs*. one) (Carpenter, 1954; Krzemiński, 2007). The species *Hylobittacus picteti* Krzemiński, 2007 has only one Pcv crossvein between the pterostigma and RP (*vs*. two in the new fossil) (Krzemiński, 2007).

In the remark appended to the description of *Tytthobittacus jarzembowski* Kopeć *et al*., 2016, it is indicated that the genus 'is characterized by the position of the Mb fork (=FM), which is situated before the fork of Rs (=FRp), and vein R4 (=RP_3) being strongly curved towards the upper margin of the wing with a crossvein between R_{2+3} and R4 at the peak of this curve' (Kopeć *et al*., 2016). However, this particular position of FM and FRp is also found, *inter alia*, in some *Bittacus*, *Symbittacus*, or *Terrobittacus*, and cannot be used as the sole character to separate the genus *Tytthobittacus* from the other bittacids (*e.g*., Byers, 1986; Chen *et al*., 2013; Du & Hua, 2017). Nevertheless, the new fossil differs from the genus *Tytthobittacus* owing to the course of the RP_3 vein and by its veins RP and M being longitudinal (*i.e*., without abrupt angle).

Conclusion

The new species presents supplementary insights into the post-K/Pg diversity of the Bittacidae family, and it could potentially be the earliest occurrence of the genus *Bittacus* (the species described from the Cretaceous amber of Myanmar being questionable). This species constitutes the first record of a hangingfly in the Paskapoo Formation. The Paskapoo Formation offers a significant window into the past diversity of insects during the Paleocene, and a point of comparison with the other Paleocene deposits (*e.g*., Menat Formation, France).

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