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**A fossil flat wasp (Hymenoptera: Bethyridae) from the early Eocene Green River Formation suggests past cosmopolitan distribution of the genus *Eupsenella* Westwood, 1874**

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**Abstract**

A flat wasp specimen attributed to the genus *Eupsenella* Westwood, 1874 is described and figured from the early Eocene compressions of the Green River Formation. This fossil is the first known outside of the Old World for this genus and documents its wide distribution during the Paleogene, while it is currently confined to Australia and New Zealand. As for several other hymenopteran genera, we assume that this regression is linked to abiotic factors, i.e., the Cenozoic climate cooling, rather than to biotic factors.

**Keywords:** Hymenoptera; Chrysidoidea; Bethyridae; Ypresian; USA

## 1. Introduction

The Green River Formation is an ancient lake system, widespread throughout western United States (Wyoming, Colorado, Texas; Smith *et al.* 2008). The thin lacustrine sediments were deposited during the Early Eocene Climatic Optimum and have exquisitely preserved vertebrates, invertebrates, and plants remains, justifying the use of the term ‘Lagerstätte’ (Hellawell & Orr 2012, MacGinitie 1969). Because of the economic importance of the Green River Formation (exploitation of oil-shale layers), its geology and physical setting are well understood (Johnson *et al.*, 2014). In contrast, its biota is far less known and particularly the entomofauna, despite the collection of more than 80,000 specimens (Dlussky & Rasnitsyn 2002).

The first studies on Green River fossil insects date back to the late 19th and early 20th centuries and were especially conducted by S.H. Scudder and T.D.A. Cockerell (Scudder 1890, Cockerell 1907, 1925). Grande (2013) revised the fauna of the deposit, highlighting the greater interest of paleoentomologists for the northern deposits of the Greater Green River Basin and the Fossil Basin. However, in the past few years, some studies focused on the insects from the Piceance Basin, in Colorado (e.g., Vršanský *et al.* 2011, Wappler *et al.* 2015).

In this paper, we describe a Bethyridae from the Piceance Basin locality of Denson, the specimen being the first flat wasp known from the Green River Formation. The Bethyridae are a cosmopolitan family, the largest within the Chrysidoidea (Azevedo *et al.* 2018). Of the nine recognized subfamilies (Colombo *et al.* 2020), eight have fossil representatives but mostly from amber deposits (Martynova *et al.* 2019). Bethyrids are rarer in compressions, with only a few known specimens (Colombo *et al.* 2021, Peñalver-Mollá 1998, Rasnitsyn 1990), mainly because of the fossorial habits and small size of these wasps.

45

## 46    **2. Material and methods**

47       The part of a Bethylidae was collected in 2006 by David Kohls at the Denson Site,  
48   Garfield County, northwestern Colorado, USA (see map in Wappler *et al.* 2015: fig. 1). The  
49   locality corresponds to the lesser-known Piceance Basin, whose insect-bearing stratum is the  
50   Parachute Creek Member. This member is the youngest of the basin, dated of the upper  
51   Ypresian (Smith *et al.* 2008, Cole & Picard 1978). The specimen is labelled UCM 58339 and  
52   housed in the Invertebrate Paleontology collection of the University of Colorado.

53       The images were captured using a Canon EOS 5D camera with 65 mm MPE Canon macro  
54   lens attached to a Stackshot macro rail. All images are digitally stacked photomicrographic  
55   composite of several focal planes, which were obtained using HeliconFocus. Adobe Illustrator  
56   CC2019 and Photoshop CC2019 software were used to compose the figures and ImageJ 1.53  
57   for measurements (Schneider *et al.* 2012). The morphological nomenclature follows Lanes *et*  
58   *al.* (2020). Main measurements and indices used are as follows: length of forewing (LFW);  
59   length of head, measured from top of vertex to apex of clypeus (LH); width of head above  
60   eyes (WH); height/width of eye (HE).

61

## 62    **3. Systematic palaeontology**

63    **Superfamily** Chrysidoidea Latreille, 1802

64    **Family** Bethylidae Haliday, 1839

65    **Subfamily** Bethylinae Haliday, 1839

66    **Genus** *Eupsenella* Westwood, 1874

67    *Eupsenella* sp.

68    Figs. 1, 2

69

70

71    Material. Specimen UCM 58339 of unknown sex, part. Right lateral aspect of the body, with  
72    legs, left hind wing and parts of the antennae missing.

73    Locality. Denson Site, Green River, Colorado, USA

74    Horizon. Lake Uinta, Piceance Basin, Parachute Creek member; upper Ypresian, Eocene, ca.  
75    48 Ma.

76    Description. Body dark brown, not especially flattened, stout (length 3.23 mm). Head ovoid,  
77    apparently longer than wide; LH: ca. 0.67 mm; WH: ca. 0.36 mm; HE: 0.21 mm; compound  
78    eyes elliptical, longer than high; antennae short, only scape and two apicalmost flagellomeres  
79    preserved, apical flagellomere tapering at apex; vertex corners rounded.

80    Mesosoma shorter than metasoma (length 1.04 mm). Fore wing micro-pubescent, without  
81    apparent colour patterns (LFW: 1.91 mm); C, Sc+R, M+Cu, 1Rs&1M, Rs+M, Rs and R1  
82    preserved and tubular; 1Rs&1M angulate at junction with Rs+M; Rs apically angulate toward  
83    wing margin; post-stigmal abscissa of R1 apically arched; [C], [R], [1M] (areolet), [1R1] and  
84    [2R1] cells closed; [1M] cell small, subpentagonal, aligned basally with [1R1] cell; [1R1] cell  
85    elongate, 1.0 x [2R1] cell; [2R1] cell 0.19 x LFW, evenly wide, as wide as [1R1] cell;

pterostigma well-defined, elongate, slightly shorter than [1R1] cell, rectangular. Hind wing hyaline, without apparent venation.

Metasoma fusiform (length 1.52 mm); segments not discernible.

#### 4. Discussion

Despite being only observable laterally and missing the legs and part of the antennae, this fossil wasp can confidently be identified as a Bethylidae of the subfamily Bethylinae, thanks to the unique reduced fore wing venation (five closed cells visible), the Rs+M vein tubular and the 1Rs&1M angled (Azevedo *et al.* 2018). The [1Cu] cell, which is always closed in bethylinae wasps, is assumed to be present as well but not preserved, as a stub of the 1cu-a vein is visible anteriorly. The comparatively high number of closed cells (six) and their combination (especially the [1M], [1R1] and [2R1] cells) for a Bethylinae strongly indicates either *Lytopsenella* Kieffer, 1911 or *Eupsenella* Westwood, 1874 within the subfamily (Azevedo *et al.* 2018). The distinction between these two genera is based on the relative length of the [1R1] and [2R1] cells and the shape of the [2R1] cell. In our specimen, the [2R1] cell is as long as the [1R1] (while it is longer in *Lytopsenella*) and evenly wide and rounded apically (while it is lanceolate in *Lytopsenella*). The specimen mostly differs from extant species by the size of the [2R1] cell, which is as long as the [1R1] cell and not significantly shorter. This characteristic occurs in all other fossils attributed to *Eupsenella* (Ramos *et al.* 2014). Yet, we cannot rule out the possibility that this specimen belongs to a brand new genus

of Bethylinae. But it is worth mentioning that no fossil genera of this subfamily are known during the Cenozoic, which is quite uncommon, possibly because of its basal position within the family (Sorg 1988, Ramos *et al.* 2014). Additionally, the fore wing pattern is very characteristic of *Eupsenella* and, except *Lytopsenella*, no other Bethylinidae have such a venation, even in a different subfamily. Therefore, we allocate this specimen in the extant genus *Eupsenella*. However, due to the lack of body features preserved, which prevents from establishing precise diagnosis, we decide to leave it unnamed.

The genus *Eupsenella* is currently composed of 52 species (Azevedo *et al.* 2018). The 45 extant species are restricted to Australia with one species occurring in the South Island of New Zealand (Fig. 3; Ramos & Azevedo 2012). During the late Eocene, four species are known from the contemporaneous Baltic amber and Rovno amber (Ramos *et al.* 2014). Two species originally attributed to *Fushunochrysis* Hong, 2002 and *Sinibethylus* Hong, 2002 from the Ypresian Fushun amber (Hong 2002) and one attributed to *Protobethylus* De Ploëg & Nel, 2004 from the Ypresian Oise amber (De Ploëg & Nel 2004) have been synonymized with this genus (Ramos *et al.* 2014). Therefore, *Eupsenella* appears to be widely distributed throughout the Palearctic during the Paleogene but the fossil from Green River is the first known of this genus outside of the Old World. A Paleogene Holarctic distribution for *Eupsenella* implies that it diverged from other bethyline genera when America and Eurasia were still connected (last connection across North Atlantic: ca. 50 Ma; Tiffney, 1985). This reflection also applies to its sister-taxa, *Lytopsenella*, now confined to Chile but with representatives known from the European Baltic and Rovno amber (Azevedo 2009, Ramos *et al.* 2014). *Eupsenella* and *Lytopsenella* are the basalmost two genera of the Bethylinae

(Ramos & Azevedo 2020), so this scenario is consistent with what is known of the subfamily phylogeny.

The regression of *Eupsenella* is likely correlated to the general climate cooling in the last 50 Ma. The Green River Ypresian Mean Annual Temperature (MAT) have been estimated for various sites (e.g., Wilf 2000, Fricke & Wing 2004, Archibald *et al.* 2011) and mid-mesothermal values have been obtained (~16°C; Wolfe 1975). The presence of crocodilians fossil remains is further evidence of a subtropical climate for the Green River Formation (Brochu 2010). The climate of the Paris basin during the early Eocene was certainly paratropical, given its occurrence during the Early Eocene Climatic Optimum and the presence of the Amazon rainforest trees *Hymenaea oblongifolia* (Jossang *et al.* 2008). Similarly, the Eocene Fushun Forest climate was moist subtropical, as suggested by the entomofauna (Wang *et al.* 2014). Finally, the distinct Baltic amber and Rovno amber forests were respectively warm-temperate and subtropical environments (Sadowski *et al.* 2017, Perkovsky, 2016). This range of climates matches what exists in today Australia, the climate being tropical in the North, subtropical along East and West coasts and warm temperate in the South and Tasmania (Sturman & Tapper 2006). Only *Eupsenella nanda* Ramos & Azevedo, 2012 have been collected in a desertic and arid environment, near Alice Springs in the center of Australia.

*A contrario*, the *Eupsenella* species for which the biology is known parasitize lepidopterous larvae belonging to the Tortricidae (Gordh & Harris 1996, Berry 1998, Paull & Austin 2006). This family has several fossil representatives in Baltic amber and two in the late Eocene Florissant beds (USA) but still currently shows a worldwide distribution (Heikkilä *et al.* 2018) unlike *Eupsenella*. Thus, the host-parasite association of *Eupsenella* and Tortricidae is not sufficient to explain the past and present distribution of the genus.



A similar pattern of regression toward tropical or subtropical latitudes has been observed in various hymenopteran families, e.g., Megalyridae (*Megalyra* Westwood, 1832 in Baltic amber; Poinar & Shaw 2007), Formicidae (*Carebara* Westwood, 1840, *Gesomyrmex* Mayr, 1868, *Tetraponera* Smith, 1852 in Baltic, Rovno and Bitterfeld ambers; Perkovsky 2016), Diapriidae (*Doliopria* Kieffer, 1910 in Baltic amber; Brazidec & Vilhelmsen 2022), Mymaridae (*Borneomymar* Huber, 2002 in Baltic amber; Engel *et al.* 2013) or Scolebythidae (*Pristapenesia* Brues, 1933 in Baltic amber; Brues 1933). The regression of *Eupsenella* could be documented by screening younger ambers from southeastern Asia, e.g., Miocene Zhangpu amber, China (Wang *et al.* 2021), Sumatra amber, Indonesia (Ngô-Muller *et al.* 2019), or McGrath Flats, Australia (McCurry *et al.* 2022).

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337 **Figure captions:**

338 **Figure 1.** Photograph of *Eupsenella* sp., specimen UCM 58339 (scale bar = 1 mm).

339 **Figure 2.** Line drawing of *Eupsenella* sp., specimen UCM 58339 (dashed lines indicate  
340 interpretations; scale bar = 1 mm).

341 **Figure 3.** Distribution map of extant and extinct species of *Eupsenella* showing type localities  
342 (green square = extant; orange star = early Eocene; red triangle = late Eocene; question  
343 mark = imprecise location).