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1 **A fossil flat wasp (Hymenoptera: Bethyridae) from the early Eocene Green River**  
2 **Formation suggests past cosmopolitan distribution of the genus *Eupsenella* Westwood,**  
3 **1874**

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12

13 **Abstract**

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

20

21 **Keywords:** Hymenoptera; Chrysidoidea; Bethylinae; Ypresian; USA

## 22 1. Introduction

23 The Green River Formation is an ancient lake system, widespread throughout western  
24 United States (Wyoming, Colorado, Texas; Smith *et al.* 2008). The thin lacustrine sediments  
25 were deposited during the Early Eocene Climatic Optimum and have exquisitely preserved  
26 vertebrates, invertebrates, and plants remains, justifying the use of the term ‘Lagerstätte’  
27 (Hellowell & Orr 2012, MacGinitie 1969). Because of the economic importance of the Green  
28 River Formation (exploitation of oil-shale layers), its geology and physical setting are well  
29 understood (Johnson *et al.*, 2014). In contrast, its biota is far less known and particularly the  
30 entomofauna, despite the collection of more than 80,000 specimens (Dlussky & Rasnitsyn  
31 2002).

32 The first studies on Green River fossil insects date back to the late 19th and early 20th  
33 centuries and were especially conducted by S.H. Scudder and T.D.A. Cockerell (Scudder  
34 1890, Cockerell 1907, 1925). Grande (2013) revised the fauna of the deposit, highlighting the  
35 greater interest of paleoentomologists for the northern deposits of the Greater Green River  
36 Basin and the Fossil Basin. However, in the past few years, some studies focused on the insects  
37 from the Piceance Basin, in Colorado (e.g., Vršanský *et al.* 2011, Wappler *et al.* 2015).

38 In this paper, we describe a Bethylidae from the Piceance Basin locality of Denson, the  
39 specimen being the first flat wasp known from the Green River Formation. The Bethylidae are  
40 a cosmopolitan family, the largest within the Chrysidoidea (Azevedo *et al.* 2018). Of the nine  
41 recognized subfamilies (Colombo *et al.* 2020), eight have fossil representatives but mostly  
42 from amber deposits (Martynova *et al.* 2019). Bethylids are rarer in compressions, with only a  
43 few known specimens (Colombo *et al.* 2021, Peñalver-Mollá 1998, Rasnitsyn 1990), mainly  
44 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** Chrysoidea 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;

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

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

89

90

91

#### 92 **4. Discussion**

93         Despite being only observable laterally and missing the legs and part of the antennae,  
94 this fossil wasp can confidently be identified as a Bethylinidae of the subfamily Bethylininae,  
95 thanks to the unique reduced fore wing venation (five closed cells visible), the Rs+M vein  
96 tubular and the 1Rs&1M angled (Azevedo *et al.* 2018). The [1Cu] cell, which is always  
97 closed in bethyline wasps, is assumed to be present as well but not preserved, as a stub of the  
98 1cu-a vein is visible anteriorly. The comparatively high number of closed cells (six) and their  
99 combination (especially the [1M], [1R1] and [2R1] cells) for a Bethylininae strongly indicates  
100 either *Lytopsenella* Kieffer, 1911 or *Eupsenella* Westwood, 1874 within the subfamily  
101 (*Azevedo et al.* 2018). The distinction between these two genera is based on the relative  
102 length of the [1R1] and [2R1] cells and the shape of the [2R1] cell. In our specimen, the [2R1]  
103 cell is as long as the [1R1] (while it is longer in *Lytopsenella*) and evenly wide and rounded  
104 apically (while it is lanceolate in *Lytopsenella*). The specimen mostly differs from extant  
105 species by the size of the [2R1] cell, which is as long as the [1R1] cell and not significantly  
106 shorter. This characteristic occurs in all other fossils attributed to *Eupsenella* (Ramos *et al.*  
107 2014). Yet, we cannot rule out the possibility that this specimen belongs to a brand new genus

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

115

116         The genus *Eupsenella* is currently composed of 52 species (Azevedo *et al.* 2018). The  
117 45 extant species are restricted to Australia with one species occurring in the South Island of  
118 New Zealand (Fig. 3; Ramos & Azevedo 2012). During the late Eocene, four species are  
119 known from the contemporaneous Baltic amber and Rovno amber (Ramos *et al.* 2014). Two  
120 species originally attributed to *Fushunochrysis* Hong, 2002 and *Sinibethylus* Hong, 2002  
121 from the Ypresian Fushun amber (Hong 2002) and one attributed to *Protobethylus* De Ploëg  
122 & Nel, 2004 from the Ypresian Oise amber (De Ploëg & Nel 2004) have been synonymized  
123 with this genus (Ramos *et al.* 2014). Therefore, *Eupsenella* appears to be widely distributed  
124 throughout the Palearctic during the Paleogene but the fossil from Green River is the first  
125 known of this genus outside of the Old World. A Paleogene Holarctic distribution for  
126 *Eupsenella* implies that it diverged from other bethyline genera when America and Eurasia  
127 were still connected (last connection across North Atlantic: ca. 50 Ma; Tiffney, 1985). This  
128 reflection also applies to its sister-taxa, *Lytopsenella*, now confined to Chile but with  
129 representatives known from the European Baltic and Rovno amber (Azevedo 2009, Ramos *et*  
130 *al.* 2014). *Eupsenella* and *Lytopsenella* are the basalmost two genera of the Bethylinae

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

133         The regression of *Eupsenella* is likely correlated to the general climate cooling in the  
134 last 50 Ma. The Green River Ypresian Mean Annual Temperature (MAT) have been  
135 estimated for various sites (e.g., Wilf 2000, Fricke & Wing 2004, Archibald *et al.* 2011) and  
136 mid-mesothermal values have been obtained (~16°C; Wolfe 1975). The presence of  
137 crocodylians fossil remains is further evidence of a subtropical climate for the Green River  
138 Formation (Brochu 2010). The climate of the Paris basin during the early Eocene was  
139 certainly paratropical, given its occurrence during the Early Eocene Climatic Optimum and  
140 the presence of the Amazon rainforest trees *Hymenaea oblongifolia* (Jossang *et al.* 2008).  
141 Similarly, the Eocene Fushun Forest climate was moist subtropical, as suggested by the  
142 entomofauna (Wang *et al.* 2014). Finally, the distinct Baltic amber and Rovno amber forests  
143 were respectively warm-temperate and subtropical environments ( (Sadowski *et al.* 2017,  
144 Perkovsky, 2016). This range of climates matches what exists in today Australia, the climate  
145 being tropical in the North, subtropical along East and West coasts and warm temperate in the  
146 South and Tasmania (Sturman & Tapper 2006). Only *Eupsenella nanda* Ramos & Azevedo,  
147 2012 have been collected in a desertic and arid environment, near Alice Springs in the center  
148 of Australia.

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



155           A similar pattern of regression toward tropical or subtropical latitudes has been  
156 observed in various hymenopteran families, e.g., Megalyridae (*Megalyra* Westwood, 1832 in  
157 Baltic amber; Poinar & Shaw 2007), Formicidae (*Carebara* Westwood, 1840, *Gesomyrmex*  
158 Mayr, 1868, *Tetraoponera* Smith, 1852 in Baltic, Rovno and Bitterfeld ambers; Perkovsky  
159 2016), Diapriidae (*Doliopria* Kieffer, 1910 in Baltic amber; Brazidec & Vilhelmsen 2022),  
160 Mymaridae (*Borneomymar* Huber, 2002 in Baltic amber; Engel *et al.* 2013) or Scolebythidae  
161 (*Pristapenesia* Brues, 1933 in Baltic amber; Brues 1933). The regression of *Eupsenella* could  
162 be documented by screening younger ambers from southeastern Asia, e.g., Miocene Zhangpu  
163 amber, China (Wang *et al.* 2021), Sumatra amber, Indonesia (Ngô-Muller *et al.* 2019), or  
164 McGrath Flats, Australia (McCurry *et al.* 2022).

165

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173

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336

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).