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

MANUEL BRAZIDEC[1,2*], VINCENT PERRICHOT[1]

[1]Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France.
manuel.brazidec@gmail.com / https://orcid.org/0000-0002-0860-8972;
vincent.perrichot@univ-rennes1.fr / https://orcid.org/0000-0002-7973-0430

[2]State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China.

*corresponding author

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; Bethylinae; 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 Fosil 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 Bethylidae from the Piceance Basin locality of Denson, the specimen being the first flat wasp known from the Green River Formation. The Bethylidae 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). Bethylids 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.

2. Material and methods

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

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

3. Systematic palaeontology

Superfamily Chrysidoidea Latreille, 1802

Family Bethylidae Haliday, 1839

Subfamily Bethylinae Haliday, 1839

Genus *Eupsenella* Westwood, 1874

Eupsenella sp.

Figs. 1, 2

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

Locality. Denson Site, Green River, Colorado, USA

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

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

Mesosoma shorter than metasoma (length 1.04 mm). Fore wing micro-pubescent, without apparent colour patterns (LFW: 1.91 mm); C, Sc+R, M+Cu, 1Rs&1M, Rs+M, Rs and R1 preserved and tubular; 1Rs&1M angulate at junction with Rs+M; Rs apically angulate toward wing margin; post-stigmal abscissa of R1 apically arched; [C], [R], [1M] (areolet), [1R1] and [2R1] cells closed; [1M] cell small, subpentagonal, aligned basally with [1R1] cell; [1R1] cell 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 bethyline 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 Bethylidae 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 *Fushunochrysites* 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).

Acknowledgments

The images are courtesy of Talia Karim, University of Colorado Museum of Natural History and we warmly thank her. We express our gratitude to the Editor-in-Chief of Palaeoentomology, Prof. Diying Huang for his guidance throughout the submission process, as well as Prof. Alexandr. P. Rasnitsyn and an anonymous reviewer for their useful comments. This work is part of Manuel Brazidec Ph.D. project on “The role of greenhouses on the diversification and evolution of chrysidoid wasps”.

References

Archibald, S.B., Johnson, K.R., Mathewes, R.W. & Greenwood, D.R. (2011) Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals. *Proceedings of the Royal Society of London (B)*, 278, 3679–3686. https://doi.org/10.1098/rspb.2011.0729

Azevedo, C.O. (2009) Synopsis of *Lytopsenella* Kieffer (Hymenoptera: Bethylidae). *Zootaxa*, 2286, 58–64. https//doi.org/10.5281/zenodo.191267

Azevedo, C.O., Alencar, I.D.C.C., Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas, J. M. & Lim, J. (2018) Global guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, 4489, 1–294. https://doi.org/10.11646/zootaxa.4489.1.1

Berry, J.A. (1998) The bethyline species (Hymenoptera: Bethylidae: Bethylinae) imported into New Zealand for biological control of pest leafrollers. *New Zealand Journal of Zoology*, 25, 329–333. https://doi.org/10.1080/03014223.1998.9518162

Brazidec, M. & Vilhelmsen, L. (2022) New species of belytines and diapriine wasps (Hymenoptera: Diapriidae) from Eocene Baltic amber. *European Journal of Taxonomy*, 813, 57–86. https://doi.org/10.5852/ejt.2022.813.1733

Brochu, C.A. (2010) A new alligatoroid from the lower Eocene Green River Formation of Wyoming and the origins of caimans. *Journal of Vertebrate Paleontology*, 30, 1109–1126. https://doi.org/10.1080/02724634.2010.483569

Brues, C.T. (1933) The parasitic Hymenoptera of the Baltic amber, Part 1. *Bernstein-Forschungen*, 3, 4–178.

Cockerell, T.D.A. (1907) A new fly (fam. Mycetophilidae) from the Green River beds. *American Journal of Science*, 136, 285–286. https://doi.org/10.2475/ajd.s4-23.136.285

Cockerell, T.D.A. (1925) Plant and insect fossils from the Green River Eocene of Colorado. *Proceedings of the United States National Museum*, 66 (2556), 1–13. https://doi.org/10.5479/si.00963801.66–2556.1

Cole, R.D. & Picard, M.D. (1978) Comparative mineralogy of nearshore and offshore lacustrine lithofacies, Parachute Creek Member of the Green River Formation, Piceance Creek Basin, Colorado and eastern Uinta Basin, Utah. *Geological Society of America Bulletin*, 89 (10), 1441–1454. https://doi.org/10.1130/0016-7606(1978)89<1441:cmonao>2.0.co;2

Colombo, W.D., Perkovsky, E.E. & Azevedo, C.O. (2020) Phylogenetic overview of flat wasps (Hymenoptera, Bethylidae) reveals Elektroepyrinae, a new fossil subfamily. *Palaeoentomology*, 3 (3), 296–283. https://doi.org/10.11646/palaeoentomology.3.3.8

Colombo, W.D., Perkovsky, E.E., Waichert, C.C. & Azevedo, C.O. (2021) Synopsis of the fossil flat wasps Epyrinae (Hymenoptera, Bethylidae), with description of three new genera and ten new species. *Journal of Systematic Palaeontology*, 19, 29–89. https://dx.doi.org/10.1080/14772019.2021.1882593

De Ploëg, G.D. & Nel, A. (2004) A new bethylid wasp from the Lowermost Eocene amber of France (Hymenoptera: Bethylidae: Bethylinae). *Geologica acta*, 2, 75–88.

220 Dlussky, G.M. & Rasnitsyn, A.P. (2002) Ants (Hymenoptera: Formicidae) of Formation
221 Green River and some other Middle Eocene deposits of North America. *Russian*
222 *Entomological Journal*, 11, 411–436.

223 Engel, M.S., McKellar, R.C. & Huber, J.T. (2013) A fossil species of the primitive mymarid
224 genus *Borneomymar* (Hymenoptera: Mymaridae) in Eocene Baltic amber. *Novitates*
225 *Paleoentomologicae*, 5, 1–8.
226 https://doi.org/10.17161/np.v0i5.4651

227 Fricke, H.C. & Wing, S.L. (2004) Oxygen isotope and paleobotanical estimates of
228 temperature and δ18O-latitude gradients over North America during the early Eocene.
229 *American Journal of Science*, 304, 612–635.
230 https://doi.org/10.2475/ajs.304.7.612

231 Gordh, G. & Harris, A. (1996) New record and a new species of *Eupsenella* (Hymenoptera:
232 Bethylidae) in New Zealand. *Journal of the Royal Society of New Zealand*, 26, 529–536.
233 https://doi.org/10.1080/03014223.1996.9517523

234 Grande, L. (2013) *The lost world of fossil lake: snapshots from deep time*. University of
235 Chicago Press, Illinois, 425 pp.

236 Heikkilä, M., Brown, J.W., Baixeras, J., Mey, W. & Kozlov, M.V. (2018) Re-examining the
237 rare and the lost: a review of fossil Tortricidae (Lepidoptera). *Zootaxa*, 4394, 41–60.
238 https://doi.org/10.11646/zootaxa.4394.1.2

239 Hellawell, J. & Orr, P.J. (2012) Deciphering taphonomic processes in the Eocene Green River
240 Formation of Wyoming. *Palaeobiodiversity and Palaeoenvironments*, 92, 353–365.
241 https://doi.org/10.1007/s12549-012-0092-6

242 Hong, Y. (2002) *Amber insects of China*. Science and Technology Press, Beijing, 653 pp.

Johnson, R.C., Mercier, T.J. & Brownfield, M.E. (2014) Spatial and stratigraphic distribution of water in oil shale of the Green River Formation, using Fischer Assay, Piceance Basin, northwestern Colorado. *U.S. Geological Survey Open-File Report*, 1059, 1–59. https://doi.org/10.3133/ofr20141059

Jossang, J., Bel-Kassaoui, H., Jossang, A., Seuleiman, M. & Nel, A. (2008) Quesnoin, a novel pentacyclic *ent*-Diterpene from 55 million years old Oise amber. *Journal of Organic Chemistry*, 73, 412–417. https://doi.org/10.1021/jo701544k

Lanes, G.O., Kawada, R., Azevedo, C.O. & Brothers, D.J. (2020) Revisited morphology applied for Systematics of flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, 4752, 1–127. https://doi.org/10.11646/zootaxa.4752.1.1

MacGinitie, H.D. (1969) *The Eocene Green River flora of northwestern Colorado and northeastern Utah*. University of California Press, Berkeley, 202 pp.

Martynova, K.V., Perkovsky, E.E., Olmi, M. & Vasilenko, D.V. 2019. New records of Upper Eocene chrysidoid wasps from basins of Styr and Stokhod rivers (Rovno amber). *Paleontological Journal*, 53, 998–1023. https://doi.org/10.1134/S0031030119100125

McCurry, M.R., Cantrill, D.J., Smith, P.M., Beattie, R., Dettmann, M., Baranov, V., Magee, C., Nguyen, J.M.T., Forster, M.A., Hinde, J., Pogson, R., Wang, H., Marjo, C.E., Vasconcelos, P. & Frese, M. (2022) A Lagerstätte from Australia provides insight into the nature of Miocene mesic ecosystem. *Sciences advances*, 8, eabm1406. https://doi.org/10.1126/sciadv.abm1406

Ngô-Muller, V., Garrouste, R., Pouillon, J., Christophersen, V., Christophersen, A. & Nel, A. (2019) The first representative of the fly genus *Trentepohlia* subgenus *Mongoma* in amber from the Miocene of Sumatra (Diptera: Limoniidae). *Historical Biology*, 33, 1–4. https://doi.org/10.1080/08912963.2019.1610948

Paull, C. & Austin, A.D. (2006) The hymenopteran parasitoids of light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) in Australia. *Australian Journal of Entomology*, 45, 142–156. https://doi.org/10.1111/j.1440-6055.2006.00524.x

Peñalver-Mollá, E. (1998) *Estudio tafonómico y paleoecológico de los insectos del Mioceno de Rubielos de Mora (Teruel)*. Instituto de studios Turolenses, Teruel, 179 pp.

Perkovsky, E.E. (2016) Tropical and Holarctic ants in late Eocene ambers. *Vestnik Zoologi*, 50, 111–122. https://doi.org/10.1515/vzoo-2016-0014

Poinar, G.O. & Shaw, S.R. (2007) *Megalyra baltica* Poinar and Shaw n. sp. (Hymenoptera: Megalyridae), a long-tailed wasp from Baltic amber. *Zootaxa*, 1478, 65–68.

Ramos, M.S. & Azevedo, C.O. (2012) Revision of *Eupsenella* Westwood, 1874 (Hymenoptera, Bethylidae). *Zootaxa*, 3539, 1–80.

Ramos, M.S. & Azevedo, C.O. (2020) Revisited phylogeny of Bethylinae (Hymenoptera, Bethylidae) solves basal polytomy. *Insect Systematics & Evolution*, 51, 296–346. https://doi.org/10.1163/1876312X-00002202

Ramos, M.S., Perkovsky, E.E., Rasnitsyn, A.P. & Azevedo, C.O. (2014) Revision of Bethylinae fossils from Baltic, Rovno and Oise amber, with comments on the Tertiary fauna of the subfamily. *Neues Jahrbuch fur Geologie und Palaontologie*, 271, 203–228.

https://doi.org/10.1127/0077-7749/2014/0385

Rasnitsyn, A.P. (1990) Hymenoptera. *In*: Ponomarenko, A.G. (Ed.), *Late Mesozoic insects of Eastern Transbaikalian.* Nauka Press, Moscow, pp. 177–205.

Sadowski, E., Schmidt, E.R., Seyfullah, L.J. & Kunzmann, L. (2017) Conifers of the 'Baltic amber forest' and their palaeoecological significance. *Stapfia*, 106, 1–73.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671–675.

https://doi.org/10.1038/nmeth.2089

Scudder, S.H. (1890) The Tertiary insects of North America. *U.S. Geological and Geographical Survey of the Territories*, 4, 1–734.

https://doi.org/10.3133/70038967

Smith, M.E., Caroll, A.R. & Singer, B.S. (2008) Synoptic reconstructions of a major ancient lake system: Eocene Green River Formation, western United States. *Geological Society of America Bulletin*, 120, 54–84.

https://doi.org/10.1130/B26073.1

Sorg, M. (1988) Zur Phylogenie und Systematik der Bethylidae (Insecta, Hymenoptera, Chrysidoidea). *Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln*, 63, 1–146.

Sturman, A.P. & Tapper, N.J. (2006) *The weather and climate of Australia and New Zealand*. Oxford University Press, 476 pp.

Tiffney, B.H. (1985) The Eocene North Atlantic land bridge: its importance in Tertiary and modern phylogeography of the Northern Hemisphere. *Journal of the Arnold Arboretum*, 66, 243–273.

311 Vršanský, P., Vidlička, L., Čiampor Jr., F. & Marsh, F. (2011) Derived, still living cockroach
312 genus *Carriblatoides* (Blattida: Blattellidae) from the Eocene sediments of Green River in
313 Colorado, USA. *Insect Science*, 19, 143–152.

314 Wang, B., Rust, J., Engel, M.S., Szwedo, J., Dutta, S., Nel, A., Fan, Y., Meng, F., Shi, G.,
315 Jarzenbowski, E.A., Wappler, T., Stebner, F., Fang, Y., Mao, L., Zheng, D. & Zhang, H.
316 (2014) A diverse paleobiota in Early Eocene Fushun amber from China. *Current Biology*,
317 24, 1606–1610.

318 https://doi.org/10.1016/j.cub.2014.05.048

319 Wang, B., Shi, G., Xu, C, Spicer, R.A., Perrichot, V., Schmidt, A.R., Feldberg, K., Heinrichs,
320 J., Chény, C., Pang, H., Liu, X., Gao, T., Wang, Z., Ślipiński, A., Solórzano-Kraemer,
321 M.M., Heads, S.W., Thomas, M.J., Sadowski, E., Szwedo, J., Azar, D., Nel, A., Liu, Y.,
322 Chen, J., Zhang, Q., Zhang, Q., Luo, C., Yu, T., Zheng, D., Zhang, H. & Engel, M.S.
323 (2021) The mid-Miocene Zhangpu biota reveals an outstandingly rich rainforest biome in
324 East Asia. *Science Advances*, 7, eabg0625.

325 https://doi.org/10.1126/sciadv.abg0625

326 Wappler, T., Guilber, E., Labandeira, C.C., Hörnschemeyer, T. & Wedmann, S. (2015)
327 Morphological and behavioral convergence in extinct and extant bugs: the systematics and
328 biology of an unusual lace bug from the Eocene. *PLoS One*, 10, e0133330.

329 https://doi.org/10.1371/journal.pone.0133330

330 Wilf, P. (2000) Late Paleocene-early Eocene climate changes in southwestern Wyoming:
331 paleobotanical analysis. *Geological Society of America Bulletin*, 112, 292–307.

332 https://doi.org/10.1130/0016-7606(2000)112<292:LPECCI>2.0.CO;2

Wolfe, J.A. (1975) Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. *Annals of the Missouri Botanical Garden*, 62, 264–279. https://doi.org/10.2307/2395198

Figure captions:

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

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

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