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Cimbicidae (Hymenoptera, 'Symphyta') in the Paleogene: revision, the new subfamily Cenocimbicinae, and new taxa from the Eocene Okanagan Highlands

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Abstract

We erect the Cenocimbicinae, a new subfamily of Cimbicidae (Hymenoptera, Symphyta), restricted to the Selandian Menat Formation of France, the oldest occurrence of the family, and the Ypresian Okanagan Highlands of far-western North America. We describe new taxa from the Okanagan Highlands: *Allenbycimbex morrisae* gen. et sp. nov. and *Leptostigma* **n. gen.** with seven new species: *L. alaemacula* **n. sp.**, *L. brevilatum* **n. sp.**, *L. fasciatum* **n. sp.**, *L. longiclava* **n. sp.**, *L. longipallidum* **n. sp.**, *L. longitenebricum* **n. sp.**, and *L. proxivena* **n. sp.** We revise the Cimbicidae from the Ypresian Green River Formation and the Priabonian Florissant Formation, both in Colorado, USA. The oldest fossil of a modern cimbicid subfamily appears with a single pachylostictine specimen in the Green River Formation, and all Cimbicidae are in modern subfamilies after the Ypresian (we did not examine one larva known from Priabonian Baltic amber). *Pseudocimbex clavatus* Rohwer 1908 from the Florissant Formation is not a cimbicid; we treat it as Tenthredinoidea *incertae sedis*. We transfer Cimbex vetusculus Cockerell to Floricimbex n. gen.

Key words: Cimbicidae, Okanagan Highlands, Florissant, Green River Formation, Paleogene

Introduction

The Cimbicidae (Hymenoptera, Symphyta, Tenthredinoidea) is a small family of herbivorous wasps with about 200 extant species in 15 genera, mostly in the subfamilies Cimbicinae (8 genera, 98 species) and Abiinae (1 and 58), both in the Holarctic and Oriental regions, and the remainder in two smaller subfamilies, the Neotropical Pachylostictinae (5 and 9) and the Palearctic Corynidinae (1 and 28) (Vilhelmsen *et al.* 2018, Vilhelmsen 2019, Vilhelmsen & Shinohara 2020). Although many are an unremarkable size, they include the impressively largest modern Symphyta, reaching three centimetres in length, hence their common name "giant sawflies" (Vilhelmsen 2019). Their larvae feed externally on angiosperm leaves and adults are known to feed on sap, nectaries and floral tissues, and insectivory has been reported (Vilhelmsen 2019, Jervis & Vilhelmsen 2000).

Cimbicidae have a modest fossil record (Table 1) with large gaps. Their oldest known occurrence is a single fossil from the Selandian (mid-Paleocene) Menat Formation of France (Nel 2004). They then appear shortly after with the fossils described here in the Ypresian (early Eocene) of the Okanagan Highlands series of localities in British Columbia, Canada and northern Washington, United States of America, and a poorly preserved specimen in the coeval Green River Formation of Colorado, United States of America (Cockerell 1925). They are not known in the Lutetian or Bartonian (middle Eocene). Four genera and species have been described from the Priabonian (late Eocene) of Florissant (Colorado, United States of America: Brues 1908, Cockerell 1908, Rohwer 1908). A larva is known from Priabonian Baltic amber (Menge 1856, Handlirsch 1907, APR pers. obs.). Cimbicidae are not known

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from the Oligocene, but are well-represented in the Miocene of East Asia (China, 12 species; Japan, 1) and France (2) (see references in Table 1). Their youngest fossil occurrence is a single species in the Pliocene of Germany (Steinbach 1967).

The Cimbicidae of the Okanagan Highlands have been briefly mentioned and illustrated, but never described (Lewis 1992, Fig. 2N as unknown Hymenoptera; as Cimbicidae by Archibald 2007, 2010; Archibald *et al.* 2018). Here, we describe them and revise the cimbicids from the Florissant and Green River Formations.

Material and methods

We examined 19 compression fossils from lacustrine shale of three sites of the Okanagan Highlands series of fossil localities: the Allenby Formation near Princeton, the McAbee location near Cache Creek, both in British Columbia, Canada, and at Republic, Washington, United States of America. We also examined photographs of one fossil from the Green River Formation (MCZ) and five fossils from the Florissant Formation (DMN, UCM, USNM).

For extant Cimbicidae we follow the systematics of Vilhelmsen (2019) and Vilhelmsen & Shinohara (2020), who recently published detailed works based on morphological characters. We follow the wing vein and cell terminology of Rasnitsyn (1969, Fig. 1) (Fig. 1). All wings are depicted with the apex to the right for ease of comparison. Drawings are taken from the part and counterpart where available, dry, and often wetted with ethanol.

Mean annual temperature (MAT) categories are *sensu* Wolfe (1975): microthermal, ≤ 13°C; mesothermal, > 13°C, < 20°C; megathermal, ≥ 20°C.

Institutions: DMN, Denver Museum of Nature and Science, Denver, CO, USA; GSC, Geological Survey of Canada, Vancouver, BC, Canada; MCZ, Museum of Comparative Zoology, Cambridge, MA, USA; RBCM, Royal British Columbia Museum, Victoria, BC, Canada; SR, Stonerose Interpretive Center, Republic, WA, USA; TRU, F numbers, Thompson Rivers University, Kamloops, BC, Canada; UCM, University of Colorado (Boulder) Natural History Museum paleontology collection, Boulder, CO, USA; USNM, Smithsonian National Museum of Natural History, Washington, DC, USA; UWBM, Burke Museum of Natural History and Culture, Seattle, WA, USA.

Character states of compared taxa are given in brackets.

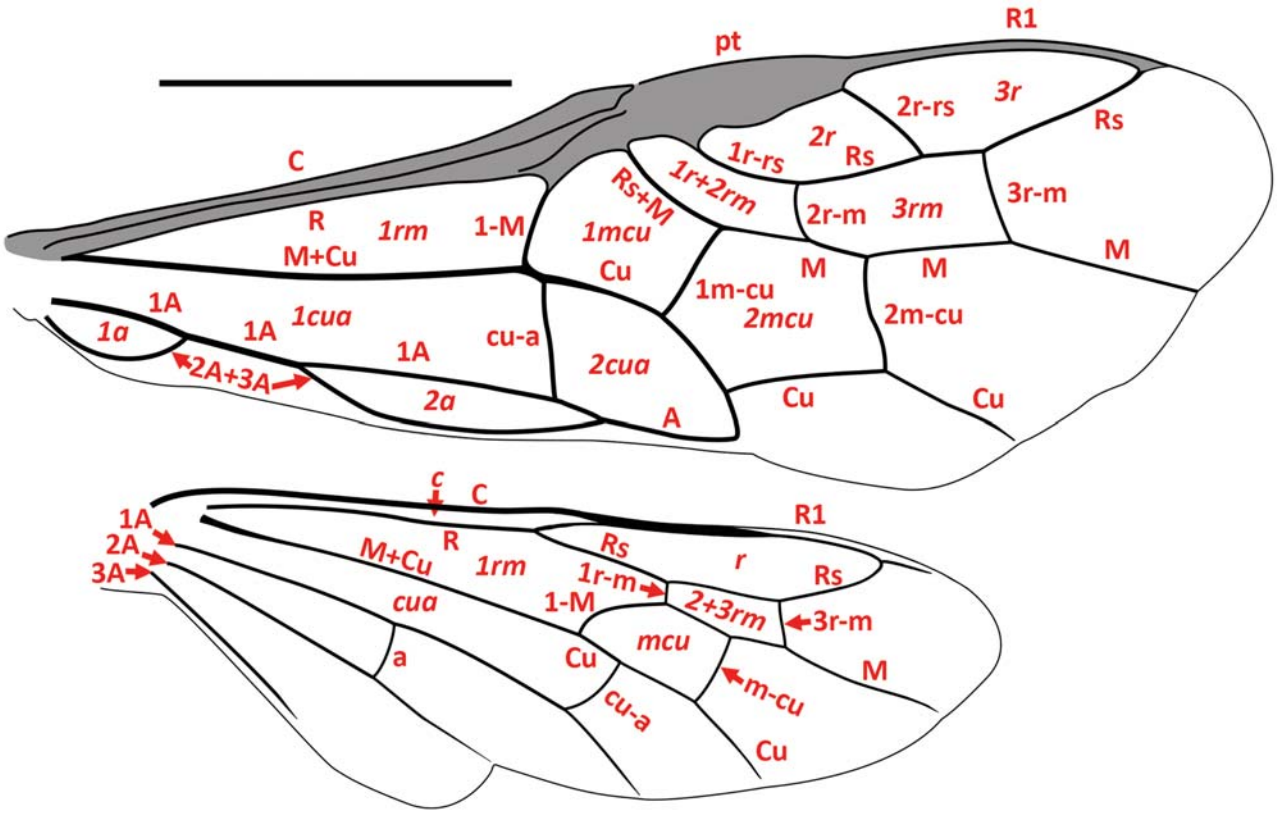


FIGURE 1. Forewing and hind wing of *Corynis crassicornis* (Rossi) (Corynidinae) with veins (roman font) and cells (italic font) labelled. Drawn from Vilhelmsen (2019) figure 15B. Scale = 2 mm.

In living Cimbicidae, species level diagnostics are mostly based on characters of colouration and morphology of the body and appendages, with a negligible role of venational characters (*cf*. Benson 1951, Zhelokhovtzev 1988, Vilhelmsen *et al.* 2018), which may be unreliable. We assume that this held true through deep time. Unfortunately, the material available for *Leptostigma* **n. gen.** consists mostly of detached wings. Therefore, only a small part of the specimens can be used to define species with enough certainty based on diagnostically reliable differences such as antennal colouration and club morphology, and for *L. proxivena*, *L. fasciatum*, and *L. alaemacula*, colouration of the wings. The remaining specimens are tentatively associated with species whenever possible based on these less reliable venational similarities, in particular see wing specimens tentatively grouped with *L. brevilatum* **n. sp.**, *L. longiclava* **n. sp.**, *L. longipallidum* **n. sp.**, and *L. longitenebricum* **n. sp.** This issue must be considered in fossil Cimbicidae, but in some other Symphyta, *e.g*., Siricidae, wing venation may be clearly informative to low taxonomic levels (see Schiff *et al.* 2012).

Localities

Menat. Wedmann *et al.* (2018) provided an overview of the Paleocene Menat Formation of Puy-de-Dôme, France. Most recently it has been considered Selandian (mid-Paleocene) (Wappler *et al.* 2009, Tanrattana *et al.* 2020). Menat is not only well-known as an important Paleocene insect locality, but it also contains a wide variety of vertebrates and plants. Its rich fossil insect record has been described since the mid-Twentieth Century.

The Okanagan Highlands. The Okanagan Highlands is comprised of a series of lacustrine shale and coal localities deposited in the second half of the Ypresian, scattered across about a thousand kilometers from north-western British Columbia near Smithers southeast to Republic, Washington. It was a temperate montane setting with mild winters in the globally hot world of the Early Eocene Climatic Optimum (review: Archibald *et al.* 2011). The localities bearing the fossils described here are estimated to have had upper microthermal MAT values (Greenwood *et al.* 2005).

The McAbee locality consists of exposures of lacustrine shale of an unnamed formation about 13 kilometers east of the village of Cache Creek in south-central British Columbia, dated as 52.10 ± 0.26 Ma. (U-Pb decay from zircons: Rubino *et al.* 2021). The fossils reported here are from the Hoodoo Face beds found immediately north of the trans-Canada Highway. Those in the collections of the GSC (Vancouver) that were collected by one of the authors (SBA) and by John Leahy are assigned GSC locality number V-016800.

The fossiliferous Vermilion Bluffs Shale Unit of the Allenby Formation in the Princeton Basin is exposed in and surrounding the town of Princeton, BC (Read 2000). An outcrop in Princeton has an estimated age of 51.85 ± 0.85 Ma. (U-Pb from zircons: Rubino *et al.* 2021).

Shale of the Tom Thumb Tuff Member of the Klondike Mountain Formation is exposed in and around the village of Republic, Washington. It is the southern-most of the Okanagan Highlands series. The Republic fossils reported here are from exposure A0307, which has an estimated age of 51.45 ± 0.12 Ma. (U-Pb decay from zircons: Rubino *et al.* 2021). A0307 is a Burke Museum locality code, also used by the Stonerose Interpretive Center.

The Green River Formation. The Green River Formation includes richly fossiliferous lacustrine shales of several large Eocene lake basins in Wyoming, Colorado, and Utah, USA. The fossil examined here (USNM 69181) is from the Piceance basin of Eocene Lake Uinta in western Colorado, at the "head of East Alkali Gulch, about 8 miles south of De Beque, CO" (Cockerell 1925, page 11). Although this locality is not dated, other Piceance basin sites have mid-late Ypresian radiometric age estimates (Smith *et al.* 2008), *i.e*., coeval with the Okanagan Highlands. Its lowland intermontane climate appears to have been much warmer than the Okanagan Highlands, with high mesothermal to megathermal MAT values (Wilf 2000, Archibald *et al.* 2011 and references therein).

The Florissant Formation. The Florissant Formation is located near the town of Florissant in eastern Colorado. It was deposited in the globally cooler latest Priabonian, 34.07 ± 0.10 Ma. (Evanoff *et al.* 2001). Like the Okanagan Highlands, it was situated in an upland with an estimated upper microthermal MAT (Allen *et al.* 2020), also with no frost days indicated by the presence of *e.g*., palms and associated Pachymerina (Coleoptera, Chrysomelidae) (Manchester 2001, Archibald *et al.* 2014).

Systematic Paleontology

Order Hymenoptera Linnaeus, 1758

Infraorder Siricomorpha Billberg,1820

Superfamily Tenthredinoidea Latreille, 1803

Family Cimbicidae Curtis, 1825

Subfamily Cenocimbicinae n. subfam.

http://zoobank.org/urn:lsid:zoobank.org:act:FA885793-D7D8-49A8-A00D-6C813ACBFC0F

Type genus. *Cenocimbex* Nel, 2004.

Diagnosis. Distinguished from all other Cimbicidae by forewing with 2r-m distinctly curved, meeting M distal of 2m-cu; cell 2r+pterostigma distinctly higher than cell 3r; and a combination of the following: eyes converging ventrally; antenna with 7–9 antennomeres, club 3-segmented; mesonotum with median longitudinal mesonotal sulcus and notauli distinct; metanotum short, with cenchri oval; tibial spur acute, long; first abdominal tergite with hind margin straight or weakly emarginated.

Remarks. Cenocimbicinae differ from individual subfamilies of Cimbicidae by: from all by 2r-m as in diagnosis; from Abiinae, Cimbicinae by eyes converging ventrally [Cimbicinae: more or less parallel; Abiinae: converging dorsally], by at least one tibial spur acute, long (equal length of first tarsomere, one known, see F-774, tentative *Leptostigma brevilatum*) [Abiinae, Cimbicinae: blunt]; from Corynidinae, Pachylostictinae by 2r-m posterior insertion distal to cell 2mcu [Corynidinae, Pachylostictinae: proximal to], by cell 2r+pterostigma distinctly higher than cell 3r [not so], antenna with more than five antennomeres [five], club 3-segmented [non-segmented], metanotum short [long]; further from Corynidinae by mesonotum with median longitudinal mesonotal sulcus and notauli distinct [reduced or absent]; from some Abiinae and Cimbicinae by cenchri oval, from some Cimbicinae also by first abdominal tergite with hind margin straight or weakly emarginated [deeply emarginated].

Attribution of the Cenocimbicinae to the Tenthredinoidea is confident by 1-M meeting R and 2r-rs meeting Rs distally to 2r-m, and to the Cimbicidae by their clubbed antenna, and a unique forewing venation characteristic of the core cimbicid subfamilies Cimbicinae and Abiinae and found nowhere else in Hymenoptera: venation complete for Hymenoptera (except Sc, Rs between Rs+M and 1r-rs, and Rs bifurcation lost), characteristically narrow (low) cell 3r, and 2r-m crossvein meets M distal to 2m-cu.

The long, curved to strongly curved crossvein 2r-m is distinct, occurring only rarely in extant Cimbicidae (very few Abiinae, *cf*. Vilhelmsen 2019, Fig. 16A; and Cimbicinae, *cf*. Vilhelmsen 2019, Fig. 16B) and in the Miocene of China (Abiinae: *cf*. Zhang *et al.* 1994, Fig. 121; Cimbicinae: *cf*. Zhang *et al.* 1994, Fig. 118), which we consider convergent.

The new subfamily comprises the oldest known Cimbicidae, from the Selandian of Menat and less than ten million years later in the Ypresian Okanagan Highlands deposits of far-western North America (Archibald *et al.* 2011), a rather narrow interval of time but across a great distance of the Holarctic.

Genera included. The type genus, *Allenbycimbex* **n. gen.** and *Leptostigma* **n. gen.**

Locality and age. Menat, France, Selandian; Okanagan Highlands (McAbee, Allenby Formation, and Republic), far-western North America, Ypresian.

Menat Formation

Genus *Cenocimbex* Nel, 2004

Figs. 2, 3E–F.

Type species *C. menatensis* Nel, 2004.

Emended diagnosis. Separated from all other Cenocimbicinae by R before base of pterostigma with dark triangular sclerite reaching 1-Rs+M near 1m-cu [vs. sclerotization not apparent, either absent or pale, small]; by wing broad, estimated length/width 2.5 [all others *ca*. 2.8 or more]; by cell 3rm short (2r-m to 3r-m length ≤ 3r-m [vs. distinctly longer]); from *Leptostigma* **n. gen.** also by pterostigma broad, maximum height distinctly more than height of C to R basal to pterostigma [*Leptostigma* **n. gen.**: similar in height to C to R basal to pterostigma]. Hind wing with r-m, m-cu and cu-a only moderately distant from each other (for about length of m-cu, so cu-a at about midlength cell mcu) [in other genera usually well before mid-length].

Remarks. Sclerotisation on R near the pterostigma, even though of much lesser size, is clearly seen in an extant cimbicine, see Vilhelmsen *et al.* 2018, Fig. 2B).

Locality and age. Menat Formation; Puy-de-Dôme, France; Selandian.

Species included. Type species only.

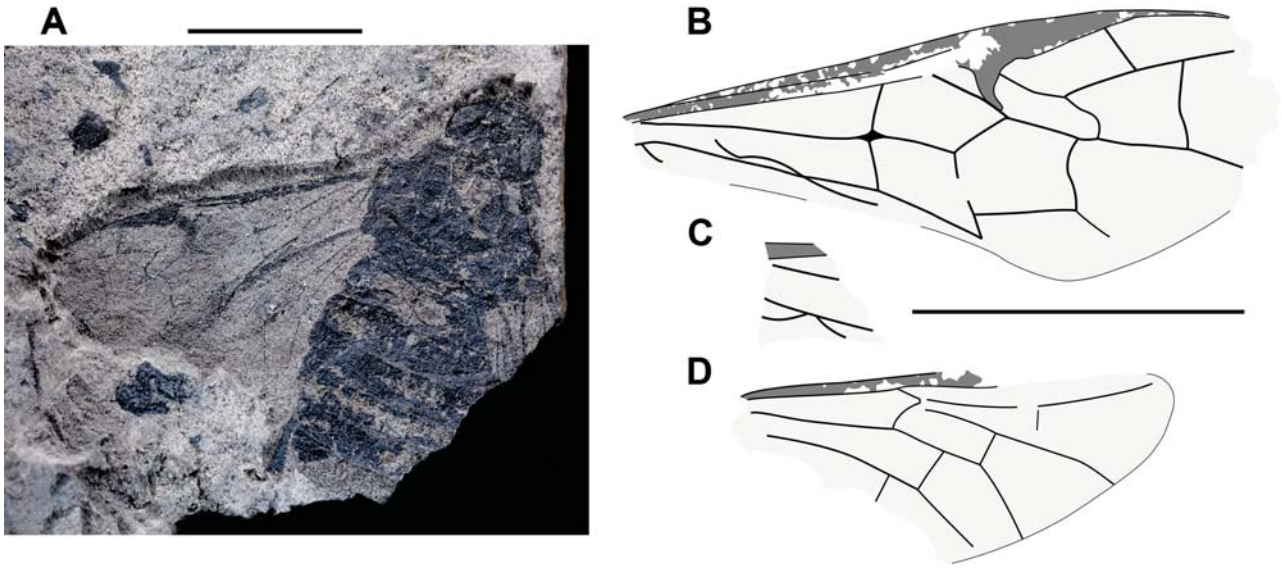


FIGURE 2. *Cenocimbex menatensis* Nel, holotype MNHN-LP-R.11195: A, extract from a reflectance transformation imaging (RTI) file (Cultural Heritage Imaging 2012); B, drawing of left forewing; C, drawing of right forewing preserved portion; D, left hind wing. Scale bars 5 mm.

Cenocimbex menatensis Nel, 2004

Figs. 2, 3E–F.

See Nel (2004).

Okanagan Highlands

Allenbycimbex n. gen.

http://zoobank.org/urn:lsid:zoobank.org:act:704AB0FB-18D0-4CF4-AB78-F48D42378EAF
Fig. 4.

Type species. *Allenbycimbex morrisae* n. sp.

Diagnosis. Distinguished from *Cenocimbex* by R lacking dark triangular sclerite before base of pterostigma reaching 1-Rs+M near 1m-cu; wing narrower (length/width *ca*. 3.0 as reconstructed) [*Cenocimbex*: 2.5]; cell 3rm long (2r-m to 3r-m distinctly longer than length of 3r-m); hind wing with m-cu placed much basally than in *Cenocimbex*; distinguished from *Leptostigma* by pterostigma broad, maximum height distinctly exceeding height of C to R basal to pterostigma.

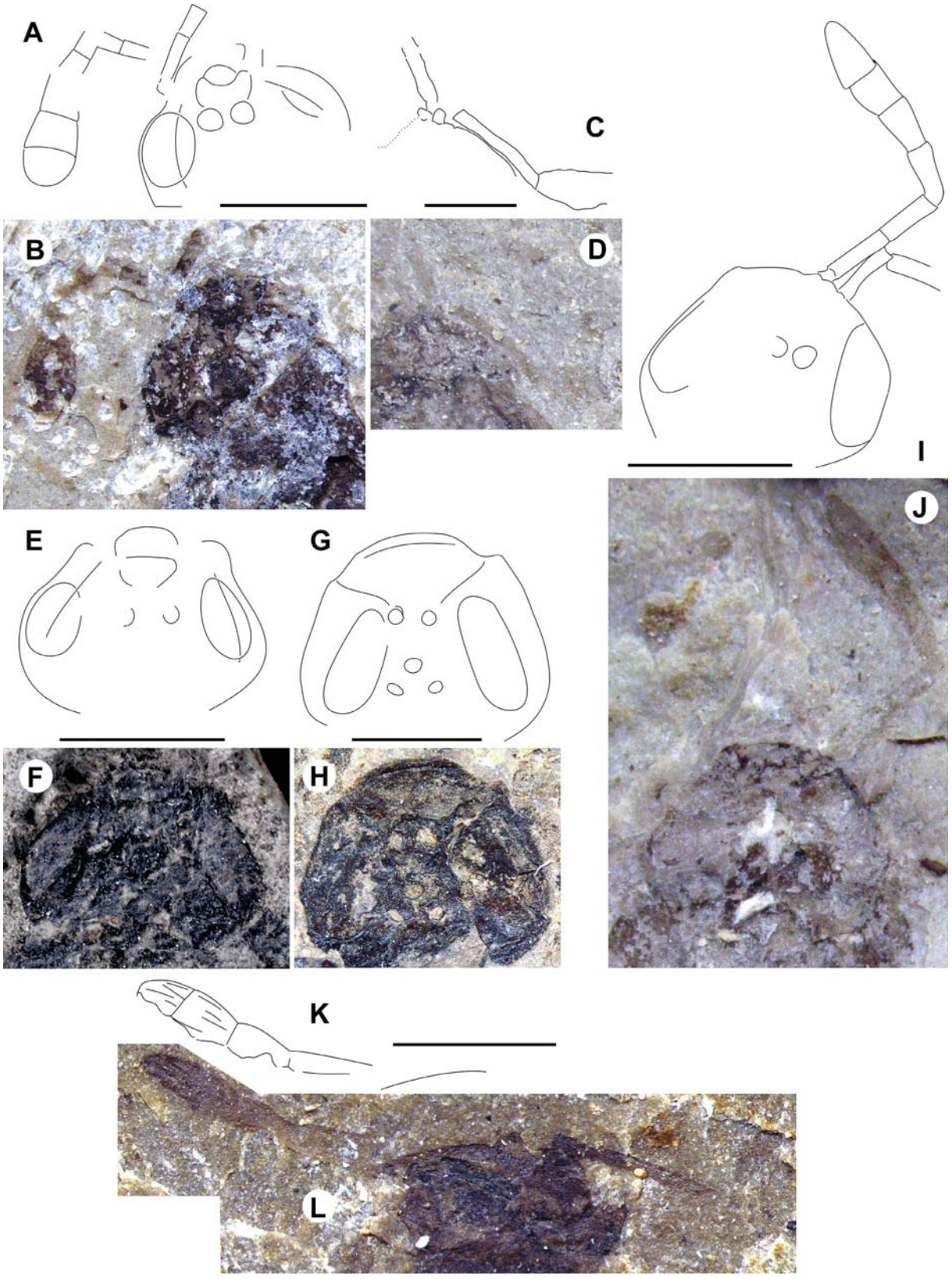


FIGURE 3. Heads of Cenocimbicinae: A, *Leptostigma brevilatum* GSC 142839, drawing; B, *L. brevilatum* GSC 142839, photograph; C, *Leptostigma longipallidum* GSC 142841, drawing; D, *L. longipallidum* GSC 142841, photograph; E, *Cenocimbex menatensis* MNHN-LP-R.11195, drawing; F, *C. menatensis* MNHN-LP-R.11195, photograph; G, *Leptostigma longipallidum* F-771, drawing; H, *L. longipallidum* F-771, photograph; I, *Leptostigma longitenebricum* F-1565, drawing; J, *L. longitenebricum* F-1565, photograph; K, *Leptostigma longiclava* RBCM.EH2017.050.4085.0001, drawing; L, *L. longiclava* RBCM.EH2017.050.4085.0001, photograph. Scale bars 2 mm.

Locality and age. Vermilion Bluffs Member of the Allenby Formation south of the village of Princeton, British Columbia, Canada; mid-Ypresian.

Species included. Type only.

Etymology. Named for the Allenby Formation, where its only specimen was found. The name is to be treated with masculine grammatical gender since it is derived from *Cimbex* (see Taeger *et al.* 2010: 188).

***Allenbycimbex morrisae* n. sp.**

http://zoobank.org/urn:lsid:zoobank.org:act:158DB20D-4B4D-41C3-B064-CCB1AB5237A9

Fig. 4.

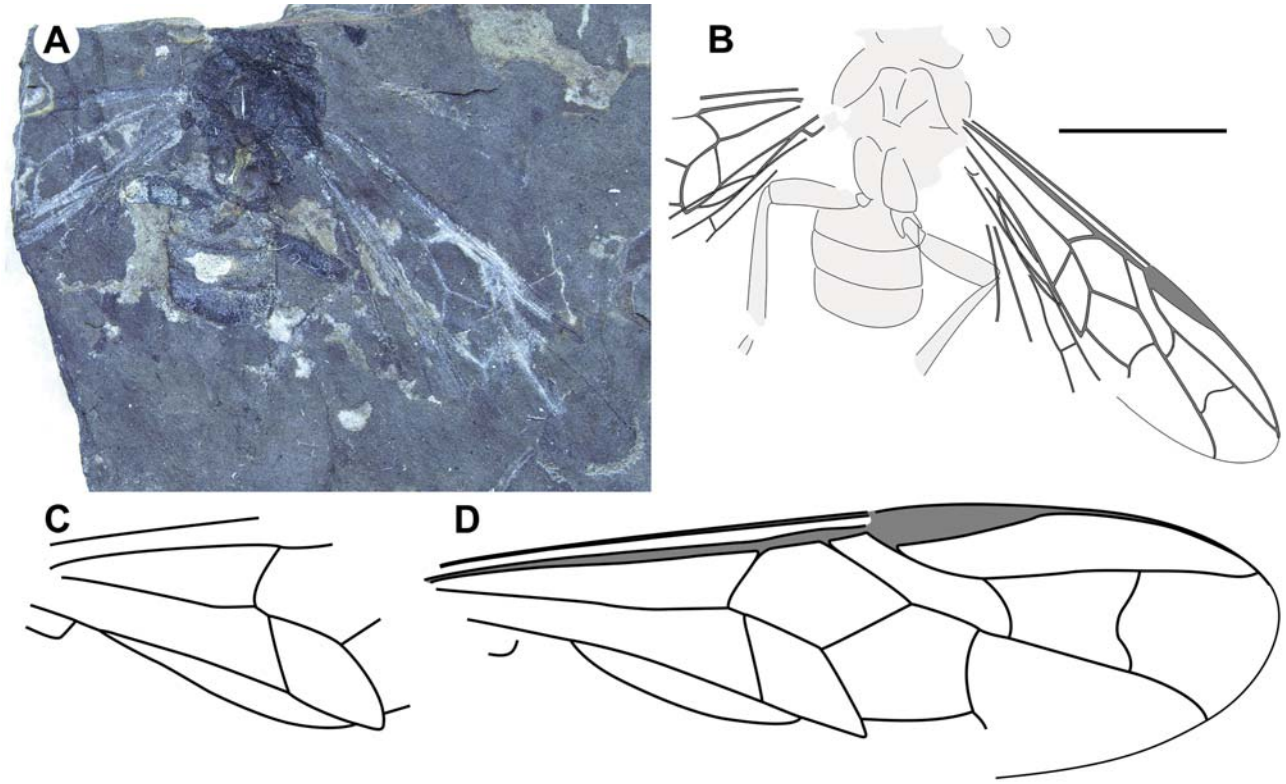


FIGURE 4. *Allenbycimbex morrisae*, holotype RBCM.EH2007.002.0001: A, photograph; B, drawing; C, drawing of right wing; D, drawing of left wing. Scale bar for A and B is 5 mm (as the fossil has been stretched by geologic shear forces, C and D are altered to the presumed unstretched configuration).

Material. Holotype RBCM.EH2007.002.0001a, b (part, counterpart). Mostly complete but somewhat deformed by geological shear forces, lacking head, fore and mid legs, hind tarsi, apical half of left wings, and apical half of abdomen; hind wings fragmentary and poorly preserved; wings lack visible colouration either originally or by preservation; collected by Muriel Morris, Allenby Formation; housed in the collections of the RBCM.

Diagnosis. As for genus.

Description. Length as preserved (stretched, see below; incomplete head and abdomen) 8.9 mm, apparently dark (preserved parts: hind tibiae, metasoma possibly paler). Temples somewhat inflated. Antennal club if correctly identified apparently short with truncated apex. Lateral pronotal lobes very wide, notauli apparently widely separated before scutellum (interpretation tentative). Hind coxae large, contiguous; femora not inflated, almost parallel-sided, shorter than abdomen wide; tibia thinner and much longer than femur. Forewing: length *ca*. 13.5 mm as preserved (distorted), the same in life if it was compressed in width, *ca*. 10 mm in life if it was stretched in length; maximum width: *ca*. 3.5 mm as preserved, about the same in life if it was stretched in length or *ca*. 4.25 if compressed in width; length/width: probably *ca*. 3.0; no membrane colouration detected (could be an artefact of preservation); pterostigma broad, distinctly wider than C-R basal to it; R+M longer than 1-M; 2r-rs not preserved; 2r-rm curved, joins Rs about same level as 2m-cu joins M, joins M behind 2m-cu for more than half length of 2r-m; 1-M almost straight; 1-M and 1m-cu diverging toward anterior; 3r-m distinctly bowed toward base; cell 2mcu with M shorter

than 1m-cu; 2m-cu curved distinctly toward base; cu-a postfurcal; anal cell contracted for distance subequal to width (height) of 1a cell, with no crossvein; basal portion of 2A+3A sharply bent toward 1A, meets 1A at steep angle. Hind wing with m-cu not preserved, r-m and cu-a far distant (for much longer than in *Cenocimbex* and more similar to that characteristic of *Leptostigma* **n. gen.**); other details obscure. Abdomen with 3 segments preserved (apparently sterna 2–4) each narrower than thorax and some 3.5× as wide as long.

Remarks. The fossil was distorted by geological shear forces during diagenesis, either stretching it along the plane of the length of its right forewing or compressing it 90° to that. These possibilities cannot be distinguished. As the forewings are about 90° to each other, we estimated its life shape by both graphically compressing the image along the length of the right forewing and by stretching it's width so that elements of its venation are of equal length to those of its left wing.

Etymology. The specific epithet is a patronymic formed from the surname of Muriel Morris, recognizing her contribution as collector and donor of the only known specimen.

Leptostigma n. gen.

http://zoobank.org/urn:lsid:zoobank.org:act:531F3657-F3D9-4A4D-86B7-1C146E74D627
Figs. 3A–D, 3G–K, 5–21.

Type species. *Leptostigma brevilatum* n. sp.

Diagnosis. Distinguished from *Cenocimbex* by lacking dark triangular sclerite on R basal to pterostigma reaching 1-Rs+M near 1m-cu (absent or undetectable being small, pale); wing narrower (length/width 2.8 or more); cell 3rm long (2r-m to 3r-m distinctly longer than length of 3r-m); hind wing with cu-a well before middle of cell mcu; distinguished from *Allenbycimbex* by pterostigma narrow, maximum height about equal to height to C to R basal to pterostigma.

Species included. The type species and *L. longiclava* **n. sp.**, *L. longipallidum* **n. sp.**, *L. longitenebricum* **n. sp.**, *L. proxivena* **n. sp.**, *L. fasciatum* **n. sp.**, and *L. alaemacula* **n. sp.**

Etymology. From the Greek *leptos*, meaning thin, and *stigma*, for the pterostigma. The name is neuter (see Examples below Art. 30.1.2, ICZN 1999).

Locality and age. Republic, Washington, United States of America, Tom Thumb Tuff Member of the Klondike Mountain Formation exposure A0307; and McAbee, British Columbia, Canada, Hoodoo Face beds; mid-Ypresian.

Leptostigma brevilatum n. sp.

http://zoobank.org/urn:lsid:zoobank.org:act:B29C5890-4E50-4408-8D67-0E073DB25546
Figs. 3A–B, 5–10.

Holotype. GSC 142839 (Fig. 3A–B, 5). Head with antennae (one incomplete), thorax, perhaps part of abdomen, parts of several legs, both forewings, both hind wings poorly preserved, collector SBA at McAbee (GSC locality V-016800), pre-1999, housed in the collections of the GSC (Vancouver).

Diagnosis. Distinguished from other species of *Leptostigma* by a combination of antenna dark, with club short and wide, with two basal flagellar segments comparatively short (combined shorter than half head width). Forewing lightly, evenly infuscate throughout. Tentatively diagnostic: R+M shorter than 1-M, 2r-rs enter cell 3rm at or before its middle, 2r-m enters M far behind 2m-cu, anal cells meet at crossvein or at most minimally separated by short fusion of 1A with 2A+3A.

Description. Holotype. Body length not known by preservation. Body as preserved (including head with antenna, thorax, femora, tibiae, abdominal base) and pterostigma dark, membrane lightly infuscate throughout, tarsal fragments (at least hind tarsomeres 1–3) darkened. Head (interpretation tentative by imperfect preservation) wider than long, with compound eyes oval, rather short, converging below, rather close to mandibles; ocelli not known, toruli close to each other, touching clypeus; clypeus small, excised apically; labrum oval, narrower and slightly shorter than clypeus; temples not inflated, scarcely exceeding eye contour. Antenna apparently with 9 antennomeres; scape, pedicel small, poorly preserved; flagellomeres possibly gradually becoming shorter, wider (but precise length sometimes obscure) except apical two of similar length; club somewhat unclear, apparently 3-segmented, short,

rounded apically. Thorax poorly known by preservation, with notauli and median longitudinal mesonotal sulcus distinct, meeting well before transverse scutellum. Forewing length 13 (holotype)–17 mm, maximum width 4–5 mm, length/width: 3.1–3.3. Pterostigma narrow, similar to width of C-R; R+M shorter than 1-M; 2r-rs before middle of cell 3rm (near middle in UWBM 54840); 2r-rm distinctly curved (F-1182 with aberrant short stub near middle in both wings), joins Rs about same level as 2m-cu joining M, joining M behind 2m-cu for more than half of 2r-m length (in F-1182, slightly less than that in right wing); 1-M straight or almost so; 3r-m almost straight; cell 1mcu with M and 1m-cu distinctly to slightly (in GSC 142840) diverging toward anterior margin, aberrant (split) in left wing of F-1182; cell 2mcu with M usually shorter than 1m-cu (as long as that in GSC 142840, slightly longer than that in F-1182); 2m-cu curved distinctly toward base (weakly so in GSC 142840); cu-a distinctly postfurcal; anal cells meet at crossvein. Hind wing with 3r-m, m-cu, cu-a present, 3r-m slightly more than its own length from m-cu; cu-a before middle of cell mcu, more than for its length before m-cu (aberrantly two cu-a present in holotype placed before and behind middle of cell mcu: which is true crossvein unclear). Legs long, narrow, hind femur widest subbasally, 2.9 times as long as wide, with lower margin smooth, hind tibia *ca*. 6 times as long as wide apically, hind apical spur long (as long as basitarsus, almost 0.4 times as long as tibia, Fig 9B), sharp, tarsomere 1–3 length ratio 1 : 0.7 : 0.45 (in GSC 142840, femora, tibiae apparently narrower, but difficult to measure), with claw apparently simple.

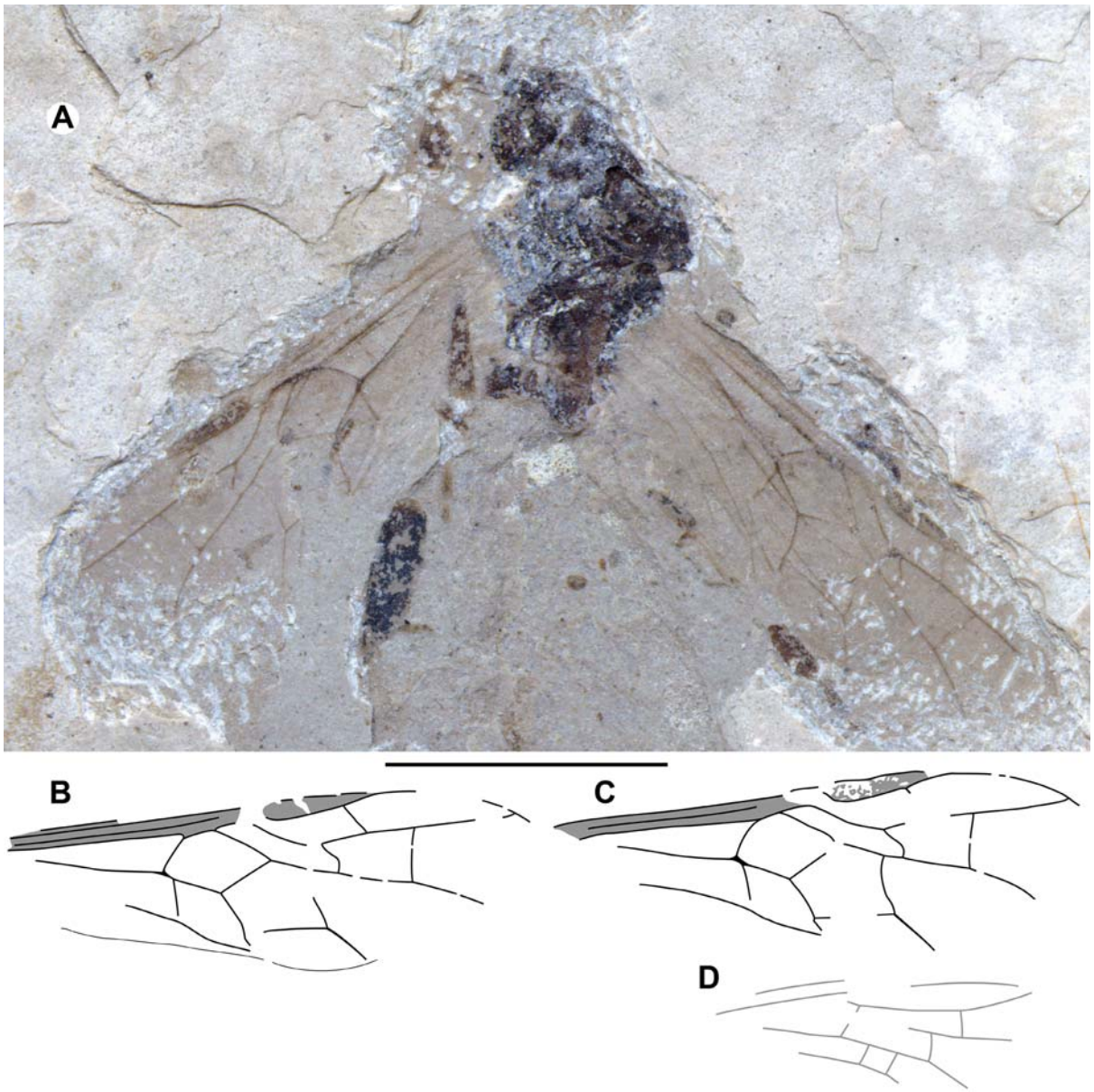


FIGURE 5. *Leptostigma brevilatum*, holotype GSC 142839. A, photograph, and B–D, drawings: B, right forewing; C, left forewing; D, right hind wing. All to scale, 5 mm.

Remarks. *L. brevilatum* **n. sp.** differs from all congeners with known antenna (*L. longiclava* **n. sp.**, *L. longipallidum* **n. sp.**, *L. longitenebricum* **n. sp.**) by its short and wide club. It additionally differs venationally from *L. longiclava* **n. sp.** in having 2r-rs at or before middle of cell 3rm, from *L. longipallidum* **n. sp.**, as well as from *L. longitenebricum* **n. sp.** in having R+M shorter than 1-M and by its anal cells being either separated by a short crossvein or at most by 1A and 2A+3A fused for a very short distance. Differs from *L. proxrvena* **n. sp.**, *L. fasciatum* **n. sp.**, *L. alaemacula* **n. sp.** with unknown antenna in having wing membrane lightly, evenly infuscate throughout (neither fascia nor macula) and 2r-m entering M far behind, not close to, 2m-cu.

Material. Holotype and tentatively (by venational characters) specimens F-1182/1183 (Fig. 6), unknown collector at McAbee, in the collections of TRU; UWBM-54840 (Fig. 7) (Lewis 1992: Fig. 2N as unknown Hymenoptera), unknown collector at Republic, in the collections of the UWBM; RBCM.EH2017.050.4628 (Fig. 8), collector John Leahy at McAbee, in the collections of the RBCM; F-774 (Fig. 9), unknown collector at McAbee, in the collections of TRU. GSC 142840 (Fig. 10), collector John Leahy at McAbee (GSC locality V-016800), in the collections of the GSC; this specimen is very tentatively attributed to the species, as it is missing 3r-m, which prevents identification of the precise position of 2r-rs with respect to cell 3rm: 2r-rs is distant from 2r-m for less that its own length, more consistent with *L. brevilatum* **n. sp.** than *L. longiclava* **n. sp.**

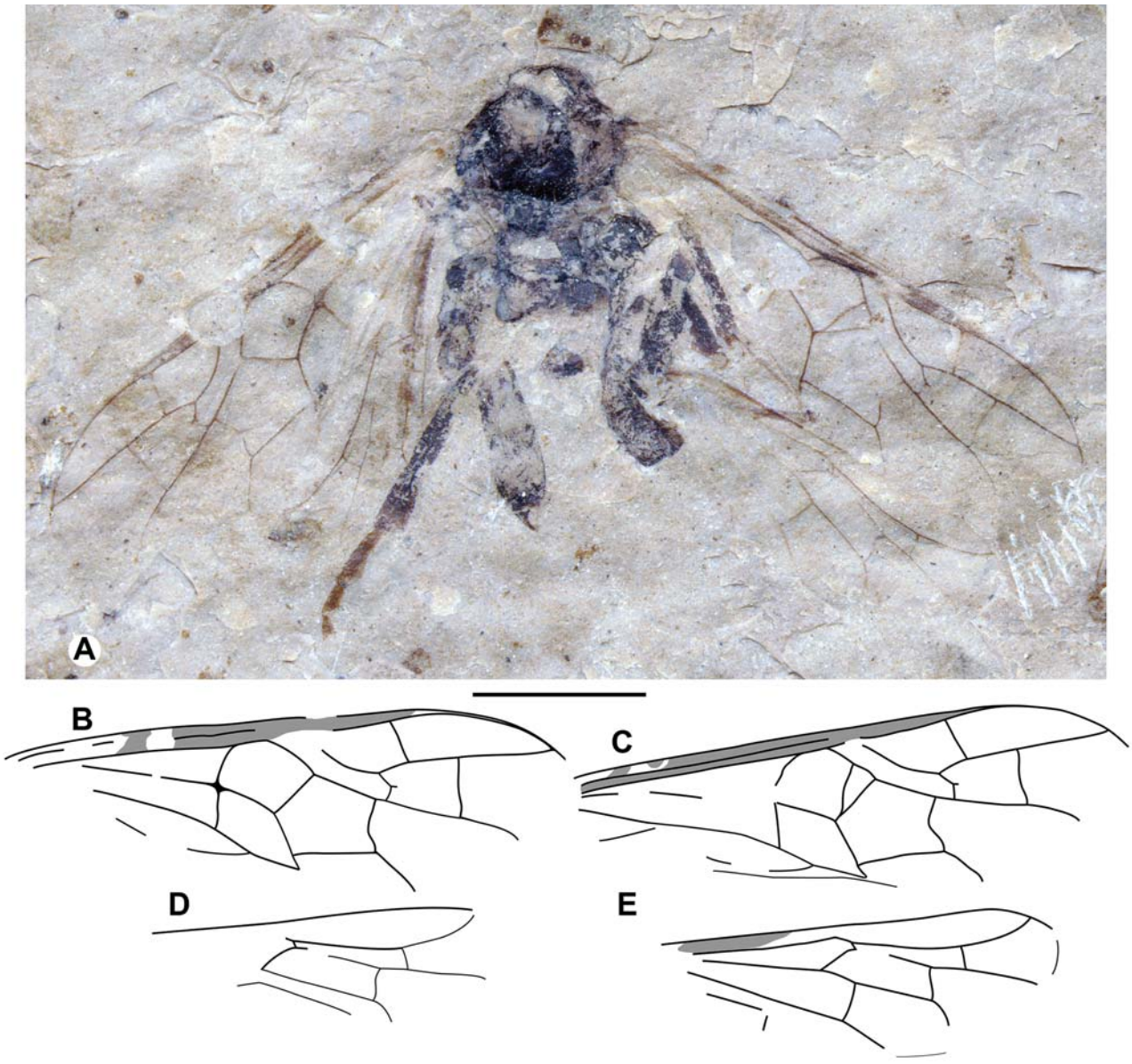


FIGURE 6. F-1182, tentative *Leptostigma brevilatum*, A, photograph, and B–E, drawings of: B, left forewing; C, right forewing; D, left hindwing, and; E, right hind wing. All to scale, 5 mm.

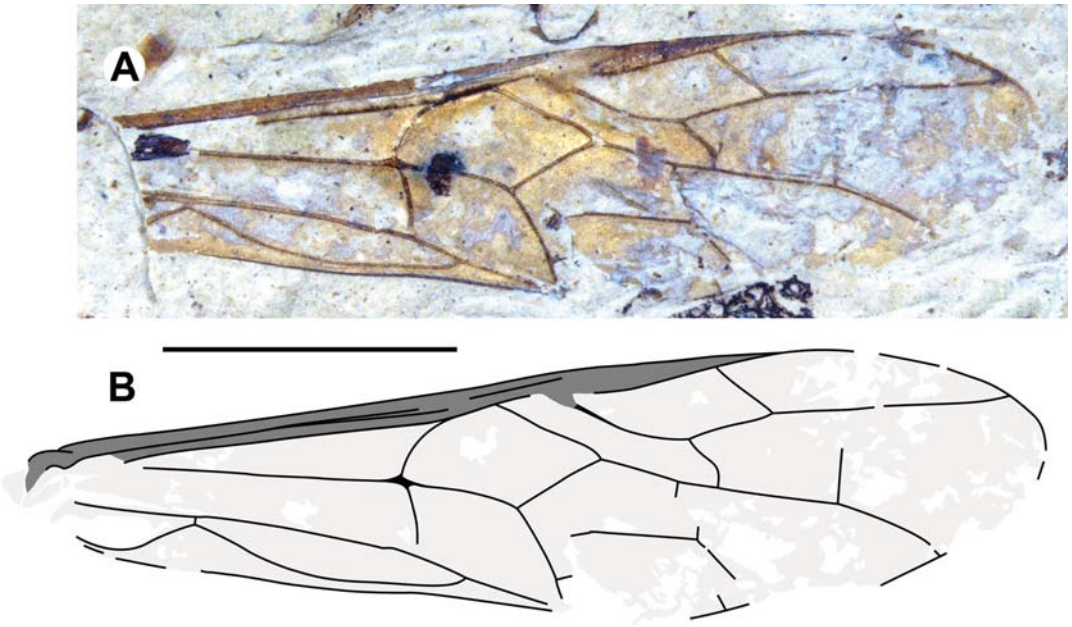


FIGURE 7. UWBM-54840, tentative *Leptostigma brevilatum*: A, photograph; B, drawing from part and counterpart. Scale bar 5 mm.

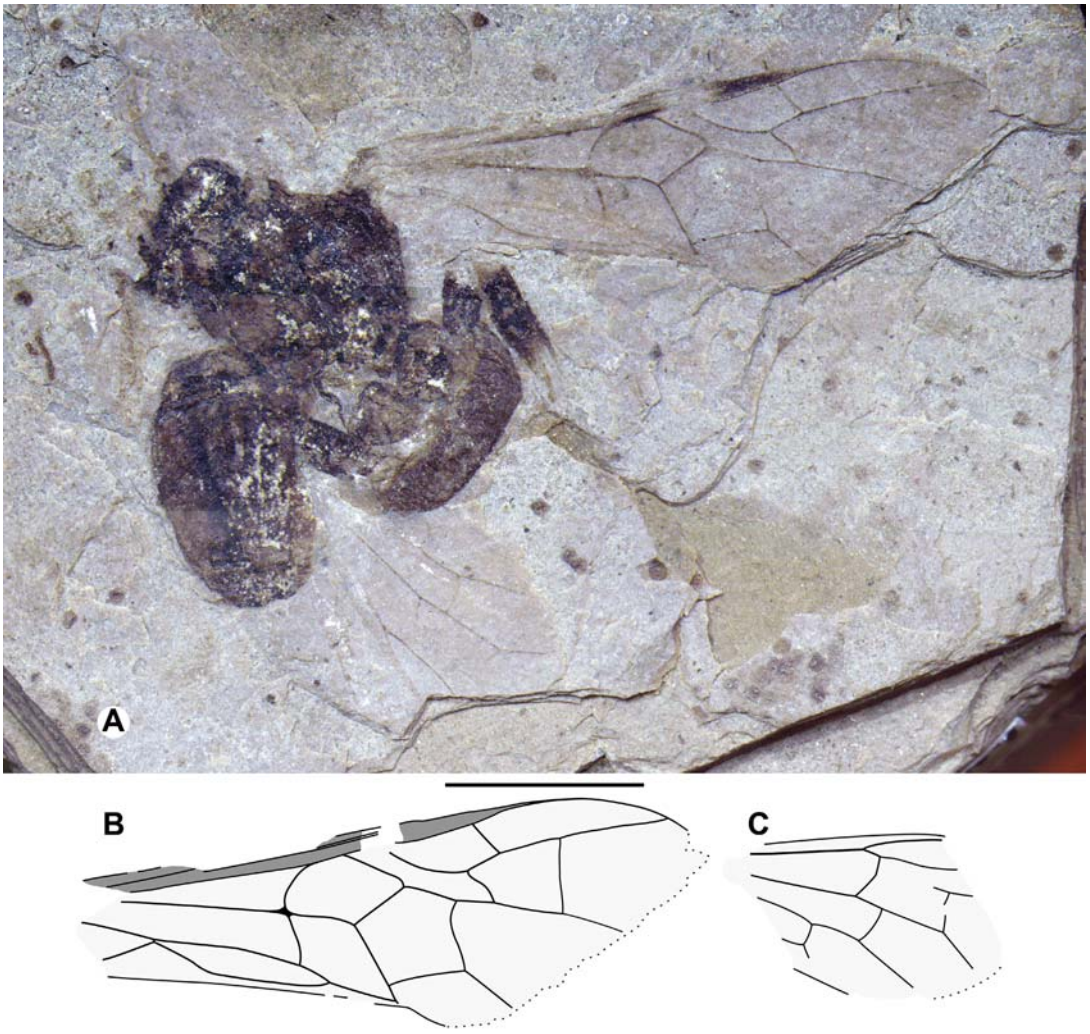


FIGURE 8. RBCM-EH2017-050-4628-001, tentative *Leptostigma brevilatum*, A, photograph, and B–C, drawings of the wings: B, right forewing; C, right hindwing. All to scale, 5 mm.

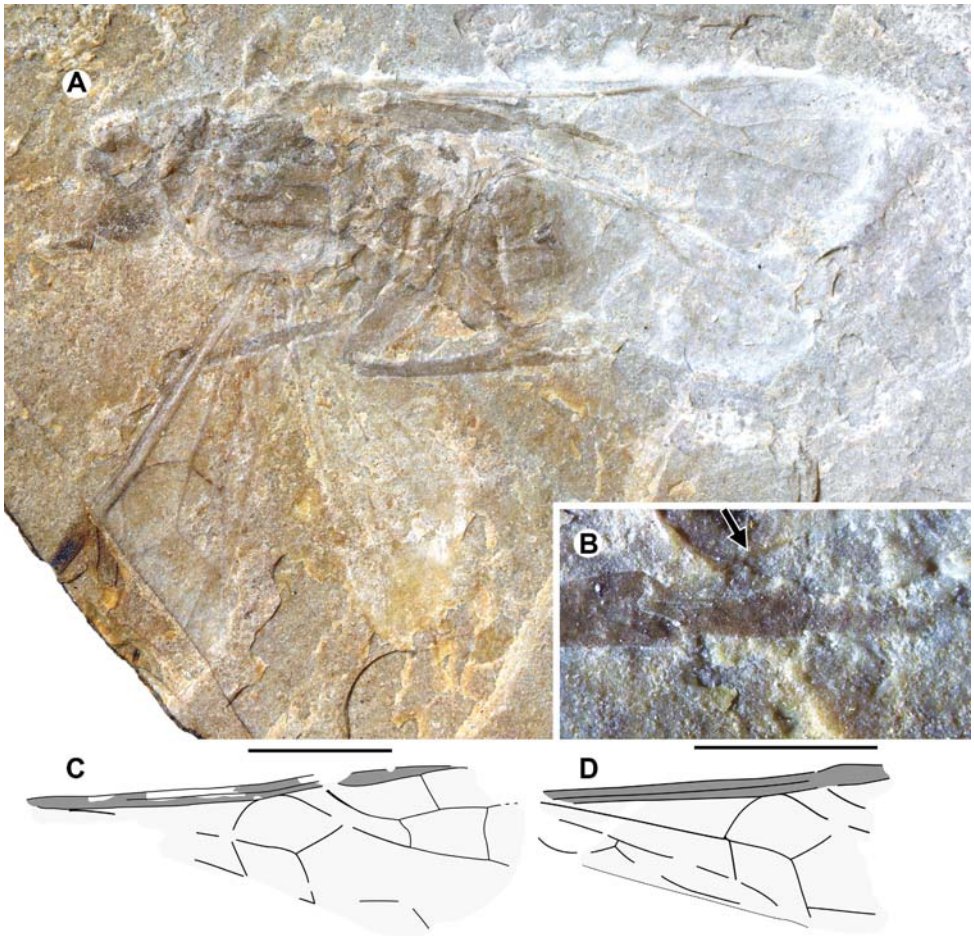


FIGURE 9. F-774, tentative *Leptostigma brevilatum*: A–B photographs and C–D, wing drawings: A, the whole fossil; B, closeup with arrow indicating the hind apical spur; C, right forewing; D, left forewing. A, C–D to 5 mm scale; B scale is 2 mm.

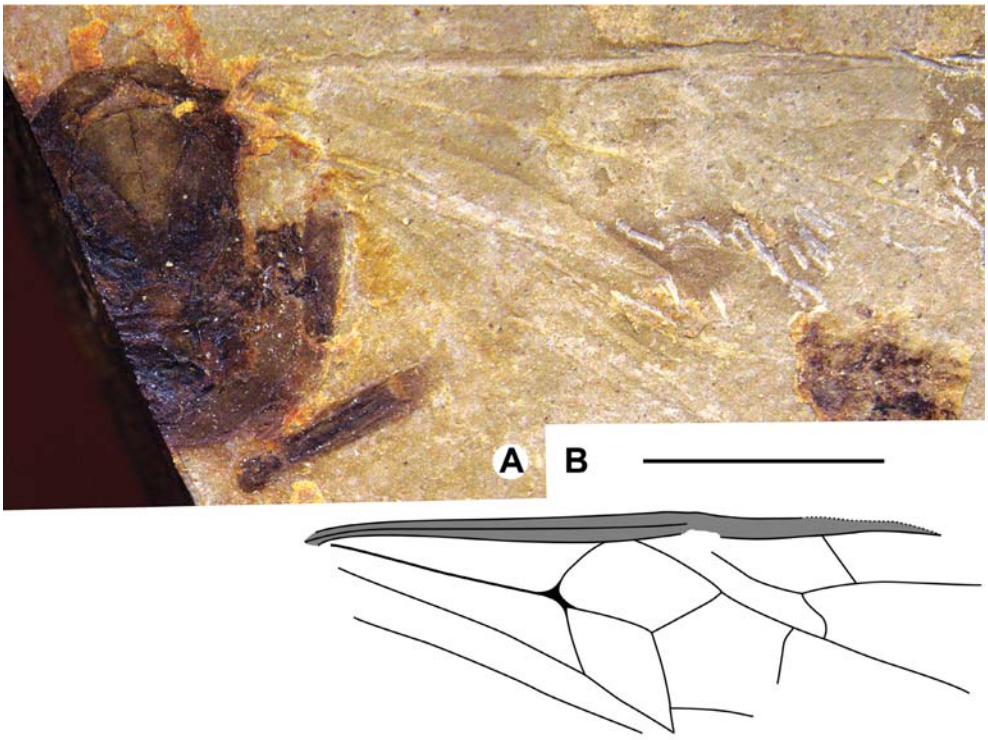


FIGURE 10. GSC 142840, tentative *Leptostigma brevilatum*: A, photograph, B, drawing of the forewing; scale is 5 mm.

Etymology. From the Latin *brevis*, meaning short and *latus*, wide, referring to the antennal club. The epithet is an adjective.

Locality and age. Republic, Washington, United States of America, Tom Thumb Tuff Member of the Klondike Mountain Formation exposure A0307; and McAbee, British Columbia, Canada, Hoodoo Face beds; both mid-Ypresian.

***Leptostigma longiclava* n. sp.**

http://zoobank.org/urn:lsid:zoobank.org:act:B8F5BDEE-1B98-4F5F-94FB-646D070B6153

Figs. 3K–L, 11–12.

Holotype. RBCM.EH2017.050.4085.0001a, b (part, counterpart) (Figs. 3K–L, 11). Mostly complete in dorsal aspect but missing much of the abdomen; collected at McAbee by John Leahy; housed in the collections of the RBCM.

Diagnosis. Distinguished from other species of *Leptostigma* by a combination of antenna with club long, darkened, penultimate segment longer than ultimate, flagellar base formed by long, dark, apparently single (entire) segment. Forewing lightly, evenly infuscate throughout (no fascia or macula). Tentatively diagnostic: R+M shorter than 1-M, 2r-rs joins cell 3rm distinctly behind its middle, 2r-m joins M far behind 2m-cu, anal cells meet at crossvein or are at most minimally separated by a very short fusion of 1A with 2A+3A.

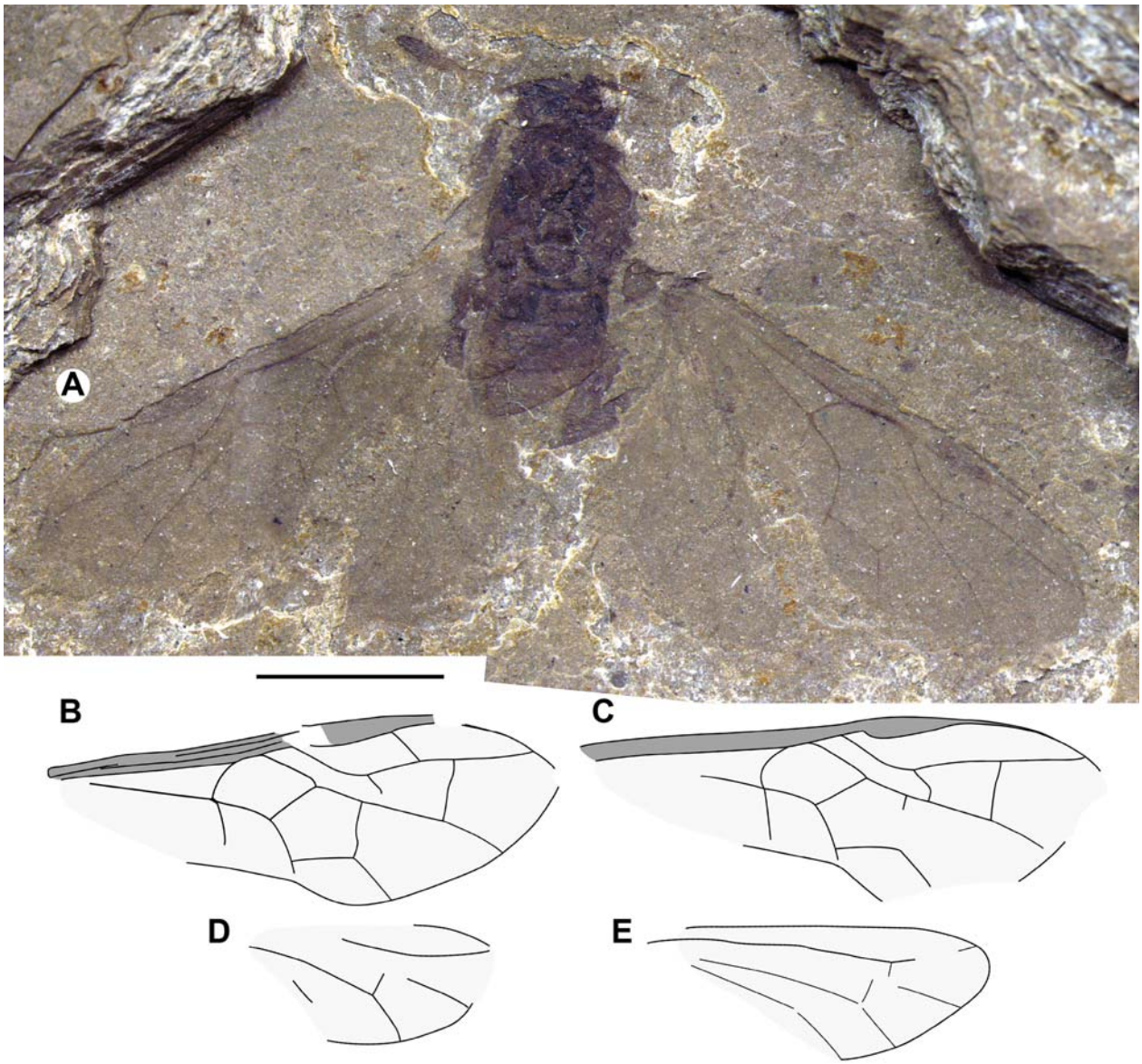


FIGURE 11. *Leptostigma longiclava* holotype RBCM-EH2017.050.4085.001, A, photograph, B–E wing drawings: B, right forewing; C, left forewing; D, left hind wing; E, right hind wing. All to scale, 5 mm.

Description. Holotype. Body. Length not known by preservation, tentative specimen F-848 *ca*. 14 mm as preserved, likely 15–16 mm in life. Head, thorax, scape, pedicel, basal flagellomere, femora dark; antennal club, pterostigma, tibiae, metasoma darkened as preserved; flagellar segment 2 rather pale, wing membrane lightly infuscate throughout. Head as preserved difficult to interpret. Antenna apparently 7-segmented, with scape, particularly pedicel very short, first flagellomere longest (about one third of flagellum), those following gradually becoming shorter and, except apical one, wider, apical one half-oval. Thorax with distinct median longitudinal mesonotal sulcus, notauli complete, meeting well before transverse scutellum; metascutellum narrow (narrower than normal in Pachylostictinae, Corynidinae), cenchri not apparent. Forewing length 14 (holotype)–16 mm, maximum width 4.5 (holotype)–5 mm, length/width 3.1–3.2; pterostigma narrow, similar to width of C&R basal of pterostigma; R+M as long as 1-M in left wing, shorter in right; 2r-rs shorter than Rs between 2rm, 2r-rs, entering Rs behind middle of cell 3rm; 2r-m distinctly curved, joins Rs about same level as 2m-cu joining M, joins M behind 2m-cu for more than half length of 2r-m; 3r-m almost straight; 1-M curved; 1-M and 1m-cu slightly diverging toward wing anterior margin; cell 2mcu with M shorter than 1m-cu; 2m-cu slightly curved or angular mid-length; cu-a slightly postfurcal; anal cells minimally separated by a very short fusion of 1A with 2A+3A, no crossvein between them (in F-848, anal cell region not preserved in holotype). Hind wing mostly indistinctly preserved, crossveins 3r-m, m-cu present, distant for less than length of 2r-m. Abdominal tergum 1 possibly split medially, with hind margin straight.

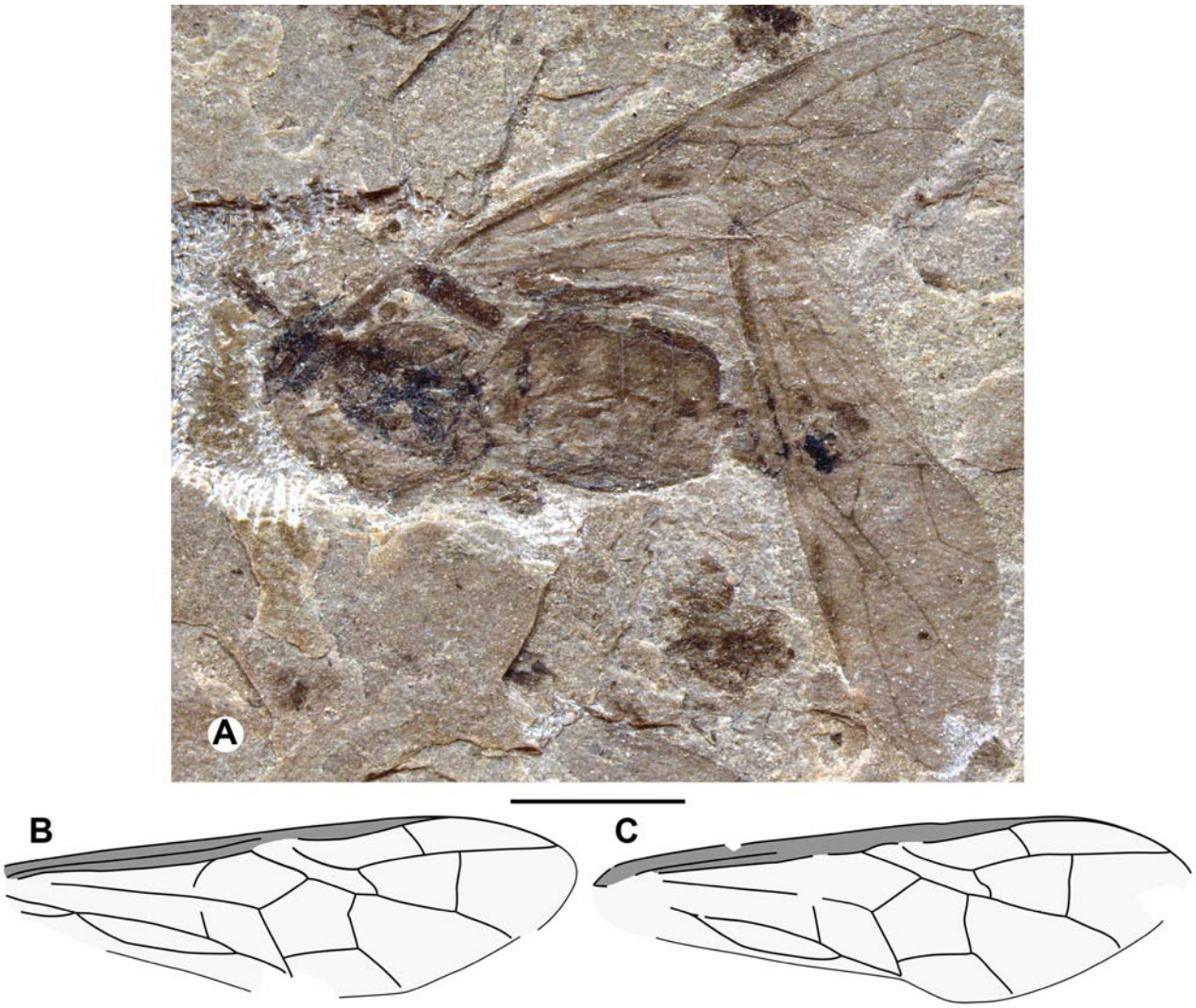


FIGURE 12. F-848, tentative *Leptostigma longiclava*, A, photograph, B–C, drawings: B, right forewing; C, left forewing. All to scale, 5 mm.

Remarks. Differs from *L. brevilatum* **n. sp.** and *L. longipallidum* **n. sp.** by its club long and darkened [short, wide, and dark in *L. brevilatum* **n. sp.**; long and pale in *L. longipallidum* **n. sp.**]; differs venationally, tentatively, from both *L. brevilatum* **n. sp.** and *L. longipallidum* **n. sp.** in 2r-rs joining cell 3rm distinctly distal to its middle [vs. at or

before middle]. Differs from *L. longitenebricum* **n. sp.** that has a generally similar antenna (club long, darkened) in that its flagellar base is formed by one long, dark segment [vs. two pale, relatively short ones], and by its penultimate club segment longer than ultimate [vs. shorter]. *L. longiclava* **n. sp.** also differs from *L. longitenebricum* **n. sp.** in having anal cells at most minimally separated [vs. distant for more than half width/height of cell 2a]. Differs from *L. proxivena* **n. sp.**, *L. fasciatum* **n. sp.**, and *L. alaemacula* **n. sp.** by its forewing lightly, evenly infuscate throughout [vs. with dark transverse fascia or macula at or basal to level of pterostigmal base] and 2r-m entering M far behind, not close to 2m-cu.

Material. Holotype and tentatively (based on venational characters) specimen F-848 (Fig. 12), collector unknown at McAbee, in the collections of TRU.

Etymology. From the Latin *longus*, meaning long, and *clava*, club, referring to the antennae. The epithet is a noun in apposition.

Locality and age. McAbee, British Columbia, Canada, Hoodoo Face beds; mid-Ypresian.

***Leptostigma longipallidum* n. sp.**

http://zoobank.org/urn:lsid:zoobank.org:act:EEEB4CA5-0EF0-4B45-985E-08D39CF2A996

Figs. 3C–D, 13–15.

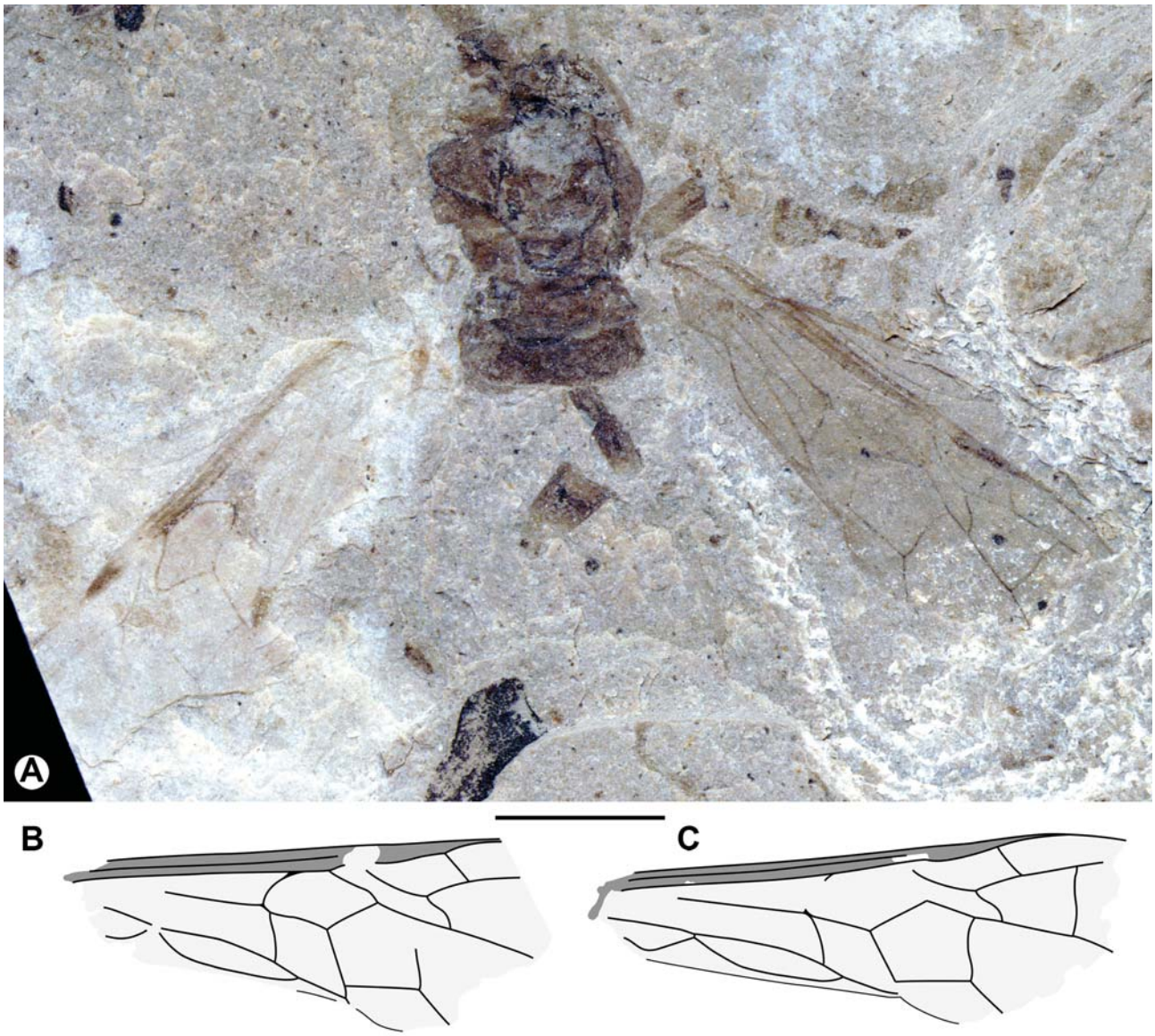


FIGURE 13. *Leptostigma longipallidum*, holotype GSC 142841, A, photograph, B–C , wing drawings: B, right forewing; C, left forewing. All to scale, 5 mm.

Holotype. GSC 142841 (part, counterpart) (Figs. 3C–D, 13). A very damaged head, thorax, partial abdomen and fragments of legs, both forewings only missing the apical regions overlaying indistinct portions of hind wings; from McAbee (GSC locality V-016800), collector John Leahy; housed in the collections of the GSC (Vancouver).

Diagnosis. Distinguished from other species of *Leptostigma* by antenna with a combination of club elongate, paler than flagellar base formed with two long darkened segments; forewing lightly, evenly infuscate throughout. Tentatively diagnostic: R+M longer than 1-M, 2r-rs joins cell 3rm at or before its middle. R+M longer than 1-M, 2r-rs joins cell 3rm at or before its middle, 2r-m joins M far behind 2m-cu, anal cells meet at crossvein.

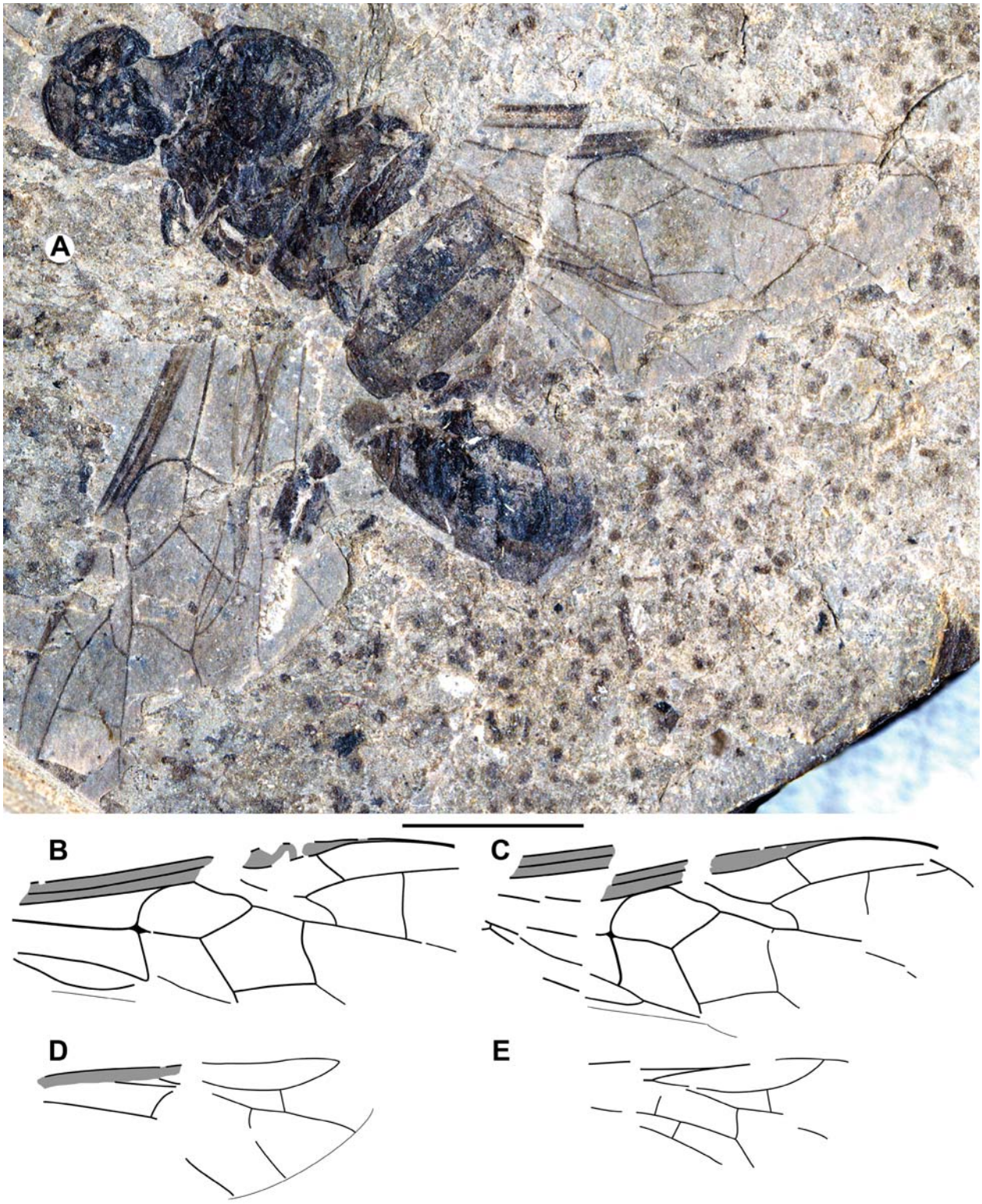


FIGURE 14. F-771, tentative *Leptostigma longipallidum*, A, photograph, B–E, wing drawings: B, right forewing; C, left forewing; D, right hind wing; E. left wing. All to scale, 5 mm.

Description. Holotype. Body length as preserved (F-777, certainly incomplete) 20 mm, dark throughout including small leg fragments, wing membrane lightly infuscate throughout, pterostigma dark; in F-1185 middle part of wing wide with long, dense pubescence (similar in some living cimbicids, *cf*. Vilhelmsen *et al.* 2018, Fig. 2A, B, 6D, 13A; Yan *et al.* 2019, Fig. 1; may be absent in other Cenocimbicinae by preservation). Head (F-777) roundish, slightly transverse, with eyes long, strongly converging forward, reaching rather close to both clypeus and occiput, ocelli in orthogonal triangle, posterior ones somewhat diminished, distant from each other for more than their greatest diameter; toruli touching clypeus, distant for more than their diameter; temples inflated, in front view toward clypeus as wide as eye; clypeus wide, moderately short. Antennal club elongate, paler than funicle, funicle 2-segmented, cylindrical, somewhat darkened. Lateral lobes of pronotum wide; median longitudinal mesonotal sulcus, notauli well developed, joined well before small transverse scutellum, metanotum short. Forewing length holotype 17.8 mm (F-1185, 15 mm; F-777, 16.5 mm), maximum width 4–5.3 mm, length/width 3.4–3.7, pterostigma narrow, tapering, similar to width of C-R basal to pterostigma, R+M longer than 1-M, maximum length of cell 2r shorter than 3r, 2r-rs same length or shorter than Rs between 2r-m and 2r-rs, joins Rs before middle of cell 3rm, 2r-rm curved (more or less sigmoidal), joins Rs similar level to 2m-cu joins M, joins M behind 2m-cu for more than half (for half only in F-1185) of 2r-m length; 1-M more or less curved, cell 1mcu with 1-M, 1m-cu sub-parallel to slightly diverging, 3r-m almost straight, cell 2mcu with M shorter than 1m-cu or (in F-1185) of similar length, 2m-cu slightly bent toward base, cu-a postfurcal (scarcely so if at all in F-777), anal cells meet at crossvein. Hind wing with 3r-m, m-cu, cu-a present, m-cu for its length from 3r-m, cu-a before middle of cell mcu, for twice its length basal to m-cu. Abdominal tergum 1 entire, with hind margin weakly convex.

Remarks. Differs from all congeners with known antenna (*L. brevilatum* **n. sp.**, *L. longiclava* **n. sp.**, and *L. longitenebricum* **n. sp.**) by its club paler than its funicle. Differs venationally from *L. brevilatum* **n. sp.** and *L. longiclava* **n. sp.** by R+M longer than 1-M, from *L. longitenebricum* **n. sp.** by its anal cells meeting at a crossvein. Differs from *L. proxivena* **n. sp.**, *L. fasciatum* **n. sp.**, *L. alaemacula* **n. sp.**, with unknown antenna by wing membrane lightly, evenly infuscate throughout (without fascia, macula) and 2r-m entering M far behind, and not close to, 2m-cu.

Material. Holotype and tentatively (by venation) specimen F-777, F-771 (part, counterpart) (Fig. 14), and F-1185 (Fig. 15), both collector unknown, in the collections of TRU.

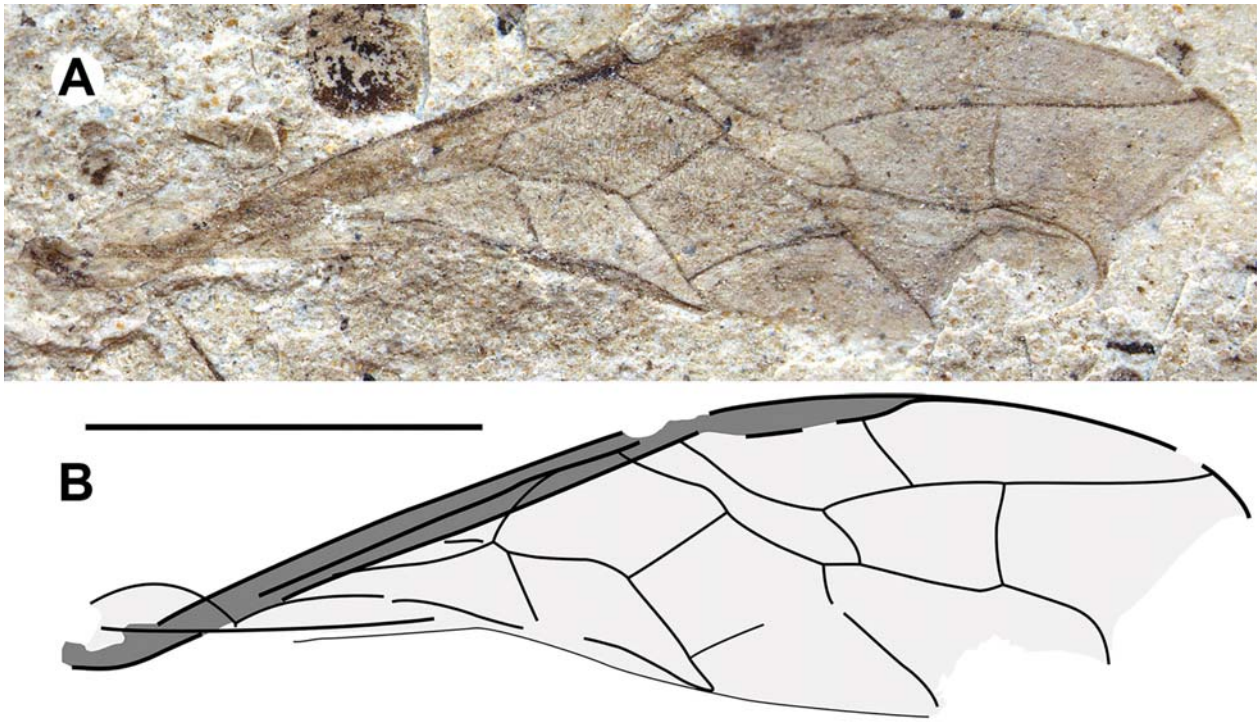


FIGURE 15. F-1185 tentative *Leptostigma longipallidum* forewing: A, photograph; B, drawing. Scale is 5 mm.

Etymology. From the Latin *longus*, meaning long, and *pallidus*, pale, referring to the antennal club. The epithet is an adjective.

Locality and age. McAbee, British Columbia, Canada, Hoodoo Face beds; mid-Ypresian.

***Leptostigma longitenebricum* n. sp.**
http://zoobank.org/urn:lsid:zoobank.org:act:82407841-CBF9-4647-A04B-A12A242B7AE0
Figs. 3I–J, 16–18.

Holotype. F-1565 (part, counterpart) (Figs. 3I–J, 16). Almost complete, in dorsal aspect, but legs, one antenna, body mostly poorly preserved, hind wings poorly preserved; from McAbee, collector John Leahy; housed in the collections of TRU.

Diagnosis. Distinguished from other species of *Leptostigma* by antenna with a combination of club elongate, darker than flagellar base, base two long, pale segments; forewing lightly, evenly infuscate throughout. Tentatively diagnostic: R+M longer than 1-M, 2r-rs enters cell 3rm at or before its middle, 2r-m enters M far behind 2m-cu, anal cells separated by 1A joining 2A+3A for at least half height of cell 2a.

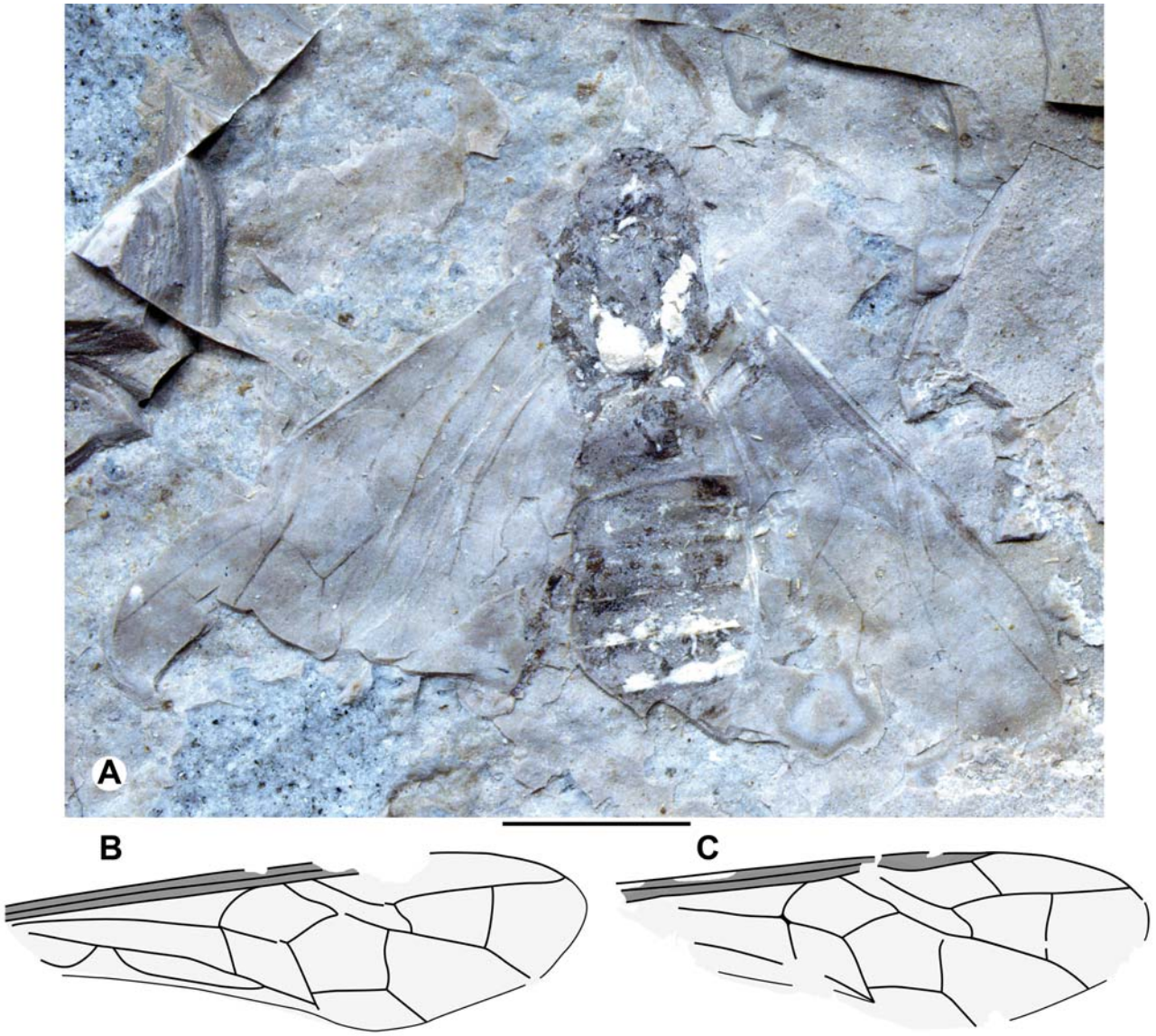


FIGURE 16. *Leptostigma longitenebricum* holotype F-1565, A, photograph, B–C, wing drawings: B, left forewing; C, right forewing. All to scale, 5 mm.

Description. Holotype. Body length *ca*. 15.5 mm, body, legs, pterostigma dark (tarsi less dark), antenna with club darkened, funicle paler, wing membrane lightly infuscate throughout. Head roundish, eyes occupying most of head sides, oval, converging ventrally, with temples weak (scarcely visible in front view), toruli close to each other. Antenna with eight antennomeres, club elongate, narrowed apically, two basal flagellar segments cylindrical, next three widened, apical one narrowed distally; basal, apical segments longest, penultimate shortest. Pronotum with wide

lateral lobes; median longitudinal mesonotal sulcus, notauli well developed, meeting well before scarcely transverse scutellum; metanotum rather narrow, with wide triangular scutellum, small, roundish cenchri. Forewing length holotype 15.5 mm (F-1563, 11.5 mm), maximum width estimated 3.5–5 mm, length/width: 3.1–3.3; pterostigma narrow, tapering, similar to width of C-R before pterostigma; R+M longer than 1-M; maximum length of cell 2r shorter than 3r; 2r-rs shorter than Rs between 2r-m, 2r-rs, joining Rs at middle of cell 3rm; 2r-rm curved, sometimes slightly sigmoidal, joins Rs at or slightly distal to 2m-cu joins M, joins M behind 2m-cu more than for half length of 2r-m; 1-M curved or (GSC 142842) almost straight; cell 1mcu with M, 1m-cu slightly divergent toward anterior margin; 3r-m near straight or (GSC 142842) distinctly bowed toward base; cell 2mcu with M similar length or (GSC 142842) shorter than 1m-cu; 2m-cu slightly curved toward base; cu-a postfurcal (holotype) or interstitial; anal cell separated by 1A fusion with 2A+3A (no crossvein) for length of almost half width of cell 2a in GSC 142842, for more than its width in F-1563. Mid, hind femora long, oval, *ca.* 3.5 times as long as wide; tibiae thin, only slightly longer than their femora, basitarsi *ca.* 0.35 as long as their tibiae. First abdominal tergum if correctly identified (F-1563 only) entire, with straight hind margin.

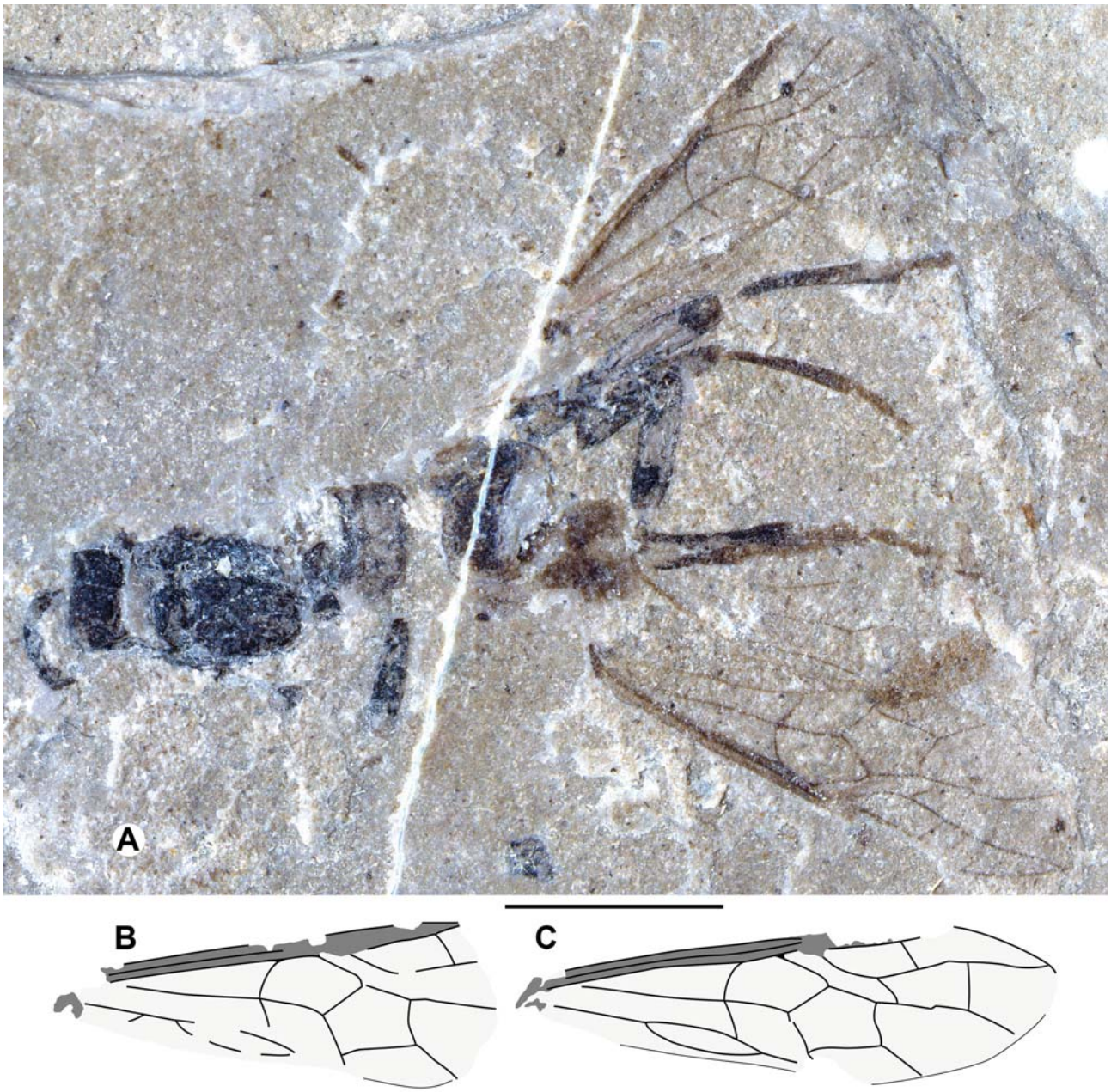


FIGURE 17. F-1563, tentative *Leptostigma longitenebricum*, A, photograph and B–C, wing drawings: B, left forewing; C, right forewing. All to scale, 5 mm.

Remarks. Differs from *L. longiclava* **n. sp.** and *L. longipallidum* **n. sp.** by flagellar base pale and, venationally, in more the distal position of 2r-rs (behind middle of cell 3rm). Differs from *L. brevilatum* **n. sp.** by its antennal club being long, also venationally by its R+M long and anal cells distinctly separated by fusion of 1A with 2A+3A. Differs from *L. proxivena* **n. sp.**, *L. fasciatum* **n. sp.**, *L. alaemacula* **n. sp.** with unknown antenna by its wing membrane lightly, evenly infuscate throughout (without fascia or macula) and by 2r-m entering M far behind, not close to, 2m-cu.

Material. Holotype and tentatively from venation F-1563 (Fig. 17), collector unknown, in the collections of TRU, and GSC 142842, collector SBA at McAbee (GSC locality V-016800), July 12, 2000 (Fig. 18), housed in the collections of the GSC (Vancouver).

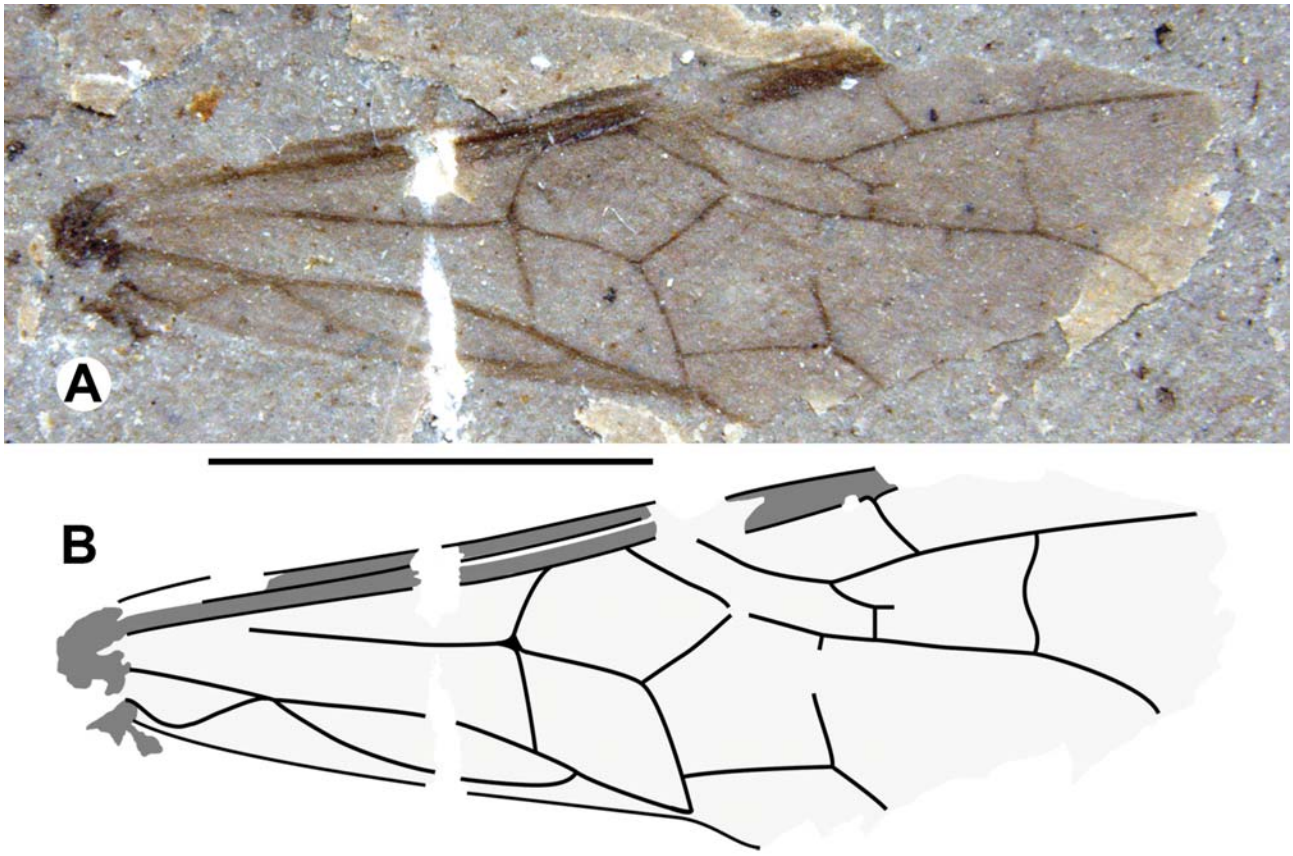


FIGURE 18. GSC 142842, tentative *Leptostigma longitenebricum* forewing: A, photograph; B, drawing. Scale bar 5 mm.

Etymology. From the Latin *longus*, meaning long, and *tenebricus*, dark, referring to the antennal club. The epithet is an adjective.

Locality and age. McAbee, British Columbia, Canada, Hoodoo Face beds; mid-Ypresian.

***Leptostigma proxivena* n. sp.**

http://zoobank.org/urn:lsid:zoobank.org:act:B78563B1-A3EB-4DB2-80D7-2EBC0B8C9F05

Fig. 19.

Holotype. F-1564 (Fig. 19). A mostly complete forewing missing the apical portion; from McAbee, collector unknown; in the collections of TRU.

Diagnosis. Distinguished from other species of *Leptostigma* by forewing mid-length with dark transverse fascia including all of cell 1mcu. Tentatively diagnostic: R+M shorter than 1-M, 2r-rs enter cell 3rm before its middle, 2r-m enters M scarcely behind 2m-cu, anal cells meet at crossvein.

Description. Holotype. Forewing length *ca*. 20 mm complete, maximum width *ca*. 6 mm (estimated), length/width 3.3. Membrane lightly infuscate throughout, darker posterior to 1r-rs in cell 1mcu and immediately posterior to this; pterostigma dark, narrow, tapering, similar to width of C-R before pterostigma; R+M shorter than 1-M;

maximum length of cell 2r shorter than 3r; 2r-rs shorter than Rs between 1r-rs, 2r-rs; 2r-m curved, slightly sigmoidal, joins Rs basal to 2m-cu joins M, joins M slightly behind 2m-cu; 3r-m slightly curved; 1-M slightly curved; cell 1mcu with first abscissa of M, 1m-cu slightly divergent toward anterior; cell 2mcu with M notably longer than 1m-cu; 2m-cu with distinct, but small curve toward base; cu-a postfurcal; anal cells meet at crossvein.

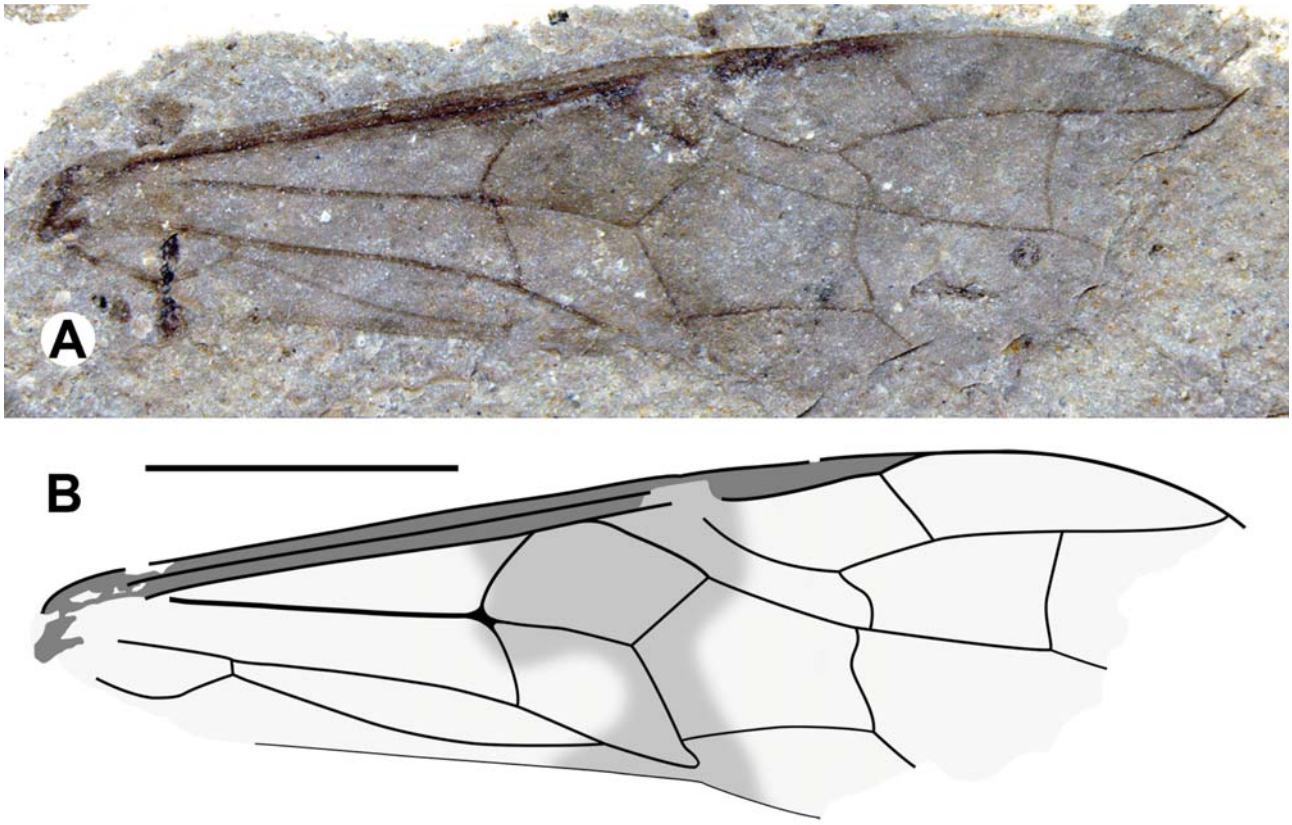


FIGURE 19. *Leptostigma proxivena* holotype F-1564, forewing: A, photograph; B, drawing. Scale bar 5 mm.

Remarks. Differs from *L. brevilatum* **n. sp.**, *L. longiclava* **n. sp.**, *L. longipallidum* **n. sp.**, and *L. longitenebricum* **n. sp.** by forewing with dark transverse fascia and 2r-m joins M close to 2m-cu. Differs from *L. fasciatum* **n. sp.** by a more basal position of 2r-rs (before middle of cell 3rm), from *L. alaemacula* **n. sp.** by anal cells meeting at crossvein (1A and 2A+3A not fused).

Material. Holotype.

Etymology. From the Latin *proxior*, meaning closer, and *vena*, vein, referring to the position of 2r-rs. The epithet is a noun in apposition.

Locality and age. McAbee, British Columbia, Canada, Hoodoo Face beds; mid-Ypresian.

Leptostigma fasciatum n. sp.

http://zoobank.org/urn:lsid:zoobank.org:act:19480AA6-435A-490A-BB68-644C50F9BD32
Fig. 20.

Holotype. GSC 142843 (Fig. 20). A mostly complete forewing, missing the apex and the basal portion of cell 1a. Collected by SBA at McAbee (GSC locality V-016800), May 16, 2001, in the collections of the GSC (Vancouver).

Diagnosis. Distinguished from other species of *Leptostigma* by a combination of forewing mid-length with dark transverse fascia, including small part of cell 1mcu. Tentatively diagnostic: R+M shorter than 1-M, 2r-rs joins cell 3rm distinctly distal to its middle, 2r-m joins M scarcely basal to 2m-cu, anal cells meet at crossvein (1A and 2A+3A not fused).

Description. Holotype. Forewing length: 11.1 mm, maximum width estimated 4.0 mm, length/width 2.8; membrane lightly infuscate throughout, darker posterior to base of pterostigma; pterostigma narrow, tapering, similar to width of C-R before pterostigma; R+M shorter than 1-M; maximum length of cell 2r shorter than 3r; 2r-rs

shorter than Rs between 2r-m, 2r-rs; 2r-m curved, slightly sigmoidal, joins Rs notably basal to 2m-cu joins M, joins M scarcely behind 2m-cu; 1-M straight; cell 1mcu almost square; 3r-m slightly curved; cell 2mcu with M shorter than 1m-cu; 2m-cu curved toward base; cu-a interstitial; anal cells meet at crossvein, with adventitious oblique crossvein in cell 2a.

Remarks. Differs from *L. brevilatum* **n. sp.**, *L. longiclava* **n. sp.**, *L. longipallidum* **n. sp.**, *L. longitenebricum* **n. sp.** in having forewing with dark transverse fascia and 2r-m joining M close to 2m-cu. Differs from *L. proxivena* **n. sp.** by a more distal position of 2r-rs (distal to middle of cell 3rm), from *L. alaemacula* **n. sp.** by anal cells meeting at crossvein (1A and 2A+3A not fused).

Material. Holotype.

Etymology. From the Latin adjective *fasciatus*, meaning striped, referring to the forewing colouration of the species.

Locality and age. McAbee, British Columbia, Canada, Hoodoo Face beds; mid-Ypresian.

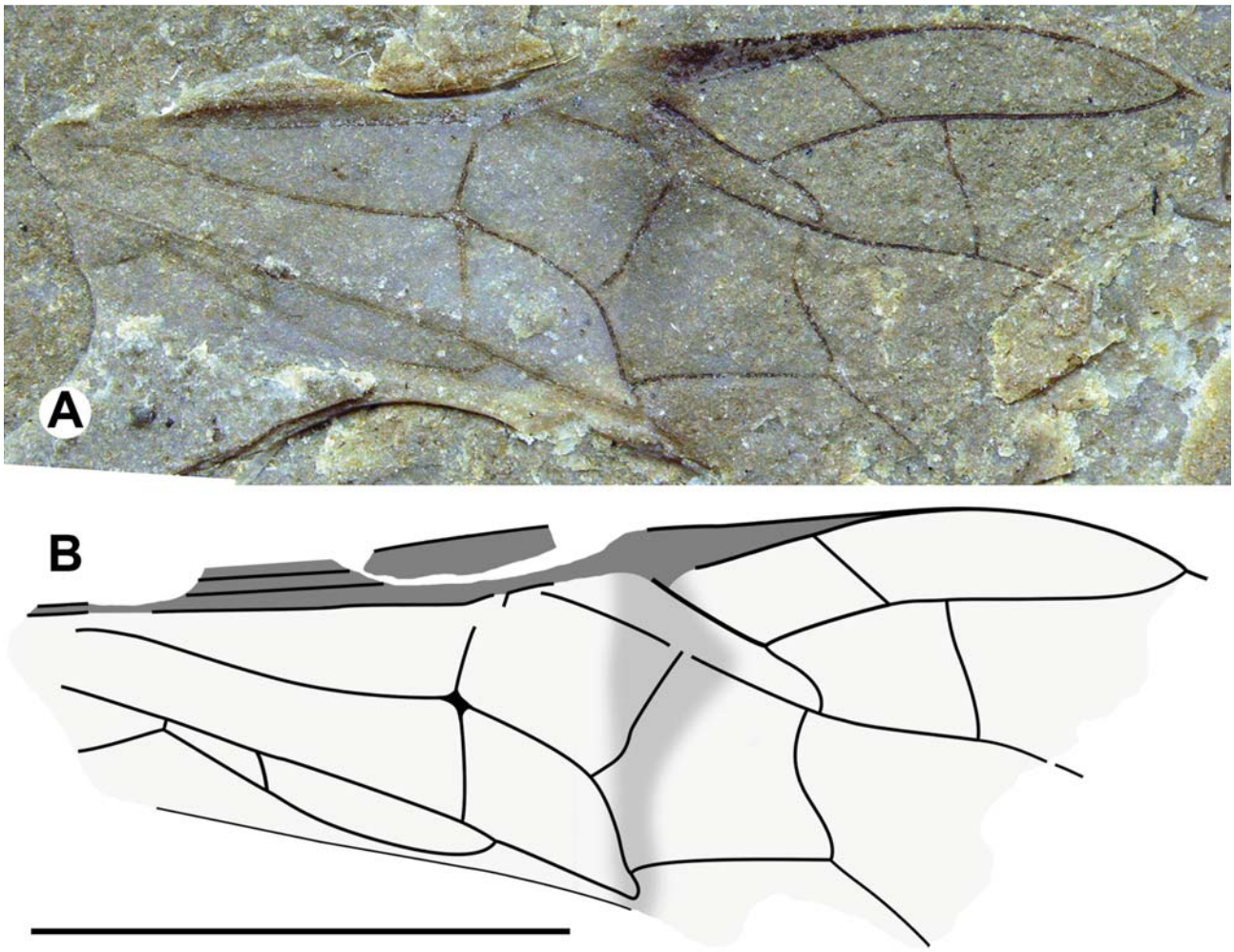


FIGURE 20. *Leptostigma fasciatum* holotype GSC 142843, forewing: A, photograph; B, drawing. Scale bar 5 mm.

***Leptostigma alaemacula* n. sp.**

http://zoobank.org/urn:lsid:zoobank.org:act:CB061CC9-BB17-4FED-B536-2A35796FCBBA

Fig. 21.

Holotype. SR 92-18-08 (Fig. 21). A forewing, collected by Carma Henry at Republic on September 25, 1992, in the collections of the SR.

Diagnosis. Distinguished from other species of *Leptostigma* by a combination of forewing dark in cell 1r+2rm. Tentatively diagnostic: R+M shorter than 1-M; 2r-rs joins cell 3rm distinctly near its middle; 2r-m joins M scarcely basal to 2m-cu; anal cells widely separated by fusion of 1A and 2A+3A, without crossvein.

Description. Holotype. Forewing length 14.2 mm, maximum width 4.1 mm, length/width 3.5; membrane lightly infuscate throughout except darker posterior to 1r-rs; pterostigma dark; R+M shorter than 1-M; maximum length of cell 2r shorter than 3r; 2r-rs shorter than Rs between 2r-m, 2r-rs, joining cell 3rm near its middle; 2r-m slightly curved, joins Rs notably basal to 2m-cu joining M, aligned with 2mcu; 1-M almost straight, sub-parallel to 1m-cu; 3r-m distinctly bowed toward base; cell 2mcu with M longer than 1m-cu; 2m-cu curved distinctly toward base; cu-a postfurcal; anal cells separated for distance greater than width of cell 2a, without crossvein between them.

Remarks. Differs from *L. brevilatum* **n. sp.**, *L. longiclava* **n. sp.**, *L. longipallidum* **n. sp.**, *L. longitenebricum* **n. sp.** by its forewing dark posterior to 1r-rs and 2r-m joins M close to 2m-cu. Differs from *L. proxivena* **n. sp.** and *L. fasciatum* **n. sp.** in which the anal cells are not separated by a fusion of 1A with 2A+3A.

Material. Holotype.

Etymology. From the Latin *ala*, meaning wing, and *macula*, spot, referring to the forewing spot. The epithet is a noun in apposition.

Locality and age. Republic, Washington, United States of America, Tom Thumb Tuff Member of the Klondike Mountain Formation exposure A0307; mid-Ypresian.

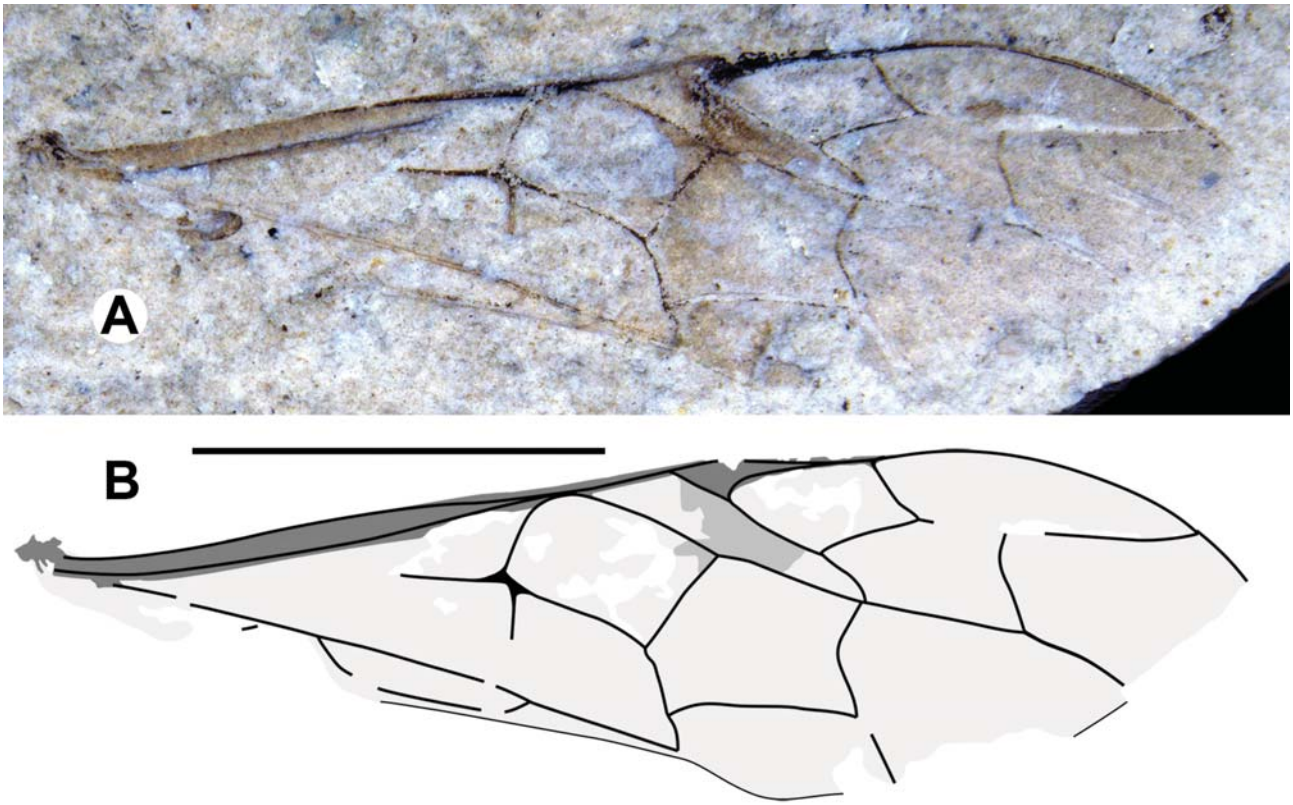


FIGURE 21. *Leptostigma alaemaculum* holotype SR 92-18-08, forewing: A, photograph; B, drawing. Scale bar 5 mm.

Cimbicidae subfamily *incertae sedis*

Genus and species *incertae sedis*

Fig. 22.

Description. Forewing (Fig. 22) length 15.5 mm, maximum width 5.4 mm, length/width 2.9; membrane lightly infuscate throughout, pterostigma dark, narrow, tapering, narrower than C-R before pterostigma; R+M shorter than 1-M; maximum length of cell 2r shorter than 3r (3r length about 1.6 2r); 2r-rs longer than Rs between 2r-m, 2r-rs, joining cell 3rm before its middle; 2r-m subvertical, short, slightly curved, joins Rs scarcely behind 2mcu; 1-M almost straight, sub-parallel to 1m-cu; 3r-m slightly angular toward base; cell 2mcu with M slightly shorter than 1m-cu; 2m-cu slightly curved toward base; cu-a postfurcal; anal cells meet at crossvein.

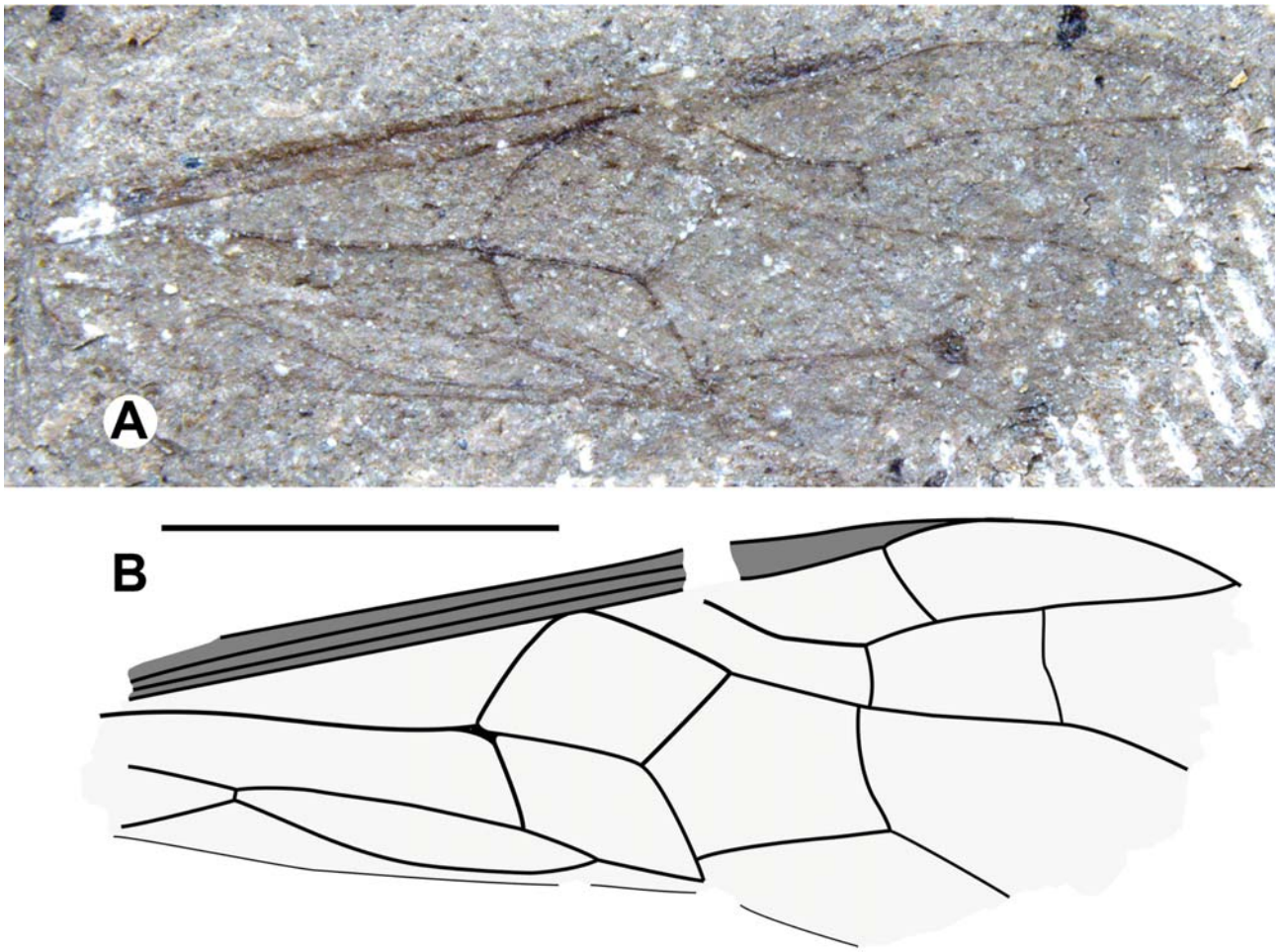


FIGURE 22. GSC 142844, Cimbicidae subfamily, genus, and species *incertae sedis*: A, photograph; B, drawing. Scale bar 5 mm.

Remarks. The straight, short 2r-m excludes this specimen from the Cenocimbicinae. Its other forewing venation is a mixture of character states diagnostic of modern subfamilies: M+Sc-R junction is close to that of Rs+M as in Pachylostictinae and Corynidinae, but the anal veins are separate throughout, joined by a short crossvein 1a as in the Cimbicinae. We refrain from assigning this specimen to a subfamily or erecting a new one based on it, or naming it pending more specimens to clarify its position. We only note that this forewing is very different not only from those of all other Ypresian Cimbicidae, but from all others. Unfortunately, the wings of the only other known Ypresian non-cenocimbicine, the Green River Formation *Eopachylosticta byrami* (Cockerell) are too poorly preserved to compare.

Material. GSC 142844, a forewing collected at McAbee by SBA (GSC locality V-016800), May 19, 2001 (Fig. 22), in the collections of the GSC (Vancouver).

Locality and age. McAbee, British Columbia, Canada, Hoodoo Face beds; mid-Ypresian.

Green River Formation

Subfamily Pachylostictinae Benson, 1938

Genus *Eopachylosticta* Malaise, 1945

Eopachylosticta Malaise, 1945, p. 14.

Type species. *Amasis byrami* Cockerell, 1925.

Emended diagnosis. Because of lack of sufficiently preserved wings and incompletely preserved body, the type and only fossil lacks many characters reliably used as diagnostic in Cimbicidae. However, generic distinction in Pachylostictinae is currently based in part on colour pattern (Vilhelmsen *et al.* 2019) which is available here, allowing at least a tentative genus diagnosis until better preserved fossils are found. The genus is distinct from others of Pachylostictinae by its dark head and thorax in contrast to its distinctly paler (somewhat infuscate) abdomen.

Remarks. *Eopachylosticta* belongs to the Pachylostictinae by a combination of its antennae with five segments and the median longitudinal mesonotal sulcus and notauli present and well developed (Vilhelmsen 2019).

Preservation of the type specimen of *Eopachylosticta byrami* suffers from the aggressive hydrochemistry of the Green River depositional environment. This is a common problem for fossil insects in parts of this formation, where the wings, legs and other body parts which were pale in life may become extremely faint or invisible as fossils. Therefore, our description and interpretation of this fossil is limited to distinguishing the genus from others of Pachylostictinae, setting aside more detailed analysis until better preserved material is available.

Species included. Type species only.

***Eopachylosticta byrami* (Cockerell, 1925)**
Fig. 23.

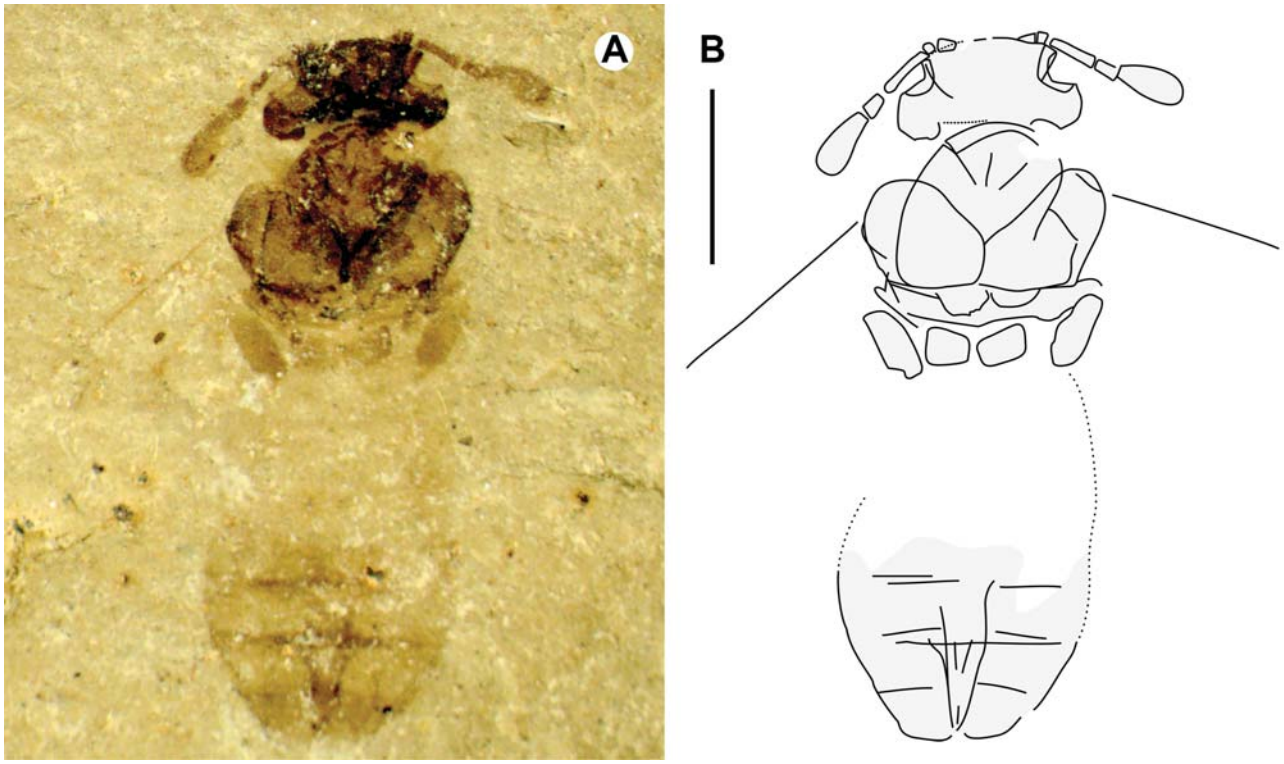


FIGURE 23. *Eopachylosticta byrami* (Cockerell) holotype, USNM-69181, Pachylostictinae, from the Green River Formation: A, photograph; B, drawing. Scale bar 5 mm.

Amasis byrami Cockerell, 1925, p. 10, plate 1, Fig. 4
Eopachylosticta byrami Malaise, 1945, p. 14.

Holotype. USNM 69181. A complete female with its body mostly well preserved, but almost no legs evident and poorly preserved wings with venation too faint to interpret. Green River Formation, about 8 miles south of De Beque, Colorado (Cockerell 1925), Ypresian.

Diagnosis. As for genus.

Description. Body length *ca*. 8.2 mm; head, antennae dark; thorax dark, hind femora somewhat infuscate (otherwise legs not visibly preserved, presumably pale), anterior abdomen light, posterior segments lightly infuscate. Head transverse, temples short; compound eyes not preserved; antenna five-segmented, with pedicel transverse, distinctly wider than flagellar base, flagellomere 1 thin, slightly widened apically, twice as long as

wide, trapezoid, flagellomere 2 wider, together about as long as thick, unsegmented club. Pronotum not distinct, mesonotum only partially visible, with median longitudinal mesonotal sulcus and notauli well developed, meeting well before presumed position of scutellum (poorly preserved); mesopleuron with percurrent mesopleural groove; otherwise, thoracic structure obscure. Hind femora short. Forewing almost entirely invisible as preserved. Abdomen short, wide; ovipositor short, not exceeding abdominal apex, sheaths not distinct.

Material. Holotype.

Locality and age. Green River Formation, about eight miles south of De Beque, Colorado (Cockerell 1925), Ypresian.

Florissant Formation

Subfamily Abiinae Ashmead, 1898a

***Genus Trichiosomites* Brues, 1908**

Fig. 24–25

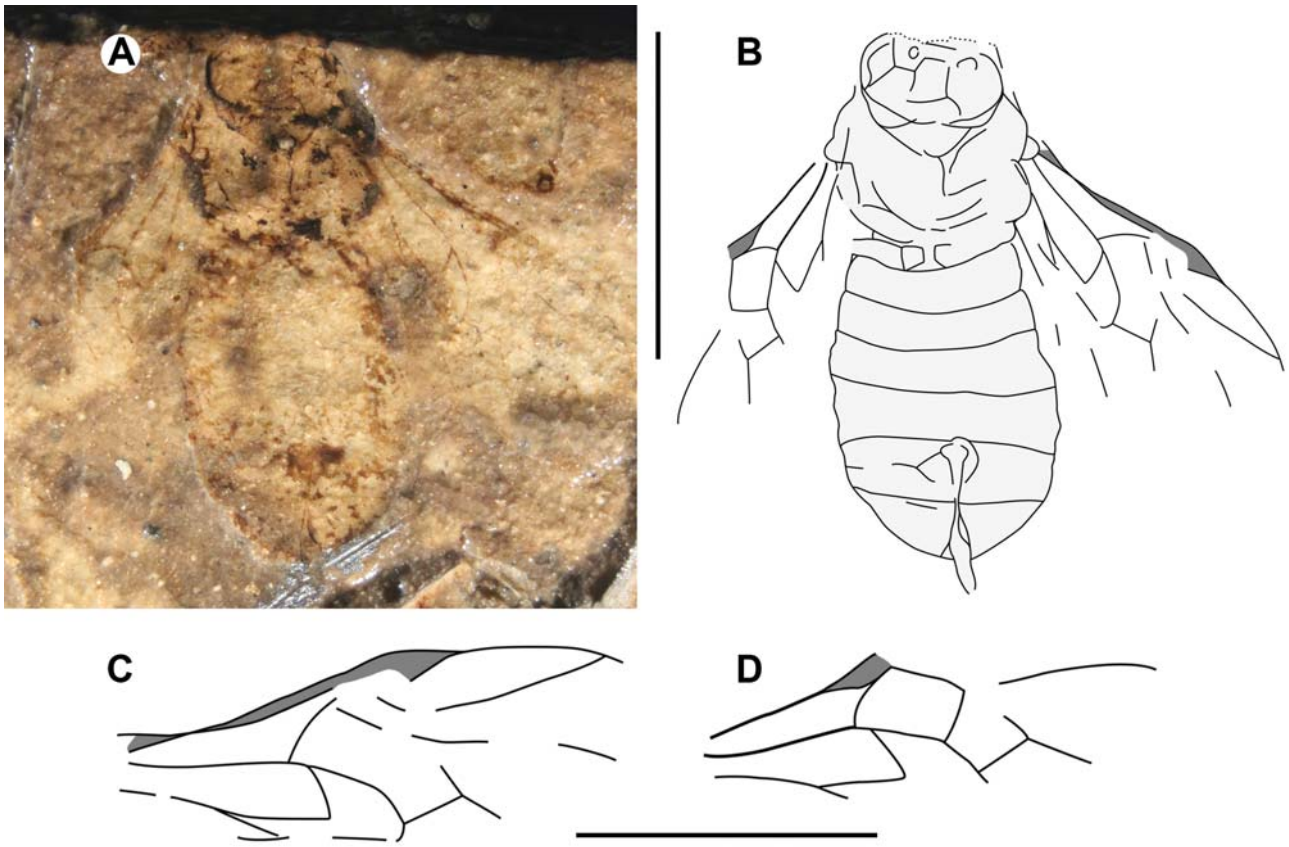


FIGURE 24. *Trichiosomites obliviosus* Brues holotype**,** MCZ-2036, Abiinae, from the Florissant Formation: A, photograph; B, drawing; C, drawing of right forewing; D, drawing of left forewing. Scale bars A–B, 5 mm; C–D, 3 mm.

Trichiosomites Brues, 1908, p. 259
Trichosomites: Abe & Smith, 1991, p. 87, misspelling

Type species. *Trichiosomites obliviosus* Brues, 1908.

Emended diagnosis. Distinct from other Abiinae by its very wide pterostigma and second flagellar segment forming the first part of the club.

Remarks. *Trichiosomites obliviosus* fits well with the Abiinae. Its distinctly segmented club excludes Corynidinae and Pachylostictinae, and widely separated anal cells exclude Cimbicinae. It is the oldest representative of the subfamily.

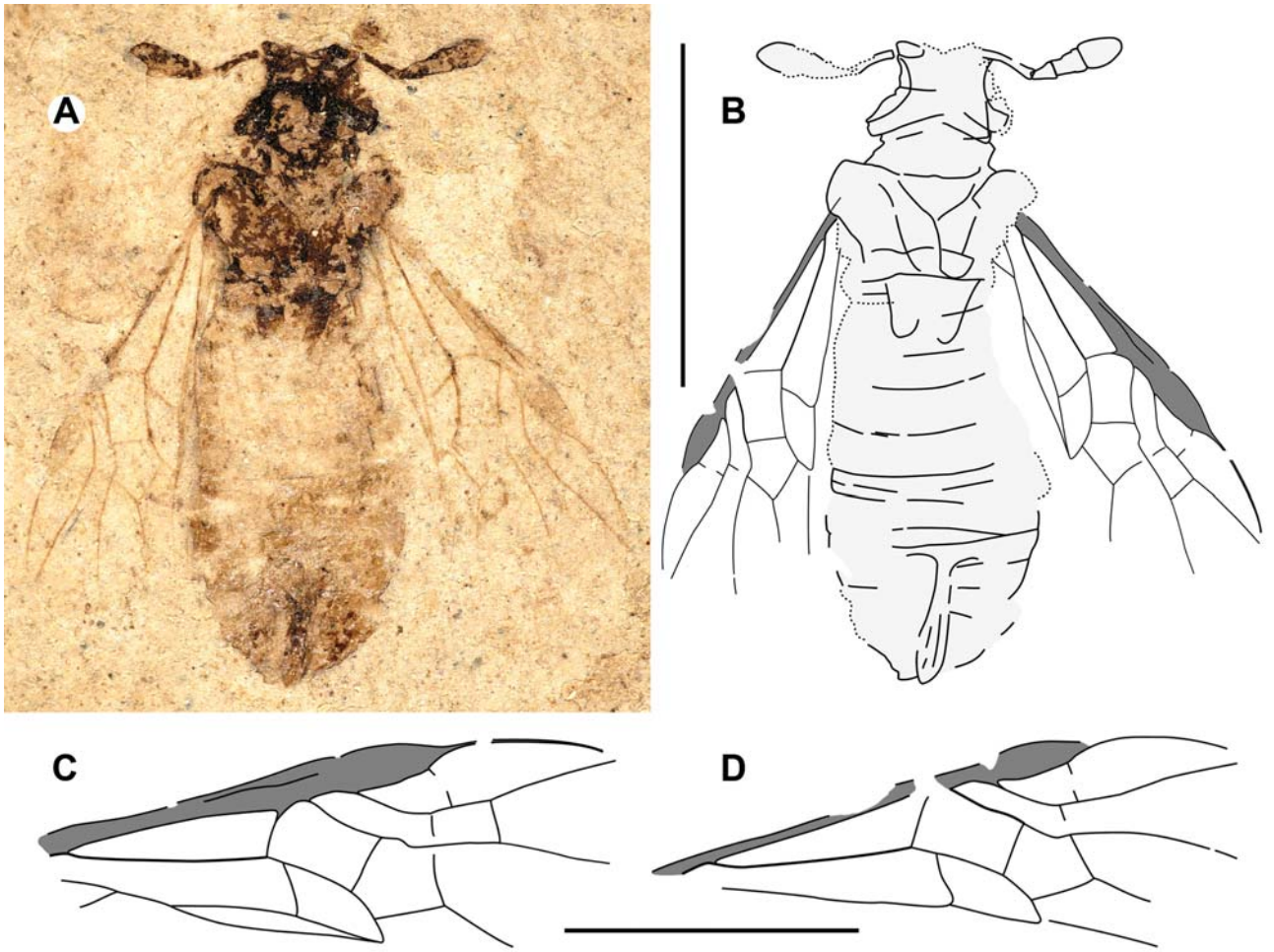


FIGURE 25. *Trichiosomites obliviosus* Brues, UCM-4570, Abiinae, from the Florissant Formation: A, photograph; B, drawing; C, drawing of right forewing; D, drawing of left forewing. Scale bars A–B, 5 mm; C–D, 3 mm.

Trichiosomites obliviosus Brues, 1908

Figs. 24–25.

Trichiosomites obliviosus Brues, 1908 p. 260, Fig. 1.

Holotype. Holotype MCZ 2036, Brues (1908). A rather complete female with head present, but positioned under thorax (not missing as Brues 1908 presumed).

Diagnosis. As for genus.

Description. Holotype MCZ 2036 (Fig. 24), female. Body: head length 0.5 mm or slightly more, width 0.87 mm; thorax length *ca*. 2.5 mm; abdomen length *ca*. 5 mm; body colouration unknown by preservation. Forewing: length *ca*. 6.0 mm, estimated maximum width *ca*. 2.0 mm, length/width: *ca*. 3.0. UCM 4570 (Fig. 25), female. Body: length *ca*. 9.2 mm; head, antenna dark; thorax dark, wings including pterostigma light; abdomen light. Head difficult to interpret as preserved; moderately transverse, occiput long, three distinct ocelli in low triangle, compound eyes not preserved, sole funicular segment thin, slightly more than half length of club; club expands gradually over three segments ("drop-like"). Thoracic dorsum only partially visible as preserved, median longitudinal mesonotal sulcus and notauli present; mesopleuron with no mesopleural sulcus visible. Forewing: membrane hyaline, length *ca*. 6.5 mm; maximum width estimated *ca*. 2.5 mm, length/width: *ca*. 2.6; pterostigma wide, *ca*. as cell 2r; R+M shorter than 1-M; maximum length of cell 2r shorter than 3r; 2r-rs longer than Rs between 2r-m, 2r-rs, joining Rs near middle of cell 3rm; 2r-rm straight, short, joins M at 2m-cu; 1-M curved; cell 1mcu with M, 1m-cu sub-parallel; 3r-m straight; cell 2mcu with M slightly longer than 1m-cu; 2m-cu straight; cu-a postfurcal; anal cell separated by

1A fusion with 2A+3A (no crossvein) for length of about a third length of cell 2a. Abdomen: long, wide; ovipositor thick, not exceeding abdomen apex.

Material. Holotype and UCM 4570, a rather complete specimen missing only the legs and much of the hind wings.

Locality and age. Florissant Formation, Priabonian.

Subfamily Cimbicinae Curtis, 1825

Genus Phenacoperga Cockerell, 1908

Fig. 26.

Perga: Cockerell, 1907, p. 446, original description of *P. coloradensis*/misidentifiation of genus.
Phenacoperga Cockerell, 1908, p. 113–114.

Type species. *Perga coloradensis* Cockerell, 1907.

Emended diagnosis. Apparently distinct from other genera of Cimbicinae by antennae short (length *ca*. 1.2 × head width), subclavate, flagellomere 2 only twice as long as wide; 1-M, 1m-cu strongly divergent toward anterior margin; crossvein 2r-m slightly bent.

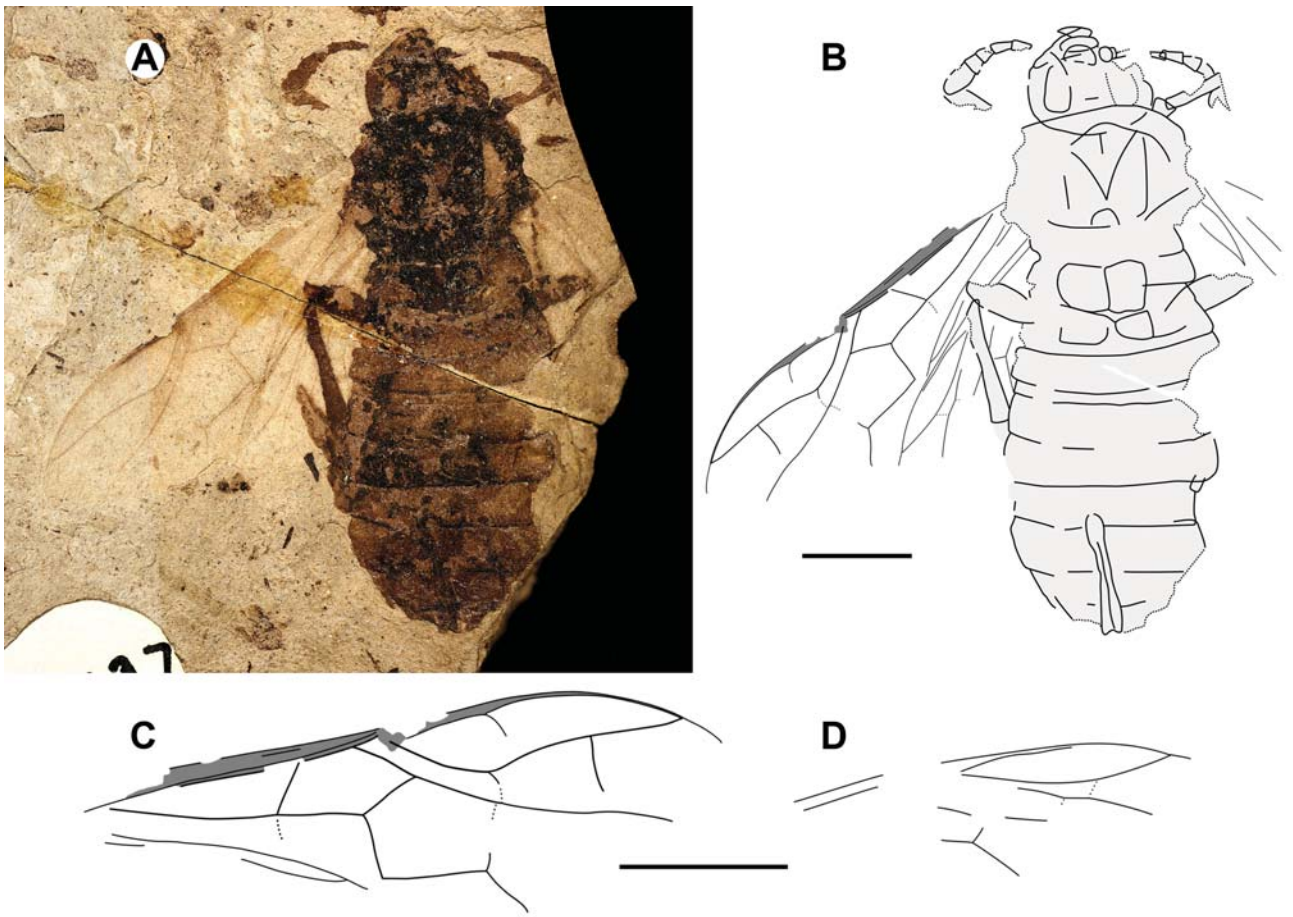


FIGURE 26. *Phenacoperga coloradensis* Cockerell holotype, UCM-4537, Cimbicinae, from the Florissant Formation: A, photograph; B, drawing; C, drawing of right forewing; D, drawing of left forewing. Scale bars A–B, 5 mm; C–D, 5 mm.

Remarks. The forewing venation of *Phenacoperga* agrees with Cimbicinae as its M+Sc-R junction is well separated from that of Rs+M, and the posterior anal vein 2+3A is complete, anal cells joined by crossvein 1a. In the key to Asiatic Cimbicidae of Wei *et al.* (2012), which includes all genera of Cimbicinae but *Labriocimbex* Yan & Wei, 2019, *Phenacoperga* keys to couplet 12 with *Pseudoclavellaria* Schulz, 1906 and *Leptocimbex* Semenov, 1896

but differs from both in its huge size, short and stout antennae and 1-M and 1m-cu strongly divergent toward anterior margin. *Phenacoperga* additionally differs from *Labriocimbex* and *Pseudoclavellaria* by its apparent absence of a rich vestiture, from *Pseudoclavellaria* by its ill-defined antennal club, and from *Leptocimbex* by its robust stature.

Phenacoperga coloradensis (Cockerell, 1907)

Fig. 26.

Perga coloradensis Cockerell, 1907, p. 446.
Phenacoperga coloradensis Cockerell, 1908, p. 113–114, new combination.

Holotype. UCM 4537 A rather complete female specimen missing most of the legs and the right wings. *"Perga" coloradensis* of Cockerell (1907) and see *Phenacoperga* of Cockerell (1908) and Rohwer (1908).

Diagnosis. As for genus.

Description. Holotype, female. Body: length *ca*. 27.7 mm; head, thorax, abdomen dark; antennae short, *ca*. 6.7 mm, 1.2 × head width (5.7 mm), dark, subclavate (very gradually widening apicad), with basal fragellomeres short (ratios of five apical segment lengths from base to apex, 1 : 1.1 : 0.8 : 0.7 : 1.7), apical one longer than two preapical combined; labrum large (*ca*. half as wide as separation of compound eyes); median longitudinal mesonotal sulcus, notauli present, well-developed. Forewing: membrane hyaline, length *ca*. 20.7 mm, maximum width estimated *ca*. 6.5 mm, length/width: *ca*. 3.3; pterostigma narrow, tapering, similar to width of C-R before pterostigma; R+M about same length as 1-M; maximum length of cell 2r shorter than 3r; 2r-rs longer than Rs between 2r-m, 2r-rs, joining Rs just basal to middle of cell 3rm; 2r-m nearly straight, short, joins M at 2m-cu; 1-M straight; cell 1mcu with M, 1m-cu divergent toward anterior margin; 3r-m straight; cell 2mcu with M longer than 1m-cu; 2m-cu apparently straight (faint); cu-a at branching of M, Cu; 2A complete, anal cells separated by crossvein 1a. Hind wing with m-cu much closer to 3r-m than to cu-a. Hind coxae small, apparently contiguous, hind femur and tibia thin. First abdominal tergum apparently not split medially, with hind margin rounded. Abdomen much wider than thorax, almost as long as forewing, ovipositor comparatively long (about one third as long as abdomen).

Locality and age. Florissant Formation, Priabonian.

Genus Floricimbex n. gen.

Fig. 27.

Cimbex: Cockerell, 1922, p. 50, placement of *C. vetusculus*.

Type species. *Cimbex vetusculus* (Cockerell, 1922).

Diagnosis. Distinct from all other genera of Cimbicinae by combination of much inflated hind male femur with mid and hind coxae touching basally.

Remarks. The genus is attributed to Cimbicinae based on wing venation: 1-M joins R distant from Rs+M, cell 2r plus the pterostigma is distinctly wider than cell 3r, and 2m-cu joins M far before 2r-m. Within Cimbicinae, the genus belongs to a group defined by Vilhelmsen (2019) to include *Cimbex* Olivier, 1791, *Labriocimbex*, *Odontocimbex* Malaise, 1934, and *Trichiosoma shojaense* Saini & Thind, 1992. This group is characterized in part by their elongate hind coxa and swollen male hind femur. However, unlike these and other large Cimbicinae (*Cimbex*, *Labriocimbex, Leptocimbex, Odontocimbex* and *Trichiosoma* Leach, 1817) its mid and hind coxae approach each other (coxae of these five genera are set distinctly distant leaving a considerable space along thorax midline). Additionally, the new genus differs from *Cimbex* by the posterior margin of its first abdominal tergum being straight, from *Odontocimbex* and *Trichiosoma* in having the hind femur apparently not toothed below (although not all of the lower margin of the hind femur is sufficiently visible), from *Labriocimbex* and *Leptocimbex* in much more swollen hind femur. These justify the generic level distinction of *Floricimbex*.

Etymology. From the Florissant locality and genus name *Cimbex*. The name is to be treated with masculine grammatical gender since it is derived from *Cimbex* (see Taeger *et al.* 2010: 188).

Species included. Type species only.

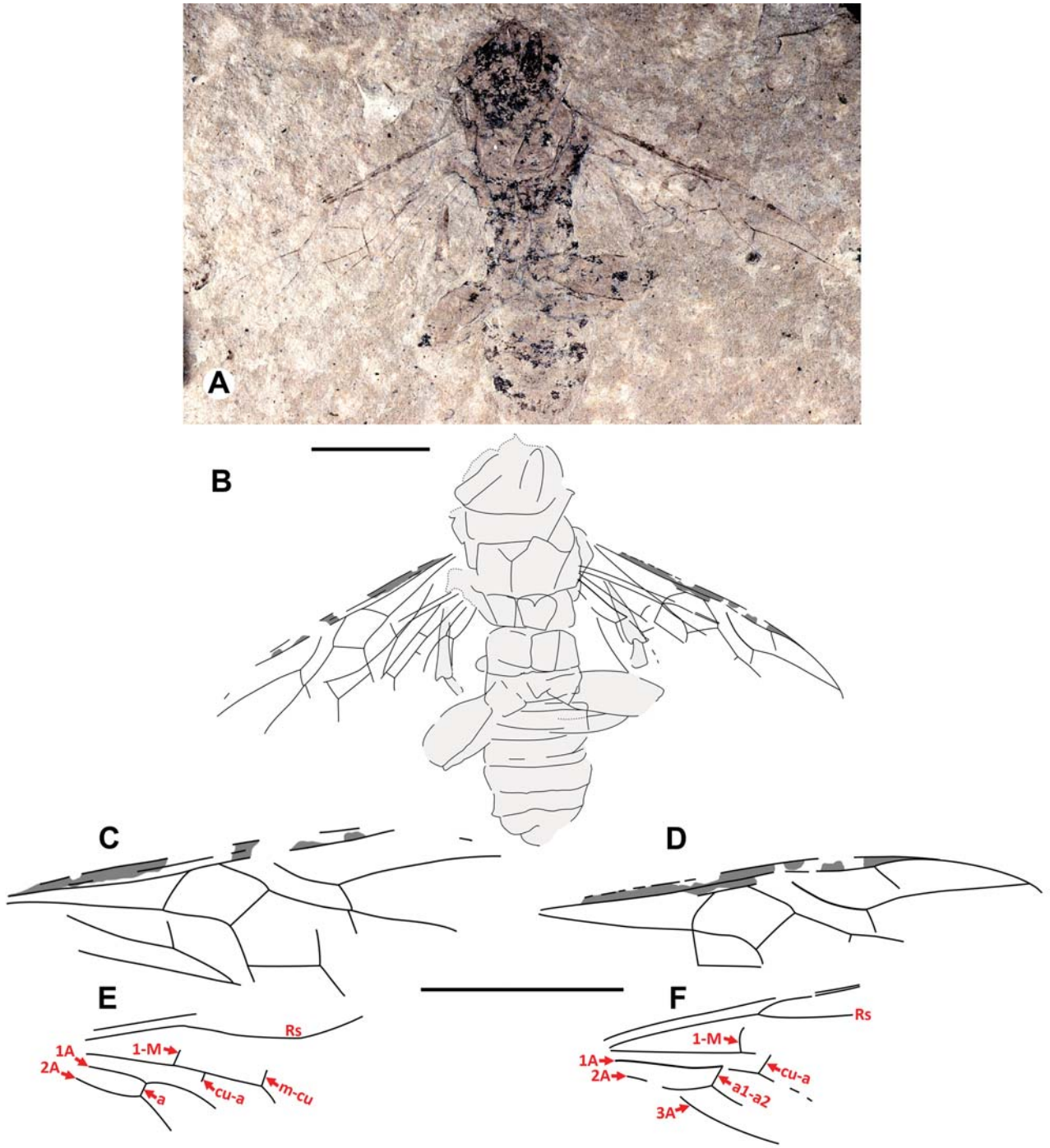


FIGURE 27. *Floricimbex vetusculus* (Cockerell) holotype, DMNH-163, Cimbicinae, from the Florissant Formation: A, photograph of the part (©DMNH); B, drawing from the part and counterpart; C, drawing of left forewing; D, drawing of right forewing; E, drawing of the left hind wing; F, drawing of the right hind wing. Scale bars A–B, 5 mm; C–F, 5 mm.

***Floricimbex vetusculus* (Cockerell, 1922)**

Fig. 27.

Cimbex vetusculus Cockerell, 1922, p. 50.

Holotype. DMNH-163A, B, type specimen, Cockerell (1922). Part, a rather complete specimen; counterpart, missing the right wings and head.

Diagnosis. As for genus.

Description. Holotype, male. Body: length 16.7 mm as preserved, colour pattern possibly mostly dark (organic matter mostly lost, obscuring colouration). No rough surface sculpture discernible. Structure of head and thorax obscure. Mid, hind coxae touching basally, slightly separated distally, hind coxae large, elongate, more or less parallel-sided, no distinct armament visible; hind femur almost regularly elliptical, 4.4 mm long, 1.9 mm wide (length to abdominal segment width *ca*. 1:2.3), other leg segments incomplete. Wings damaged, incompletely known. Forewing length 13.9 mm, maximum width 4.4 mm or slightly more, length/width > 3.1; membrane possibly lightly infuscate behind R+M; pterostigma dark; R+M shorter than 1-M; maximum length of cell 2r shorter than 3r; 2r-rs slightly longer than Rs between 2r-m, 2r-rs, joining cell 3rm slightly before its middle; 2r-m straight, joins Rs distal to 2m-cu joining M, well distal 2mcu; 1-M almost straight, sub-parallel to 1m-cu; 3r-m incompletely preserved, its form obscure; cell 2mcu with M apparently subequal to 1m-cu; 2m-cu incompletely preserved, apparently slightly curved toward base; cu-a interstitial; anal cells not preserved. Hind wing with M base basal to level of Rs base, m-cu present, cu-a before middle of cell mcu, a1-a2 basal to level of Rs base, Cu with distinct free apex, 1A and 2A with long free apex. Abdomen narrow, slightly widening caudally (widest at segments 5–6), tergum 1 with straight hind margin, genitalia not distinct.

Material. Holotype.

Locality and age. Florissant Formation, Priabonian.

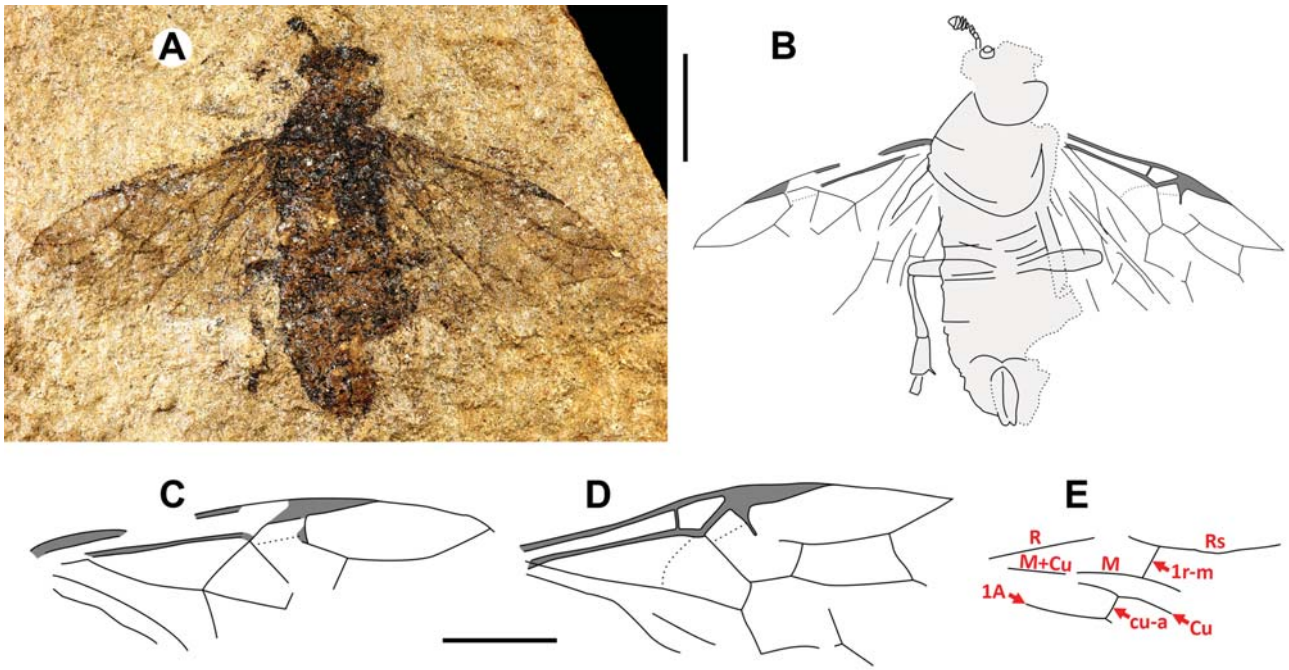


FIGURE 28. *Pseudocimbex clavatus* Rohwer holotype, UCM-18614, Tenthredinoidea *incertae sedis*, from the Florissant Formation: A, photograph; B, drawing; C, drawing of right forewing; D, drawing of left forewing; E, drawing of left hind wing. Scale bars A–B, 5 mm; C–D, 3 mm.

Tenthredinoidea *incertae sedis*

Genus *Pseudocimbex* Rohwer, 1908

Fig. 28.

Pseudocimbex Rohwer, 1908, p. 526.

Type species: *Pseudocimbex clavatus* Rohwer, 1908, by original designation.

Diagnosis. Distinct from all other Symphyta by hind wing with M+Cu branching to M, Cu unusually basally; M and Cu at a low angle to M+Cu, almost aligned with it; cell mcu long, narrow, wedge-shaped; cu-a present, vertical.

Also distinct from all other Symphyta by comparatively short antenna (about as long as half head width) with subspherical club consisting of several very short segments. Additionally distinct from Cimbicidae by lack of 2r-rs; by its wide costal space; and by presence of vein Sc.

Remarks. 2r-rs is not detected in the forewing in some cimbicid specimens described here, presumably by preservation. It is, however, confidently absent in both forewings of *Pseudocimbex* examined dry and wetted with ethanol (Fig. 28). The very short antenna does occur in various Pergidae, however, there it is combined with an elongate and non-segmented club. In comparison with extant species, a placement of this fossil in either Cimbicidae or Pergidae remains ambiguous.

Species included. Type species only.

Pseudocimbex clavatus Rohwer, 1908

Fig. 28.

Pseudocimbex clavatus Rohwer, 1908, p. 527, Fig. 1a, e.

Holotype. UCM 18614, Rohwer (1908). An almost complete specimen missing most of the legs, one antenna.

Diagnosis. As for genus.

Description. Holotype, female. Body: length 17.6 mm as preserved; head, thorax darker than abdomen. Surface sculpture not discernible. Structure of head, thorax obscure. Antenna very short (flagellum 1.8 mm long, less than half head width), capitate, apparently 11-segmented, scape and pedicel very short, with funicle of four segments gradually shortening distally from twice as long as wide up to strongly transverse and almost round club of possibly five segments, four very short and apical one longer. Hind tibia 4.6 mm long, other leg segments incompletely or not preserved. Forewing length 12.9 mm, maximum width 5.5 mm, length/width 2.4; membrane lightly infuscate, more so toward base; pterostigma dark, narrow, short, wedge-shaped; C, R basal to pterostigma thin, widely separated, slightly more so distally, with crossvein-like Sc between; pterostigma small, wedge-shaped; 1-M at or very close to Rs+M on R; 1r-rs short, 2r-rs lost; Rs+M very short; 2-Rs (separating cells 1r and 2rm) possibly detected (as dotted line in Fig. 28); Rs distal of 1r smoothly curved, meeting R_1 at wing margin; 2r-rs absent; 2r-m, 3r-m present, well spaced, straight, near 0.4 and 0.7 length of cell 3r; M notably angled at 1m-cu; 1m-cu short, just more than half length of 1-M, diverging with 1-M toward anterior margin, 1m-cu and 2m-cu join cells 2rm and 3rm, respectively; 1m-cu converging to 1-M forward; 2m-cu slightly curved toward base; cu-a interstitial; anal cells incompletely preserved: cell 1a apparently open posteriorly, distally (2+3A not reaching a1-a2 crossveins), cell 2a closed basally, not preserved distally (distal portion of 2+3A obscured by fore margin of hind wing). Hind wing partially known, with unusual venation; uniformly infuscate as forewing; 1r-m about its length distant from Rs base; with Rs, M+Cu, M, Cu, cu-a and 1A detected, M+Cu forking far basally of RS base, with fork narrow, M and Cu both almost aligned with M+Cu; cu-a slightly reclival, long, placed slightly basal of Rs base; 2r-m, m-cu not evident; 1A evident, with at least short free end preserved. Abdomen moderately narrow, with few details discernible; ovipositor short (length 0.65 mm), barely exceeding abdomen apex.

Material. Holotype.

Locality and age. Florissant Formation, Priabonian.

Cenocimbicinae and the history of Cimbicidae

The Cimbicidae first appears in the fossil record with one fossil of the extinct subfamily Cenocimbicinae in the Selandian, which is dominant and diverse in the Ypresian and disappears after. A single specimen of the extant Pachylostictinae is known in the Ypresian. A small assemblage of the extant subfamilies Abiinae and Cimbicinae appears in the late Priabonian, the family is unknown the Oligocene, and then it reappears in the Miocene showing the modern pattern of dominance by the Cimbicinae and Abiinae (Table 1).

The family might have originated in the Paleocene, but this might also simply reflect the paucity of Paleocene and Late Cretaceous shale insect localities. They—and Symphyta in general—are almost entirely absent in amber for an unknown reason. Their rich record in the Okanagan Highlands could be an artefact of unknown taphonomic factors favouring their preservation there.

TABLE 1. Fossil record of Cimbicidae with selected references.

Paleogene	
Paleocene	
Selandian	
Menat Formation, France	
Cenocimbicinae	
Cenocimbex menatensis Nel, 2004	Nel (2004)
Eocene	
Ypresian	
Okanagan Highlands, Canada and USA	
Cenocimbicinae	
Allenbycimbex morrisae **n. gen.** and **sp.**	herein
Leptostigma alaemacula **n. gen.** and **sp.**	herein
Leptostigma brevilatum **n. gen.** and **sp.**	herein
Leptostigma fasciatum **n. gen.** and **sp.**	herein
Leptostigma longiclava **n. gen.** and **sp.**	herein
Leptostigma longipallidum **n. gen.** and **sp.**	herein
Leptostigma longitenebricum **n. gen.** and **sp.**	herein
Leptostigma proxivena **n. gen.** and **sp.**	herein
Subfamily *incertae sedis*	
Genus and species *incertae sedis*	herein
Green River Formation, Colorado, USA	
Pachylostictinae	
Eopachylosticta byrami (Cockerell, 1925)	Cockerell (1925), Malaise (1945)
Priabonian	
Florissant Formation, United States of America	
Abiinae	
Trichiosomites obliviosus Brues, 1908	Brues (1908)
Cimbicinae	
Floricimbex vetusculus (Cockerell, 1922)	Cockerell (1922)
Phenacoperga coloradensis (Cockerell, 1907)	Cockerell (1907, 1908), Rohwer (1908)
Baltic amber, Russia	
Subfamily *incertae sedis*	
Cimbex sp. (larva)	Menge (1856), Handlirsch (1907), APR pers. obs.
Neogene	
Miocene	
Aquitanian/Burdigalian	
Masaragawa Formation, Japan	
Cimbicinae	
?*Cimbex* sp.	Fujiyama (1985)
Burdigalian/Langhian	
Shanwang Formation, China	
Cimbicinae	
*Cimbex chromoptera** Zhang, 1989	Zhang (1989)
Pseudoclavellaria autochthona (Zhang)	Zhang (1989), Taeger *et al.* (2010)
Pseudoclavellaria bicolor Zhang, 1989	Zhang (1989)

.....continued on the next page

TABLE 1. (Continued)

Cimbicinae	
Pseudoclavellaria longiclava (Zhang, 1989)	Zhang (1989), Taeger *et al.* (2010)
Sinocimbex pellucidus Zhang *et al.*, 1994	Zhang *et al.* (1994)
Sinocimbex silaceus Zhang *et al.*, 1994	Zhang *et al.* (1994)
Cimbicinae?	
Abia cf. *lonicerae* Linnaeus, 1758	Zhang *et al.* (1994)
Pseudoclavellaria molpa (Zhang *et al.*, 1994)	Zhang *et al.* (1994), Taeger *et al.* (2010)
Abiinae	
Abia maculosa Zhang, 1989	Zhang (1989)
Abia paurocephala Zhang, 1989	Zhang (1989)
Abia shandongensis (Hong & Wang, 1985)	Hong & Wang (1985), Taeger *et al.* (2010)
Abia shanwangensis (Hong, 1984)	Hong (1984), Taeger *et al.* (2010)
Tortonian	
Andance, Ardèche, France	
Cimbicinae	
Cimbex? *miocenica* Riou, 1992	Riou (1992), Nel (2004)
Cimbex? *turoliana* Riou, 1992	Riou (1992), Nel (2004)
Pliocene	
Piacenzian	
Willershausen/western Harz Mountains, Germany	
Abiinae	
Abia (as *Zarea*) sp.	Steinbach (1967)

*Misspelled *chromptera* by Taeger *et al.* (2010, #2263)

Alternatively, this record might closely reflect their actual history (see Archibald *et al.* 2018). Cimbicidae feed on the leaves of angiosperms: Abiinae and Cimbicinae on Betulaceae, Caprifoliaceae, Dipsacaceae, Rosaceae, and Salicaceae; and the Corynidinae on Crassulaceae, Geraniaceae and Papaveraceae (the hosts of Pachylostictinae are little known) (summarized by Vilhelmsen 2019, see references therein). All of these are present in the Okanagan Highlands except the Dipsacaceae and Geraniaceae, and many genera of these families that are important today first appear there (*e.g.*, Crane & Stockey 1987, Wolfe & Wehr 1987; Wehr & Hopkins 1994; Greenwood *et al.* 2005; Moss *et al.* 2005; Devore & Pigg 2007, 2010; Mathewes *et al.* 2016; Pigg & Devore 2016). The temperate montane Okanagan Highlands had a high diversity of insects and plants (woody dicots analysed) associated with climatic factors (Archibald *et al.* 2010), and may have been the setting for the origin of modern microthermal northern forests that the great majority of extant Cimbicidae prefer which later spread downslope into lowlands in the globally cooler Neogene (Graham 2011).

The only fossil Pachylostictinae known is from the Ypresian megathermal lowland Green River Formation. The Priabonian record of the Cimbicidae (excluding the single Baltic amber larva) is at Florissant, another upper microthermal montane forest, where only modern subfamilies are present. Such montane forest communities are rare in the insect fossil record, which might further bias our knowledge of the history of the family.

The limited morphological information available in known fossils indicates that the Cenocimbicinae forms a clade with the Cimbicinae and Abiinae based on at least two synapomorphies of the forewing: 1, cell 2r together with the pterostigma is distinctly higher than cell 3r (Corynidinae and Pachylostictinae: at most as high as 3r), and 2, crossvein 2r-m joins M distal of 2m-cu (basal in Corynidinae and Pachylostictinae). The strongly bent crossvein 2r-m of Cenocimbicinae separates it from the Cimbicinae+Abiinae, where it is straight or gently curved (we treat rare occurrences of a similar 2r-m in Cimbicinae and Abiinae as convergent).

This implies an unknown presence of Corynidinae and Pachylostictinae at least to the Selandian, and of Cimbicidae originating earlier in the Paleocene or perhaps the Late Cretaceous.

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