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Diptera of the middle Eocene Kishenehn Formation. I. Documentation of diversity at the family level

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ABSTRACT

The Coal Creek Member of the Kishenehn Formation in northwestern Montana, USA, is an emerging middle Eocene Lagerstätte. While fish, plant, mammal and molluscan fossils are present, the most numerous and well-preserved fossils are those of insects. In this study, we initiate an effort to enumerate, at the family level, the diversity of flies (Insecta: Diptera) at this locality. Seventeen specimens from 17 different families (15 families with Limoniinae and Cylindrotominae within Tipulidae s.l.), 15 new species and three new genera are described. These include *Tipula fji* sp. nov. (Tipulidae), *Ellipteroides kishenehn* sp. nov. (Limoniidae), *Cyttaromyia lynnae* sp. nov. (Cylindrotomidae), *Sylvicola silibrarius* sp. nov. (Anisopodidae), *Efcookella nigra* sp. nov. (first fossil known in the genus) (Scatopsidae), *Bibiodes kishenehnensis* sp. nov. (Bibionidae), *Eosciarites hermes* gen. et sp. nov. (Sciaridae), *Rymosia hypnolithica* sp. nov. (Mycetophilidae), *Litoleptis araeostylus* sp. nov. (Rhagionidae), *Kishenehnoasilus bhl* gen. et sp. nov. (Asilidae), *Drapetis adelomedos* sp. nov. (Hybotidae), *Salishomyia eocenica* gen. et sp. nov. (Dolichopodidae), *Agathomyia eocenica* sp. nov. (first known fossil in genus) (Platypezidae), *Lonchoptera eocenica* sp. nov. (Lonchopteridae) and *Aenigmatias kishenehnensis* sp. nov. (Phoridae). Two specimens in the families Psychodidae and Pipunculidae are described but not assigned to a genus. In addition, we revise several related fossil species housed at the NMNH. *Asilopsis fusculus* Cockerell, 1921, formerly described in Asilidae, is transferred to *Cyttaromyia* (Cylindrotomidae) as *C. fuscula*, *Sciara florissantensis* Cockerell, 1917 is assigned to Sciaroidea incertae sedis, and *Sciara gurnetensis* Cockerell, 1916, *Sciara lacoei* Cockerell, 1915 and *Sciara protoberidis* Cockerell, 1915, are assigned to Sciaridae incertae sedis. Given their diversity and high degree of preservation, continued characterization of the Coal Creek Member fossils may help elucidate the Eocene radiation of Diptera in North America.

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INTRODUCTION

Diptera constitute one of the largest and most diverse groups of organisms on Earth. The order appears to have originated in the Permian, based both on molecular divergence studies (Wiegmann et al., 2011; Misof et al., 2014) and the existence of eight dipteran families in the 223–235 Ma Cow Branch Formation in Virginia (Blagoderov et al., 2007). The clade Schizophora, which includes the majority of dipteran families, is relatively recent, having undergone extensive and rapid radiations between the early Paleocene and the middle Eocene (Wiegmann et al., 2011). Despite their modern diversity, including about one-third of all extant dipteran species, Schizophora have a relatively poor fossil record. Evenhuis (2017) indicated that approximately 64% of all fossil species (45.6% of genera) were “Nematocera” or lower Diptera, and only 17% of all described fossil species (about 28.5% of genera) were schizophorans. Less than 1% of fossil species (2.25% of genera) belonged to the younger Calyptratae. Given these numbers, the discovery and proper description of new fossil flies is always relevant, but fossil discoveries documenting higher dipterans would be of critical importance for understanding the recent history of the order.

The middle Eocene Coal Creek Member of the Kishenehn Formation in northwestern Montana, USA, is an emerging Conservat Lagerstätte. Fossil insects from this site display a high degree of preservation of both morphological detail and original biomolecular components (Greenwalt et al., 2013, 2016). Taphonomic processes have produced a unique entomofauna, with a strong size bias against large specimens; fossil insects 1 cm or longer in length are rare and, with the exception of isolated wings, invariably poorly preserved. On the other hand, very small insects (e.g., ptiliid beetles and mymarid wasps) that are rarely found as compression fossils in other Lagerstätten, are frequently preserved in the Kishenehn Formation’s oil shales (Huber and Greenwalt, 2011; Shockley and Greenwalt, 2013; Greenwalt et al., 2015a). As a result, the Coal Creek Member entomofauna provides insights into insect diversity that are not available from other major North American Lagerstätten.

Although detailed studies of several individual families of Coal Creek Member insects have been published, documentation of the overall diversity of the entomofauna is more important and the goal of the current study. While there are at least 17 insect orders represented in the Coal Creek Member (Greenwalt et al., 2015a), enumeration of the total number of families has not been attempted. The current study of the families of the order Diptera is an initial effort towards this goal. Since documentation of diversity at the family level, vs. descriptions of new species per se, is the purpose of this study, new species descriptions are purposefully limited to one for each family. In some instances, families are represented by specimens not identified to genus level. A total of 17 dipteran families are identified herein; combined with those already published (Dixidae, Culicidae, Bolitophilidae and Bombyliidae), the total diversity of the Coal Creek Diptera, at the family level, currently numbers 21. This number will increase as the Kishenehn Formation specimens continue to be characterized. In addition to the description of these new specimens, we revise several fossil species in relevant families from similar geological ages in North America that are housed at the NMNH.

MATERIALS AND METHODS

Specimens described herein were collected from the Kishenehn Formation, exposed along the Middle Fork of the Flathead River in northwestern Montana, USA, between 2009 and 2016 in accordance with USFS Authorization HUN281. Exposures there are from the middle sequence of the Coal Creek Member, which have been estimated to be 46.2±0.4 Ma by ^{40}Ar/^{39}Ar analysis and 43.5±4.9 Ma by fission-track analysis (Constenius, 1996). Specimens were photographed with an Olympus SZX12 microscope equipped with a Q-Color5 Olympus camera. Image-Pro Plus 7.0 software (Media Cybernetics, Inc., Bethesda, MD) was used to capture and record the images. Kishenehn Formation fossils were immersed in 95% ethanol for examination and photography. Measurements were made with the Image-Pro Plus 7.0 software. A thin plate spline analysis was performed to show the direction of the changes from fossil to modern wing veination (for *Lonchoptera eocenica*). Comparison to a modern species was made by landmarking photographs using the program TPS-Dig. Landmarks were transformed using Procrustes analysis as implemented in PAST 3.22 (Hammer et al., 2001), and a comparative thin plate spline generated in the same program.

Venational terminology is from Cumming and Wood (2017). Although recent evidence (e.g., Ribeiro, 2008; Petersen et al., 2010; Zhang et al., 2016) suggests that Limoniidae is paraphyletic, this group is treated as a family herein. The holotypes of *Asilopsis fuscula* Cockerell, 1921 (USNM 66572), *Rhagio fossitus* Melander, 1949 (USNM 112626), *Sciara florissantensis* Cockerell, 1917 (Cockerell 1917a) (USNM 61995), *S. gurnetensis* Cockerell, 1915 (USNM 61435), *S. locoei* Cockerell, 1915 (USNM 61436) and *S. protoberidis* Cockerell, 1915 (USNM 61437) are housed at the NMNH, in Washington, D.C. Numbers of extant genera and species/family were taken from Pape et al. (2011). The number of fossil species for each individual family was obtained from the Paleobiology database. Institution acronyms and abreviations used herein are PBDB (Paleobiology Database), FDB (Florissant National Monument Fossil Database), EDNA (EDNA Fossil Insect Database), EOL (Encyclopedia of Life), NMNH (National Museum of Natural History), USNM (United States National Museum = NMNH depository), and LACM (Los Angeles County Museum).

Although specimens of modern, extant insect species have been reported in some older papers on Mexican and Baltic amber (Doutt, 1973; Masner, 1969; Mockford, 1972; Rozen, 1971), the assumed timespan of insect species has been estimated to be 3–10 My (Grimaldi and Engel, 2005). We have therefore limited comparisons of new species described herein to fossils of the Eocene Epoch.

Database Searches

The number of dipteran families from major Eocene localities was obtained from online digital databases and, for the Okanagan/Republic locality, a review of the literature. Given their universal value and huge potential, especially with the advent of database-based research, it is very disappointing that all on-line digital databases, including the PBDB (PBDB, 2018), FDB (Meyer, 2002), EDNA (EDNA, 2017), Bishop Museum Fossil Diptera Catalog (Evenhuis, 2017) and Systema Dipterorum (Pape and Thompson, 2013), are woefully underfunded. As a result, some databases are more up-to-date than others and different databases occasionally provide different results. The material that follows is not meant to be a criticism of the digital databases but rather straightforward documentation of the status of specific records.

The EDNA database was searched for Green River Formation dipteran families, with the parameters "Order equals Diptera", "Country equals U.S.A." and "Era equals Cenozoic" ("Period equals Paleogene" yields a null set) and yielded 442 records. Searches of "Formation contains Green", "Site: [any field] contains Green" and "Reference: Title contains Green" in place of "Country equals U.S.A." yielded 4, 28 and 10 records respectively. Obvious undesired locations (e.g., the Barstow, Kishenehn and Florissant Formations) as well as all junior synonyms were deleted from the 442 records to provide 155 records overall. Numerous records were assigned to local sites (e.g., Twin Creek, East Alkali Gulch, Little Duck Creek, Little Tommies Draw) that belonged to the Green River but were not originally recorded as such. Evidently, this is due to data entry based solely on the original publication; this also results in the geological age of Green River Formation specimens being listed as both Eocene and Oligocene. Most records of senior synonyms were entered without the Green River locality designation that accompanied the original junior synonym. The majority of the 155 records were listed solely as originating in the U.S.A. or, in some cases, a particular state (Colorado, Utah and Wyoming). Queries of the literature for more than 90 of these latter records eliminated many entries, nearly all of which were from the Florissant but not designated as such in the database. Corrections included transfer of *Anthomyia winchesteri* Cockerell, 1921 (Cockerell 1921a), from Anthomyiidae Robineau-Desvoidy, 1830, to unplaced Brachycera (Michelsen, 1996), *Culex proavitus* Scudder, 1877 from Culicidae Meigen, 1818, to Psychodidae Newman, 1834 (Edwards, 1923), and *Heteromyza detecta* Scudder, 1877, from Palaeopleciidae Rohdendorf, 1962 to Heleomyzidae Bezzi, 1911 (Evenhuis, 2017). *Rhingia zephyrea* Hull, 1945, is listed as a junior synonym of *Geron oligocaenica* Timon-David, 1944; however, Evenhuis (1994) transferred *Phthiria oligocenica* Timon-David, 1944, to the genus *Geron* Meigen, 1820 as *G. oligocaenica* within Bombyliidae. Nel (2006) considered the specimen to be Bombyliidae Latreille, 1802, subfamily and genus undetermined. In addition, *Rhingia zephyrea* was collected by Hull (1945) from the Florissant.

Corrections to the EDNA database relative to Baltic amber Diptera are as follows: Sciadoceridae, as the subfamily Sciadocerinae Schmitz, 1929, is currently placed in Phoridae Curtis, 1833 (Brown, 2007). Although often used during most of the twentieth century, Leptidae is an invalid synonym for Rhagionidae (Kertész, 1908; Malloch, 1931). Species of Palaeopleciidae are now included in the extinct family Protopleciidae Rohdendorf, 1946 (Blagoderov, 1996). Rachiceridae, as the subfamily Rachicerinae Curran, 1934, is placed in Xylophagidae (Clapham, 2016).

In the Florissant Fossil Database, the single species of Xylophagidae Fallén, 1810, *Dialysis revelata* Cockerell, 1908, was originally described in the family Leptidae (invalid family name; = Rhagionidae Latreille, 1802) and is listed in Systema Dipterorum in Xylophagidae. However, Melander (1949) placed *D. revelata* in Rhagionidae. The genus *Dialysis* Walker, 1850, was revised by Webb (1978). *Melieria atavina* Cockerell, 1917 (Cockerell 1917b), and *M. calligrapha* Melander, 1949, were originally placed in the family Otitidae Aldrich, 1932 and these two are the sole species ascribed to Otitidae in the FDB. However, Gentilini et al. (2006) have transferred both species to Ulidiidae Macquart 1835 (see Kameneva and Korneyev, 2006 for Otitidae as a junior synonym of Ulidiidae). The FDB lists five species in the family Anthomyiidae: *Mecistoneuron perpetuum* Melander, 1949, and *Ophyra vetusta* Melander, 1949, *Anthomyia atavella* Cockerell, 1913, *A. persepulta* Cockerell, 1917 (Cockerell 1917b) and *A. laminarum* Cockerell, 1917 (Cockerell 1917c). Evenhuis (1994) reassigned *O. vetusta* to Muscidae Latreille, 1802 and Michelsen (1996) reassigned *M. perpetuum* to Platypezidae Latreille, 1802. Michelsen (1996) designated all eleven compression fossils of the genus *Anthomyia* available at that time as *nomina dubia*.

A Note on Taxonomic Paleoentomology

The uncertain and often invalid status of many generic assignments of fossil insects is, if not fully appreciated, well known. Many such assignments were made in the nineteenth and early twentieth centuries, when attitudes and protocols were much less rigorous than they are today. Unfortunately, descriptions of new species with similarly suspect generic assignments continue to be published for both extinct and extant specimens (e.g., Hong, 2002; Park and Carlton, 2014). Poor preservation and/or the absence of the morphological detail required for rigorous generic identification forms the basis of most invalid assignments. In the absence of required morphological data, it is not uncommon for paleoentomologists to indicate uncertainty in their generic assignment. This has taken several forms. "Open nomenclature" wherein, for example, a question mark is added to the generic epithet (Richter, 1943; Bengtson, 1988) is commonly utilized. Unfortunately, subsequent literature rarely includes the punctuation mark and, with time, the generic assignment becomes more definitive than was originally intended. This is particularly problematic as it relates to modern digital databases, none of which record the question mark as an indicator of uncertainty.

Another common convention that can convey uncertainty and confusion in subsequent studies is the addition of prefixes such as litho-, archeo-, palaeo-, etc. to the stem of the name of an extant genus to create often unwarranted genera. For example, *Lithobibio* Beier, 1952, was based on an inaccurate interpretation of wing venation and was corrected by Nel (1994) to *Bibio* Geoffroy, 1762. *Miopsiloptera savchenkoi* Gentilini, 1984, from the Miocene of Italy, was placed in *Symplecta* Meigen, 1830, by Evenhuis (1994). The dipteran *Mesotanyderus* Riek, 1955 is now recognized as a mecopteran and *Protocyrtus* Rohdendorf, 1938, originally described as a fly, is now assigned to Hymenoptera (Evenhuis, 1994). Use of such prefixes, when applied to a genus that can be shown, based on preserved morphological details, to be related to but definitively distinct from an extant genus, can be informative and legitimate; when applied to specimens that lack enough detail to allow differentiation from another taxon, it simply confounds the taxonomy of that taxon.

Designation of specimens as incertae sedis, undetermined or simply "sp." may often be more appropriate and scientifically accurate. The problem is that most modern digital databases (e.g., the EDNA fossil insect database) are entirely species-based and do not record specimens that are designated as indeterminate, "sp." or incertae sedis. This results in the loss of valuable information since unassigned specimens can be of highly significant scientific value (e.g., Talamas and Buffington, 2015; Lak and Nel, 2009). Different approaches are currently taken regarding this conundrum. Talamas and Buffington (2015) figured specimens in Dominican amber from 25 extant genera, but described and assigned species names to only two. They argued that "quality morphology-based taxonomy requires examination of primary types and specimens from a broad geographical range to provide a context for interpreting morphology and intraspecific variation. Without synthetic work that provides a sound basis for accurate identification, the description of new species is of little use to taxonomy and can result in the proliferation of unstable species names, which are ultimately detrimental to understanding biodiversity and evolutionary history." A less extreme but still stringent approach was taken by Palmer et al. (1957) who stated that fossil "species are named only if critical morphological features of species rank are preserved on the specimens". An approach, perhaps at the opposite end of the spectrum, was taken by Pierce (1966) who stated simply "we need to have names to associate our findings."

SYSTEMATIC PALEONTOLOGY

Order DIPTERA Linnaeus, 1758
Family TIPULIDAE Latreille, 1802
Genus TIPULA Linnaeus, 1758

Type Species. *Tipula oleracea* Linnaeus, 1758

Subgenus *Trichotipula* Alexander, 1915

Type species. *Tipula oropezoides* Johnson, 1909

Tipula (Trichotipula) fji De Jong, sp. nov.
Figures 1-3

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Etymology. The specific epithet (to be pronounced as efyaï) is the Latin genitive case for FJ, which stands for Floris-Jan Muys, a young Dutch researcher.

Holotype. USNM 625687, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Spring site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. This species of *Tipula* is distinguished by the short vein Rs, the parallel-sided and pentagonal discal cell, the petiolate cell m_1, the length and position of crossvein m-cu, and the shape of the male terminalia.

Description

Adult male (Figure 1.1), body length about 13.5 mm, wing length about 11.5 mm. Specimen preserved in lateral view.

Head. Eyes well-developed, large, almost covering entire head, dorsally with narrow separation. Rostrum shorter than remainder of head, nasus invisible (Figure 2.1). Antenna about 4.5 mm long, longer than head and thorax combined, with elongate scape, pedicel not identifiable, flagellum consisting of 11 cylindrical flagellomeres with enlarged base that carries a set of verticils; flagellomeres becoming shorter towards apex of antenna, apical flagellomere abruptly much shorter than preceding one; most flagellomeres have become separated in

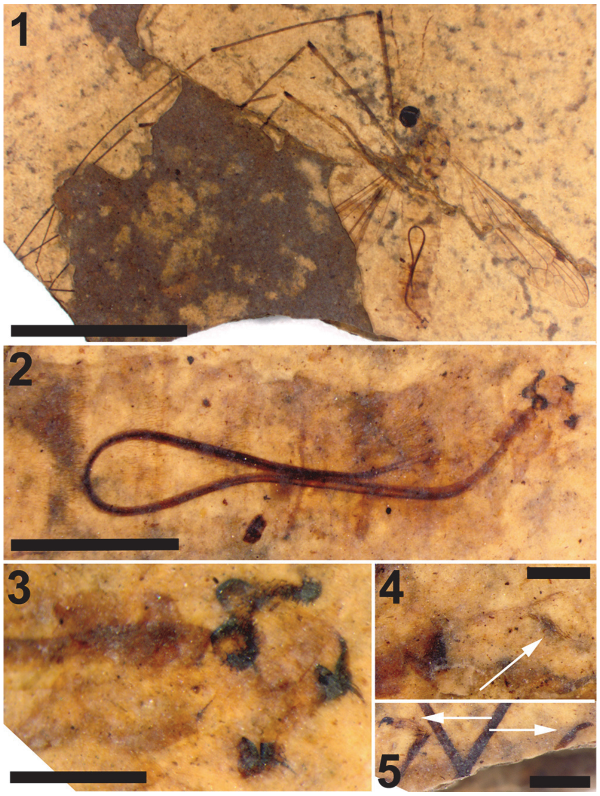

FIGURE 1. *Tipula (Trichotipula) fji* sp. nov., USNM 625687, male. **1**, Habitus; **2**, Posterior portion of the abdomen showing aedeagus; **3**, Terminalia; **4**, Halter; **5**, tarsal claws. The arrows point to the front tarsal claw (left) and the terminal tarsomere of either the middle or back leg (right). Scale bars equal 10.0 mm (**1**), 2.0 mm (**2**) and 0.5 mm (**3**-**5**), respectively.

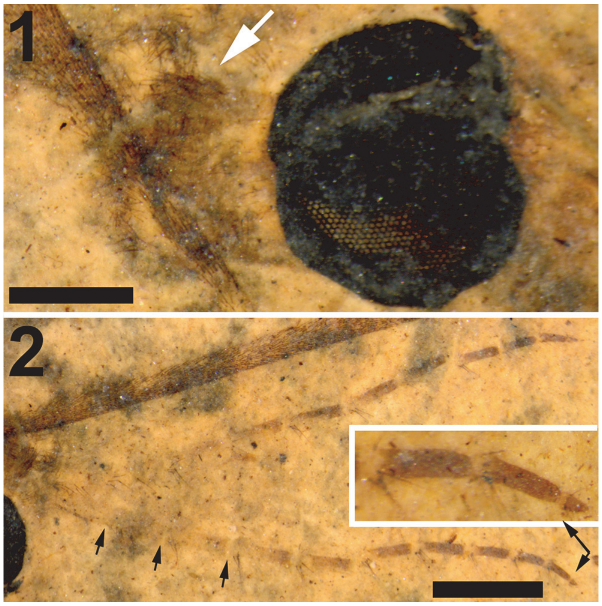

FIGURE 2. *Tipula (Trichotipula) fji* sp. nov., USNM 625687. **1**, Head. Arrow denotes palpus; **2**, Antennae. Arrows denote boundaries between basal flagellomeres, double arrows point to verticils at the base of the terminal flagellomere. Scale bars equal 1.0 mm (**1**) and 0.5 mm (**2**).

fossil. Palp not clearly segmented, apparently densely set with setae (Figure 2.2).

Thorax. Scutum with dorsum moderately curved. Contours of halter indicated, halter about 1.2 mm long.

Wings. Right wing visible (Figure 3.1), although partly broken, apical part of left wing missing. Pterostigma distinct, dark-brown. Microtrichia on membrane visible. Subcosta long, terminating in R_1 just apical of origin of Rs (Figure 3.2). R_1 long, almost straight, terminating in costa near midlength of pterostigma. Rs very short and curved, forking near proximad side of pterostigma. R_{2+3+4} short, forking into R_{2+3} and the long R_4 at distad end of pterostigma (Figure 3.3). R_4 almost straight towards wing margin. Base of R_5 aligned with crossvein r-m; long apical section of R_5 slightly curved. M forking into short basal sections of M_{1+2} and M_{3+4}. Discal cell with anterior and posterior margins almost parallel-sided, discal cell pentagonal. M_{1+2} forming petiole apicad of discal cell, then forks into a gradually widening cell m_1 towards wing margin. M_3 curves with anteriorly concave bow towards wing margin. M_4 fuses with crossvein m-cu for a short distance near proximal part of discal cell and from there curves with an anteriorly concave arch towards wing margin. Crossvein m-cu strong and distinctly longer than Rs. CuA upturned and slightly angled at point of contact with crossvein m-cu; apical section of crossvein CuA rather abruptly curved just before wing margin. False vein immediately posterior to CuA present. CuP gradually deviating from CuA from wing base towards wing margin. A_1 long, slightly sinuous. Anal area of wing well-developed.

Legs. Left legs partly preserved, left foreleg almost complete. Femora and tibiae darkened at extreme tips. No tibial spurs identifiable. Apical tarsomere of foreleg with claw carrying a basal tooth (Figure 1.5).

Abdomen and genitalia. Abdomen made up of rather short segments. Male outer and inner genitalia partly visible (Figure 1.3). Posterior margin of tergite nine with a pair of lateral bulbous extensions that are ventrally set with dark spines; area between the lateral extensions U-shaped emarginate and (ventro-?) medially blackish, sclerotized;

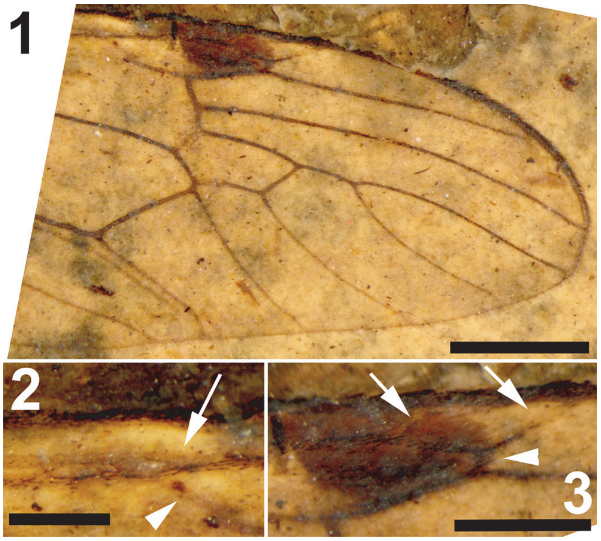

FIGURE 3. *Tipula (Trichotipula) fji* sp. nov., USNM 625687. **1**, The apical half of the right wing; **2**, Detail of vein Sc. The arrow denotes the terminus of Sc, the arrowhead points to a dislocation of a portion of Rs; **3**, Detail of anterior radial veins. The arrows point to R_1 and the second abscissa of R_2 (left and right respectively) and the arrowhead denotes the first abscissa of R_2. Scale bars equals 1.0 mm (**1**), 0.3 mm (**2**) and 0.5 mm (**3**).

black spines along (ventral side of) posterior margin. A pair of blackish-brown gonostyles visible with broad base and slender, somewhat sinuous anterior part that ends in a narrow point; a bundle of thick black, curved setae on dorsal margin. Broad and dark-brown aedeagus clearly visible through integument, runs anterior from ill-defined sperm pump in segment seven to segment three and from there loops back to aedeagal guide in terminal segment (Figure 1.2).

Allotype. Female unknown.

Syncompressions. Coprolite (1).

Remarks

Tipulidae s.str. currently include 38 recent genera and 4,294 species and subspecies; the genus *Tipula* comprises 40 recent subgenera with 2,634 species and subspecies (Oosterbroek, 2018). The higher-level classification of the Tipulidae does not necessarily reflect phylogenetic relationships within the family and is in need of revision. Over 100 fossil species are described in Tipulidae, most of them are classified in *Tipula* sensu lato. The few fossil species that have been assigned to a subgenus of *Tipula* include *T.* (*Electrotipula*) *pinetorum* Alexander, 1931 (Alexander, 1931a), *T.* (*Platytipula*) *anatolica* Kania and Nel, 2013, *T.* (*Tipula*) *oligocenica* Kania and Nel 2013, and *T.* (*Trichotipula*) *paicheleri* Kania and Nel, 2013. *Electrotipula* Alexander, 1931 (Alexander, 1931a) is the only described extinct subgenus of *Tipula*.

The present fossil is placed in the genus *Tipula* because of its relatively small size, the presence of simple flagellomeres with a whorl of verticils at their enlarged bases (Figure 2.2), the long Sc ending apical of the origin of Rs, the petiolate cell m_1 and the fusion of M_4 with m-cu near the proximal part of the discal cell. It is provisionally placed in the subgenus *Trichotipula* because of the short vein Rs, the shape of the discal cell (Figure 3.1), the shape and armament of the posterior margin of tergite nine and the shape and sclerotization of the inner gonostylus. The inner gonostylus and the posterior margin of tergite nine are reminiscent of that of the type species of *Trichotipula*, *T. oropezoides* (cf. Alexander, 1965, figure 31). The exceptionaly well-preserved aedeagus may suggest that this particular cranefly was teneral and the post-eclosion period too short to have allowed cuticular sclerotization.

Trichotipula includes 46 recent species, of which 34 are known from the Nearctic region; eight species are recorded from the Neotropical region, four from the East Palaearctic and one from the Oriental region; one species occurs in both the Nearctic and Neotropical regions. Most, but not all, *Trichotipula* species have at least some macrotrichia on the membrane of the wingtip; in the present fossil, microtrichia can be observed quite clearly, but macrotrichia are absent.

The fossil species from the late Oligocene of Turkey classified by Kania and Nel (2013) in *Trichotipula* does not belong to this subgenus, or even to the genus *Tipula*. The very short vein Rs, the sessile cell m_1 and the position of crossvein m-cu proximal of the discal cell indicate that it belongs to the genus *Nephrotoma* Meigen, 1803. For these reasons, the species *paicheleri* is formally transferred to the genus *Nephrotoma* as *Nephrotoma paicheleri* (new combination).

Family LIMONIIDAE Rondani, 1856

Genus ELLIPTEROIDES Becker, 1907

Type species. *Ellipteroides piceus* Becker, 1907

Subgenus *Ellipteroides* Becker, 1907

Type species. *Ellipteroides piceus* Becker, 1907

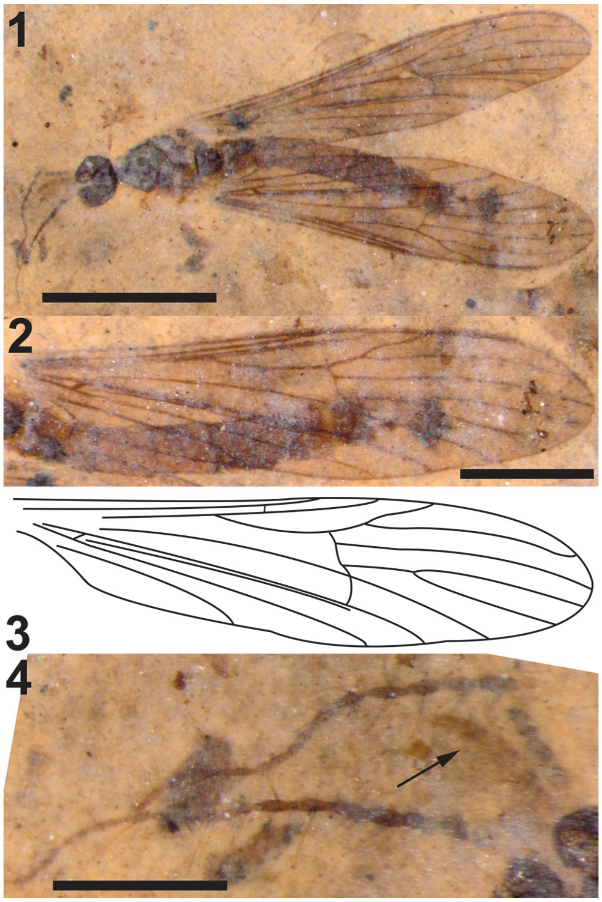

FIGURE 4. *Ellipteroides (Ellipteroides) kishenehn* sp. nov., USNM 621123. **1***,* Habitus; **2**, Left wing; **3**, Line drawing of left wing; **4**, Antennae and palpus. Arrow points to palpus. Scale bars equal 2.0 mm (**1**), 1.0 mm (**2**) and 0.5 mm (**3**).

Ellipteroides (Ellipteroides) kishenehn De Jong, sp. nov.

Figure 4

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Etymology. The specific epithet is regarded here to be a noun in apposition to the genus name *Ellipteroides*, which is masculine.

Holotype. USNM 621123, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Park site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. This species of the genus *Ellipteroides* is distinguished by the length of vein Sc, absence of vein R_2, wide cell r_3, absence of the discal cell and the shape of cell m_1.

Description

Adult male (Figure 4.1), body length about 5.0 mm, wing length about 5.1 mm. Specimen preserved in dorsal view.

Head. Head round. Eyes large covering most of sides of head, widely separated medially. Rostrum hardly visible but by inference very short. Antenna about 0.7 mm long, number of segments not distinguishable, basal segments short and somewhat bulbous, becoming more elongate and slender apically towards antennal tip; intermediate and apical flagellomeres with long verticils that exceed length of segments (Figure 4.4). Palp only vaguely indicated. Occiput dark brown.

Thorax. Hardly any distinguishing characters; metatergite distinct from remainder of thoracic dorsum. Thorax dark brown.

Wings. Both wings entirely preserved, right wing somewhat folded along M. Pterostigma not visible (Figure 4.2-3). Sc terminating in costa at level of first fork of Rs. The position of crossvein sc-r is uncertain, but it is possibly present at some distance proximad of apex of Sc. R_1 long, straight, terminating in costa near level of fork of $R_{(2+)3}$ and R_4. Rs long, originating at level of apex of A_1, gradually curved. $R_{(2+)3+4}$ with short petiole, free section of R_2 absent, R_3 slightly sinuous and subparallel to apex of R_1, R_4 long, slightly sinuous. R_5 long, evenly curved towards wing tip. Crossvein r-m rather long, a bit curved and oblique. Discal cell absent. M branches into M_{1+2} and M_4 (M_3 absent). M_{1+2} with short petiole before branching into M_1 and M_2. M_4 aligned with M. Crossvein m-cu touches M at its branching point, appearing somewhat curved possibly due to deformation of fossil. CuA almost straight, not upcurved at contact with crossvein m-cu, apical section of CuA aligned with preceding part of vein. False vein immediately posterior to CuA distinct from base of wing to level of crossvein m-cu. CuP gradually diverging from CuA from wing base to margin. A_1 long, gradually bowed to posterior wing margin. Anal area well developed, anal corner evenly rounded.

Legs. Missing.

Abdomen and genitalia. Abdomen entirely present, but covered by wings, dark-brown. Genitalia preserved in dorsolateral view, but no details discernible.

Allotype. Female unknown.

Syncompressions. None.

Remarks

The family Limoniidae currently includes 147 recent genera and 10,578 described species (Oosterbroek, 2018). The genus *Ellipteroides* is divided into six subgenera, *Ellipteroides* sensu stricto (with 15 species), *Progonomyia* Alexander, 1920 (55), *Protogonomyia* Alexander, 1934 (38), *Ptilostenodes* Alexander, 1931b (9), *Ramagonomyia* Alexander, 1968 (2) and *Sivagonomyia* Alexander, 1968 (1). *Ellipteroides* is a taxonomic derivative of a huge clade that is dominated by the large genus *Gonomyia* Meigen, 1818. The systematics of this group is based on venational characters as the length of Sc, presence or absence of R$_2$, depth of cell r$_3$, presence or absence of the discal cell, shape of cell m$_1$ and the structure of the male and female terminalia. The classification is in need of revision and given the present situation, the fossil is best filed under the subgenus *Ellipteroides* (*Ellipteroides*). Placement in the genus *Ellipteroides* is based on the long Rs, the apically wide cell r$_3$, the very long R$_4$ (much longer than R$_{(2+)3+4}$), the position of m-cu near the fork of M, branching of M into M$_{1+2}$ and M$_4$. Placement in the subgenus *Ellipteroides* s.s is based on the absence of a free section of R$_2$, the absence of a discal cell, and the petiole of M$_{1+2}$ being shorter than its fork. In the Nearctic region, the genus *Ellipteroides* is represented by only four recent species that are classified in the subgenus *Progonomyia*. No fossils of *Ellipteroides* s.l. have previously been described.

Family CYLINDROTOMIDAE Schiner, 1863
Genus CYTTAROMYIA Scudder, 1877

Type species. *Cyttaromyia fenestrata* Scudder, 1877

Cyttaromyia lynnae De Jong, sp. nov.
Figures 5, 6

zoobank.org/D2C5FED7-813C-418A-B1B4-A35C286BD427

Etymology. The specific epithet is the Latin genitive case of the first name of the wife of the author (HDJ).

Holotype. USNM 621109, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Park site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. This species of *Cyttaromyia* is distinguished by the presence of an additional crossvein r'-m', a wide and long discal cell, four complete but relatively short medial veins, and a female terminalia with a long and curved extension of tergite 10, slender and curved cerci and broad hypogynial valves.

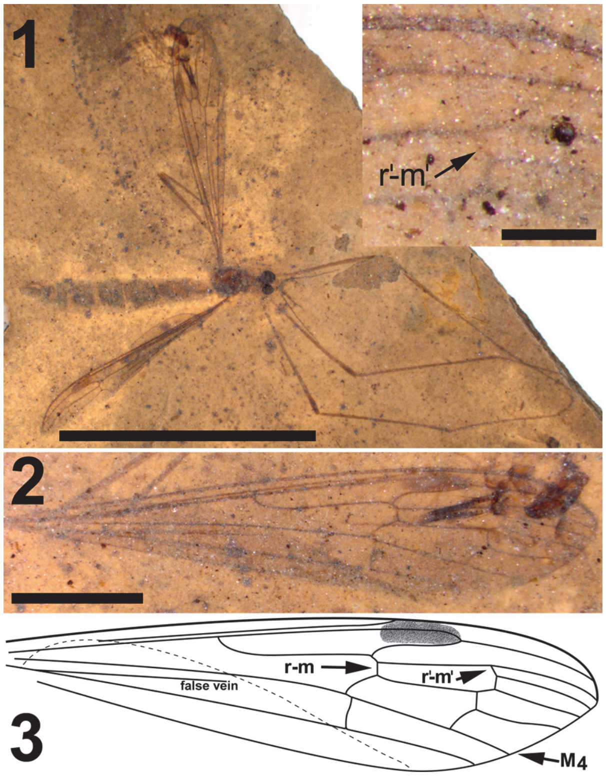

FIGURE 5. *Cyttaromyia lynnae* sp. nov., USNM 621109. **1**, Habitus. Inset: details of venation, right wing. Arrow points to the r'-m' crossvein; **2**, Left wing; **3**, Line drawing of left wing. The dotted line represents a fold in the postero-basal portion of the wing. Scale bars equal 10.mm (**1**), 0.5 mm (Inset) and 2.0 mm (**2**).

Description

Adult female (Figure 5.1), body length about 10 mm, wing length about 10 mm. Specimen preserved in dorsal view.

Head. Eyes well-developed, large, dorsally widely separated though distance not measurable due to crushed state of head (Figure 6.3). Occiput dark brown colored. Antenna 2.4 mm long, about as long as head and thorax combined, consisting of short scape and pedicel, and slender flagellum including 14 cylindrical flagellomeres. Some verticils at base of flagellomeres preserved, distinctly shorter than length of flagellomeres. Rostrum short. Palp with third to fifth segments visible, this part measuring about 0.9 mm, third and fourth segments robust, fifth irregularly shaped and about as long as third and fourth combined (Figure 6.1).

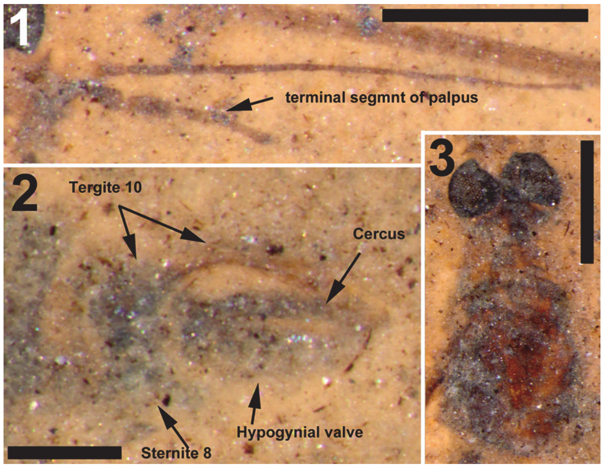

FIGURE 6. *Cyttaromyia lynnae* sp. nov., USNM 621109. **1**, Antenna and palpus, arrow denotes the 5th segment of the palpus; **2**, Genitalia; **3**, Mesosoma. Scale bars equal 1.0 mm (**1**), 0.5 mm (**2, 3**).

Thorax. Pronotum with well-developed antepronotum and broad postpronotum, scutum with visible transverse suture in posterior part. Thorax brownish in groundcolor, dark-brown on postpronotum and with broad dark-brown medial stripe and lateral sides on scutum.

Wings. Elongate and slender, anal areas folded under in both wings (Figure 5.2-3). Pterostigma distinct, located between C and first section of R_{2+3+4}, dark-brown. Sc long, terminating in C well beyond level of first fork of Rs and anterior to pterostigma. The positions of crossvein sc-r and R_1, if they exist, are uncertain. Rs long, almost 2.0 mm, about 0.75 X as long as entire R_{2+3+4}. R_5 evenly curved towards wing margin. Crossvein r-m connecting Rs with discal cell slightly distad of first fork of Rs. Vein M long, forking at proximad end of discal cell in a long first section of M_{1+3} and a short first section of M_{3+4}. Discal cell elongate, gradually widening towards wing margin, cell remarkably longer than apical sections of M_1-M_4. M_{1+2} shortly petiolate distad of discal cell where it forks into M_1 and M_2. Base of apical part of M_1 almost perpendicular to M_2, before turning towards apex of wing; M_1 here connected to R_5 by additional crossvein (r'-m'). Apical section of M_2 almost continuous with petiole of fork of M_{1+2}. M_{3+4} forks at distal part of discal cell, apical section of M_4 almost continuous with M_{3+4} and base of M_3 making angle of about 70^o with M_{3+4} and M_4. Apical section of M_3 subsinuous from discal cell towards wing margin. Crossvein m-cu located at proximad corner of discal cell. CuA only very slightly bent at point of contact with crosvein m-cu; visible part of apical section of CuA straight. Remainder of venation invisible.

Legs. Front legs and left midleg almost completely preserved; what appears as right midleg with femur and part of tibia preserved. Femora somewhat broader at tip, apex darkened. Tibiae without visible apical spurs. No claws detected.

Abdomen and genitalia. Abdomen, 7.6 mm long, broadening from segment one to five and from there narrowing towards ovipositor. Ovipositor preserved in lateral view, showing long curved extension of tergite ten dorsal of cerci and hypogynial valves. Cerci long, curved and rather slender, hypogynial valves shorter than cerci and broad (Figure 6.2).

Allotype. Male unknown.

Syncompressions. Gastropods (8).

Remarks

Cylindrotomidae is a small family of Tipuloidea with only nine recent genera, including 70 species (Oosterbroek, 2018). The recent genera occurring in North America are *Cylindrotoma* Macquart, 1834 (with two recent North American species), *Liogma* Osten Sacken, 1869 (1), *Phalacrocera* Schiner, 1863 (4), and *Triogma* Schiner, 1863 (1). The genera can be easily separated using wing venational characters (Alexander and Byers, 1981). In a phylogenetic analysis of both molecular and morphological data, Petersen et al. (2010) recovered this group as monophyletic and sister to Tipulinae but were unable to confidently resolve the combined group within Tipuloidea; they treat the group as a subfamily within Tipulidae.

Fossil Cylindrotomidae have been described in the extant genera *Cylindrotoma* and *Diogma* Edwards, 1938 and the extinct genus *Cyttaromyia* Scudder, 1877 (Table 1) (Cockerell 1921a, 1925, 1926; Freiwald, 1991; Freiwald and Krzemiński, 1991; Krzemiński, 1998; Podenas, 2000; Scudder, 1877, 1894; Séguy, 1934). All fossil Cylindrotomidae are characterized by the presence of four medial veins reaching the wing margin (recent *Diogma* always show only three medial veins). The genus *Cyttaromyia* was created by Scudder (1877) based on the apical half of an isolated wing. Scudder redefined the genus in 1894 based on several more intact specimens from the Florissant Formation. Members of *Cyttaromyia* differ from most *Cylindrotoma* and *Diogma* (and the other recent Cylindrotomidae) by the presence of additional crossvein r'-m'. This additional crossvein connec-

TABLE 1. Fossils of Cylindrotominae.

Name	Sex	Current designation	Age (Ma)	Locality/country	Reference
Cylindrotoma biamoensis	?	Valid	38.0–33.9	Biamo/Russia	Freiwald and Krzemiński (1991)
Cylindrotoma borealis	?	Valid	56.0–47.8	Fur/Denmark	Freiwald (1991)
Cylindrotoma larssoni	female?	Valid	56.0–47.8	Fur Formation/Denmark	Freiwald (1991)
Cylindrotoma monikae	?	Valid	56.0–47.8	Fur Formation /Denmark	Freiwald (1991)
Cyttaromyia veterana	?	Not tipuloid	50.3–46.2	Green River/USA	Cockerell (1921a); Brown (1988)
Cyttaromyia brevicornis		Limoniidae	38.0–33.9	Baltic amber	Loew (1850); Krzemiński (1991a)
Cyttaromyia cancellata	?	*Cyttaromyia princetoniana*	37.2–33.9	Florissant/USA	Scudder (1894); Krzemiński (1991a)
Cyttaromyia clathrata	?	*Cyttaromyia princetoniana*	37.2–33.9	Florissant/USA	Scudder (1894); Krzemiński (1991a)
Cyttaromyia fenestrata	?	Valid	37.2–33.9	Green River/USA	Scudder (1877); Cockerell (1921a)
Cyttaromyia frelloi	male	Valid	38.0–33.9	Baltic amber	Krzemiński (1998)
Cyttaromyia longicornis		Limoniidae	38.0–33.9	Baltic amber	Loew (1850); Krzemiński (1991a)
Cyttaromyia longipes		Limoniidae	38.0–33.9	Baltic amber	Loew (1850); Krzemiński (1991a)
Cyttaromyia lynnae	female	Valid	46.6–45.8	Kishenehn/USA	This paper
Cyttaromyia obdurescens	female	Valid	50.3–46.2	Green River/USA	Cockerell (1925)
Cyttaromyia oligocena	?	*Cyttaromyia princetoniana*	37.2–33.9	Florissant/USA	Scudder (1894); Krzemiński (1991a)
Cyttaromyia princetoniana	?	Valid	37.2–33.9	Florissant/USA	Scudder (1894)
Cyttaromyia quievreuxi	male	Valid	33.9–28.1	Middle Salt/France	Séguy (1934)
Cyttaromyia rayona	?	Valid	38.0–33.9	Biamo/Russia	Freiwald and Krzemiński (1991)
Cyttaromyia reclusa	male	Valid	50.3–46.2	Green River/USA	Cockerell (1925)
Cyttaromyia scudderi	?	Valid	56.0–47.8	Ølst Formation/Denmark	Freiwald (1991)
Cyttaromyia succini		Limoniidae	38.0–33.9	Baltic amber	Loew (1850); Krzemiński (1991a)
Cyttaromyia vahldieki	female	Valid	56.0–47.8	Ølst Formation/Denmark	Freiwald (1991)
Diogma gelhausi	male	Valid	38.0–33.9	Baltic amber	Podenas (2000)
Oryctogma sackenii	?	Limoniidae	37.2–33.9	Florissant/USA	Scudder (1894); Evenhuis (1994)

ting the base of M_1 with R_5 is sometimes also found in aberrant specimens of both the North American and Palaearctic subspecies of the recent *Cylindrotoma distinctissima* Meigen, 1818 (cf. Brodo, 1967, fig. 46; Peus, 1952, fig. 14) and in the Eastern Palaearctic and Oriental *C. taiwanica* Alexander, 1929 (Alexander, 1929, fig. 4).

Scudder (1894) described *Cyttaromyia* as lacking tibial spurs. This character state, in addition to the presence of r'-m', could more definitively define *Cyttaromyia* relative to *Cylindrotoma.* However, *Cyttaromyia frelloi* Krzemiński, 1998, the only specimen of the genus in Baltic amber, was described as with ”distinct tibial spurs present; single on the forelegs and midlegs, paired on hind legs. The spur of the foreleg is especially large, of a size not met till now in the Tipulidae and Limoniidae.” Tibial spurs have not been reported in the more poorly preserved compression fossils of this genus.

The structure of the ovipositor of the fossil described here (Figure 6.2) shows close similarity with that known from recent *Cylindrotoma*, where tergite ten is posteriorly extended into a long, curved and apically forked extension that is positioned dorsal of the cerci (cf Brodo, 1967, figs. 21, 22; Peus, 1952, figure 7b, c, 30). Krzemiński (1991a) previously suggested the similarity of the ovipositor of *Cyttaromyia* to that of *Cylindrotoma*. The species is placed in the genus *Cyttaromyia* because of the presence of additional crossvein r'-m', which it shares with all other species of *Cyttaromyia*. The crossvein can be present in aberrant specimens of some species of the extant genus *Cylindrotoma*.

Cyttaromyia lynnae differs from *C. vahldieki* Freiwald, 1991, and *C. rayona* Freiwald and Krzemiński, 1991, in not having a distinct patterning of the wings and from *C. frelloi, C. quievreuxi* Séguy, 1934, and *C. reclusa* Cockerell, 1925, in being female. There are numerous differences in the venation of *C. lynnae* compared to both *C. princetoniana* Scudder, 1894, and *C. fenestrate* Scudder, 1877. In the former, Rs is relatively short (Rs/R_{2+3} = 1.4; 1.8 in *C. lynnae*), R_1 is distinct and the distance between the 1st fork of M and m-cu is subequal to the length of r-m whereas that value is < 0.25 in *C. lynnae*. The ratio of the discal cell's L/W = 2.4 in *C. fenestrata* and 3.3 in *C. lynnae*. In addition, Sc terminates in C in-line with the 2nd half of the supplemental discal cell in *C. fenestrata* but just beyond the r-m in *C. lynnae.* Cells m_1 and m_2 are equal in length in *C. fenestrata* whereas m_2 is longer in *C. lynnae*. The terminus of r-r is in line with r'-m' in *C. fenestrata* but greatly basad of r'-m' in *C. lynnae*. Given the poor preservation of *C. scudderi*, it is difficult to identify differences with respect to *C. lynnae* except perhaps the shape of the pterostigma. The venation of *C. obdurescens* Cockerell, 1925 is also very similar to *C. lynnae*, although Cockerell (1926) stated that it was "similar" to *C. oligocena* Scudder, 1894 and "may prove a synonym of *C. reclusa*". The reliance on slight differences in venational morphology potentially diminishes the probable status of many of the fossil *Cyttaromyia* as separate species. Brodo (1967) has figured a large degree of intraspecific variability in the venation of multiple different specimens of the extant species *Cylindrotoma distinctissima* and *C. tarsalis* Johnson, 1912, as well as in specimens from three additional related genera. Given the existence of numerous specimens of some of the North American species (for example, there are 12 specimens of *Cyttaromyia reclusa* [Brown, 1988]), it would be of interest to study the intraspecific variability in their venation patterns.

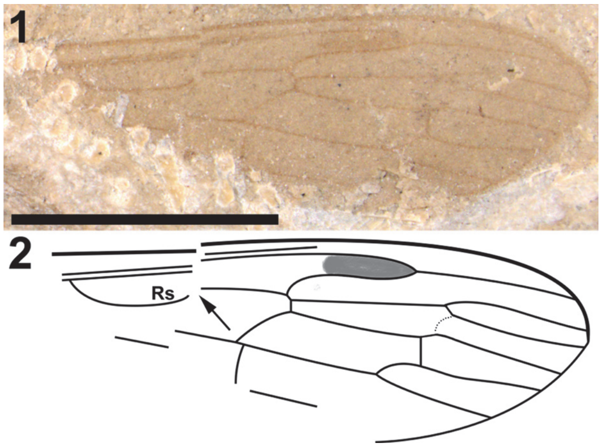

FIGURE 7. *Cyttaromyia fuscula* Cockerell, 1921 (new combination), USNM 66572. **1***,* Wing. Arrow points to a defect in the wing where the distal portion of the wing has shifted anteriorly relative to the basal portion causing an upwards curving of the basal portion of Rs; **2**, Line drawing of the wing. Scale bar equals 3.0 mm (**1**).

Cyttaromyia fuscula Cockerell, 1921 (Cockerell, 1921a, Brodo, 1967)
Figure 7
Asilopsis fusculus Cockerell, 1921 (Cockerell, 1921a)
Asilopsis fuscula Cockerell, 1921 (Evenhuis, 1994)

Material examined. Holotype, wing only. USNM 66572 (NMNH; examined).

Type horizon. Middle Eocene, Green River Formation**.**

Type locality. White River, Colorado, USA

Redescription

This specimen consists of a single wing (Figure 7.1-2). The shape of what can be interpreted as R_{2+3+4} and R_1, the shape and size of the discal cell, the position of what appears to be M_1, and the shape of cell m_2, which narrows toward the wing margin, indicate that this is a representative of Cylindrotomidae. Scudder (1877) described *Cyttaromyia fenestrata* from White River, but *C. fenestrata* has a shorter and apically much wider discal cell, and a very wide cell m_3 compared to *C. fuscula*. The short section between the first forking of vein M and the position where crossvein m-cu touches the discal cell in *C. fusculus* differs from the other known *Cyttaromyia* species; *Cyttaromyia fuscula* appears to be a distinct species.

Remarks

Originally assigned to Asilidae by Cockerell (1921a), *Asilopsis fusculus* was discussed as possibly a member of Asilinae or Laphriinae or its own new subfamily Asilopsinae. Hull (1962) discussed the fossil and stated "... the ultimate interpretation of *Asilopsis* Cockerell must rest upon the presence or absence of a proboscis and the character of the pretarsus. Without further material and for the reasons given above, I reject a subfamily based upon this fly." The specimen was subsequently assigned to Tipulidae by Brodo (1967). Twenty years later, Brown (1988), in a review of fossil *Cyttaromyia*, relied on the input of Curtis Sabrosky and Aubrey Scarbrough who stated "We believe it is a primitive asilid ... and not at all tipuloid." However, neither Sabrosky nor Scarbrough, who were Brachycera specialists, appear to have been well-acquainted with the diversity of crane flies. Brodo (1967) followed the North American concept of "Tipulidae" in which Tipulidae s.l. includes Tipulidae s.str. (as Tipulinae), Cylindrotominae, Limoniinae and Pediciinae; the rest of the world treats these four taxa as families. We believe that this specimen represents neither Tipulidae s.str. nor Limoniidae; the only other crane fly possibility other than Cylindrotomidae would be Pediciidae (based on what in that case would be R_{4+5}), but then the shape of R_1, R_2 and R_3 would be very unusual, the discal cell much too large and its shape atypical, and the number of M veins would be 'incorrect' for Pediciidae. With the caveat that the specimen is poorly preserved, we propose that wing venation is similar to that of Cylindrotomidae: *Cyttaromyia*.

Family PSYCHODIDAE Newman, 1834
BRUCHOMYIINAE Alexander, 1921
Bruchomyiinae incertae sedis
Figure 8

Holotype. USNM 619952, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Disbrow Creek site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. Based only on the wing, Bruchomyiinae is distinguished from all other Psychodidae by the following combination of character states: measured at their greatest value, distance from base to apex at least three times that of anterior to posterior wing margin; five radial veins present; base of R_1 prominent, thickened, setose; apex of CuA reaching wing margin.

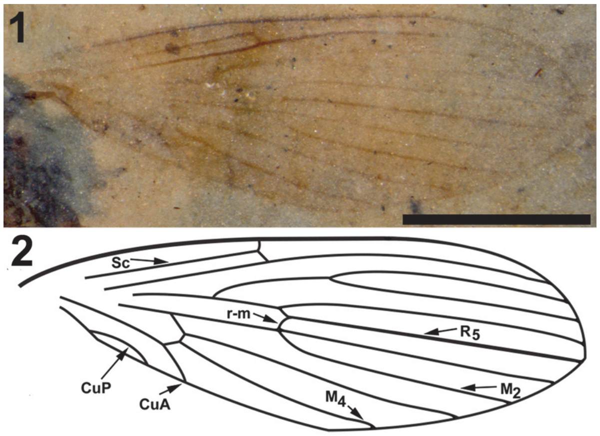

FIGURE 8. Bruchomyiinae sp., USNM 619952. **1**, Right wing; **2**, Drawing of the right wing. Scale bar equals 1.0 mm (**1**).

Description

Two wings (Figure 8.1-2), the left wing missing a portion of it postero-apical end, attached to remnants of the mesosoma.

Wings. Wing length, 3.08 mm, 1.02 mm wide; macrotrichia not present/preserved. No costal breaks beyond base. Distances from wing base - Rs fork - Sc terminus - r-m - R_{2+3} fork - wing apex are 1.08, 0.22, 0.12, 0.25 and 1.35 mm; ratio of the length of the stem of R_{2+3} to the length of the fork is 0.5. Apex of wing between R_4 and R_5. M_2 originating at the end of second basal cell (i.e., at r-m).

Allotype. Sex unknown.

Syncompressions. None

Remarks

Approximately 150 genera and 3,020 species of Psychodidae have been described (Pape et al., 2011); although estimates suggest the actual diversity is much greater (Wagner and Ibañez-Bernal, 2009). In addition to Bruchomyiinae, there are an additional six subfamilies including Datziinae Stebner et al., 2015, which are known only from fossil species. Despite their occurrence in a variety of habitats and frequent numerical abundance (Brown, 2005; Wagner and Ibañez-Bernal, 2009), most psychodids are poorly known. In contrast, many phlebotomine species are well known due to their role as vectors of *Leishmania* Ross, 1903 spp. and other disease agents.

There is a rich fossil record for psychodids dating to the early Jurassic (Ansorge, 1994) and possibly the late Triassic (Fraser et al., 1996; Blagoderov et al., 2007); however, Blagoderov et al. (2007) note that *Triassopsychoda olseni* Blagoderov and Grimaldi in Blagoderov, Grimaldi and Fraser, 2007 has a unique wing veination with several plesiomorphies and its relationship to other psychodomorphs is unclear. As summarized by Stebner et al. (2015), approximately 30 genera and more than 100 fossil psychodid species have been described, yet, like the extant fauna, many species remain undescribed.

Bruchomyiinae, with six genera, 53 extant species and eight fossil species (Curler and Jacobson, 2012; Wagner and Stuckenberg, 2012; Wagner and Stuckenberg, 2016; Stebner et al., 2015), is among the less-taxonomically diverse subfamilies of Psychodidae. Adults of this group are readily distinguished from other psychodids by their relatively large size as well as the diagnostic wing characters provided previously. Male and female genitalia characters are important for distinguishing genera and species (Curler and Jacobson, 2012; Wagner and Stuckenberg, 2016).

Fossil Bruchomyiinae are described from Baltic, Dominican and Burmese amber with the oldest specimen preserved in middle Cretaceous amber from Myanmar (Schluter, 1978; Stebner et al., 2015; Wagner, 2006; Wagner and Stuckenberg, 2012; Wagner, 2017). All fossil species of this subfamily, previously placed in *Nemopalpus* Macquart, 1838, were recently transferred to other genera (Wagner, 2017). Baltic amber species are placed in *Palaeosycorax* Meunier, 1905 or *Hoffeinsodes* Wagner, 2017 while Burmese amber species are grouped in *Palaeoglaesum* Wagner, 2017 and Dominican amber species are included in *Boreofairchildia* Wagner and Stuckenberg, 2016.

The wing venation of the Kishenehn specimen is similar to, for example, extant *Bruchomyia* Alexander, 1921, species and fossil *Hoffeinsodes* species in that M_2 originates at the level of r-m. Regardless, this character state occurs in other extant and fossil genera (Wagner and Stuckenberg, 2012; Wagner personal commun.); therefore, it may be a plesiomorphy within the subfamily. Considering the ambiguity of wing venation and the lack of other preserved characters, it is impossible to identify the Kishenehn specimen beyond subfamily.

This is the first compression fossil of a bruchomyiine species to be discovered and it is the first fossil of this subfamily from the Nearctic Region to be reported. With the exception of *Notofairchildia zelandiae* Alexander, 1921 (New Zealand), and *N. stuckenbergi* Wagner, 2012 (Chile, Valdivia) (Wagner and Stuckenberg, 2012), extant Bruchomyiinae are apparently absent from the temperate zone. Nonetheless, this new record and the growing number of species described from various ambers (Wagner, 2006, 2017) indicate that the group was once more widespread and morphologically diverse. In addition to the bruchomyiine specimen, psychodids taken from the Kishenehn Formation include over 20 specimens of Psychodidinae with potential for further study.

Family ANISOPODIDAE Knab, 1912
Genus SYLVICOLA Harris, 1776

Type species. *Sylvicola brevis* Coquillett, 1910 (SD)

Sylvicola silibrarius Greenwalt, sp. nov.
Figures 9-11

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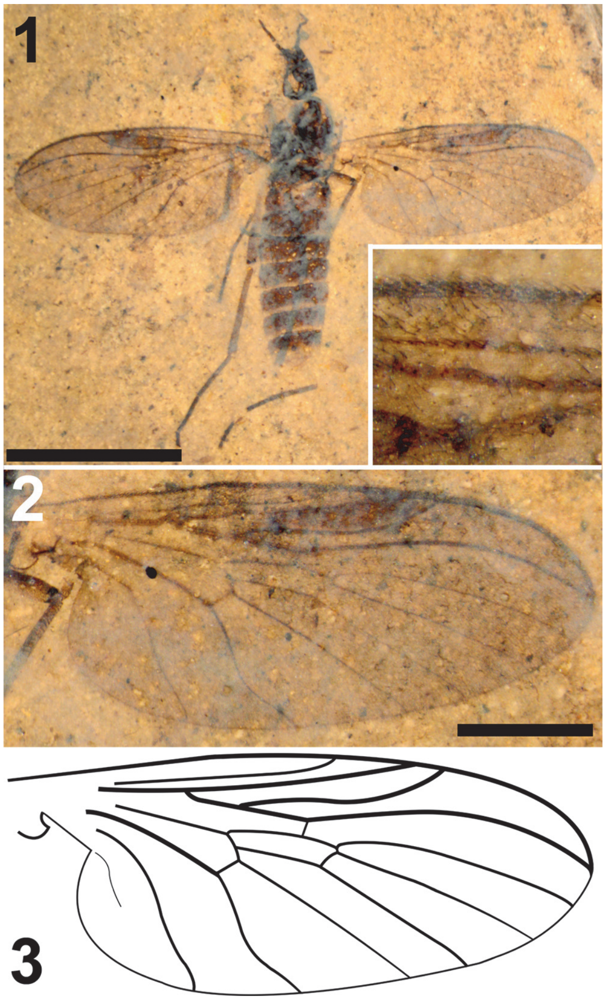

FIGURE 9. *Sylvicola silibrarius* sp. nov., USNM 626077. **1**, Habitus; **2**, Right wing. Inset: Left wing macrotrichia from area proximal of Sc terminus; **3**, Line drawing of right wing. Scale bars equal 3.0 mm (**1**), 1.0 mm (**2**).

Etymology. The specific epithet is a combination of the abbreviation SI (for the Smithsonian Institution) and the Latin term librarius (pertaining to books) and is in appreciation for the essential services that the Smithsonian libraries perform.

Holotype. USNM 626077, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Deep Ford site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. This species of *Sylvicola* is distinguished by the basal separation of M_1-M_2 1/6 of that between M_2 and M_3; pterostigma extended along cell r_1.

Description

Female (Figure 9.1), head and thorax dark brown/black, abdomen brown. Body length 5.3 mm, wing length 4.4 mm.

Head. Antenna setose; with, probably, 14 flagellomeres, basally wider than long, becoming thinner, longer than wide apically; apical flagellomere 2.5 x long as wide. Scape with ring of fine setulae in a single row. Terminal segment of palpus visible, protruding well beyond oral margin. Three occipital bristles present (Figure 10.1).

Thorax. 1.25 mm long. Scutum setose. Femur distinctly shorter than tibia; tarsomere 1 twice the length of tarsomere 2 which, in turn, is about twice the length of tarsomere 3, tarsomeres 4 and 5 short; legs setose.

Wing. Slightly dusky, membrane covered with macrotrichia. Wing shorter than body, 1.82 mm wide. C ending at R_{4+5}; pterostigma extended along cell r_1; radial veins much thicker than posterior veins, with fine setulae. M_1, M_2 and M_3 connected directly to discal cell, no forks. Distance between M_1 and M_2 at base about 1/6 of that between M_2 and M_3. CuP faint, anal lobe present (Figure 9.2-3).

Abdomen and genitalia. Abdomen, 3.4 mm long, 1.2 mm wide; uniformly brown, evenly covered with black setulae. A single sclerotized spermatheca present, 82 μm in diameter. Cerci indistinct, poorly preserved (Figure 10.2).

Allotype. Male unknown.

Syncompressions. None.

Paratype. A second specimen of *Sylvicola silibrarius* (USNM621508) is designated as a paratype (Figure 11). The specimen more clearly shows the small spherical shape of the head, the setose flagellomeres, a short arched scutum and additional legs. The specimen was collected at the Dakin site which is 0.6 km from the Deep Ford site, a possible indication of the of prevalence of the species.

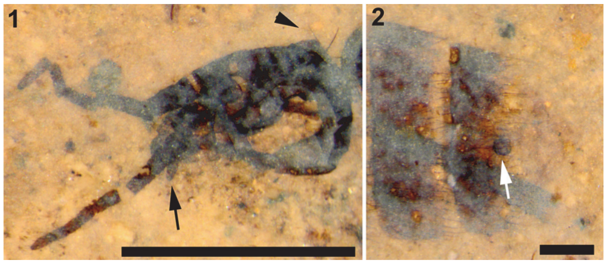

FIGURE 10. *Sylvicola silibrarius* sp. nov., USNM 626077. **1**, Head and antennae. Arrow denotes terminal palpomere. Arrowhead points to occipital bristles; **2**, Terminalia, female. Arrow denotes the spermatheca. Scale bars equal 1.0 mm (**1**) and 0.25 mm (**2**).

Remarks

The family Anisopodidae consists of 15 extant genera and more than 200 species and is widely distributed (Kania et al., 2019). The fossil record, with 49 described species (EOL, 2017; PBDB, 2018), is rich, ancient and controversial. Michelsen (1999), in reference to the unsettled Mesozoic record of anisopod stem groups, stated "all fossil family-group names ... may by necessity be referred incertae sedis to the lineage Anisopodidae." New Mesozoic species continue to be described, however, and the genera *Mesorhyphus* Handlirsch, 1920, and *Megarhyphus* Kovalev, 1990, date back to the Lower Jurassic (Ewa et al., 2010). The family has been proposed as sister to the Bibionomorpha (Wiegmann et al, 2011). Twelve of the fossil species date from the Eocene epoch. The genus *Sylvicola* contains 78 extant species and nine fossil species, the oldest of which, *Sylvicola prisca* Brodie, 1845, is from the Early Cretaceous of the Middle Purbeck; seven described species are from the Eocene (Wojtoń et al., 2018; PBDB, 2018). Pratt and Pratt (1980) proposed division of the genus *Sylvicola* into two subspecies, *Anisopus* Meigen, 1803, and *Sylvicola* Harris, 1776 s. str., based, in part, on the distance between M_1 and M_2 at base of cell m1 ≤ 1/4 (*Anisopus*) or ≥ 2/3 (*Sylvicola*) the length of the vein separating M_2 and M_3 (Krivosheina and Menzel, 1998). This proposal was rejected by Amorim and Tonzoni (1994) and Michelsen (1999).

Sylvicola silibrarius differs from the four Eocene species of *Sylvicola* as follows: *S. cadaver*

FIGURE 11. *Sylvicola silibrarius* sp. nov., USNM 621508. Paratype.Scale bar equals 2.0 mm.

Scudder, 1890, from the Green River Formation, is slightly smaller (wing length, 3.5 mm vs. 4.4 for *S. silibrarius*), its bm is "about half as long as the wing", and its br terminates apically "scarcely beyond the tip of" Sc. In addition, M_1-M_2 is 2/3 (left wing) or nearly equal to (right wing) the length of M_2-M_3, as determined from the Scudder's figure 17. *Sylvicola hooleyi* Cockerell, 1921 (Cockerell 1921b), from the Isle of Wight, is an isolated wing. The distance between the bases of M_1 and M_2, as determined from Cockerell's original figure, is 62% of that between M_2 and M_3 (vs. 17% for *S. silibrarius*). In addition, in *S. silibrarius*, the wing length is slightly shorter (4.4 mm vs 5.2 mm), lacks apical pigmentation, has the r-m crossvein contacting the discal cell at its apical half rather than its basal half and has a much wider cell m_3 relative to the discal cell (1.5 x vs. 0.8 x) measured at or as a continuation of the vein separating M_2 and M_3. The description of *S. splendida* Meunier, 1907, mentions only the large pulvilli and claws of this species. *S. silibrarius*, which is slightly smaller (5.3 mm vs. 5.75 mm in length) differs from *S. splendida*, a male from Baltic amber, in having smaller tarsal claws (< the width of the base of the tarsomere). *Sylvicola silibrarius* differs from the male and female specimens of *S. thiriona* Meunier, 1904, also from Baltic amber, in that *S. thiriona* has a filiform antenna, pedicel < twice the width of F12 (pedicel more stout, > twice the width of the terminal flagellomere in *S. silibrarius*), R_1 reaching C closer to Sc than to the end of R_{2+3}, M_1-M_2 ≥ 2/3 of M_2-M_3 and terminal tarsomeres with small claws (plate 17, figure 14 in Meunier, 1904a).

Sylvicola baltica, S. hoffeinsorum and *S.punctata* were recently described by Wojtoń et al. (2018); *S. baltica* (male) and *S. punctata* (female) are both based on single specimens from Baltic amber whereas eight specimens of *S. hoffeinsorum* (both male and female) were studied, seven from Baltic amber and one from Bitterfield amber. *Sylvicola silibrarius* differs from all of these specimens in having m'-m' much shorter than m-m. In addition, *S. baltica* has a terminal flagellomere six times as long as wide and all flagellomeres longer than wide; the terminal flagellomere of *S. librarius* is three times as long as wide. *Sylvicola punctata* has an undulating M_4 and the ratio of the distances between Sc and R_1 and R_1 and R_{2+3} is 3 whereas it is about 2 in S. *librarius.*; this ratio is 1.5 in *S. hoffeinsorum*. In all three of the species described by Wojtoń et al. (2018), r-m terminates in the middle of dm whereas the cross vein intersects with dm at the distal third of the cell in *S. librarius*.

Notes on some other fossil *Sylvicola*: Lewis (1987) figured the wing of an anisopodid from the Oligocene Ruby River Basin in southwestern Montana. The entire insect was said to have been preserved. The specimen was identified as resembling the type species of *Sylvicola, S. brevis* Harris, 1780 [*Tipula fenestralis* Scopoli, 1763]. The specimen was not described, and a repository was not designated. Although the specimen was collected by H. Becker, of the New York Botanical Gardens, sometime between 1950 and 1970, an inquiry made to the New York Botanical Gardens established that the specimen was not housed at the Gardens. Inquiries to St. Cloud State University, where Lewis' collection is reported to be housed, have gone unanswered.

Evenhuis (1994) treated the name *Rhyphus lugubris* Heer, 1849, under *Sylvicola*. However, Heer (1849) neither described nor mentioned *Rhyphus lugubris*. Evidently, Evenhuis had made a typographical error for *Plecia lugubris* Heer, 1849, which is in the text immediately after the description of *Sylvicola maculata* Heer, 1849 (N.L. Evenhuis., personal commun., 2017).

Family SCATOPSIDAE Newman, 1834
Genus EFCOOKELLA Haenni, 1998

Type species. *Efcookella albitarsis* Zetterstedt, 1850

Efcookella nigra Greenwalt, sp. nov.
Figure 12

zoobank.org/B16260A9-30BA-4765-9CEA-98FFDF806172

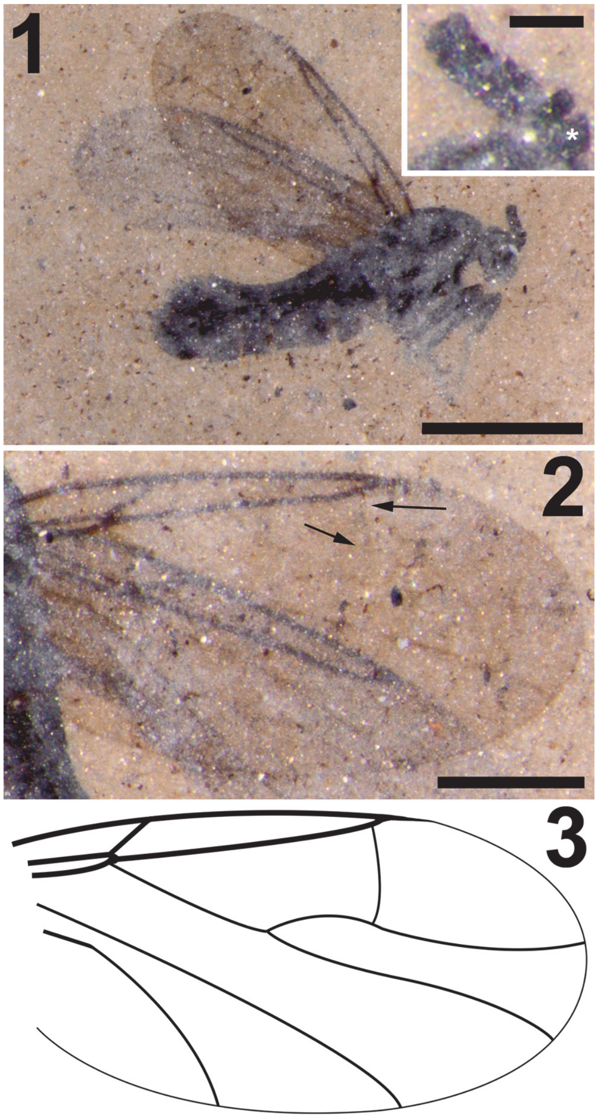

FIGURE 12. *Efcookella nigra* sp. nov., USNM 618088. **1**, Habitus. Inset: antennae, asterisk denotes the pedicel; **2**, Left wing. Arrows mark the R_5-M_1 cross vein; **3**, Line drawing of wing. Scale bars equal 1.0 mm (**1**), 0.1 mm (Inset) and 0.5 mm (**2**).

Etymology. The specific epithet is derived from the Latin term nigra for black, the colour of the insect.

Holotype. USNM 618088, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Dakin site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. This species of *Efcookella* is distinguished by R_1 very short, C terminating just beyond R_{4+5} significantly basal of the wing apex, the presence of a complete R_{4+5}-M_1 cross vein, M_1 and M_2 diverging abruptly close to the wing margin and CuA not sigmoidal in shape. Flagellomeres compact, much wider than long.

Description

Body length 2.3 mm long, sex undetermined; entire body black (Figure 12.1).

Head. Head 0.24 mm long, 0.30 mm high; antennal flagellum, 0.28 mm long, eight flagellomeres, transverse, approximately 25 μm long and 65 μm wide.

Thorax. Scutum 0.64 mm long, tibia about 2/3 length of tarsus.

Wing. Membrane uniformly covered with microtrichia; wing length 1.99 (left), 1.81 mm (right), right wing width, 0.96 mm (Figure 12.2-3). Anterior veins C, R_1 and R_{4+5} darkly pigmented; R_1 short, extending only about 1/4 the length of the wing, costa ending just distal of apex of R_{4+5}, well before wing apex; cross vein r-m minimal. Relatively long R_{4+5} extends to 0.62 (left) and 0.65 (right) of wing length. M very lightly sclerotized, forked, M_1 and M_2 diverging abruptly before wing margin, faint R_{4+5}-M_1 cross vein present, CuA strongly curved towards wing margin but not sigmoidal, CuP not visible.

Abdomen and genitalia. Abdomen 1.50 mm long, 0.4 mm in height, bulbous apically, genitalia not preserved sufficiently for characterization.

Allotype. Sex unknown.

Syncompressions. None.

Remarks

Scatopsidae is a family of very small flies, with 407 species in four subfamilies and 34 genera (Pape et al., 2011). The genus *Efcookella* contains 21 extant species (EOL, 2017). The fossil record of Scatopsidae was reviewed by Amorim (1998), subsequent to which new species have been added by Nel and Prokop (2004), Fate et al., (2013) and Nel and Coty (2016); there currently are 18 species of fossil Scatopsidae. Of the fossil species, 13 belong to extant genera although *Scatopse grassaris* Meunier, 1907 and *S. crassicornis* Meunier, 1907 are considered Scatopsidae incertae sedis. Additionally, Amorim (1998) has suggested that *Procolobostema incisum* Cook, 1971, and *P. obscurum* Cook, 1971 may be synonyms of *P. hurdi* Cook, 1971. According to Amorim (1998), most males of this genus lack the crossvein R_{4+5}-M_1 while females have an incomplete R_{4+5}-M_1, cross vein. Several specimens from Cretaceous amber from Myanmar, Canada, New Jersey and Lebanon have been reported but not described (Pike, 1994; Grimaldi et al., 2000; Rasnitsyn and Ross, 2000; Poinar and Milki, 2001).

Sinoscatopse eocenica Hong, 2002, is a potentially interesting specimen but it does not appear to be a scatopsid. As described by Hong (2002), *S. eocenica* has a four segmented palpus (vs. a one segmented palpus in Scatopsidae), antennae "like the antennae of a female mosquito" with its flagellomeres longer than wide and "plumose" with a pair of setae/segment ≥ in length than the flagellomeres themselves, whereas the flagellomeres of scatopsids are compact and wider than long. In addition, *S. eocenica* has prominent tibial spurs on all legs (absent in Scatopsidae). Most interesting is the wing venation: Rs originates at the mid-point of the wing with the first abscissa of M > 1/2 wing length. In all scatopsids, the cubital fork is at the very base of the wing vs. the presence of a significant stem in *S. eocenica*. The specimens described in Hong (2002) are stated to be housed in the Chinese Geology Museum, the Beijing Natural History Museum or personal collections; however, no single specimen has its location indicated. Until the specimen can be located and re-examined, it must be considered as Diptera incertae sedis.

Of the 18 described fossils of Scatopsidae, 17 are in amber. The exception, *Reichertella fasciata* Melander, 1949, was described from the 34 myo Florissant Formation. This specimen is unique amongst the Scatopsidae in having a long R_{4+5} that closely parallels the costa for most of its length. Amorim (1998) elected to preserve the original placement. Meyer (2002) lists and figures another specimen (PU-6943) of *R. fasciata* that was collected by the Princeton scientific expedition of 1877. This specimen, housed at the NMNH (USNM 112563), is not a type specimen. Inspection of this specimen (Figure 13) does not support its assignment to the family Scatopsidae. The body is 4.5 mm in length, large for a scatopsid, with numerous bristles on the head, scutum and scutellum. This specimen is either lacking its antennae or has antennae unlike that in Scatopsidae. Most importantly, the venation is very unlike that of a scatopsid. The anterior veins are not particularly more strongly pigmented than the posterior veins. Both medial and cubital forks are present, and CuA is subparallel to M_4 and does not curve markedly towards the posterior margin, as is the case in all Scatopsidae. This specimen is assigned to Diptera indeterminate.

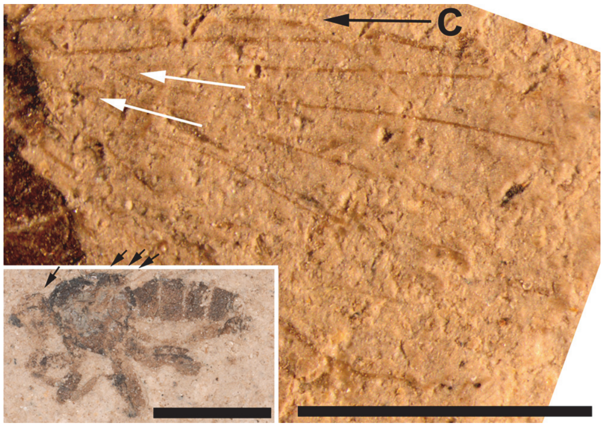

FIGURE 13. *Reichertella fasciata* (PU-6943; USNM 112563). Left wing. White arrows denote the medial and cubital forks. Inset: habitus; black arrows denote bristles. Scale bars equal 2.0 mm

Efcookella nigra keys to Scatopsinae Newman, 1834, as Aspistinae Rondani, 1840 (C swollen at junction of R_{4+5}), Ectaetiinae Enderlein, 1936 (stem of M_{1+2} arising distal to base of R_{4+5}) and Psectrosciarinae Cook, 1963 (base of M_2 arising at base of R_{4+5}) are characterized by states not found in the fossil. Critical character states that define the tribes of Scatopsinae, Rhegmoclematini Cook, 1955 (CuA sigmoid in shape), Scatopsini Newman, 1834 (basal third of CuA gently curved towards wing margin and medial fork without a "constriction" midway to apex/R_{4+5}-M_1 cross vein absent), Swammerdamellini Cook, 1972 (R_{4+5} not extending beyond middle of wing — this is not the case for the genus *Pararhexosa* Freeman, 1990; this genus however has ten flagellomeres) and Colobostematini Amorim, 1994 (basal third of CuA strongly curved towards wing margin) suggest that this specimen can be assigned to Colobostematini (Amorim, 2009). Of the six genera in Colobostematini, the specimen keys to *Efcookella* (formerly *Cookella* — see Haenni, 1998) based on CuA not sigmoidal, R_{4+5}-M_1 cross vein present and scutum longer than wide. The single fossil species of *Efcookella, E. eocenica* Nel and Prokop, 2004, was described from 53 Mya amber from Le Quesnoy, France. *Efcookella nigra* is larger than *E. eocenica* (2.3 mm body length vs. 1.86 mm, 124%), its wings are approximately 50% longer, its scutum is 71% longer (0.64 mm vs. 0.375 mm) and the shape of the cell formed by the cross vein R_{4+5}-M_1 and the terminal abscissa of M_1 is markedly different in shape: the terminal abscissa of M_1 in *E. eocenica* angles downwards from R_{4+5}-M_1 at an angle of 33° while that of *E. nigra* is inline with the more basal abscissa of M_1.

Family BIBIONIDAE Fleming, 1821
Genus BIBIODES Coquillett, 1904

Type species. *Bibiodes halteralis* Coquillett, 1904

Bibiodes kishenehnensis Fitzgerald, sp. nov.
Figures 14, 15

zoobank.org/E6A8DA89-FB03-4061-B16B-25FD8DD11FDF

Etymology. The specific epithet is named after the Kishenehn Formation in which the holotype was preserved.

Holotype. USNM 625738 deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

FIGURE 14. *Bibiodes kishenehnensis* sp. nov., USNM 625738. **1**, Habitus (ventral aspect); **2**, Right wing showing the fusion of Rs and M; **3**, Line drawing of the right wing. Scale bars equal 3.0 mm (**1**) and 1.0 mm (**2**).

Type locality. Spring site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. *Bibiodes kishenehnensis* is a typical representative of the bibionid genus *Bibiodes* that is distinguished from other genera by the elongated coalescence of the stem of M and Rs veins. *B. kishenehnensis* is distinguished from fossil congeners by the following combination of characters: coalescence of stem of M and Rs longer (coalescence 0.43 mm and slightly longer than base of Rs), wings brown fumose (especially at anterior apical portion of wing), stigma strongly pigmented, legs black and hind basitarsus about four times as long as wide (width measured at midpoint).

Description

Female (Figure 14.1), body length (excluding antennae) 6.8 mm.

Head. Black, antennae and palps black, number of flagellomeres not discernible, as base of antennae are hidden (Figure 15.1).

Thorax. Ventral and visible lateral portions black, dorsum hidden from view.

Wings. 5.2 mm long (base of wing estimated for measurement) by 1.8 mm wide (measured at level of apical end of coalescence of stem of M and Rs (Figure 14.2-3). Anterior veins except Sc (C, radial veins, base of M including junction with Rs) bold, strongly pigmented dark brown. Sc and apical tips of medial veins faint, light brown, remainder of veins unpigmented. Sc long, fading out before stigma (presumably not reaching C as in extant species). Pterostigma strongly pigmented, dark brownish black, elongate. Wing membrane distinctly brown fumose along anterior margin from stigma to just beyond apical end of C and slightly light brown fumose elsewhere, but especially along wing edge to about M_4. Costa continued only slightly as tiny stump beyond junction with R_{4+5}.

Legs. Black. Length of spur of anterior tibia not discernible. Hind femur about 1.4 mm long (base of femur estimated), swollen, 0.44 mm wide (width measured at widest area on apical third). Hind tibia not swollen, straight-sided, but gradually thickened distally, 1.5–1.6 mm long by 0.28–0.30 mm wide (width measured at apex; Figure 15.3). Hind basitarsus slender, gradually slightly more robust distally, about four times as long as wide, 0.48-0.60 mm long by 0.16 wide (width measured at midpoint of basitarsus).

Abdomen and genitalia. Abdomen brown, broad, as is typical for females. Cerci light brown, ovate, with fine setae, projecting posteriorly (Figure 15.2).

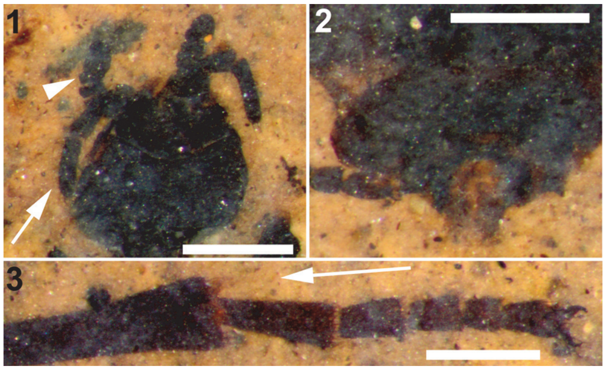

FIGURE 15. *Bibiodes kishenehnensis* sp. nov., USNM 625738. **1**, Head. Arrowhead points to the antenna; arrow points to the terminal palpomere; **2**, Genitalia; **3**, Left metatibia and tarsi. Arrow points to the tibial spur. Scale bars equal 0.5 mm (**1, 2**, **3**).

Allotype. Male unknown.
Syncompressions. None.

Remarks

The family Bibionidae *sensu stricto* (excluding *Hesperinus* Walker, 1848, but including both fossil and extant forms) consists of nine genera (Fitzgerald, 2004; Skartveit, 2008) and 1,102 species (Pape et al., 2011), and is distributed worldwide. Roughly 328 of these are fossil species (PBDB, 2018), an unusually large number given the relatively small number of extant species, which is perhaps an indication of the clade being more diverse or at least more abundant in the past. However, Skartveit and Nel (2017) recently synonymized the fossil *Bibio conformans* Théobald, 1937, with *B. celasensis* Theobald, 1937, and suggested that *B. obtusus* Théobald, 1937, and *B. tenuiapacalis* Théobald, 1937, may also be synonyms. The validity of many other fossils is uncertain. Most (70%) of the fossil species date from the Miocene and Oligocene, with 79 species from the Eocene epoch.

The genus *Bibiodes* contains four extant species. Five fossil species, *B. balticus* Skartveit 2008, *B. intermedia* James, 1937, *B. confluens* Cockerell 1915, *B. provincialis* Skartveit and Nel, 2017, and *B. nanus* Skartveit, 2008, have been described from the Eocene and Oligocene (Cockerell, 1915; James, 1937; Skartveit, 2008; Skartveit and Nel, 2017). *Bibiodes kishenehnensis* differs from most fossil congeners in part by the longer coalescence of the stem of M with the base of Rs (Figure 14; see additional characters in diagnosis) and in this regard is more similar to extant western Nearctic species of *Bibiodes*.

The Kishenehn Formation fossil insect collection contains 162 specimens of Bibionidae, including additional specimens of *Bibiodes* and several putative new species. The holotypes of *Plecia akerionana* Fitzgerald, 1999, and *Bibiodes* (=*Bibiodites*) *confluens* are housed at the NMNH.

Family SCIARIDAE Billberg, 1820
Genus EOSCIARITES Greenwalt, gen. nov.

zoobank.org/B5BA26D4-17C9-47B6-BFF3-7CA229FB6999

Type species. *Eosciarites hermes* Greenwalt, gen. et sp. nov., by monotypy.

Eosciarites hermes Greenwalt, sp. nov.
Figures 16, 17

zoobank.org/C0541528-F65E-4593-9B09-9C1CB318C6C2

Etymology. The generic epithet is a combination of the greek word Eos (early, dawn), the genus name *Sciara* and the suffix “-ites” (Latin for ”having the nature of”). *Eosciarites* is a collective parataxon as defined by Rasnitsyn (1986; 1996). The specific epithet is the Greek word Hermes (mythical messenger of the gods).
Holotype. USNM 624633, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.
Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.
Type locality. Dakin site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).
Differential Diagnosis. The absence of macrotrichia on veins M and Cu and flagellomeres with cylindrical nodes or necks differentiates this specimen from *Sciara*. A three-segmented palpus, R_1 joining C prior to medial fork and significantly longer than half the length of R, M+CuA significantly greater than bm-m, middle and hind tibia with a single apical tibial spur are all diagnostic of this specimen.

Description

Female (Figure 16.1). Total length 2.2 mm, light brown in colour.
Head. Black, spherical, 0.27 mm diameter; eye about 0.12 mm in diameter. Maxillary palpus three-segmented, about 0.19 mm in length, terminal two segments slightly longer than wide. Antennal base situated in a distinct depression, flagellomeres brown, quadrate basally. Apical flagellomeres not preserved (Figure 17.1).
Thorax. Black to dark red, legs light brown. Scutum covered with short scattered setae. Mediotergite with several bristles on its posterior margin,

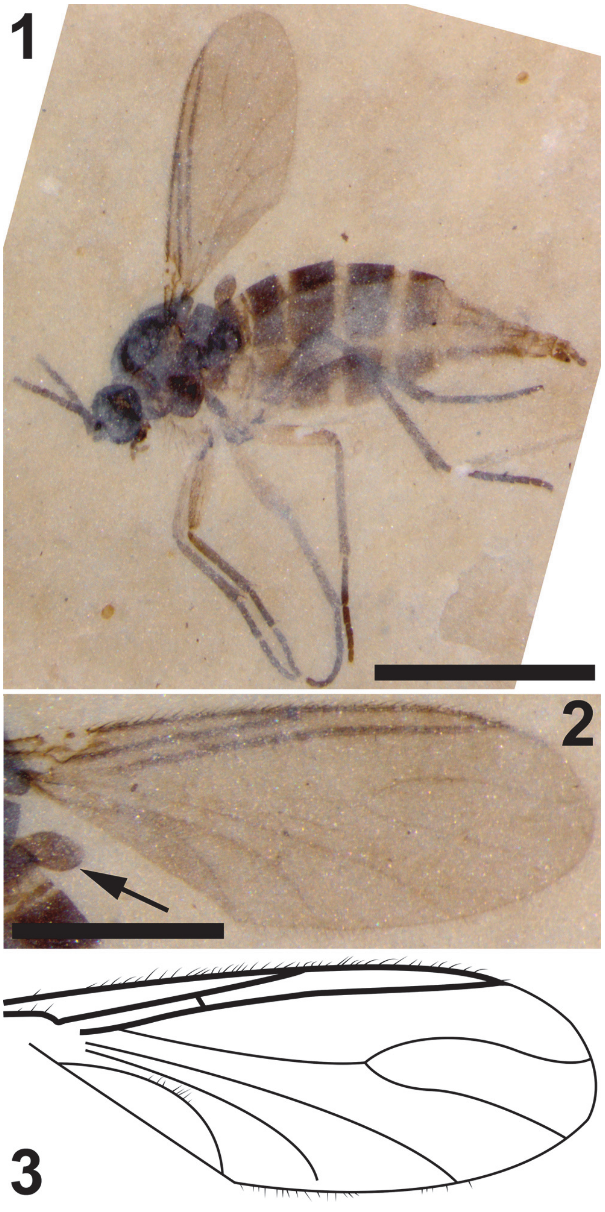

FIGURE 16. *Eosciarites hermes* sp. nov., USNM 624633. **1**, Habitus; **2**, Right wing, arrow points to the halter; **3**, Line drawing of the right wing. Scale bars equal 1.0 mm (**1**) and 0.5 mm (**2**).

katepisternum not attentuated. Haltere light brown, knob about 0.09 mm wide and 0.16mm long.

Legs. Setose, light brown basally, tibia and tarsi darker. Forecoxa with long setae along ventral margin, hind tibia with line of spines posteriorly; middle and hind tibia with one and possibly two apical spurs respectively, spurs longer than tibia diameter; foretibia with a spur longer than foretibial diameter on either side of a dark triangular area of setae (Figure 17.2).

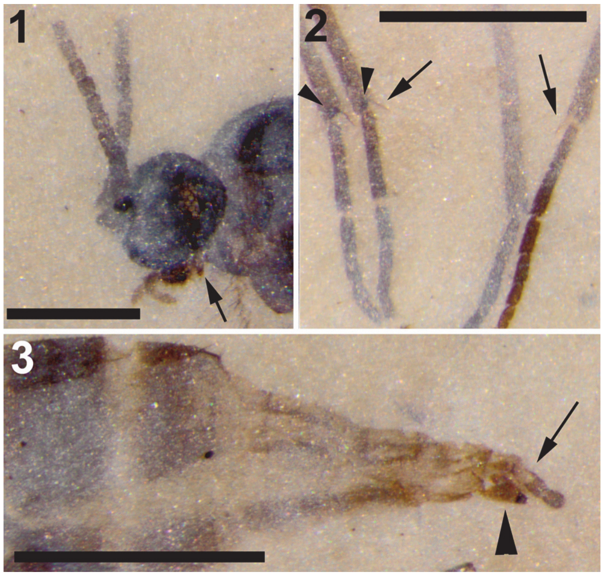

FIGURE 17. *Eosciarites hermes* sp. nov., USNM 624633. **1**, Head, arrow points to the labellum; **2**, Tibial spur of foreleg (left arrow) and tibial spur of midleg (right arrow). Arrowheads denote a small dark patch of setae; **3**, Terminalia, female. Arrow and arrow head denote the two-segmented cercus and sternite 10, respectively; Scale bars equal 0.3 mm (**1**) and 0.5 mm (**2**, **3**).

Wings. Length: 1.45 mm, width: 0.52 mm (Figure 16.2-3). Membrane with microtrichia, macrotrichia restricted to C, R_1 and R_{4+5}. C extending beyond apex of R_{4+5}, about half way to M_1. Sc short, free, R_1 significantly longer than half of R, R_1 with a short, brief posterior turn basally, ending well-short of medial fork. R_{4+5} reaching C well before wing tip. Rs oblique to R_{4+5}. Base of M and stem of M_4 both shorter than r-m cross vein, ratio of r-m to M-petiole 1:2.6. M_{1+2} inconspicuous, slightly longer than medial fork, M_1 and M_2 slightly divergent; cubital fork very long, with origin basal to origin of M_{1+2}. CuP inconspicuous or not preserved.

Abdomen and genitalia. Female, length 1.58 mm, brown; basal tergites wider than long. Tergites 3–5 with short setae at posterior margin; cercus two-segmented (Figure 17.3).

Allotype. Male unknown.

Syncompressions. Thysanoptera (1), Diptera (1).

Remarks

The family has 92 genera and 2,455 species, with a very complex taxonomy. *Sciara* Meigen, 1803, with approximately 700 extant species, is one of the most species-rich genera in the class Insecta — although many of these species may be misplaced. Sciara is the largest genus in the family Sciaridae and constitutes nearly 30% of the family's extant species. *Sciara* has obviously served as a default assignment for poorly preserved fossils; 89 of all 168 fossil Sciaridae are assigned to the genus (PBDB, 2018). Species epithets such as *rottensis*, *defectuosa*, *deperdita, diabolica*, *difficilis*, *ignorata*, etc. may reflect authors' frustrations in the identification of their fossil specimens (Heyden, 1870; Scudder, 1878; Meunier, 1904b). The presence or absence of macrotrichia on veins M and/or Cu is an essential morphological character in the identification of *Sciara*. A common question with fossil specimens is whether the macrothrichia were ever present or whether they were just not preserved. The near universal presence of these structures on the costal and radial veins however, should serve as an internal control. Neither macrotrichia nor their sockets are preserved in veins C, R_1 and R_{4+5} in the three species re-examined below.

While this new specimen does not appear to belong to the genus Sciara, due to the absence of macrotrichia on veins M, the fact that it is a female and the inability to determine morphological characters such as the absence or presence of a neck on the flagellomeres (Figure 17.1), make it difficult to assign the specimen to an extant genus. For an impression fossil, preservation of this specimen is exceptional, but although the claws do not appear to have teeth and the labial palps do not appear to have setae, their absence can not be definitively established. *Dolichociara* and *Angustosciara* can be eliminated due to the absence of macrotrichia on the M veins; *Sciarotrichia* can be eliminated due to the length of the terminal segments of its labial palps; *Edidapus* and *Pnyxia* can be eliminated as they lack a patch of anteroapical setae on their foretibia and the presence of an attenuated katepisternum; *Scatopsciara* can be eliminated due to R_1 less than half the length of R, *Euricrium* can be eliminated as it has an M fork bell-shaped, wider basally than distally; *Bradysia* is eliminated as its foretibia have two apical spurs; *Rhynchomegalosphys* and *Scythropochroa* can be eliminated as M+CuA is much longer than bm-m; *Ceratiosciara* is eliminated as it has strongly shortened convex flagellomeres; *Eugnoriste* is eliminated due to its greatly elongated mouthparts; *Cratyna* and *Archicratyna* are eliminated due to the presence of two midtibial spurs; *Hyperlasion* and *Cosmosciara* are eliminated due to the presence of an attenuated katepisternum (Menzel and Smith, 2017). This does not mean that the specimen does not belong to an extant genus. However, until additional specimens are collected that may assist in such an assignment, the generic epithet Eosciarites is provided.

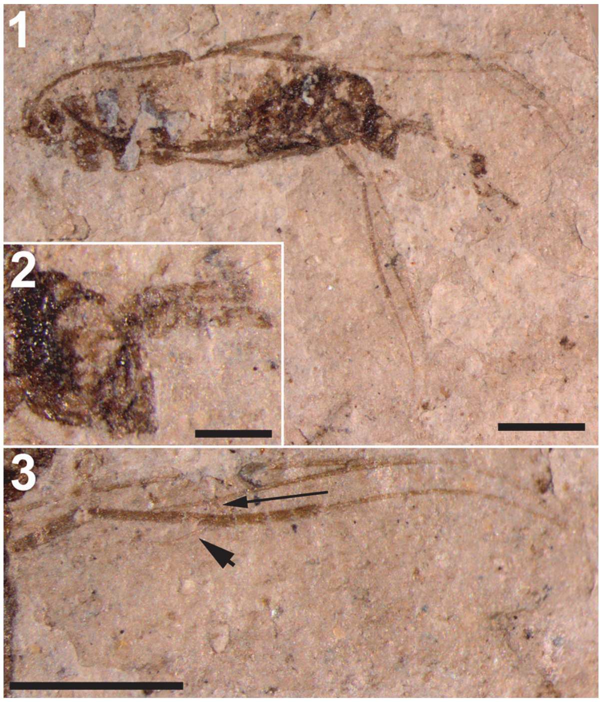

FIGURE 18. *Sciara florissantensis* Cockerell 1916, USNM 61995. **1**, Habitus; **2**, Head and antennae; **3**, Right forewing. Long arrow denotes 1st abscissa of Rs; the arrowhead points to remnants of the r-m crossvein. Scale bar equals 1.0 mm (**1**, **3**), 0.25 mm (**2**).

Sciara florissantensis Cockerell, 1917, reassigned.
Figure 18

Material examined. Holotype, USNM 61995, housed in the National Museum of Natural History, Washington, D.C., USA.

Type horizon. Florissant Formation, latest Eocene.

Type locality. Florissant, Colorado.

Remarks

Sciara florissantensis was described by Cockerell (1917a) as a male. The body length is 4.5 mm, wing 3.6 mm; wings hyaline, veins not setose; Sc colorless, R_1 long, its length 60% of R_{4+5}; r-m approximately 0.38 mm long, fork of media not preserved; first two antennal joints short and broad, following ones cylindrical, longer than broad; apical part of gonostyle slender (Figure 18.1-3). This specimen was not figured by Cockerell. Figure 18.3 herein shows that nothing of the medial or cubital veins is preserved. Although Cockerell pro-

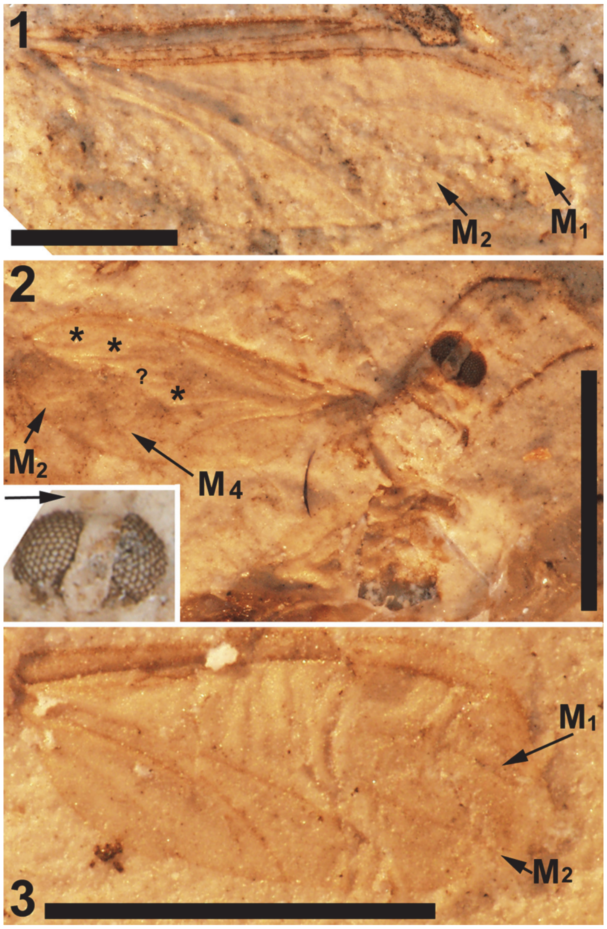

FIGURE 19. *Sciara gurnetensis* Cockerell, 1915, USNM 61435 and *S. lacoei* Cockerell, 1915, USNM 61436. **1**, *Sciara gurnetensis* (wing only). M_1 and M_2 labeled; **2**, *S. lacoei*, habitus. CuA_1 and distal portion of M_2 labeled. "Veins" under each of the three asterisks are artifacts; the "?" denotes the vein Cockerell identified as M_1. Inset: Head (Arrow points to base of antenna); **3**, *S. lacoei*, (#7583). M_1 and M_2 labeled. Scale bars equal 1.0 mm (**1**, **2**, **3**).

vided a measurement for the stem of M, this vein is not visible in the fossil. There is some pigmentation at the base of the costal cell, but the preservation of Sc is debatable — a tibia covers part of this portion of the wing. There is nothing to indicate that the specimen belongs to Sciaridae let alone *Sciara*. We therefore assign this specimen to Sciaroidea incertae sedis.

Sciara gurnetensis Cockerell, 1915, reassigned
Figure 19.1

Material examined. Holotype, USNM 61435, housed in the National Museum of Natural History, Washington, D.C., USA.

Type horizon. Bembridge Marls, UK, latest Eocene

Type locality. Gurnard Bay, Isle of Wight, UK

Remarks

Sciara gurnetensis was described, but not figured, by Cockerell (1916) as an isolated wing, 3.4 mm in length. However, the apical portion of the wing is deformed; its width is 1.27 mm. None of the veins have macrotrichia or remnants thereof. R_1 and R_{4+5} are 0.6 and 0.9 of the wing length. Both the base of M and the cubital stem are shorter than cross vein r-m; the stem and fork of M are 1.2 mm and 1.5 mm long, respectively (4:5). The very long "cubital fork" (actually M_4 originating very basally in the wing) in this species and in *S. lacoei* is seen in a few Cecidomyiidae, the rangomaramid genera *Ohakunea*, *Colonomyia* etc. and some mycetophilids. It is impossible to establish *Sciara gurnetensis* as a member of Sciaridae let alone *Sciara*. We, therefore, assign *S. gurnetensis* to Sciaroidea incertae sedis.

Sciara lacoei Cockerell, 1915, reassigned
Figure 19.2-3

Material examined. Holotype, USNM 61436, and specimen 7583, both housed in the National Museum of Natural History, Washington, D.C., USA.

Type horizon. Bembridge Marls, UK, latest Eocene

Type locality. Gurnard Bay, Isle of Wight, UK

Remarks

This fossil is of the dorsal aspect of the insect (Figure 19.2). The specimen is an impression fossil with the head, with well-preserved and clearly separated eyes, having formed a deep hemispherical depression in fine-grained mud; the face of the head contacted the bottom of the depression. Poorly preserved remnants of the basal antennomeres lie on the surface of the fossil above the hemispherical depression. The posterior portion of the head is not preserved and it is therefore impossible to determine whether or not an eye bridge is present.

C, R_1 and R_{4+5} are clearly present; Sc is absent (there is a gouge in the fossil at that point). R_1 and R_{4+5} extend to 0.48 and 0.89 of the wing's total length. The cubital veins are well preserved, but the medial veins are not. The fossil contains several creases that confound identification of these veins. In Cockerell's figure, there is a short apical portion of M_2 preserved, and this vein does indeed appear to be present in the fossil. M_1, labeled with a "?" in figure 18.3, if not a crease, takes an uncharacteristically straight path to the margin; the base of the medial fork appears to be too basal for Sciaridae. As discussed above, M_4 originating very basally in the wing in this species is seen in some Cecidomyiidae, Rangomaramidae and Mycetophilidae. The very long R_5 also suggests that *S. lacoei* is not a sciarid. We, therefore, assign this specimen to Sciaroidea incertae sedis.

A second specimen (#7583, also labelled USNM 61436) is not a type but is labelled *Sciara lacoei*. This specimen (Figure 19.3) is 1.7 mm long, although the end of the abdomen is not visible; it contains no structures of value other than the wing. The preserved portion of the wing (the apical portion is missing) is approximately 1.4 mm in length, the same length as that of the holotype. R_1 is preserved, but the end of R_{4+5} is not. Apical portions of M_1 and M_2 are preserved, but the base of the fork is not. This specimen appears to be a sciarid, although it is impossible to assign this specimen to *Sciara*; we assign it to Sciaridae incertae sedis.

Sciara protoberidis Cockerell, 1915, reassigned
Figure 20

Material examined. Holotype, USNM 61437, housed in the National Museum of Natural History, Washington, D.C., USA.

Type horizon. Bembridge Marls, UK, Latest Eocene

Type locality. Gurnard Bay, Isle of Wight, UK

Remarks

Sciara protoberidis is an insect body of 1.83 mm in length through tergite 5, 2.23 mm to the end of what may be the terminalia. Head not elongate. Wing length, 1.87 mm (left) and 1.71 mm (right), width 0.63 mm. No macrotrichia visible on any of the veins. Right wing R_1 and R_{4+5} 1.16 mm and 1.5 mm in length, respectively (7:9). Fork of M 0.73 mm in length, maximum width twice that at the wing's margin, as figured by Cockerell; stem of M not preserved, at most as long as fork, probably shorter. There are no morphological characters present that distinguish this specimen from the many genera of the family or the families within Sciaroidea. We assign *S. protoberidis* to Sciaroidea incertae sedis.

Family MYCETOPHILIDAE Newman, 1834
Genus RYMOSIA Winnertz, 1863

FIGURE 20. *Sciara protoberidis* Cockerell 1915, USNM 61437; Habitus. Distal portions of M_1 and M_2 labeled. Scale bars equal 1.0 mm.

Type species. *Mycetophila discoidea* Meigen, 1818, p. 268 = *Rymosia fasciata* (Meigen, 1804, p. 131); by designation of Johannsen, 1909, p. 102.

Rymosia hypnolithica Kerr, sp. nov.
Figures 21, 22

zoobank.org/8C1B7B7A-C82A-400D-AC71-CA596FF9DC50

Etymology. The specific epithet is a combination of the Greek terms hypnos (sleep) and litho (stone), meaning asleep in stone.

Holotype male. USNM 624134, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Dakin site, Middle Fork of the Flathead River (Pinnacle, Montana, USA.).

Differential diagnosis. This species of *Rymosia* is differentiated from all other fossils of the genus by the combination of its small size; cubital fork basal of r-m terminus; wings hyaline, without color; and heavily sclerotized gonostylus with dorsoapical process.

Description

Body length 3.50 mm (4.05 mm including genitalia), male, head and scutum black, abdomen light brown to brown, darkening distally (Figure 21.1).

Head. Ovoid, 0.5 mm high, 0.40 mm wide, vertex and face setose. Antenna with 14 flagellomeres, flagellomere two poorly defined, terminal flagellomere longer than wide, 0.40 mm wide, 0.10 mm long. Pedicel poorly defined, with two longer setae dorsally, approx. 0.60 mm and 0.10 mm in length, respectively (Figure 21.1).

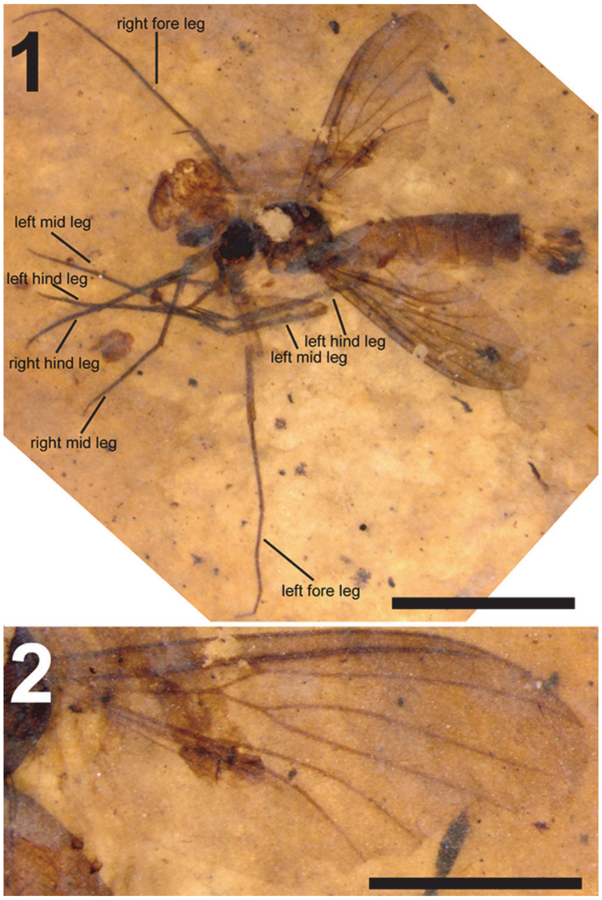

FIGURE 21. *Rymosia hypnolithica* sp. nov., USNM 624134, male. **1**, Habitus; **2**, Right forewing. Scale bars equal 2.0 mm (**1**), 1.0 mm (**2**).

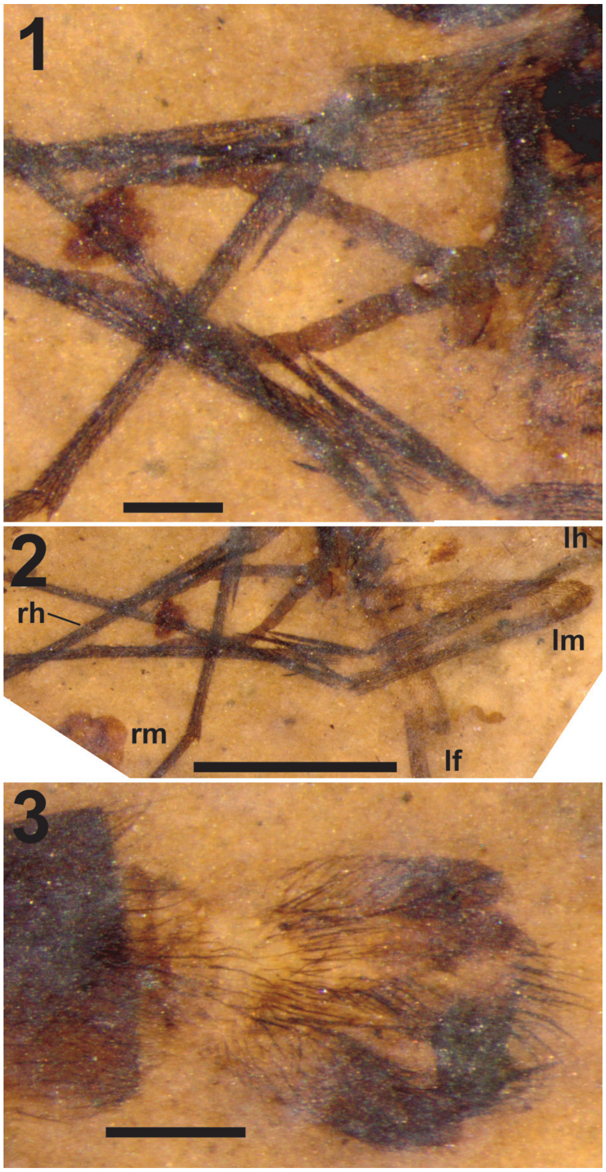

FIGURE 22. *Rymosia hypnolithica* sp. nov., USNM 624134, male. **1**, antennae; **2**, Spines and spurs of the legs; **3**, Terminalia. Abreviations: lf, lm, lh, rm and rh are left front, left mid, left hind, right mid and right hind legs respectively. Scale bars equal 0.25 mm (**1**, **3**) and 1.0 mm (**2**).

Thorax. Length 0.90 mm. Scutal setae on dorsal surface, proepisternal bristles present, but other pleura not distinguishable, a single pair of very long (0.44 mm) bristles at posterior end of scutellum.

Wings. Left wing, 2.75 mm long, 1.0 mm wide; right wing 2.65 mm long, 1.15 mm wide (Figure 21.2); wings hyaline, covered with microtrichia arranged in rows. Stem of M much shorter than fork (0.225 mm to 1.5 mm, left; 0.225 mm to 1.55 mm, right). Branches of anterior fork do not reach wing margin. M and CuA veins without setulae. CuP strong, extending beyond CuA + M_4 furcation.

Legs. Fore coxa, 0.48 mm long; fore and mid femur 0.92 mm and 0.96 mm, respectively [hind femur not observable]; tibia of fore, mid and hind legs, 0.86, 1.18 mm and 1.46 mm in length, respectively; tarsomeres (T1–T5) of fore leg, 1.02–1.08 mm, 0.52–0.54 mm, 0.36–0.38 mm, 0.28 mm and 0.22–0.24 mm in length, respectively; mid leg tarsomeres (T1–T5), 0.96 mm, 0.48 mm, 0.34–0.36 mm, 0.22–0.24 mm, and 0.16–0.20 mm in length, respectively; hind leg tarsomeres (T1–T5), 1.04 mm, 0.40 mm, 0.28 mm, 0.20 mm and 0.18 mm in length, respectively (Figure 22.2). All legs with setae in parallel rows. Tibial spurs 1: 2: 2; fore tibial spurs, 0.22–0.23 mm, tibial spurs at midleg 0.27 mm and 0.37 mm long, and tibial spurs at hind leg, 0.38–0.47 mm and 0.59 mm long.

Abdomen and genitalia. Length, 2.35 mm (not counting genitalia), width, 0.7 mm (at tergite 4), uniformly setose. Genitalia, 0.52 mm long, 0.52 mm wide; tergite nine with pair of elongate setae, approximately 0.4 mm long. Dorsal branch of gonostylus subovate with dorsoapical process measuring 0.09 mm, ventral branch of gonostylus elongate, heavily setose (Figure 22.3).

Allotype. Female unknown.

Syncompressions. None.

Remarks

The large family Mycetophilidae consists of 180 extant genera with 4,150 species and is distributed worldwide. There are 415 known fossil species, the oldest of which date from the earliest Cretaceous. Most (220) of the fossil mycetophilids are Eocene in age. The genus *Rymosia* s.l. (Kjærandsen, 2006; Søli et al., 2000) contains 87 extant species and eight fossil species, six of which are from the Eocene; *R. miocenica* Lewis, 1969 and *R. foersteri* Theobald, 1937 date to the Miocene and Oligocene respectively (PBDB, 2018).

Unfortunately, the original descriptions of *R. edwardsi* Cockerell, 1921 (Cockerell, 1921b)*, R. ferruginea* Cockerell, 1921 (Cockerell, 1921b)*, R. grisea* Cockerell, 1921 (Cockerell, 1921b) and *R. rufescens* Cockerell, 1921 (Cockerell, 1921b)*,* all from the Isle of Wight, were exceedingly terse. None of the specimens was identified as either male or female. All four descriptions, however, were accompanied by a figure of a wing. *Rymosia hypnolithica* differs from *R. edwardsi* in that the latter's wing is 5.1 mm long, two and three times that of the male and a possible female of the new species, respectively. In addition, the wing of *R. edwardsi* is markedly patterned. The cubital forks of *R. ferruginea* and *R. grisea* are quite basal of the medial terminus of r-m whereas these two points are nearly aligned in *R. hypnolithica*. While the stem of M_{1+2} in *R. grisea* is half the length of r-m, in *R. hypnolithica*, the two are nearly the same length. The wing of *R. rufescens* is about as long as that of the male of *R. hypnolithica,* but the wing of *R. rufescens* (and *R. ferruginea*) was reported to be reddish in color. Krzemiński et al. (in press) recently suggested that *Rymosia edwardsi* Cockerell, 1921, *R. ferruginea* Cockerell, 1921 and *R. rufescens* Cockerell, 1921, most probably belong to the tribe Mycetophilini. The body of *R. longicalcar* Meunier 1904 (Meunier 1904b) is 7 mm long vs. 3.5 mm for *R. hypnolithica*, its flagellomeres are twice as long as wide, and its cubital fork is distal to its medial fork. *Rymosia strangulata* Scudder 1890 is a nearly complete specimen, although the apical quarter of the wing and the genitalia are still buried under matrix material. Scudder (1890) stated that "the drawing is incorrect" and, in his figure, Rs and r-m are both missing. He also stated that "the stalk of the upper discoidal vein" as drawn was too long. The specimen is in the collections of Harvard University Museum of Comparative Zoology and a photograph (https://mczbase.mcz.harvard.edu/specimen_images/entomology/paleo/large/PALE-4967_Rymosia_strangulata_type.jpg) clearly shows a short r-m. The ratio of its length to the distance from the beginning of the fork in M to the anterior edge of the wing is 2.3; this ratio is 1.5 in *R. hypnolithica*.

Paratype specimens of *Rymosia hypnolithica* provide supportive morphological details. USNM 622565 is a paratype male with a dorsal view of the genitalia; USNM 626133 is a paratype male with black gonostyli with apical process and 9th (epandrial) sclerite with pair of long bristles. Male specimens USNM 626148 and USNM 621302 may constitute a distinct species, with gonostyli black, of a different form (more compact/elongate), without visible apical process. In addition, leg setation appears relatively longer and antennal segments more compact (not as long relative to width). Unfortunately, these fossils are not preserved with enough morphological detail to merit description of another new species at this time. USNM 623928 (male) represents an additional related, undescribed mycetophilid. Since the mycetophilids found here belong to more than one closely related species, and species are primarily distinguished by male features, the species identity of female USNM 624494, also an exechiine mycetophilid, remains uncertain.

Family RHAGIONIDAE Latreille, 1802
Genus LITOLEPTIS Chillcott, 1963

Type species. *Litoleptis alaskensis* Chillcott, 1963

Litoleptis araeostylus Greenwalt, sp. nov.
Figure 23

zoobank.org/A3D6DD5B-109E-4C06-84AD-110E46CF4C54

Etymology. The specific epithet is a combination of the Latin term araios (thin, narrow) and stylus and refers to the thin seta at the end of the flagellum.

Holotype. USNM 624657, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Dakin site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. This species of *Litoleptis araeostylus* is distinguished by its small size, cerci widely separated, tergum 9 short, partially retracted within T8, tergum 10 absent, majority or

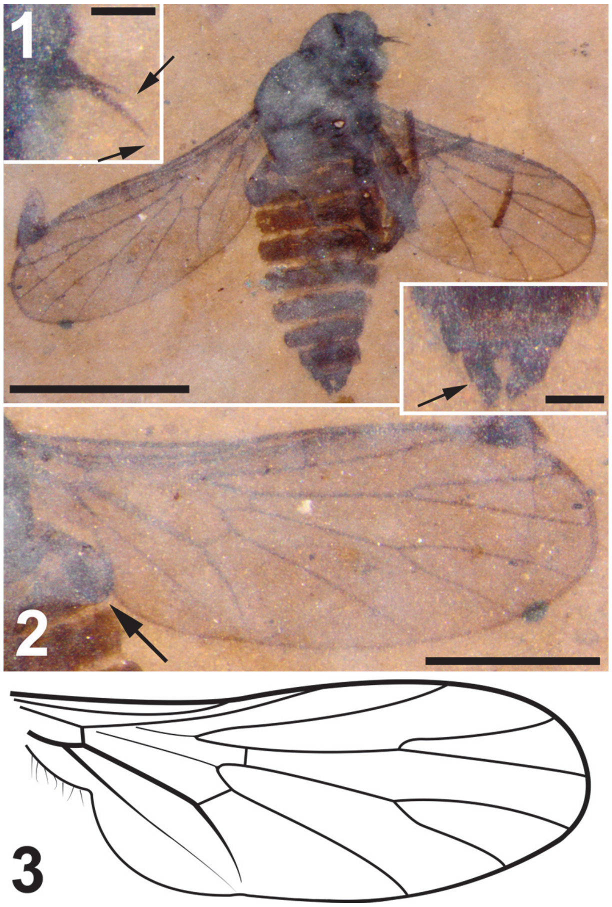

FIGURE 23. *Litoleptis araeostylus sp. nov.,* USNM 624657. **1***,* Habitus. Upper inset: Arrows denote the thin termini of the arista. Lower inset: genitalia, arrow denotes boundary between segments of the cercus; **2**, Left wing, arrow points to the halter; **3**, Line drawing of left wing. Scale bars equal 1.0 mm (**1**), 0.10 mm (**insets**), 0.50 mm (**2**).

entire length of the length of flagellum long, tapered, ending in a relatively long seta.

Description

Female (Figure 23.1) 2.0 mm in length, not including cerci; head and notum black, abdomen reddish brown.

Head. Unfortunately, it is difficult to determine if the visible basal-most portion of the antenna is the pedicel or the basal bulbous portion of F1. Observable antennal length 0.257 mm; if pedicel not visible (this portion of the antenna lacks setae), basal portion of F1 bulbous, 48 µm long x 60 µm long, with thin tapering style 157 µm long and 18 µm wide at its base; needle-like seta approximately 40 µm in length at its terminus.

Thorax. Wing, 1.72 mm long and 0.65 mm maximum width (Figure 23.2-3). Halter, 0.3 mm in length, knob, 134 µm wide and 180 µm long, stem 65 µm wide. Legs without tibial spurs.

Abdomen and genitalia. Abdomen, 1.18 mm in length and 0.65 mm wide at maximum width; lengths and widths of T7, T8 and T9, 0.46 x 0.13, 0.34 x 0.16 and 0.22 x 0.36 mm, respectively. Basal half of T9 appears to be withdrawn into T8 (Figure 23.1 inset). Spermatheca not preserved/ sclerotized. Cercus 2-segmented, lengths and widths of C1 and C2 60 x 46 µm and 50 x 40 µm, respectively.

Allotype. Male unknown.

Syncompressions. Thysanoptera (3), Chaoboridae (8), dipteran pupae (3), Diptera (1), Corixidae (1), Bibionidae (1), Hymenoptera (1), Aphididae (1), Hemiptera (1).

Remarks

The family Rhagionidae consists of 47 genera and 756 described species. There are 89 species of fossil Rhagionidae mostly in extinct Mesozoic genera. Of the fossil species, 57 date to the Mesozoic and 27 to the Eocene, with 21 of the latter in Baltic amber. The oldest known Rhagionidae s.l., *Gallia alsatica* Krzemiński and Krzemińska, 2003, is from the early Triassic. Solórzano Kraemer and Nel (2009) reviewed the fossil record of Rhagionidae. *Litoleptis* Chillcott, 1963 is a small genus with nine described extant members (Imada and Kato, 2016). The EDNA (EDNA, 2017) and Bishop Museum fossil insect databases (Evenhuis, 2017) list *Litoleptis* in the family Spaniidae Stuckenberg, 2001, a taxon proposed by Stuckenberg, but rejected by Kerr (2010). The subfamily Spaniinae Nagatomi, 1982, is unique within the Rhagionidae in the absence of a discal cell, tergite 9 short and withdrawn into T8, tibia, without spurs amongst other characters.

The only described fossil of *Litoleptis, L. fossilis* Arillo et al., 2009, from Lower Albian San Just amber (Spain) (Arillo et al., 2009), is not closely related to either *L. araeostylus* or the extant members of the genus, in that the costa does not extend around the wing margin but terminates at R_5, the tibia of the middle leg (the only preserved leg) has a spur as well as marked differences in the female genitalia (e.g., cerci not widely separated). It also differs from all other species of the genus in that the stem of R and M are both longer than their forks, with R_4 curving anteriorly, parallel to the terminal portion of R_{2+3}.

The six extant species of *Litoleptis* from Japan have been divided into two groups, one of which contains only *L. japonica* Imada and Kato, 2016.

This species is differentiated from the others by a number of characters, including the presence of a long stout seta at the tip of the flagellomere, a character shared by *L. araeostylus*. *Litoleptis japonica* is differentiated from *L. araeostylus* by its larger size, 3.4 mm wing length vs. 1.7) and wing longer than body. *Litoleptis araeostylus* differs from *L. chilensis* Hennig, 1972, in that the latter has the fork of R$_{4+5}$ distal of the fork of M$_{1+2}$, CuA reaching the wing margin and wing 3.0 mm long (Hennig, 1972). *Litoleptis orientalis* is larger than *L. araeostylus* (2.7 mm wing length vs. 1.7 mm), and the fork of R$_{4+5}$ is distal to the fork of M$_{1+2}$. *Litoleptis alaskensis* Chillcott, 1963, also has the fork of R$_{4+5}$ significantly distal to the fork of M$_{1+2}$; it also lacks the needle-like seta at the terminus of the flagellum (Chillcott, 1963).

Litoleptis is distributed worldwide, albeit sparsely, with extant specimens described from Alaska, Japan and the Philippines. It is of particular interest to note that, while a number of rhagionids are hematophagous, the larvae of *Litoleptis* are obligate miners of liverwort thalli (Imada and Kato, 2016), with species restricted to a single genus of host. Of those species whose host is known, only *L. japonica* feeds on a species in the liverwort family Conocephalaceae Grolle, 1972. There are 13 fossil species of the genus *Rhagio* Fabricus, 1775 (Evenhuis, 2017); the holotype of one of these, *Rhagio fossitus* (USNM 112626), is housed at the NMNH and is refigured here (Figure 24). Although the posterior margin of the wing is not preserved, the separation between the distal termini of CuP and CuA suggests the presence of an open anal cell, a characteristic that distinguishes *Rhagio* from all other genera in the family Rhagionidae. The specimen is left as is without additional comment.

Family ASILIDAE Latreille, 1802

Genus KISHENEHNOASILUS Dikow, gen. nov.

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Type species. *Kishenehnoasilus bhl* Dikow, gen. et sp. nov., by monotypy.

Figures 25, 26

Etymology. *Kishenehn* refers to the Kishenehn formation from which this species is described, *asilus* is a common part of generic names in Asilidae: Asilinae. Refers to the placement of this genus in the Asilinae and is to be treated as masculine.

Holotype. USNM 624491, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Dakin site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. Small asilid flies, with antennal postpedicel tapered distally and a simple cylindrical stylus; compound eye posterior margin straight or slightly curved throughout; cells r$_1$, m$_3$, and cua closed and petiolate; all femora expanded; femora and tibiae with numerous macrosetae in rows; presutural and postsutural dorsocentral macrosetae present; female with ovipositor comprised of 8th and following segments.

Kishenehnoasilus bhl Dikow, sp. nov.

Figures 25, 26

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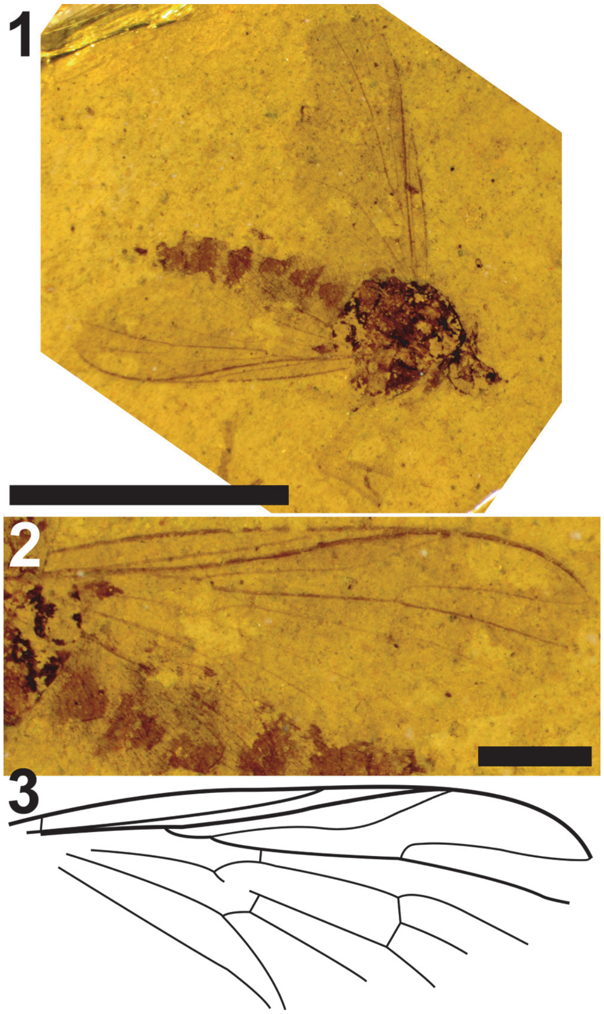

FIGURE 24. *Rhagio fossitus* Melander, 1949. USNM 112626. **1**, Habitus; **2**, Right wing; **3**, Line drawing of right wing. Scale bars equal 5.0 mm (**1**) and 1.0 mm (**2**).

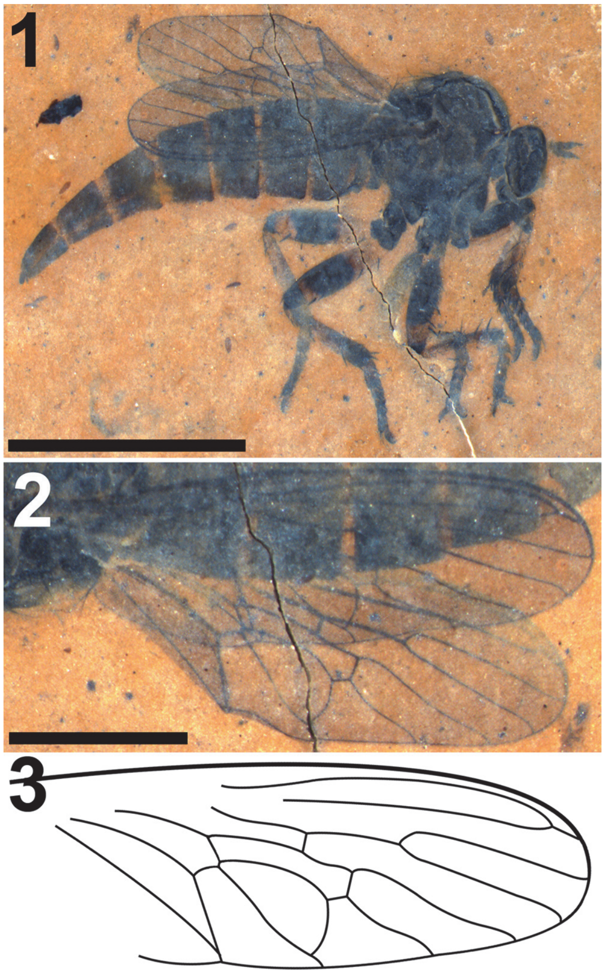

FIGURE 25. *Kishenehnoasilus bhl* gen. et sp. nov., USNM 624491, female. **1**, Habitus; **2**, Wings; **3**, Drawing of wing (composite). Scale bars equal 5.0 mm (**1**) and 2.0 mm (**2**).

Etymology. The specific epithet refers to the Biodiversity Heritage Library (www.biodiversitylibrary.org), abbreviated BHL and pronounced "bee aitch el", and is to be treated as a noun in apposition. *Kishenehnoasilus bhl* sp. nov. is providing us a window in to the past and so is the digitization effort of the BHL by making available digitally natural history literature with emphasis on publications published prior to 1923.

Description

Female (Figure 25.1), 12 mm in length, including genitalia; head, thorax and abdomen black.

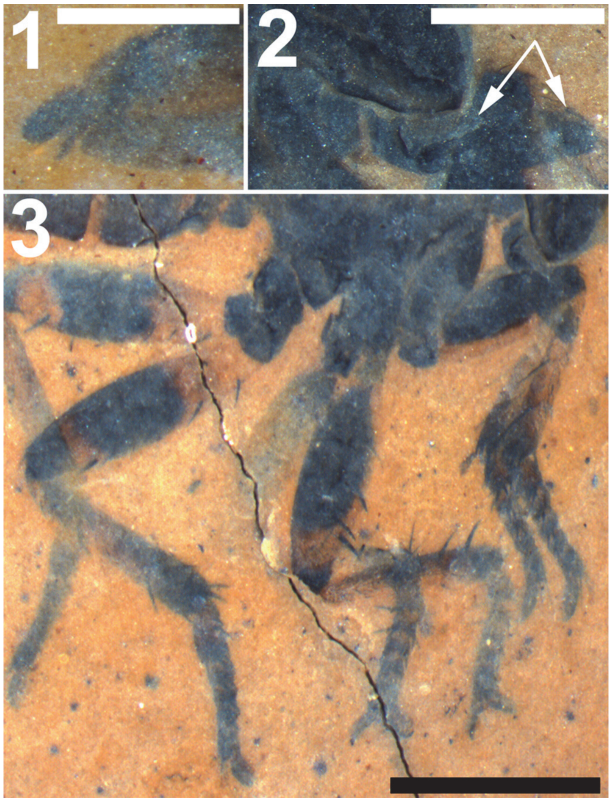

FIGURE 26. *Kishenehnoasilus bhl* gen. et sp. nov., USNM 624491, female. **1**, Terminalia; **2**, Proboscis, arrows point to the distiproboscis; **3**, Legs. Scale bars equal 0.5 mm (**1**) 1.0 mm (**2**) and 2.0 mm (**3**).

Head. Head shape in anterior view not observable, black; vertex shape not observable; facial swelling not observable, pubescence not observable; mystax not observable, mystax extent not observable; ommatidia size not observable; postgena posterior margin simple, smooth; frons (at level of antennal insertion) not observable, pubescence not observable, setation not observable; ocellar tubercle not observable, setation not observable; vertex pubescence not observable, setation not observable; median occipital sclerite setation not observable; postocular (pocl) setae not observable; occiput setation not observable, pubescence not observable; compound eye posterior margin straight or slightly curved throughout (in lateral view). Proboscis and maxillary palpus: proboscis straight, black; postmentum plate-like, straight, setation not observable; prementum cross section not observable, dorso-median development not observable, setation not observable; labella rounded; maxillary palpus not observable; stipites not observable (Figure 26.2).

Antenna. Black, pubescence not observable; scape not observable; pedicel setation not observable; postpedicel tapering distally, asetose; stylus comprised of one element, asetose; apical seta-like sensory element situated apically on stylus.

Thorax. Dark brown to black; prosternum not observable; proepisternum not observable; cervical sclerite not observable; antepronotum not observable; postpronotum not observable; postpronotal lope not observable; pleuron pubescence not observable; proepimeron not observable; anepisternum setation not observable; anterior basalare not observable, posterior basalare not observable; setation of anepimeron, katepisternum, katepimeron, katatergite, meron + metanepisternum, metakatepisternum, metepimeron, and anatergite not observable; scutum pubescence not observable, scutum setation only partially observable: one npl seta, spa and pal setae absent, two presutural and two postsutural dc macrosetae, acrostichal setae not observable, median posterior scutum setation not observable; scutellum pubescence not observable, ds sctl setae not observable, ap sctl setae present, two long macrosetae; postmetacoxal area not observable.

Leg. Light brown to brown, pubescence not observable, all setae circular in cross section (Figure 26.3); pro coxa black, pubescence not observable, asetose; pro femur black, no macrosetae, setation not observable; pro tibia light brown to brown, short black setose, black macrosetose: three long in one ventro-posterior row, four short in 1 posterior row, distal tip with four thick, black, medium length macrosetae; mes coxa black, pubescence not observable, asetose; mes femur black, distally brown, short black setose, black macrosetose: 2 long in one anterior row distally, two long in one ventral row; mes tibia light brown to brown, short black setose, black macrosetose: three long in one anterior row, two to three short in distal ½ anteriorly and dorsally; met coxa black, pubescence not observable, asetose, anteriorly without any protuberance; met trochanter setation and median shape not observable; met femur black, brown proximally and distally, short black setose, black macrosetose: two long in one anterior row distally, five long in one antero-ventral row; met tibia light brown to brown, straight, short black setose, long black macrosetose: four in one antero-dorsal row, one to two in one antero-ventral row distally, two to three antero-distally; proximal pro and mes tarsomeres slightly longer than tarsomere two, proximal met tarsomere as long as following two tarsomeres combined, pro tarsomeres short black setose dorsally, longer black macrosetose ventrally; mes tarsomeres short black setose dorsally, longer black macrosetose ventrally, met tarsomeres short black setose dorsally, longer black macrosetose ventrally; pulvilli well-developed (as long as claw); claw abruptly angled distally, pointed; empodium setiform, minute or entirely absent.

Wing. Length, 6.3 mm, hyaline, evenly microtrichose (Figure 25.2-3); C circumambient, R_{2+3} distally relatively straight, r_1 closed, R_1 and R_{2+3} meet apically and form a stalk vein (petiolate); R_4 terminating anterior to wing apex, relatively straight, stump vein (R_3) absent; r_4 open, R_4 and R_5 more or less parallel; R_5 terminating posterior to wing apex; r_5 open; M_1 terminating posterior to wing apex; cell d closed by base of M_2 and m-m, M_2 and m-m not aligned, r-m situated in distal half; m_3 closed and petiolate; cua closed and petiolate; alula not observable; microtrichia on posterior wing margin arranged in a single plane.

Abdomen. Black, tergites smooth, setae with small sockets only; T1 setation and pubescence not observable, dorsal surface smooth, without protuberances; T2–8 entirely sclerotized, predominantly black, pubescence not observable, setation in general not observable (some distal setae on T6–7 discernible), marginal macrosetae absent from T2–8, medial macrosetae absent from T2–8; S1–8 color, setation and pubescence not observable, asetose.

Female abdomen. T7 and S7 without modifications, ovipositor comprised of 8th and following segments, T6–8 pubescence and setation not observable; T8 internal apodeme not observable, S8 keel-like throughout; T9 and T10 not fused, T10 undivided (single sclerite), acanthophorite spines absent (Figure 26.1).

Allotype. Male unknown.

Syncompressions. None.

Remarks

Kishenehnoasilus gen. nov. clearly belongs to the Asilinae. Although it is in general well-preserved, few characters can be observed that would help to provide more information on it's placement within this diverse taxon. Features that support the placement within the Asilinae are (1) antenna (postpedicel tapering distally, stylus comprised of one element, apical seta-like sensory element situated apically on stylus), (2) wing venation (r_1 closed, R_4 and R_5 more or less parallel, cell d closed by base of M_2 and m-m, m_3 closed and petiolate, cua closed and petiolate, Figure 25), (3) prothoracic and mesothoracic coxae orientation (directed ventrally and not posteriorly), (4) femora development (all femora expanded), (5) development of dorsocentral (dc) macrosetae (prominent pre- and postsutural dc setae present), (6) abdomen shape (somewhat tapered abdomen), and (7) ovipositor development (elongated, simple for placing eggs on vegetation or dropping them to the ground; Figures 25.2, 26.1 and 26.3).

Dikow (2009) published a comprehensive morphological phylogeny of Asilidae in which some 32 species from 29 Asilinae genera (of 183 currently known genera) were included. The relationships among these genera could not be resolved in much detail based on the characters employed. Despite the general good preservation of *Kishenehnoasilus bhl* sp. nov., it cannot be placed within this phylogeny because of the many features that cannot be observed. A more in-depth phylogeny of Asilinae is in preparation by Rodrigo Vieira (personal commun.), and it is hoped that the findings in that study will shed some light on the relationships within Asilinae and of *Kishenehnoasilus bhl* sp. nov.

Notes on *Asilopsis fusculus* Cockerell, 1921

While preparing the description of *Kishenehnoasilus bhl* sp. nov., it seemed important to reexamine the holotype of *Asilopsis fusculus*, which is deposited in the NMNH. This fossil (Figure 7.1-2) is based on a single, partially broken wing, which might make a placement difficult. It was immediately obvious that the wing does not have any features of an Asilidae, but that it clearly belongs to another family. Through the help of Jon Gelhaus and Herman de Jong, we established that the wing venation is similar to that of Cylindrotomidae (Tipuloidea) and *Asilopsis fusculus* is here transferred to that family (see under Cylindrotomidae for a redescription and further comments).

Family DOLICHOPODIDAE Latreille, 1809
Subfamily MEDETERINAE Fischer von Waldheim, 1819
Genus SALISHOMYIA Bickel, gen. nov.

zoobank.org/DD02F2B7-F02B-4083-92BF-B2D10F4B30B3

Type species. *Salishomyia eocenica* Bickel, gen. et sp. nov., by monotypy.

Figure 27

Etymology. *Salishomyia* is a combination of the name of the indigenous Salish people who inhabited the region in Montana where the Kishenehn formation occurs (and who were referred to by outsiders as “Flatheads”), and “myia” from Greek meaning “fly”. The gender is feminine.

Holotype. USNM 622501, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

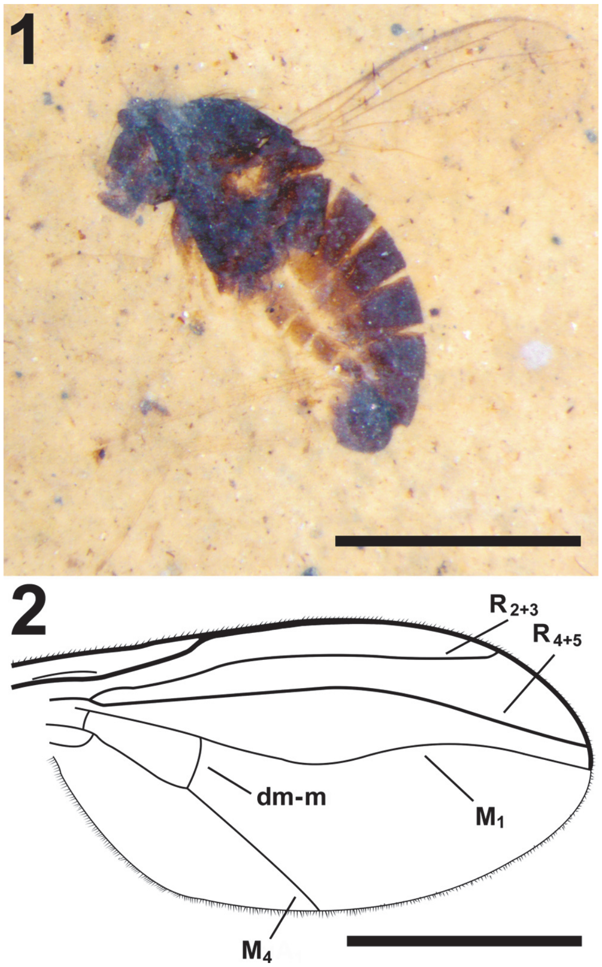

FIGURE 27. *Salishomyia eocenica* sp. nov., USNM 622501. **1**, Habitus; **2**, Right wing. Scale bars equal 1.0 mm (**1**) and 0.5 mm (**2**).

Type horizon. Middle Eocene Coal Creek member, Kishenehn Formation.

Type locality. Dakin site, Middle Fork of the Flathead River (Pinnacle, Montana).

Differential diagnosis. Small (<1.5 mm body length) flies in the subfamily Medeterinae; antenna short; postpedicel subrectangular and rounded, with apical arista, dorsal postcranium concave; posterior mesonotum apparently flattened; legs elongate, without strong setation and without evidence of anterior preapical setae on femora II and III; hypopygium with epandrium spheroidal and fully exserted, not enclosed by anterior postabdominal segments; wing rather broad; R_{2+3} joining costa at 5/6 distance from base; R_{4+5} in gentle anterior arc and joining C just anterior to wing apex; vein M basally diverging from R_{4+5}, and at midlength with gentle bend to arch forward towards R_{4+5} with the two veins becoming subparallel in distal sixth of wing, and M joining margin at apex; crossvein dm-m positioned basally, with ratio of length of dm-m crossvein/distal section M_4 = 0.3.

Salishomyia eocenica Bickel, sp. nov.
Figure 27

zoobank.org/ACCE57D9-7CDD-49F8-ADAF-8E2674E9124A

Etymology. The specific epithet refers to this species' occurrence in the Eocene period.

Description

Male, body length: 1.7 mm (Figure 27.1).

Head. Ovate in lateral view; dorsal postcranium concave and appearing to partially enclose anterior mesonotum; palp with short apical seta; proboscis short, subrectangular; antenna short; postpedicel subrectangular and rounded (possibly reniform) with apical arista; arista threadlike and shorter than head height.

Thorax. Dark brown to black; dorsal setae (probably dorsocentral setae) evident; posterior mesononotum distinctly flattened, scutellum with distinct lateral and median setae.

Leg. Coxa I apparently infuscated basally, with coxae II and III yellowish; remainder of legs apparently yellow, with little evident setation and no indication of anterior preapical setae on femora II and III; [relative lengths of podomeres are representative ratios, not measurements and given in the following formula and punctuation for each leg: femur; tibia; tarsomere 1/ 2/ 3/ 4/ 5]; leg I: 3.7; 3.6, distal podomeres obscured; leg II: all podomeres obscured; leg III: 4.0; 3.4; 1.0/ 1.2/ 0.6/ 0.4/ 0.4.

Wing. Length and width, 1.4 and 0.7 mm (Figure 27.2); hyaline, C reaches wing apex, joining vein M; R_{2+3} joining costa at 5/6 distance from base; R_{4+5} in gentle anterior arc and joining costa just anterior to wing apex; M basally diverging from $R_{4+5,}$ and at midlength with gentle bend to arch towards R_{4+5} with the two veins becoming subparallel in distal sixth of wing, and M joining margin at apex; crossvein dm-m positioned basally, with ratio of length of dm-m crossvein/distal section M_4 = 0.3; lower calypter and halter not visible.

Abdomen. Tergites with only short setation, without long marginal setae; tergite one short and adjacent to metapostnotum; tergites two to five each well-developed, with corresponding sternite; tergite six prominent; hypopygium spheroidal with short digitiform surstylus; cercus subtriangular; hypandrium (or phallus?) curved and projecting beyond hypopygium near sternite 5.

Allotype. Female unknown.

Syncompressions. None.

Remarks

The family Dolichopodidae comprises some 7,300 species in 230 genera in the recent fauna. It is often rich and abundant in Tertiary amber deposits, a result of their use of tree trunks for both feeding and mating, thereby increasing their chance of becoming entrapped by resin flows. Dolichopodids are also numerous in marine and lacustrine littoral habitats and correspondingly are known as compression fossils from a number of fine-grained lacustrine deposits. The new genus *Salishomyia* from the Kishenehn Formation clearly belongs to the dolichopodid subfamily Medeterinae, based on the following characters: antenna short; postpedicel subrectangular and rounded (possibly reniform) with apical arista, dorsal postcranium concave; posterior mesonotum apparently flattened; legs without strong setation, femora II and III without preapical setae, hypopygium large and external, not enclosed by anterior postabdominal segments. *Salishomyia* appears to have a classical *Medetera*-like venation, with vein M basally diverging from $R_{4+5,}$ and at midlength bending gently to arch forward towards vein $R_{4+5.}$ However, in *Medetera*, the dm-m crossvein connects M_4 with M at the bend in vein M, while in *Salishomyia,* the dm-cu crossvein is positioned basad of the vein M bend, and the wing is broader. This wing character is diagnostic for *Salishomyia.*

The Kishenehn Formation dolichopodid fauna, as of 2017, consists of 78 specimens. Other than *Salishomyia eocenica*, 30 additional specimens are of potential interest. Among these are two species in a genus near *Hercostomus* Loew (possibly *Gymnopternus* Loew), one with six males (USNM 621409, 622506, 622656, 625273, 625526 and 626174) and the other with one male (USNM 621182) and two females (USNM 622026 and 624021) of uncertain specific association. The two species can be separated by the shape of surstyli projecting from the hypopygium. *Hercostomus* acts as a cosmopolitan "holding genus" for many described species and remains poorly defined and is undoubtedly a polyphyletic assemblage (Brooks, 2005). Although additional work is needed to resolve the phylogenetic relationships of this complex cosmopolitan genus, it is important to note the presence of *Hercostomus*-like species in the Kishenehn formation to demonstrate regional historical-biogeographical relationships. The genus *Gymnopternus* is closely related to *Hercostomus*; *Gymnopternus lacustris* was described from the

Miocene Florissant beds of Colorado (Bickel, 1995).

There are a number of additional specimens that are of interest but lack critical morphological detail. These include: 1) a species with some similarities to the recent genus *Chrysotimus* Loew but with a slighter build and an enlarged hypopygium (12 specimens, both males [USNM 620106, 620817, 621111, 622587 and 623229] and females [USNM 621246, 621939, 623788, 623828, 624434, 712964 and 712965]), 2) a species where veins R_{4+5} and M bowed with respect to each other beyond the dm-m crossvein (three females [USNM 609598, 624638 and 712963] and one male [USNM 620605]), 3) a species with similar venation to "*Chrysotus molestus* Meunier" (which is not in the genus *Chrysotus*) from Baltic amber, with a wide wing and vein M ending well behind the wing apex (two females [USNM 620633 and 620464] and a possible male [USNM 620994]), 4) a species possibly near the abundant Baltic amber genus *Palaeomedeterus* Meunier (one male [USNM 624586]), and 5) a species appearing similar to the recent genus *Rhaphium* Meigen (one male [USNM 620398]).

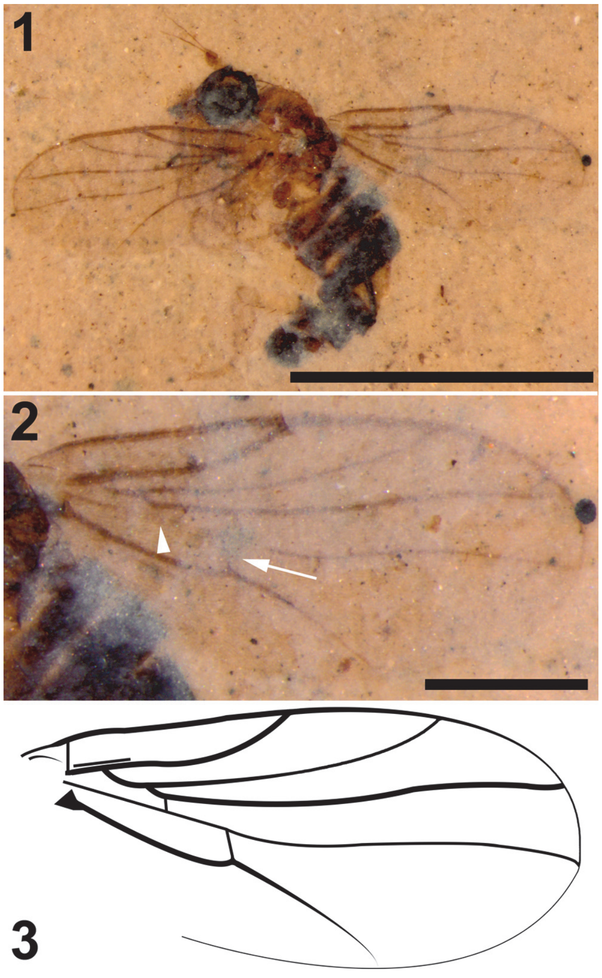

FIGURE 28. *Drapetis adelomedos* sp. nov., USNM 621705. **1**, Habitus; **2**, Right wing. Arrowhead and arrow denote r-m and m-cu cross veins respectively; **3**, Line drawing of wing. Scale bars equal 2.0 mm (**1**) and 0.5 mm (**2**).

Family HYBOTIDAE Macquart, 1827
Genus DRAPETIS Meigen, 1822

Type species. *Drapetis exilis* Meigen, 1822

Drapetis adelomedos Greenwalt, sp. nov.
Figures 28, 29

zoobank.org/A993F24D-BC6A-4035-B36A-02E3DFE65FE1

Etymology. The specific epithet is derived from the Greek words adelos (obscure) and medos (plan) and references the lack of preserved morphological detail of the genitalia.

Holotype. USNM 621705, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Tunnel Creek site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. Antenna with long terminal arista-like stylus, pedicel with marginal setae but without visible ventral bristle; proboscis stronger at

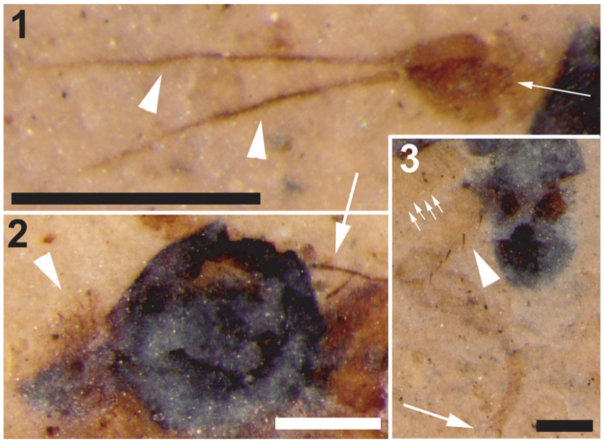

FIGURE 29. *Drapetis adelomedos* sp. nov., USNM 621705.**1**, Antennae. Arrow denotes a row of setae at the apical margin of the pedicel and arrowheads point to setae on the arista; **2**, Head. Arrow denotes two occipital bristles. Arrowhead points to setae at base of proboscis; **3**, Hind leg and terminalia. Arrowhead points to posteroventral femoral spines; four small arrows denote short setae on the hind femur; large arrow points to the claws. Scale bars equal 0.25 mm (**1**), 0.2 mm (**2, 3**).

base. One pair of vertical bristles visible on head. Rs longer than bm-cu cross vein, cell br much shorter than cell bm, cell dm absent, and radial and medial veins not forked; cup absent/not visible, CuP very weak. Scutum about as long as broad.

Description

Male. (Figure 28.1). Length, including terminalia, 2.5 mm.

Head. (Figure 29.1-2). Black/dark brown, spherical, diameter 0.4 mm, dark. Proboscis subtriangular in shape, 0.22 mm in length, 0.12 mm wide at base, heavily setose at base. Antennae reddish brown, 0.52 mm in length with apically concave pedicel with marginal fringe of short setae; first flagellomere triangular, concave at base, 90 µm long, 67 µm wide, L/W = 1.35. Arista 0.35 mm long, covered with short setae, approximately 8 µm in length. Head with one pair of occipital bristles, about 0.1 mm in length.

Thorax. Redish, 0.73 mm long, scutum barely longer than wide, as long as head.

Wings. (Figure 28.2-3). Length, 1.75 mm (right), width 0.8 mm; hyaline; microtrichia arranged in parallel longitudinal lines; costal setulae well developed; Rs about one-third length of cell bm, longer than bm-cu cross vein, cell br length about half that of cell bm; R_{2+3} strongly arched upwards, extending to beyond midlength of wing, R_{4+5} slightly sinuous, barely divergent from M_{1+2}; crossvein r-m nearly transverse, dm-m less so.

Legs. Forelegs and middle legs not preserved; hind femur with row of several short weakly sclerotized posteroventral bristles (Figure 29.3); hind tibia 0.52 mm long, 0.12 mm wide, with posteroventral row of stout bristles, about 0.06 mm in length. Hind tarsus 0.75 mm in length, 1st tarsal segment longest, 0.34 mm long.

Abdomen and genitalia. 1.37 mm in length, reddish/dark brown. Details of the male genitalia not preserved.

Allotype. Female unknown.

Syncompressions. None.

Remarks

The family Hybotidae consists of 2,005 species in 75 genera. It contains 48 described fossils, most (27) of which are from the Eocene. The genus *Drapetis* was originally separated into two subgenera, *Drapetis* and *Crossopalpus* Bigot, 1857, by Melander (1918), but the two are now recognized as separate genera. *Crossopalpus*, which contains 34 species, is distinguished by the pedicel with a distinct ventral bristle. *Drapetis*, with 156 extant species, is represented in the fossil record by six species, five in Baltic amber (Meunier, 1908) and one, *D. dissentis* Solórzano Kraemer et al., 2005, from Miocene Chiapas amber. The Chiapis specimen and the Baltic amber species described by Meunier are all smaller than *D. adelomedos*, ranging from 0.75 to 1.75 mm in length. Other differences exist. *Drapetis brevis* Meunier, 1908 has a subapical arista and r-m and m-cu nearly touching. In our view, this specimen does not belong to *Drapetis* and is here designated as Hybotidae undetermined. *Drapetis decolorata* Meunier, 1908 has cell bm triangular in shape, with origin of m-cu cross vein at the level of the Rs fork. *D. vitiosum* Meunier, 1908 has m-cu origin much closer to the level of the Rs fork than the R_1 terminus. However, CuP of *Drapetis*, when present, is weak, faint and concave (absent in *D. adelomedos*) whereas CuP in *D. vitiosum* is figured by Meunier as strong and distinctly convex. *Drapetis vitiosum* does not appear to belong to *Drapetis* and is here designated as Hybotidae undetermined. *Drapetis decoratum* Meunier, 1908, has a single apical tibial spine. Its wings were not figured by Meunier, who described them as “a little longer than the body and quite wide. Length = ¾ mm.” Given the absence of a detailed description of the venation, these specimens (both the male and female were described) must be re-examined before they can be reliably assigned to the genus *Drapetis*. *Drapetis mortuum* Meunier, 1908, has F1 convex at its base and an L/Wmax ratio = 2.2 (vs. 1.3 for *Drapetis sp.*). *Drapetis dissentis* differs from *D. adelomedos* in that its R_{4+5} is strongly divergent from M_{1+2}.

Family PLATYPEZIDAE Latreille, 1829
Genus AGATHOMYIA Verral, 1901

Type species. *Callomyza antennata* Zetterstedt, 1819

Agathomyia eocenica Tkoč, sp. nov.

Figures 30, 31

zoobank.org/AD4A9FE2-B217-444B-84BA-770423E2F470

Etymology. The specific epithet, a Latin adjective, refers to the geologic epoch (Eocene) in which this species lived.

Holotype. *Agathomyia eocenica* Tkoč, female; NMNH, USNM 553697.

Type horizon. Middle Eocene Coal Creek member, Kishenehn Formation.

Type locality. Dakin site, Middle Fork of the Flathead River (Pinnacle, Montana).

Differential diagnosis. This species has the typical wing shape and wing venation of *Agathomyia*,

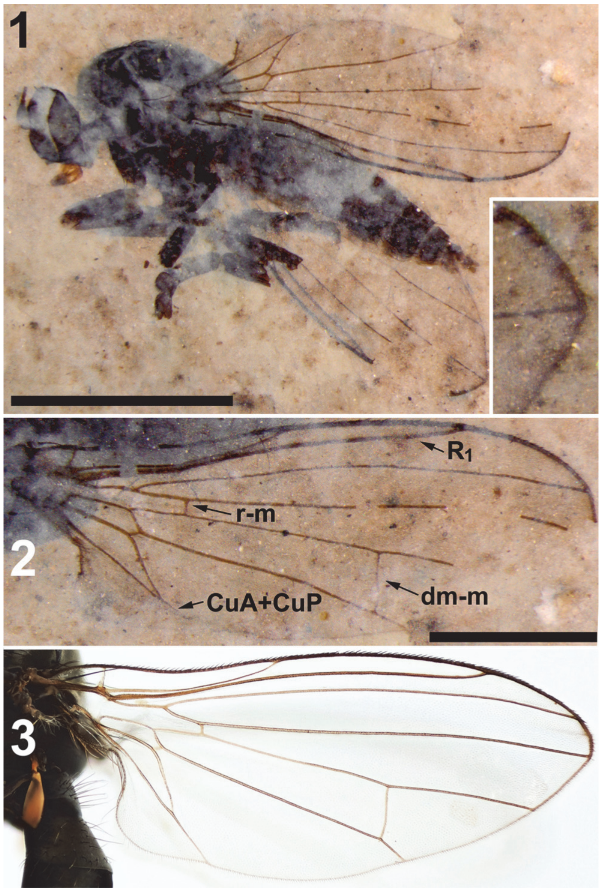

FIGURE 30. *Agathomyia eocenica* sp. nov., USNM 553697. **1**, Habitus; **2**, Left wing; **3**, Wing of extant species *Agathomyia antennata*. Scale bars equal 2.0 mm (**1**) and 1.0 mm (**2**). Inset: Apical terminus of R_{4+5} at costa (right wing).

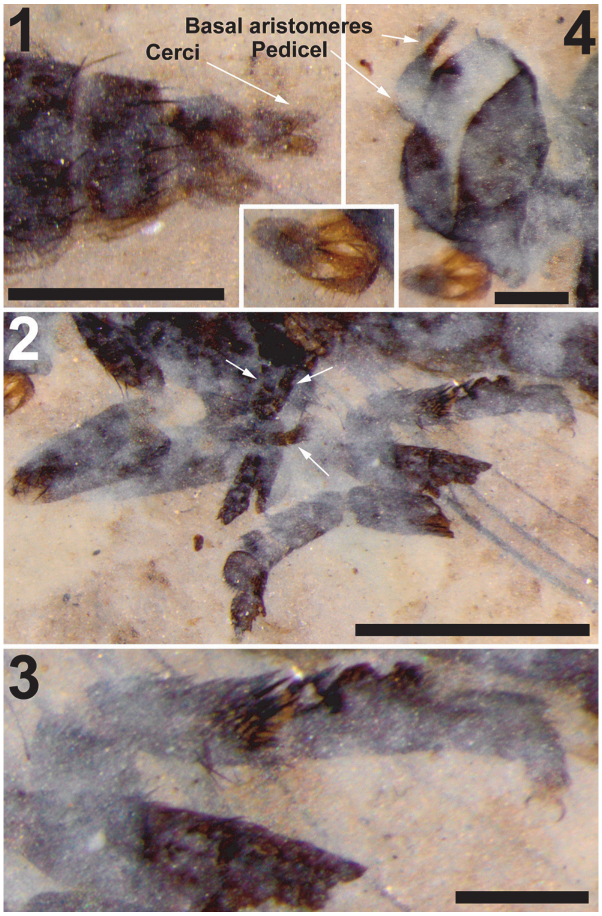

FIGURE 31. *Agathomyia eocenica* sp. nov., USNM 553697. **1**, Terminal part of abdomen; **2**, Legs. Arrows point to three tarsi of the front and middle legs; **3**, Hind leg; **4**, Head. Long arrow denotes apical marginal setae of the pedicel, short arrow denotes several basal aristomeres – the terminal aristae are missing. Inset: Labellum with postero-ventral setae. Scale bars equal 0.5 mm (**1**), 1.0 mm (**2**) and 0.25 mm (**3**, **4**).

i.e., it has seven longitudinal veins (Sc, R_1, R_{2+3}, R_{4+5}, M_{1+2}, M_4, CuA+CuP), two crossveins (r-m, dm-m) and three non-costal cells are present (rm, bm, cua). Body and legs are dark brown in color; head and abdomen are black to gray; wing with microtrichia, M_{1+2} not forked; antenna with first flagellomere conical and several basal aristomeres; tarsomeres of hind leg broad, tarsomere I the longest, both tarsomere II and III wider than long.

Description

Female (Figure 30.1), body dark brown, body length, 4.4 mm, wing length 3.6 mm.

Head. Dark brown, 0.49 mm long, 0.87 mm high (Figure 31.4). Labellum 0.31 mm long, setose with setae approximately 50 µm long; first flagellomere 0.15 mm long, conical, with maximum width 0.10 mm, narrowed apically with three basal aristomeres approximately 50 µm x 30 µm (L x W). Arista not preserved. Proboscis and palpus light brown.

Thorax. Length, 1.51 mm; 4 notopleural setae (two short, two long) visible, one long prescutellar dorsocentral seta and one supraalar seta.

Wing. Length, 3.6 mm, at the middle, width1.3 mm, with microtrichia (Figure 30.2). First longitudinal vein (R_1) devoid of any spines. Costal cell (c) a little longer than portion of C on subcostal cell (sc), 1.26:1.10 mm. Length of discal cell (d) 1.55 mm, cell cup, 0.89 mm, bm, 0.57 mm, and rm, 0.77 mm. Plane of crossvein r-m intersects cell c at 59% of its 1.26 mm length. Posterior crossvein (dm-m) almost twice as long (0.34 mm) as distal part of M_4, 0.20 mm. Cell cua elongated, its length about three times portion of vein (CuA+CuP) beyond it.

Legs. Legs dark brown (Figure 31.2-3). Front coxa with long setae. Apex of front femur and basal parts of tibia (= "knees") of lighter color. Setation of front and middle legs not visible. Visible hind tarsomeres slightly flattened, with dark bifurcated setae (an apomorphic character for family Platypezidae, see Tkoč et al. [2017]).

Abdomen and genitalia. Length, 2.63 mm long, maximum height 0.76 mm; abdominal segments narrowed gradually towards apex, T6–T7 with a row of erect blackish setae at posterior margin (Figure 31.1), approximately 0.13 mm in length (margins of the more anterior tergites not visible). Setae of two basal segments not visible. Cercus 0.16 mm in length, 43 µm in height.

Allotype. Male unknown.

Syncompressions. Diptera (1).

Remarks

The family Platypezidae, with the other flies in Platypezoidea, is thought to be sister to all other Cyclorrhapha (Wiegmann et al., 2011). Within the Platypezoidea, the family is sister to the clade (Opetiidae + *Microsania*) (Tkoč et al., 2017). The family is relatively small, with more than 250 extant species in 17 extant genera (Tkoč et al., 2017). The Paleobiology Database reports 17 fossils of Platypezoidea, most of which from the early Cretaceous (Mostovski, 1996). Evenhuis (1994) listed 11 species of Platypezidae (including Opetiidae) in nine genera. Amorim et al. (2018) have recently updated the positions of the Cretaceous biota. Four platypezid fossils are Eocene in age: Two species have been described from the Green River Formation (*Callomyia hypolitha* Cockerell, 1909 and *C. torporata* Scudder, 1890), one species from the Florissant (*Eucallimyia fortis* Cockerell, 1911) and *Oppenheimiella baltica* Meunier, 1893 from Baltic amber.

The specimen *Agathoymia eocenica* sp. nov. from the Kishenehn Formation is the first described extinct species of *Agathomyia*. Its inclusion into any *Agathomyia* species group is, however, problematic. Some of the important characters required to establish its position within the genus (exact colouration, color of setae on tergites 1–2, setation on middle tibia) are not preserved in the fossil. Figure 30.3 provides a comparison with the recent species *Agathomyia antennata* (Zetterstedt, 1819). The venation is very similar to this species, but there are observable differences: 1) cell cua is more elongated in *A. eocenica*; 2) the anal lobe has a different shape; 3) the cell between M_4 and CuA+CuP is narrower and not lobate posteriorly in *A. eocenica*; 4) the costal cell (c) is slightly longer than the portion of costa on subcostal cell (sc) in *A. eocenica*.

FIGURE 32. *Lonchoptera eocenica* sp. nov. USNM 625379. Scale bar equals 2.0 mm.

Family LONCHOPTERIDAE Macquart, 1835
Genus LONCHOPTERA Meigen, 1803

Type species. *Lonchoptera lutea* Panzer, 1809, p. 20, by subsequent monotypy.

Lonchoptera eocenica Amorim and Brown, sp. nov.
Figures 32-34

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Etymology. The specific epithet, a Latin adjective, refers to the geologic epoch in which this species lived.

Holotype. USNM 625379, compression fossil, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek member, Kishenehn Formation.

Type locality. Spring site, Middle Fork of the Flathead River (Pinnacle, Montana).

Differential diagnosis. Similar to modern lonchopterids, but can be clearly separated from the recent species by the broader shape of the wing, slightly more rounded apically; R_{2+3} not as close to R_{4+5} as in modern species of the genus; R_{4+5} reaching C slightly before wing tip (while in recent

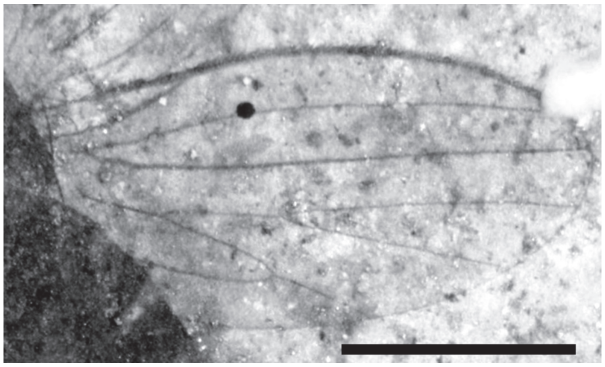

FIGURE 33. *Lonchoptera eocenica* sp. nov. USNM 625379. Close-up of wing.

species R_{4+5} characteristically ends at tip of wing); probably related to the general shape of the wing, the medial fork wider, with M_1 and M_2 relatively more separated at the wing margin; the distal end of M_4, close to the margin, is almost straight, while in recent species it is slightly curved posteriorly.

Description

Female (Figure 32), body dark brown, body length 2.8 mm, wing length 2.7 mm.

Head. Relatively small, flattened; flagellomere 1 apically pointed.

Thorax and wings. Thorax stout. Sc weakly sclerotized (as in recent species), slightly separated from R_1; R_1 short, extending to about one-third of visible wing length; R_{2+3} convex, slightly converging towards wing apex; R_{4+5} extended to wing apex, reaching C just before wing tip; costal setae ending at R_{4+5}; r-m originating at R_{4+5} just beyond origin of R_{2+3}, strongly curved basally; CuA+CuP joining M_4 before wing margin (as in modern females); fused vein CuA+CuP about as long as base of medial fork; wing cells br, bm, and cua (this latter hard to delimit) small, displaced to the base of the wing. Setulae visible on veins R_1, M_{1+2}, M_2, M_4, and base of CuA+CuP.

Legs. Legs apparently slightly shorter than in recent species.

Abdomen and genitalia. Abdomen shorter than recent species, tergites and sternites apparently well sclerotized. Terminalia short, only a short cercus visible.

Allotype. Male unknown.

Syncompressions. None.

Remarks

Lonchopteridae is a small family of extant flies that is found nearly worldwide. The modern fauna is represented by a single genus, *Lonchoptera* Meigen, for which about 50 species have been described. The Nearctic species and much of the information about the genus were reviewed by Klymko and Marshall (2008). The common name for this group, “spear-winged flies”, is based on the narrowed wing with pointed apex. Other distinctive characters are the setulose wing veins, the shortened wing veins R_1 and Sc, and the sexually dimorphic wing venation, with CuA+CuP joining M_4 in females, but extended to the wing margin in males.

Fossils assigned to this family are few, basically two species of uncertain relationships to modern lonchopterids (Grimaldi and Cumming 1999). They both are, however, considerably different relative to the modern genus *Lonchoptera* and, if they belong at all to the clade, they would clearly belong to the stem group of the family. Indeed, Amorim et al. (2018) suggested that *Lonchopterites* Grimaldi and Cumming could be a stem-group Opetiidae, not a Lonchopteridae.

Few details of the head, thorax, legs, abdomen, and terminalia are visible in the specimen (Figure 32). Nevertheless, the wings are largely well preserved and visible, and there is scarcely any doubt that this species fits together with the recent species of *Lonchoptera* as a clade. Recent *Lonchoptera* species are considerably similar in the wing shape and the wing venation. Some modified wing venation features present in *Lonchoptera* are shared with Opetiidae and Phoridae within the Platypezoidea (Amorim et al., 2018), particularly the very basal origin of R_1, the stronger R_{4+5}, the reduction in size of cells bm, br, and cua, the loss of the dm-m crossvein and the shape of the long medial fork (some of these features secondarily modified in the phorids). A number of apomorphic conditions are seen in the wing of the recent species of *Lonchoptera*. These include the typical elongate shape of the wing, with a pointed tip, the displacement of R_1 to a considerably basal position in the wing, the weakly sclerotized and short Sc, a convex R_{2+3}, the tip of R_{2+3} displaced to close to the wing tip, R_{4+5} reaching precisely the acute wing tip, the strong displacement of the posterior end of r-m towards the base of the wing, CuA distally fused to M_4 in females and a very short CuP actually coming out from the wing margin (actually, the circumambient C) to join CuA.

All of these features are present in the Eocene species described here, except the lack of the general elongate shape and pointed wing apex —

while the CuP emerging from the wing margin cannot be verified (Figure 33). Some of the features in *L. eocenica* are modified, but not to the same degree as in recent species: this includes the displacement R_1 to the base, of R_{2+3} to the apex and R_{4+5} ending at the very tip of the wing.

This set of features does not leave any doubt about the position of the species together with the recent *Lonchoptera*. A thin plate spline analysis was performed to show the direction of the changes from the fossil to modern wing veins (Figure 34.1-2; dots indicate modern venation, line bases the fossil equivalent). The analysis makes clear that the distance between R_1 and R_{2+3} is expanded (orange/red) in the recent species, while R_{2+3} is compressed towards R_{4+5} (light/dark blue). Also, R_1 is in an even more basal position in the recent species. The process of narrowing the wing in the modern species takes place in both the anterior and posterior portions of the wing.

It is quite unfortunate that the some details of the fossil cannot be fully described, particularly the head, thorax, and legs. The very characteristic shape of the head of recent *Lonchoptera* and the quite elongate thorax cannot be properly checked in *L. eocenica*, but the fossil seems to be slightly stouter. The legs of *L. eocenica* seem to be also shorter. Based on the discussion above, *L. eocenica* appears to be the sister species to the recent species of *Lonchoptera*. In other words, the Eocene fossil described here is a stem *Lonchoptera*. Despite some differences in the wing shape and in the wing venation, we do not see any particular reason to have a separate monotypic taxon of generic rank to hold the fossil species. It is worth noting that Bouchenak-Khelladi et al. (2010) date the crown node of Poaceae (i.e., BEP+PACCMAD) at the early Eocene, 57 Ma. The larvae of recent species have quite varied habitats, but adults are associated with grassy habitats (Klymko and Marshall, 2008), and the genus may have largely expanded its distribution with the diversification of grassy, open environments at the mid of the first half of the Cenozoic. This fossil will certainly bring important benefits to calibration in studies on age divergence in the Cyclorrhapha.

Family PHORIDAE Curtis, 1833
Genus AENIGMATIAS Meinert, 1890

Type species. *Aenigmatias blattoides* Meinert, 1890

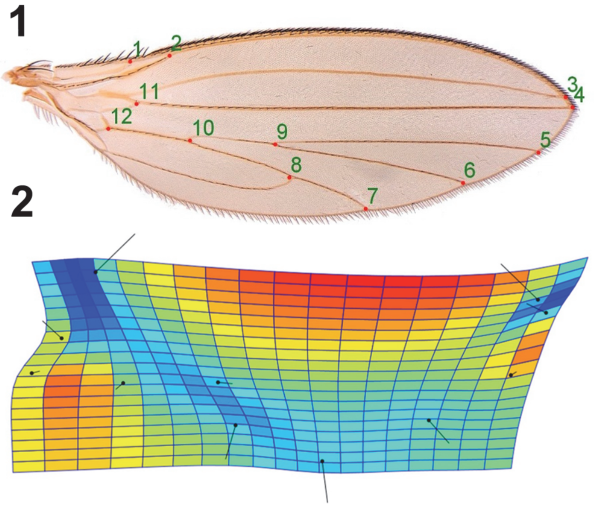

FIGURE 34. A thin plate spline analysis demonstrates the direction of the changes from fossil to modern wing veination. **1**, Wing of modern *Lonchoptera* sp. (from the Puyehue National Park, Chile), showing placement of landmarks; **2**, Expansion (red) and compression (blue) of wing venation of a modern species of Lonchoptera relative to *Lonchoptera eocenica*. Basal, left; distal, right. Base of lines represent fossil landmark; dots at tips of lines represent modern landmark.

Aenigmatias kishenehnensis Brown, sp. nov.
Figure 35

zoobank.org/28A4C2F4-40E2-45AF-83A4-FADAD0EBD616

Etymology. The specific epithet denotes the geological Formation in which the specimen was preserved.

Holotype. USNM 625132, deposited in the Department of Paleobiology, National Museum of Natural History (NMNH), Smithsonian Institution, Washington, District of Columbia, USA.

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. The Spring site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. This species of *Aenigmatias* is distinguished by the presence of wings, very short C, R_1 and Rs veins, the absence of R_{2+3} and an apparently nonlimuloid body shape.

Description

Body length (head to the end of tergite 6) 1.5 mm. Female (Figure 35.1).

Head. Four large setae present at vertex and at least six large setae on frons (all frontal setae absent in modern species, often reduced in num-

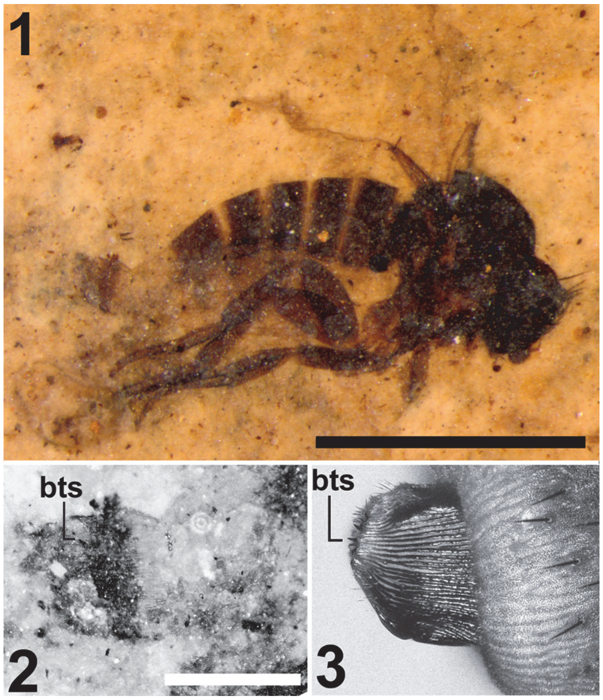

FIGURE 35. *Aenigmatias kishenehnensis* sp. nov., USNM 625132. **1**, Habitus; **2**, Terminalia, (bts = blunt thick setae); **3**, Terminalia of an extant female *Aenigmatias sp.* Scale bars equal 1.0 mm (**1**) and 0.2 mm (**2**).

ber and size in fossils). Postpedicel rounded. Palpus with well-developed setae.

Thorax. Most details of thorax not visible, but not appearing to be highly limuloid. One pair of short setae visible (possibly posterior dorsocentral setae) and one longer pair (scutellars?) near base of wing.

Wings. C short, but costal setae long. R_{2+3} absent. Base of radial veins possibly with row of setulae.

Legs. Foretibia not preserved. Midtibia with one large seta near base. Hind legs preserved, but details not visible.

Abdomen and genitalia. Abdomen unmodified, unlike flattened modern species. Abdominal segment 7 with dense striation and blunt thick setae. (Figure 35.2, bts; as in modern species, Figure 35.3).

Allotype. Male unknown.

Syncompressions. None.

Remarks

The family Phoridae consists of 302 genera and about 4,300 species. The fossil record of the family is quite good, with 103 fossil species (47 genera), 95% of which are in amber (about half of these in Baltic amber). Many extant phorids exhibit a parasitoid lifestyle and several genera are myrmecophilous (Brown, 2018). The 14 extant species of the genus *Aenigmatias* are presumed to be larval parasitoids of ant pupae. Members of the genus are markedly sexually dimorphic, with the female wingless and limuloid in shape, the latter an adaptation that provides defense against attack by ants (Brown, 2017; Brown et al., 2017). Brown (1999), in an examination of fossil phorids in Baltic and Fushun amber, concluded that many of the specimens assigned to extant genera actually belong to more primitive stem-groups. *Protophorites fimbriatus* Brues, 1939, was synonymized with *Protoplatyphora tertiaria* Brues, 1939 (holotype lost), which was thought to be a stem group of a clade with the modern *Aenigmatias* species, based on a less limuloid body shape, the presence of wings (*Protophorites fimbriatus* is a female) and the presence of large setae on the vertex and scutellum. Brown (2017), in a phylogenetic analysis of the fossil *Aenigmatias* and related genera, transferred *Protoplatyphora tertiaria* and *Chaetopleurophora multisetosa* Brown, 2007 to *Aenigmatias* and described three new species from Baltic amber. With *Aenigmatias kishenehnensis*, there are currently a total of six fossil species in the genus: *A. tertiarius* Brues, 1939, *A. bisetosa* Brown, 2007, *A. longicornis* Brown, 2017, *A. primitivus* Brown, 2017 and *A. nigeroticus* Brown, 2017. Only *A. tertiarius*, Brues 1939, *A. kishenehnensis* and an additional specimen (LACM 159804) are females.

Aenigmatias kishenehnensis can be differentiated from *A. tertiaria* in having a much shorter costa (0.24 mm vs. 0.5 mm), R_{2+3} vein absent, and the frons with large setae; from *A. bisetosa* in having a much shorter body length (1.5 mm vs. 4.3–4.4 mm), a much shorter costa and R_{2+3} absent; from *A. longicornis* in having a rounded first flagellomere (vs. elongate) and a much shorter costa (0.24 mm vs. 0.43 mm); from *A. primitivus* in having a much shorter costa (0.24 mm vs. 0.48 mm); and from *A. nigeroticus* in having a much shorter costa (0.24 mm vs. 0.48 mm), R_{2+3} absent and the frons with large setae. *Aenigmatias kishenehnensis* is also differentiated from *Aenigmatias* sp. indet. (LACM ENT 159804; Brown, 2017), a female, in having a much shorter costa (0.24 mm vs. 0.71 mm). Apparently, the set of extinct species of *Aenigmatias* do not constitute a clade sister to the extant species of the genus, but rather a grade.

The 21 fossil phorid flies of the Kishenehn formation are intriguing. With the exception of *A. kishenehnensis*, they are difficult to place to any modern group. None of the specimens exhibit proclinate supra-antennal setae, a condition found in most phorids of the subfamily Metopininae, which is the numerically dominant group today. The earliest undoubted metopinines are known from Baltic amber, and even there they are a smaller portion of the fauna than today, suggesting that the metopinine radiation is indeed an evolutionarily recent (i.e., post-Eocene) event. Other character states visible in the Kishenehn phorids are not considered synapomorphic of any modern groups, with a single exception of *A. kishenehnensis.*

Modern *Aenigmatias*, and most fossil species of the genus (Brown, 2017), have a series of setulae along the radial vein, more than four scutellar setae and longitudinal, irregular rows of tightly-packed setulae (setal palisades) on the hind tibia in addition to the limuloid body form. None of these character states was convincingly observed in *A. kishenehnensis*, but the much more distinctive structure of the female terminal segments is clearly visible: the ovipositor has heavily striate membrane and thick, peglike setae. This structure is known from at least one fossil species, *A. tertiarius,* and all examined modern species, but no other phorids. The life history of two of the 14 modern species has been studied and both found to be parasitoids of *Formica* Linnaeus 1758 ant pupae (Donisthorpe, 1927). No studies have been done on the function of this peculiar ovipositor, which is unlike those of other parasitoid phorids that attack adult ants, but it is likely related to the parasitic lifestyle.

Family PIPUNCULIDAE Walker, 1834
PIPUNCULINAE Walker, 1834

Type species. *Pipunculus campestris* Latreille, 1802

Pipunculinae incertae sedis
Figure 36

Type horizon. Middle Eocene Coal Creek Member, Kishenehn Formation.

Type locality. Deep Ford site, Middle Fork of the Flathead River (Pinnacle, Montana, USA).

Differential diagnosis. This specimen is distinguished by antennal pedicel with prominent bristle and shorter setae, and a long, thin arista; body without long setae/bristles; wing with costa extending beyond apex to M_1, R_{4+5} ending at the apex of the wing, M_2 present, CuA_2 merges with A_1 just before margin.

Description. Ventral aspect, female. Total length 3.64 mm (actual), 4.0 mm (estimated); color black. NMNH, USNM 625934 (Figure 36.1).

Head. Large, 1.27 mm wide, 0.89 mm long. Ocellar bristles absent. Occiput, if present, obscured/destroyed by crack. Antenna well-preserved. Scape not clearly distinguishable. Pedicel 0.13 mm wide, length 74 µm, with one prominent ventral bristle 0.12 mm long plus some smaller bristles and at least eight smaller but distinct (30–80 µm) setae on the dorsal surface. Visible portion of F1 spherical, 73 µm wide, with several thin 33 µm setae. Arista long (0.46 mm), thin, basal portion 86 µm long, 26 µm wide (Figure 36.1).

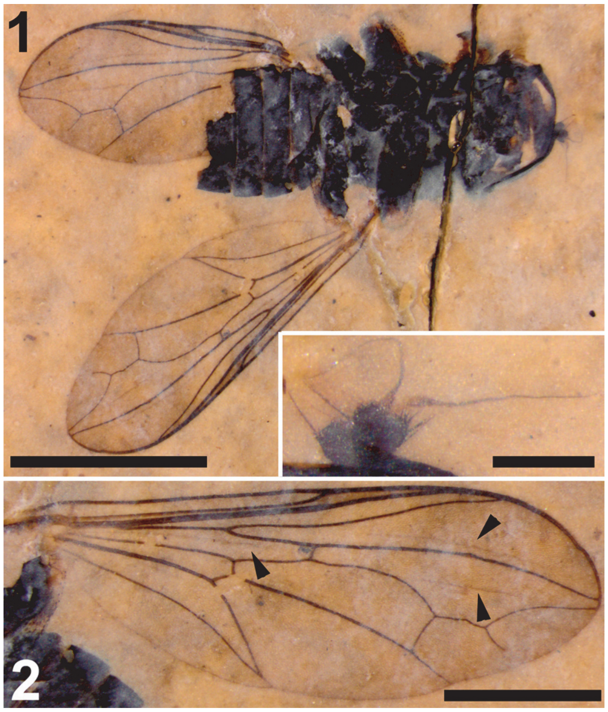

FIGURE 36. Pipunculidae sp. USNM 625934. **1**, Habitus. Inset: antennae; **2**, Left wing. Arrowheads denote spurious veins; Scale bars equal 2.0 mm (**1**), 0.25 mm (inset) and 1.0 mm (**2**).

Thorax. Quadrate, both length and width 1.43 mm. Scutum and scutellum not visible as the fossil is of the ventral aspect of the insect.

Wings. Length, 4.0 mm, width, 1.33 mm (left), 1.48 mm (right) (Figure 36.2). Pterostigma present, as long as 3rd costal section. Ratio of length of 2nd, 3rd and 4th costal sections 4.5:2.2:1. R_{4+5} meets margin at wing apex, C extends beyond apex to reach M_1; r-m at 0.27 of length of discal cell. M_{1+2} distal of r-m curved, convex. M_2 present, 0.61 of length of last abscissa of M_{1+2}; M_1 curved, convex, dm-cu slightly curved, CuA merges with CuP just before margin. Spurious veins in both wings in the basal radial cell and cells r_{1+2} and r_{4+5}. Anal lobe present.

Legs. Five legs visible including yellow fore and hind tibiae; tibiae with short black setae. Front femur wide, black.

Abdomen. Sternites 1-5 length, 0.2 mm, 0.23 mm, 0.27 mm, 0.26 mm and 0.41 mm, respectively, wider than long, sternite 3, 1.3 mm wide. Lateral abdominal setae, if present, short. Terminalia not preserved. Length of sternite 5 strongly suggests that the specimen is a female, since males have sternite 5 considerably reduced compared to sternites 2–4 due to the genitalia complex that follows S5.

Allotype. Male unknown.

Syncompressions. None.

Remarks

Pipunculidae contains approximately 1,428 species in 22 extant genera placed in four subfamilies: Chalarinae Aczél, 1939a, Nephrocerinae Aczél, 1939b, Pipunculinae Walker, 1834, and Protonephrocerinae Aczél, 1948. According to molecular dating, the diversification of this family began approximately 85 Mya (Wiegmann et al., 2011). The oldest, albeit undescribed, fossil is from the Fur Formation (about 55 Mya; Bonde et al., 2008). Members of the crown group of the family (with M_2 absent), however, existed as early as 51 Mya (Archibald et al., 2014a). To date, 16 fossil specimens have been described (Archibald et al. 2014a; Kehlmaier et al., 2014; this study).

The crack in this fossil has destroyed any remnant of an occiput. The first flagellomere is very small (smaller than the pedicel, which is not the case in any extant species), which raises the possibility that only the uppermost portion of this structure is visible. Except for the pedicel, no other long setae or bristles are visible on the head, thorax, legs or abdomen. This feature, in combination with the wing venation, eliminates the possibility that this species belongs to the Chalarinae, Protonephrocerinae (eliminated based on R_{4+5} ending at the apex of the wing), part of Nephrocerinae (Nephrocerus Zetterstedt, 1838) and part of Pipunculinae. *Priabona* Archibald et al., 2014 (Nephrocerinae) is not well enough known. In extant Pipunculinae, long and numerous (>5) bristles on pedicel occur especially in *Claraeola* Aczél, 1940 (Eudorylini Rafael and De Meyer, 1992) of which many extant species also have M_2. Skevington and Yeates (2001) regard long bristles on the pedicel as a plesiomorphy while a larger number of bristles as an apomorphic condition. Despite the destroyed occiput, the fossil can be safely placed in the Pipunculinae. The characters required for a confident assignment to a tribe, however, let alone a genus, cannot be observed. The specimen is here assigned to Pipunculinae incertae sedis.

This Kishenehn Formation pipunculine is small relative to most fossils of the family. Pipunculidae species A (Archibald et al., 2014a), *Metanephrocerus belgardeae* Archibald, Kehlmaier and Mathewes, 2014, *Protoverallia succinea* Meunier, 1903, *Nephrocerus oligocenicus*, Carpenter and Hull, 1939, *Metanephrocerus collini* Carpenter and Hull, 1939, *M. hoffeinsorum* Kehlmaier and Skevington in Kehlmaier, Dierick and Skevington, 2014, and *M. groehni* Kehlmaier and Skevington in Kehlmaier, Dierick and Skevington, 2014, have wing lengths of 5.9, 9.2, 6, 8, 6, 6.7 and 6 mm, respectively. The body length of *Eudorylas* Aczél, 1940 species A is only 2.2 mm, while *Eudorylas* species A and B (De Meyer, 1995) and Pipunculinae species A (Archibald et al., 2014a) lack vein M_2. Unlike this incertae sedis Pipunculinae, both *Protoverallia succinea* and *Metanephrocerus collini* have long abdominal bristles; *Metanephrocerus collini* also has M_2 at the wing margin; *Cephalosphaera baltica*, according to Carpenter and Hull, 1939, has "smoky wings", but this feature was not mentioned by Aczél (1948). *Cephalosphaera baltica* is larger than the Kishenehn Formation specimen as its wings are 5.5 mm in length (Aczél, 1948). Pipunculidae species A, *Metanephrocerus hoffeinsorium* and *M. groehni* differ markedly from this Pipunculinae incertae sedis in the ratios of the 2nd, 3rd and 4th costal sections length. Carpenter and Hull (1939) briefly reviewed Meunier's (1903) fossils and indicated that *Verrallia exstincta* Meunier, 1903, was conspecific with what Meunier termed a "variety" of *V. exstincta* which he referred to as *V. kerteszia* Meunier, 1903. Aczél (1948) however, stated that "according to the figure, the 3rd and 4th costal sections are shorter than the 5th (in *V. kerteszia*), while the 3rd and 4th costal sections of *V. exstincta* are much longer than the 5th." In any case, both of these fossil specimens of *Verrallia* are twice the length of the Kishenehn specimen.

DISCUSSION

There are currently 163 extant families in the order Diptera (Pape et al., 2011; Papp, 2011), including the families Mythicomyiidae (Melander, 1902), Pseudopomyzidae (McAlpine, 1966) and Uluromyiidae (Michelsen and Pape, 2017). Most (116 or 71%) of these are represented in the fossil record. There are 54 additional taxa with family rank that are extinct (Nagatomi and Yang, 1998; Poinar, 2010; Pape et al., 2011; Zhang et al., 2011; Zhang, 2012). In North America, the Eocene Florissant, Green River and Okanagan/Republic Lager-

TABLE 2. Families and species of the order Diptera from the 46 Ma Coal Creek Member of the Kishenehn Formation and the oldest described fossil of each family.

Family	Genus species	Museum/Number	Reference	Oldest known age (Ma)	Reference
Tipulidae	*Tipula fji*	USNM 625687	This study	206–222	Krzemiński (1992)
Limoniidae	*Helius constenius* *Ellipteroides kishenehn*	CMNH 34935 USNM 621123	Krzemiński (1991b) This study		Krzemiński (1992)
Cylindrotomidae	*Cyttaromyia lynnae*	USNM 621109	This study	49–56	Freiwald (1991)
Psychodidae	Bruchomyiinae sp.	USNM 619952	This study	182–183	Ansorge (1994)
Dixidae	*Dixella intacta* *Dixella eomarginata* *Dixella curvistyla* *Dixella spinilobata*	USNM 546204 USNM 553521 USNM 546860 USNM 553522	Greenwalt and Moulton (2016)	190–202	Lukashevich (1996)
Culicidae	*Culiseta kishenehn* *Culiseta lemniscata* *Culiseta?* sp.	USNM 546528 USNM 547065 USNM 559050	Harbach and Greenwalt (2012); Greenwalt et al. (2013)	94–100	Borkent and Grimaldi (2011)
Anisopodidae	*Sylvicola silibrarius*	USNM 626077	This study	190–202	Rohdendorf (1962); Krzemińska et al. (2010)
Scatopsidae	*Efcookella nigra*	USNM 618088	This study	94–100	Fate et al. (2013)
Bibionidae	*Bibiodes kishenehnensis*	USNM 625738	This study	123–126	Ren et al. (1995)
Sciaridae	*Eosciarites hermes*	USNM 624633	This study	100–113	Kaddumi (2007)
Mycetophilidae	*Rymosia hypnolithica*	USNM 624134	This study	122–125	Ren et al. (1995)
Bolitophilidae	*Bolitophila warreni*	USNM 595138	Greenwalt and Blagoderov (2019)	46*	Greenwalt and Blagoderov (2019)
Rhagionidae	*Litoleptis araeostylus*	USNM 624657	This study	242–247	Krzemiński and Krzemińska (2003)
Bombyliidae	*Eoanomala melas*	USNM 595155	Greenwalt et al. (2015b)	56–59	Nel (2008)
Asilidae	*Kishenehnoasilus bhl*	USNM 624491	This study	113–123	Grimaldi (1990)
Dolichopodidae	*Salishomyia eocenica*	USNM 622501	This study	125–130	Grimaldi and Cumming (1999)
Hybotidae	*Drapetis adelomedos*	USNM 621705	This study	125–130	Hennig (1970)
Platypezidae	*Agathomyia eocenica*	USNM 553697	This study	113–126	Mostovski (1995)
Lonchopteridae	*Lonchoptera eocenica*	USNM 625379	This study	129	Grimaldi and Cumming (1999)
Phoridae	*Aenigmatias kishenehnensis*	USNM 625132	Thu study	46	This study
Pipunculidae	Pipunculinae sp.	USNM 625934	This study	48–56	Archibald et al. (2014a)

stätten have, to date, produced described species in 36, 26 and 15 families, respectively (Table 2) (Rice, 1959; Wilson, 1977, 1978; Douglas and Stockey, 1996; Wehr and Barksdale, 1996, 1998; Meyer, 2003; Archibald, 2007; Archibald et al., 2010, 2013, 2014a, 2014b). For reference, Baltic amber has produced described species in 81 dipteran families, only one of which, Hoffeinsmyiidae, is extinct (Michelsen, 2009; EDNA, 2017). The insect fauna of the Coal Creek Member of the Kishenehn Formation in northwestern Montana is dominated by flies, and studies to date, including the material herein addressed, have described 23 species of Diptera in 21 families (including Limoniidae and Cylindrotomidae; Table 2).

Of the 21 familes described from the Kishenehn Formation, including the 17 described herein, only three, Platypezidae, Phoridae and Pipunculidae belong to Cyclorrhapha. Pipunculidae has recently been proposed to be sister to the Schizophora (Pauli et al., 2018). No schizophorans have been described to date from the Kishenehn Formation although Calyptratae near Muscidae and acalyptrates near Chloropidae have been

TABLE 3 Families of the order Diptera from four North American Compression fossil Lagerstätten..

Dipteran family	Kishenehn	G. River	Florissant	Okanagan
Agromyzidae		x	x	
Anisopodidae	x	x		
Asilidae	x	x	x	
Bibionidae	x	x	x	x
Blephariceridae		x		
Bolitophilidae	x			x
Bombyliidae	x		x	
Cecidomyiidae		x	x	
Chironomidae		x	x	
Conopidae		x		
Culicidae	x	x		
Cylindrotomidae	x	x	x	
Dixidae	x			
Dolichopodidae	x		x	
Empididae		x	x	x
Eophlebomyiidae†		x		
Glossinidae			x	
Heleomyzidae		x	x	
Hybotidae	x			
Keroplatidae		x		x?
Lauxaniidae			x	
Limoniidae	x	x	x	
Lonchopteridae	x			
Lygistorrhyinidae				x?
Muscidae		x	x	
Mycetophilidae	x	x	x	x
Mydidae			x	
Mythicomyiidae		x		
Nemestrinidae			x	
Oestridae		x		
Phoridae	x		x	
Piophilidae			x	
Pipunculidae	x		x	x
Platypezidae	x	x	x	
Psychodidae	x			x
Ptychopteridae			x	x
Rhagionidae	x		x	x
Richardiidae			x	
Scathophagidae			x	
Scatopsidae	x		x	
Sciaridae	x	x	x	x
Sciomyzidae		x	x	x
Sepsidae			x	
Stratiomyidae		x	x	
Syrphidae		x	x	x
Tabanidae			x	
Tachinidae		x		
Therevidae			x	
Tipulidae	x	x	x	x
Trichoceridae				x?
Ulidiidae			x	
Xylomyidae			x	

identified (Bickel, personal commun., 2017). In contrast, 18 families of Cyclorrhapha have been described from the three other North American Eocene compression fossil Lagerstätten, including 10 Schizophora and five Calyptratae (Glossinidae Theobald, 1903, Muscidae Latreille, 1802, Oestridae Leach, 1815, Scathophagidae Robineau-Desvoidy, 1830 and Tachnidae Robineau-Desvoidy, 1830 [Table 3]).

Classification of Kishenehn Formation specimens to extant genera reflects, in part, their high degree of preservation of morpholpgical detail. It also reflects the relative longevity of dipteran genera. Analysis of all described fossil Diptera (Evenhuis, 2017) reveals that 55% of all genera represented by species from the Eocene epoch are extant. The percentage increases to 79% for genera in which the oldest representative is from the Oligocene. The former percentage is actually much higher as the value is negatively affected by the 79 new and mostly unnecessary genera created by Hong (2002). In the current studies, different approaches have been taken by different authors. Two of the specimens have been identified to subfamily incertae sedis. Although the bruchomyiine (Psychodidae) specimen can be keyed to the genus *Nemopalpus* (Quate and Alexander, 2000), the observations that all existing bruchomyiine fossils have been assigned to this genus and many, if not the majority of these assignments are thought to be inaccurate (Wagner and Stuckenberg, 2016) have elicited a conservative assignment of this specimen. In the case of the asiline (Asilidae) specimen, the new genus *Kishenehnoasilus* is, in essence, a placeholder assignment, useful until additional and better preserved specimens can be obtained and/or the extant North American fauna is better understood.

Several factors affect the preservation of dipteran diversity in the Kishenehn Formation. Very small insects are often well-preserved (Huber and Greenwalt, 2011; Shockley and Greenwalt, 2013). Culicidae, of which over 70 specimens have been collected from the Coal Creek Member, have not been recorded as described species from either the Florissant or the Okanagan. Specimens of the families Dixidae Schiner, 1868, and Bolitophilidae Winnertz, 1863, both described from the Kishenehn Formation (Greenwalt and Moulton, 2016; Greenwalt and Blagoderov, 2019), have not been reported from any of the three North American Lagerstätten. There appears to be a taphonomic size bias such that specimens greater than 1 cm in length are rarely preserved in the Kishenehn Formation. For example, large 3-dimensional flies such as horse flies, house flies, etc. are, if present, invariably very poorly preserved. This of course has a negative impact on the documentation of existing diversity at that time. The Diptera of the Coal Creek Member of the Kishenehn Formation are dominated by families that have aquatic immatures. As with the size bias, the shallow lacustrine environment in which the insects were preserved both limits and promotes the preservation of diversity. Kishenehn Formation specimens from numerous additional families including Ceratopogonidae Newman, 1834, Chaoboridae Newman, 1834, Chironomidae Newman, 1834, Chloropidae Rondani, 1856, Empididae Latreille, 1804, Microphoridae Collin 1960, Muscidae Latreille, 1802, Syrphidae Latreille, 1802, Xylomyidae Verrall, 1901 and others, have been identified and await description.

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