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The fossil record of female sexual ornamentation in Empididae (Diptera: Empidoidea), with description of four new species

DALE E. GREENWALT[1] & BRADLEY J. SINCLAIR[2,*]

[1]*Department of Paleobiology, National Museum of Natural History MRC 121, Smithsonian Institution, 10th & Constitution Ave. NW, Washington, D.C. 20013-7012, USA*

[2]*Canadian National Collection of Insects and Canadian Food Inspection Agency, K.W. Neatby Bldg., C.E.F., 960 Carling Ave., Ottawa, ON K1A 0C6, Canada*

GreenwaltD@si.edu; https://orcid.org/0000-0002-9811-6356

bradley.sinclair@inspection.gc.ca; https://orcid.org/0000-0001-6413-1606

**Corresponding author*

Abstract

Females of the subfamily Empidinae (Diptera: Empididae *s.s.*) often exhibit sexual ornamentation, an adaptation that, within the animal world at large, is most often associated with males, especially in vertebrates. Ornaments of female Empidinae include: 1) legs with rows of relatively large pennate scales, 2) enlarged and/or darkly pigmented wings and 3) inflated abdominal sacs. Ornamentation makes the females appear larger, a characteristic that may make them appear, albeit deceptively, more fecund, and therefore more attractive to potential mates. Given the rarity of female sexual ornamentation, these flies, particularly those of the tribe Empidini, have become a model system for study of this phenomenon. The family's fossil record consists of 111 known occurrences including several genera from the middle Jurassic. This fossil record however is dominated by two genera, *Empis* and *Rhamphomyia*, which account for nearly 60% of all fossil occurrences. Unfortunately, there has been no fossil record of empidine sexual ornamentation other than pennate leg scales. Herein, we review this fossil record and describe the first empidine fossils, all from the Middle Eocene Kishenehn Formation, with enlarged and/or darkly pigmented wings, *Rhamphomyia kitadai* **sp. nov.** and *R. brunnipennis* **sp. nov.**, and two new species of *Rhamphomyia* which display pennate leg scales, *R. decens* **sp. nov.** and *R. pennipes* **sp. nov.** *Rhamphomyia enena* Cockerell, 1921, the oldest known fossil that exhibits pennate leg scales, is redescribed.

Keywords: *Rhamphomyia*, Empidinae, fossil insects, new species, Kishenehn Formation, middle Eocene

Introduction

Species within the family Empididae (Diptera: Empidoidea) are important behavioral models in studies of female sexual ornamentation (Cumming, 1994; Hunter & Bussière, 2019; Murray *et al*., 2020, 2022). The basis for this phenomenon is the dependence of females on the presentation of a prey-based meal—their only protein meal as adults—by males immediately prior to mating. To attract males, the females have evolved several structures that make them appear large and gravid and, as a result, more fecund, and more attractive to males. Ornaments include inflatable (pleural) sacs in their abdomens, feather-like (pennate) scales on legs that, when placed immediately adjacent to the abdomen, make the abdomen appear larger, and increased size and dark pigmentation of the female's wings, again, characters that make the female appear larger and/or easier to target.

Various steps in the evolution of empidid sexual ornamentation have been suggested by Kessel (1955, 1959) and, more recently, Turner (2012) and Hunter & Bussière (2019) have speculated on ecological and behavioral factors that may have led to female empidid ornamentation. However, very little is known about the actual timeframe(s) involved. We herein review the fossil record of sexual ornamentation in Empidinae, a record that consists entirely of species of *Empis* Linnaeus and *Rhamphomyia* Meigen. We describe the first empidine fossils, from the middle Eocene (Lutetian) Kishenehn Formation of northwestern North America, that exhibit ornamentally darkened and enlarged wings. We also describe two new species of *Rhamphomyia* from this same

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formation that display pennate leg scales. *Rhamphomyia enena* Cockerell, 1921, from the early (Ypresian) Eocene Green River Formation, provides the oldest evidence of sexual ornamentation in Empidini (pennate leg scales) and is redescribed. *Rhamphomyia enena*, originally described as *Rhamphomyia* (?) *enena* by Cockerell (1921), was listed by both Melander (1928) and Evenhuis (1994), in the absence of any examination, analysis or redescription of the specimen, as *Rhamphomyia enena*. Open nomenclature qualifiers such as "(?)" frequently and inexplicably disappear from the literature with the first subsequent mention of the species (Ibid.; personal observations).

Material and methods

New species described in this study were collected from the Kishenehn Formation in northwestern Montana, USA, in accordance with USFS Authorizations HUN 281 and 465. Exposures there are from the middle sequence of the Coal Creek Member, which has 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 *et al*., 1989; Constenius, 1996). A specimen (USNMENT00471634) of the extant species *Rhamphomyia fumosa* Loew was obtained from the Entomology Department of the Smithsonian National Museum of Natural History.

This and all other specimens were photographed with either an Olympus SZX12 microscope equipped with a Q-Color5 Olympus camera and Image-Pro Plus 7.0 software (Media Cybernetics, Inc., Bethesda, MD) or with an Olympus DSX 100 microscope. Length and width measurements were made with the Image-Pro Plus 7.0 software. Wing areas were determined through use of the shoelace algorithm with SketchAndCalc. Fossil specimens, with the exception of the holotype of *Rhamphomyia enena* (USNM 66921), were immersed in 95% ethanol for examination and photography. Venational terminology is from Cumming & Wood (2017). Numbers of genera and species/tribe were taken from the Catalogue of Life (2022). The number of fossil species for each individual taxon were obtained from the Paleobiology Database. Institutional acronyms and abbreviations used herein are COL (Catalogue of Life), PBDB (Paleobiology Database), NMNH (National Museum of Natural History) and USNM (United States National Museum = NMNH depository), M_2/d = length of vein M_2: greatest length of discal medial cell (discal cell), M_4 ratio is the length of the dm-m crossvein/distal section of M_4 (Bickel, 1994), lw:ww = greatest length of wing (from basicosta to apex)/greatest width of wing, WA = wing area and TAL = length of the thorax plus abdomen (without cerci).

Systematic palaeontology

Order Diptera Linnaeus, 1758
Superfamily Empidoidea Latreille, 1804
Family Empididae Latreille, 1804
Subfamily Empidinae Latreille, 1804
Genus *Rhamphomyia* Meigen, 1822

***Rhamphomyia brunnipennis* sp. nov.**
(Figs 1, 11C)

Holotype. Female, USNM 623786, deposited in the Paleobiology collections of the National Museum of Natural History in Washington, D.C.

Etymology. The specific epithet is from the Classical Latin *brunneus* (brown) and *pennis* (wing) and refers to the color of this specimen's wing pigmentation.

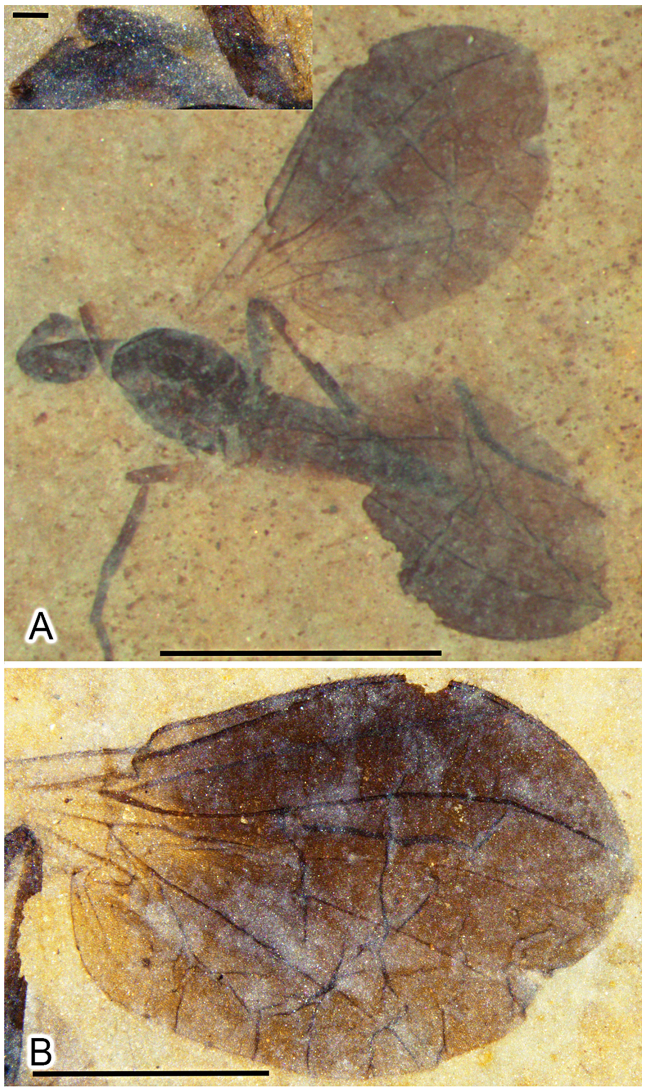

FIGURE 1. *Rhamphomyia brunnipennis* **sp. nov.**, female, USNM 623786. **A**, Habitus, insert = antennae. **B**, Right wing. Scale bars = 2.0 mm (insert 0.1 mm) (**A**), 1.0 mm (**B**).

Diagnosis. Females of this species are distinguished from all previously described fossils of the genus by its darkly pigmented and enlarged wings. It is distinguished from *R. kitadai* **sp. nov.** by the size, shape (L/W ratio) and degree of pigmentation of the wings and the L/W ratio of its postpedicel (6.8 *vs*. 4.6). It is also distinguished from *R. kitadai* **sp. nov.** by its shorter abdomen (1.63 mm *vs*. 2.1 mm) and its thorax/abdomen ratio of 0.71 (*vs*. 0.50).

Locality and horizon. Dakin site, Kishenehn Formation, Colorado (USA); Middle Eocene (Lutetian).

Description. Female. Length 3.46 mm (with cerci). Head 0.64 mm long, brown/black, without observable setae. Antenna black, 0.55 mm long, scape 79 µm long, pedicel 58 µm long, setose apically; postpedicel 0.41 mm in length, L/W_{max} = 6.8, stylus 66 µm long. Mouthparts not preserved (Fig. 1A). Thorax brown/black, 1.18 mm long. Wing with basal portion of anterior edge slightly folded/overlapped, 2.7 mm long, 1.76 mm wide, area 3.5 mm^2, TAL = 1.3, lw/ww = 1.55; basal sixth of wing hyaline, remainder dark brown; length of cell br > cell bm > cell cua, vein CuA recurved and confluent with underside of cell cua (Figs 1B, 11C). Legs black to brown, only portions of four legs preserved, not pennate. Abdomen brown/black, 1.66 mm in length, thorax/abdomen length ratio 0.71, cerci approximately 0.22 mm in length.

Male. Unknown.

***Rhamphomyia decens* sp. nov.**
(Figs 2, 3, 10B)

Holotype. Female, USNM 623106, deposited in the Paleobiology collections of the National Museum of Natural History in Washington, D.C.

Etymology. The specific epithet is from the Latin *decens*, becoming or comely, and refers to the extensive sexual ornamentation of this species.

Diagnosis. Females of this species are distinguished from *Rhamphomyia kitadai* **sp. nov.** and *R. brunnipennis* **sp. nov.** by the absence of darkly pigmented and/or enlarged wings. They are distinguished from all other female Eocene fossils of the genus that display sexual ornamentation as follows: *R. pennipes* **sp. nov.** and the previously described fossil species *R. enena*, *R. insolita* Meunier, *R. media* Meunier and *R. obtusa* Meunier, based on being significantly longer (4.44 mm *vs*. ≤ 3 mm or, in the case of *R. interita* Melander, shorter (4.44 mm *vs*. 6.75 mm); *Rhamphomyia decens* **sp. nov.** has a relatively short and stout postpedicel with a L/W ratio of 3.1 which distinguishes it from *R. obtusa* (6.3), *R. pennipes* **sp. nov.** (4.4), *R. kitadai* **sp. nov.** (4.6) and R. *brunnipennis* **sp. nov.** (6.8); *Rhamphomyia decens* **sp. nov.** can be differentiated from the previously described species *R. infernalis* Melander, by having pennate scales on the mid femora and tibiae; it is distinguished from *R. ablata* Meunier by the latter's femora lacking scales.

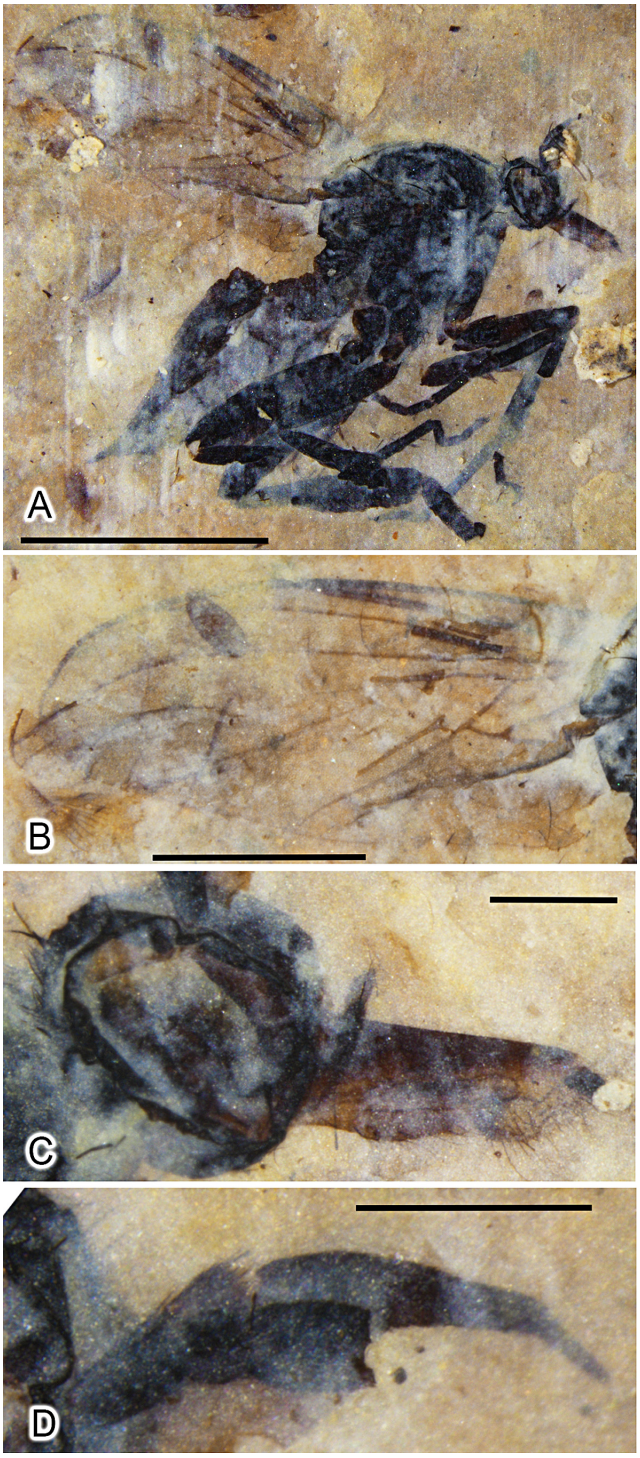

FIGURE 2. *Rhamphomyia decens* **sp. nov.**, female, USNM 623106. **A**, Habitus. **B**, Wings. **C**, Head and proboscis. **D**, Antennae. Scale bars = 2.0 mm (**A**), 1.0 mm (**B**), 0.25 mm (**C**, **D**).

Locality and horizon. Disbrow Creek site, Kishenehn Formation, Colorado (USA); Middle Eocene (Lutetian).

Description. Female. Length (lateral view) 4.5 mm long, black (Fig. 2A). Head 0.55 mm long, 0.58 mm high, proboscis 0.58 mm long, with setae along ventral surface.

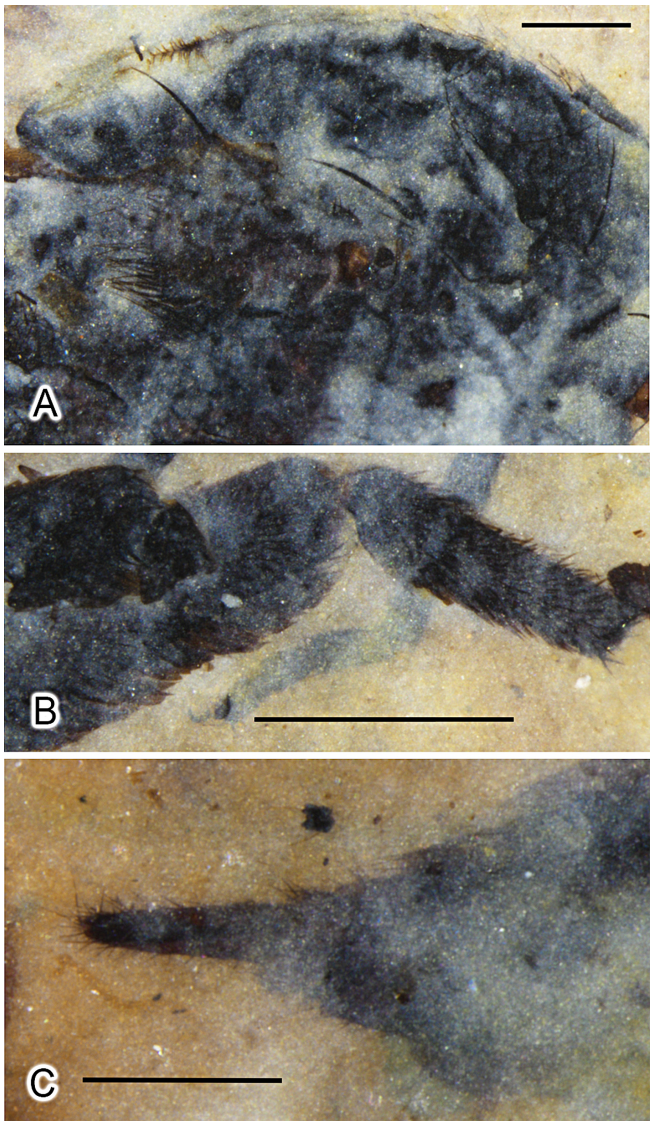

FIGURE 3. *Rhamphomyia decens* **sp. nov.**, female, USNM 623106. **A**, Thorax, lateral view. **B**, Hind tibia and tarsus. **C**, Cerci. Scale bars = 0.25 mm (**A, C**), 0.5 mm (**B**).

Palpi (one behind the other) setose apically, 250 mm long, 45 µm wide (Fig. 2C). Antenna 0.6 mm long, both scape and pedicel setose apically, 0.12 mm and 80 µm long respectively; postpedicel length 0.31 mm long, ratio of L/W_{max} = 3.1, style 95 µm long, 20 µm wide. (Fig. 2D). Thorax black, approximately 1.64 mm long, laterotergite with row of long, dark setae, other setae, possibly postpronotal, notopleural and postalar, also present (Fig. 3A). Wing poorly preserved, length approximately 2.86 mm, width 1.25 mm, lw/ww = 2.29, length of cell br > cell bm > cell cua, vein CuA recurved and confluent with underside of cell cua (Fig. 2B). Legs black, hind femur, tibia and tarsomere 1 enlarged, fore, mid and hind femora and tibiae and hind tarsomere 1 all with pennate scales; lengths and widths (scales not included) of hind femur, tibia and tarsomere 1 approximately 1.45 mm × 0.35 mm, 1.57 × 0.22 mm, and 0.64 mm × 0.13 mm, respectively (Figs 2A, 3B, 10B). Abdomen 2.45 mm in length, cerci setose, relatively small, approximately 0.25 mm long (Figs 2A, 3C).

Male. Unknown.

Rhamphomyia enena Cockerell, 1921

(Figs 4, 5)

Rhamphomyia (?) *enena* Cockerell, 1921: 30.

Rhamphomyia enena: Melander, 1928: 191 [checklist]; Evenhuis, 1994: 354 [catalogue].

Holotype. Female, USNM 66921, deposited in the Paleobiology collections of the National Museum of Natural History in Washington, D.C.

Diagnosis. Females of this species are distinguished by the weakly infuscate wings, wing length 2.6 mm long, body length/wing length > 1 and presence of pennate scales on the hind femur. It is distinguished from *R. pennipes* **sp. nov.** by its shorter terminal abdominal segments (2.4 mm *vs*. 4.3 mm).

Locality and horizon. Cathedral Bluffs, Green River Formation, Colorado (USA); Early Eocene (Ypresian).

Description. Female. Length 3.1 mm. Body color light brown as preserved, head darker, with setae on face. Antenna approximately >0.41 mm in length, boundaries of scape, pedicel and postpedicel not well preserved, bulbous portion of postpedicel 0.17 mm wide, terminus of postpedicel and stylus buried under matrix (The figure of Cockerell (1921) is, charitably, an educated guess at the shape and length of the antenna and its various segments). Proboscis setose, approximately 1.8 mm long (Fig. 4A, B). Thorax 0.92 mm in length, scutum setose with largest setae > 0.15 mm in length; laterotergite not discernable. Wing 2.6 mm in length, weakly infuscate, several long basal costal setae present; R_{4+5} unbranched. Ratio of wing length to width (lw/ww) = 2.3, cell dm shorter than cell bm, M_2/d = 2; R_{4+5}, M_1, M_2 and M_4 all reaching wing margin although weakening near margin; alular incision, calypter and halter not preserved (Fig. 5A, B). All legs setose, hind femur and tibia 1.1 long × 0.3 mm wide and 1.0 long × 0.2 mm wide, respectively; ventral (and dorsal?) edges of hind femur and dorsal edge of hind tibia with pennate scales (Fig. 4A, D). If ventral edge of hind tibia with scales, they appear smaller and less sclerotized than those of dorsal edge. Abdomen (with terminalia) 2 mm in length; cercus long, about 0.15 mm, and slender.

Male. Unknown.

Remarks. Cockerell's original description included little that would identify this specimen as the genus *Rhamphomyi*a other than a statement that the venation was "apparently normal for the genus"; he referred to

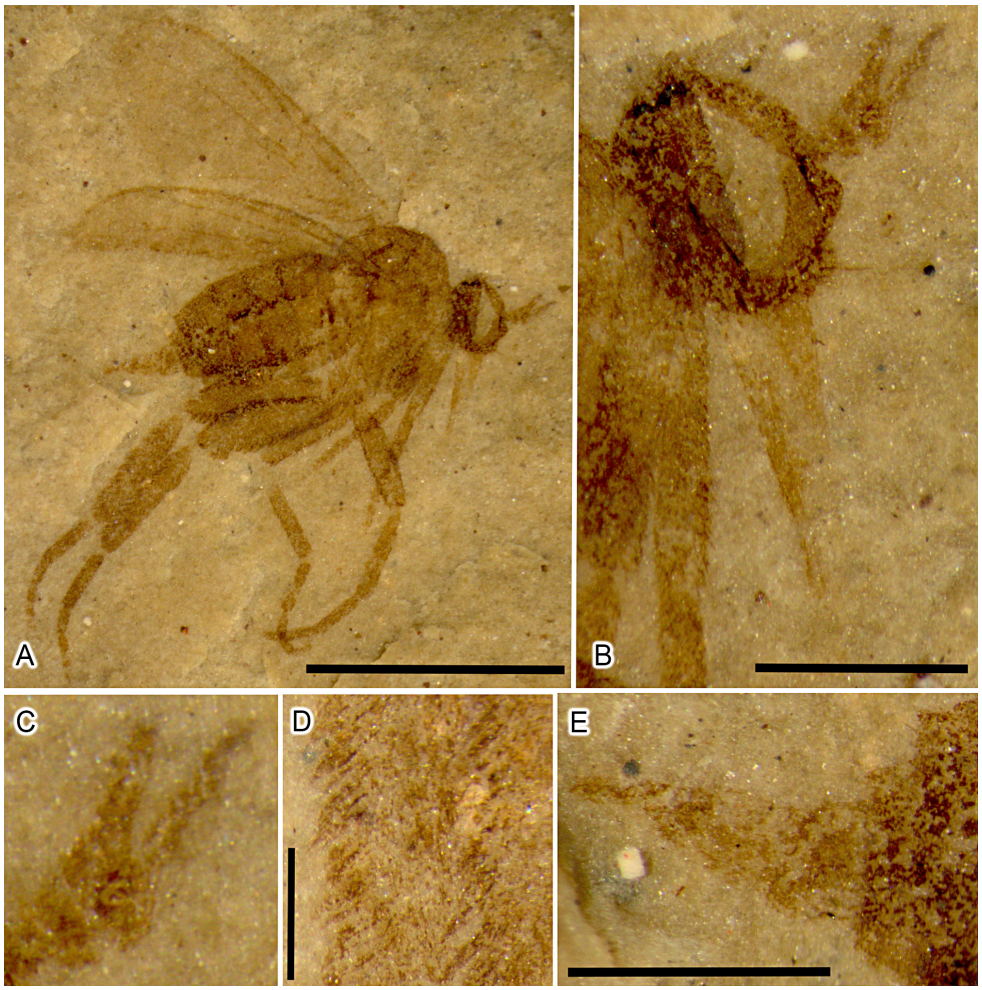

FIGURE 4. *Rhamphomyia enena*, female, USNM 66921. **A**, Habitus. **B**, Head and proboscis. **C**, Antennae. **D**, Hind tibia with pennate scales. **E**, Terminalia. Scale bars = 2.0 mm (**A**), 0.5 mm (**B**), 0.2 mm (**D**) and 0.5 mm (**E**); **C** is intentionally left without scale bar.

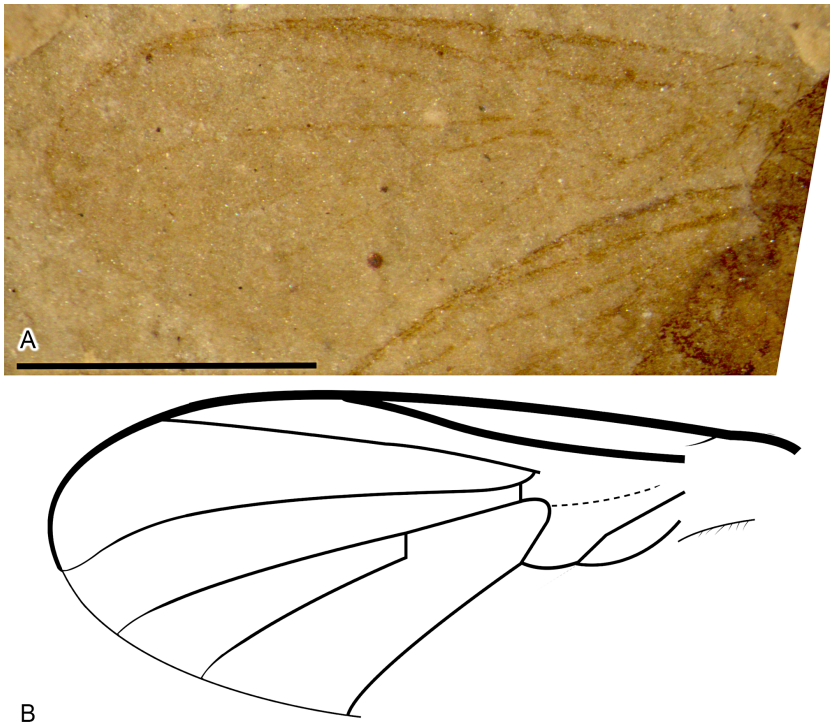

FIGURE 5. *Rhamphomyia enena*, female, USNM 66921. **A**, Left wing. **B**, Drawing of wing. Scale bar = 1.0 mm.

it as *Rhamphomyia* (?) *enena*, an indication that his identification was not to be considered definitive. His report of "thin rather long hair" on the thorax did not refer to the laterotergite's group of dark setae, a character that separates Empidini from Hilarini. He did however observe that the specimen's legs were "unusually stout, especially the hind femora and tibiae; the hind legs quite thickly beset with short hairs" which are identified here as scales. Pennate legs are found in many species of *Empis* and *Rhamphomyia* and at least one undescribed specimen of *Hilara* Meigen (Empidinae: Hilarini) has been reported (Cumming, 1994) with such ornamentation. Given the rarity of this character state in genera other than *Empis* and *Rhamphomyia*, and the inability of the presence/absence of a forked R_{4+5} to differentiate between these two genera (Rhodén & Wahlberg, 2020), we propose that Cockerell's original open nomenclature (Bengtson, 1988) assignment be changed to the more definitive *Rhamphomyia enena* (*i.e.*, without the question mark).

Cockerell (1921) also reported an isolated wing from a different Green River site (Roan Mountain, Colorado), the venation of which he described, as "agrees with *R. enena*". The venation of this specimen is much better preserved than in the holotype of *R. enena*, but it can be assigned only to *Rhamphomyia*.

***Rhamphomyia kitadai* sp. nov.**
(Figs 6–8)

Holotype. Female, USNM 622529, deposited in the Paleobiology collections of the National Museum of Natural History in Washington, D.C.

Etymology. The species name is in honor of Leland Kitada, who joined the Peace Corps to teach as his ethnicity prevented him from pursuing a career as a science teacher in the United States.

Diagnosis. Females of this species are distinguished from all previously described fossils of the genus by its darkly pigmented and expanded wings. *Rhamphomyia kitadai* **sp. nov.** is distinguished from *R. brunnipennis* **sp. nov.** by its longer abdomen (2.1 mm *vs*. 1.6 mm) and the resulting thorax/abdomen length ratios (0.5 *vs*. 0.71).

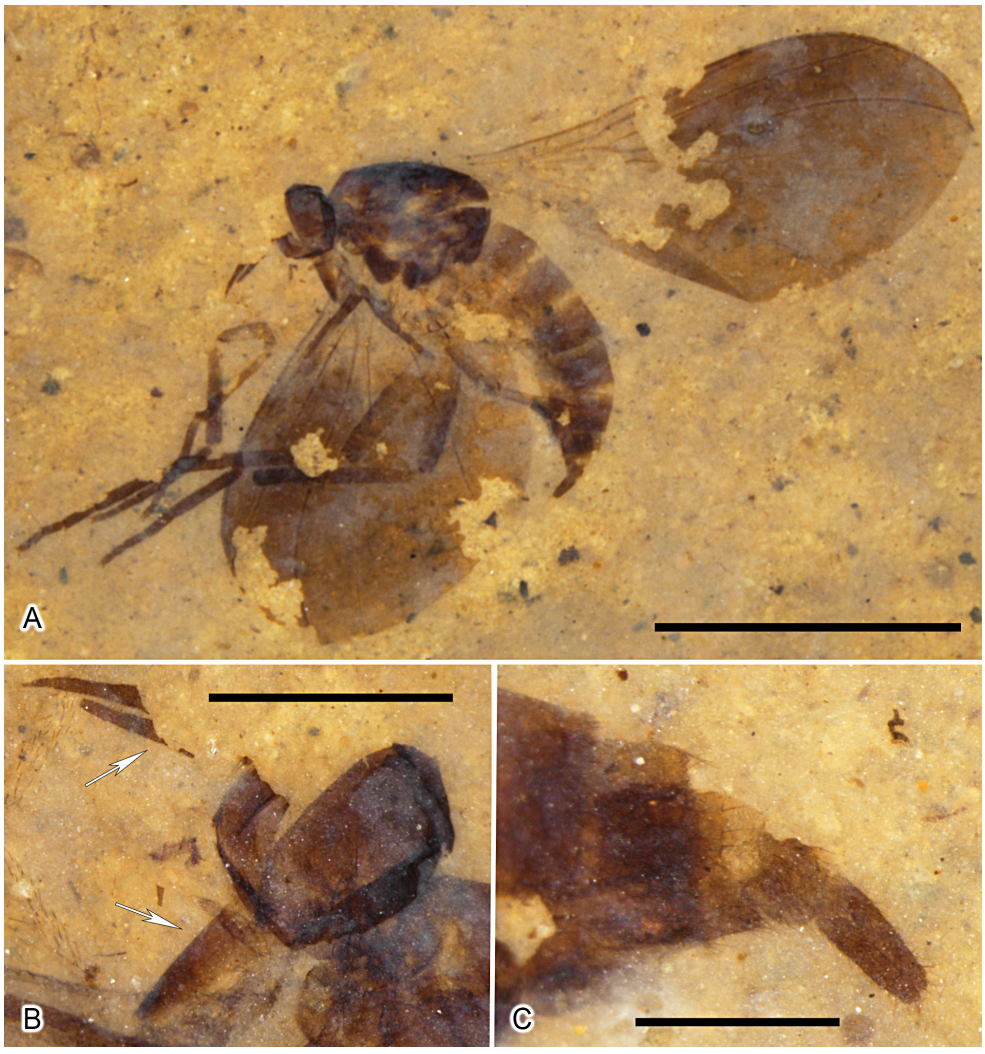

FIGURE 6. *Rhamphomyia kitadai* **sp. nov.**, female, USNM 622529. **A**, Habitus. **B**, Head, proboscis and antennae. **C**, Terminalia. Scale bars = 2.0 mm (**A**), 0.5 mm (**B**), 0.25 mm (**C**).

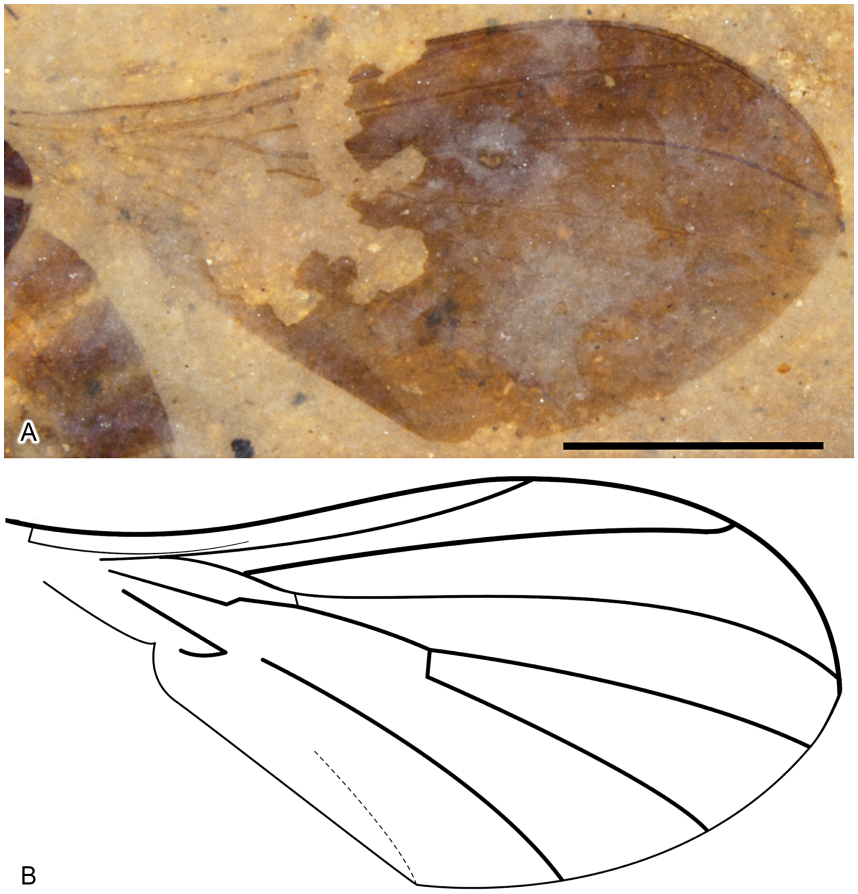

FIGURE 7. *Rhamphomyia kitadai* **sp. nov.**, female, USNM 622529. **A**, Left wing. **B**, Drawing of wing. Scale bar = 1.0 mm.

Locality and horizon. Disbrow Creek site, Kishenehn Formation, Colorado (USA); Middle Eocene (Lutetian).

Description. Female. Length about 3.5 mm. Head 0.42 mm long, 0.49 mm high, dark brown, without observable setae. Antenna brown, 0.52 mm long, scape setose apically, pedicel not preserved, stylus 64 µm long with apical process 20 µm × 8 µm wide (Fig. 6A); proboscis brown, setose, relatively short, 0.33 mm long, 0.14 mm wide at base; palpus 0.2 mm long, 50 µm in width, setose apically (Fig. 6A, B). Thorax dark reddish brown, 1.06 mm in length, setae not preserved/visible. Legs mostly brown, coxae and base of at least hind femur pale, not pennate, hind femur 0.92 mm long, 0.17 mm wide, heavily setose, hind tibia 1.09 mm long × 0.11 mm wide and hind tarsus 1.12 mm long, 90 µm wide (T1). Right wing 2.7 mm long × 1.6 mm wide, area 3.6 mm^2, apparent wing area/thorax + abdomen length (TAL) = 1.3 (both wings); R_{4+5} unbranched, cells bm and dm incompletely preserved, M_2/d = 1.8, lw/ww = 2.1 (Figs 7, 11). Abdomen brown with intersegmental areas unpigmented, 2.1 mm in length, hind marginal setae on all tergites; ratio of thorax/abdomen lengths = 0.5. Cerci 175 µm × 33 µm, setose (Fig. 3C).

Male. Unknown.

Paratype. Female, USNM 626127, deposited in the Paleobiology collections of the National Museum of Natural History in Washington, D.C.

Locality and horizon. Deep Ford site, Kishenehn Formation, Colorado (USA); Middle Eocene (Lutetian).

Description. Female. Length 3.85 mm (with cerci). Head 0.45 mm long, 0.5 mm high, dark brown, without observable setae. Antenna brown, 0.5 mm long, scape 60 µm long, pedicel 60 µm long, setose apically; postpedicel 0.27 mm in length, L/W_{max} = 4.6, stylus 40 µm long with apical process 30 µm long; proboscis reddish brown, setose, (Fig. 8A, B). Thorax dark brown, 0.98 mm long (Fig. 8A, B). Wing 3.0 mm long, 1.37 mm wide, area 2.9 mm^2, TAL = 0.9, lw/ww = 2.2 (Fig. 8C); basal fifth of wing hyaline, remainder darkly pigmented; length of cell br > cell bm > cell cua, vein CuA recurved and confluent with underside of cell cua (Fig. 8C). Legs light to dark brown, coxae and base of at least hind femur pale, not pennate, hind femur 0.91 mm long, 0.17 mm wide, with ventral row of setae, hind tibia 0.99 mm long, 87 µm wide and hind tarsus 0.95 mm long, 79 µm wide (T1). Abdomen brown, 2.49 mm in length with intersegmental areas unpigmented, ratio of thorax/abdomen lengths =

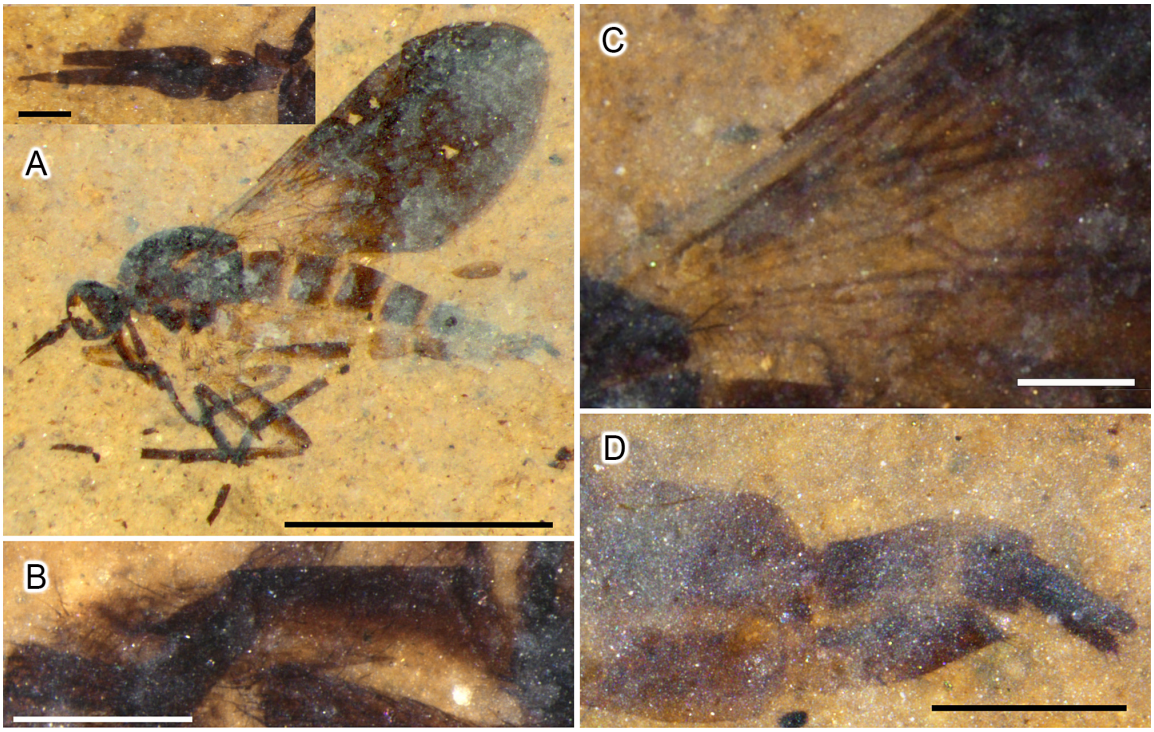

FIGURE 8. *Rhamphomyia kitadai* **sp. nov.**, paratype female, USNM 626127. **A**, Habitus, insert = antennae. **B**, Proboscis. **C**, Basal portion of wing. **D**, Terminalia. Scale bars = 2.0 mm (insert 0.1 mm) (**A**), 0.2 mm (**B**) and 0.25 mm (**C**, **D**).

0.39, cerci setose, 0.17 mm in length, 24 µm wide (Fig. 8D).

***Rhamphomyia pennipes* sp. nov.**
(Figs 9, 10A)

Holotype. Female, USNM 620447, deposited in the Paleobiology collections of the National Museum of Natural History in Washington, D.C.

Etymology. The specific epithet is from the Latin *pennipes* (wing-footed) and refers to the pennate scales of the hind legs of this specimen.

Diagnosis. Females of this species are distinguished from the seven previously described Eocene fossils of females of the genus that display sexual ornamentation as follows: its small size (2.86 mm) differentiates it from *R. ablata*, *R. infernalis* and *R. interita* (all 4.5 mm or greater in length); *R. pennipes* **sp. nov.** has narrow mid tibiae without scales while *R. media* has fringed middle tibiae; *R. pennipes* **sp. nov.** is distinguished from *R. media* and *R. obtusa* by the L/W ratio of its postpedicel (4.4 *vs*. 3.17 and 6.33, respectively). *Rhamphomyia insolita* and *R. obtusa* have wings half again as long as *R. pennipes* **sp. nov.** (3.0 mm *vs*. 2.0 mm); *R. enena* differs from *R. pennipes* **sp. nov.** in the size and shape of their terminal abdominal segments and the more enlarged/stout hind tibia of *R. enena*; *R. pennipes* **sp. nov.** is distinguished from *R. decens* **sp. nov.** by its smaller size (2.86 mm *vs*. 4.5 mm), its color and the L/W ratio of its postpedicel (4.4 *vs*. 3.1), and is distinguished from *R. kitadai* **sp. nov.** and *R. brunnipennis* **sp. nov.** by the absence of pigmented and/or enlarged wings; it is also differentiated from *R. brunnipennis* **sp. nov.** by the L/W ratio of its postpedicel (4.4 *vs*. 6.8).

Locality and horizon. Park site, Kishenehn Formation, Colorado (USA); Middle Eocene (Lutetian).

Description. Female. Length (ventral view) 2.86 mm (Fig. 9A). Head dark brown, 0.33 mm long, 0.37 mm high, setae visible at dorsal base of proboscis and ventral portion of head; proboscis 0.33 mm long. Neither scape nor pedicel completely visible, right postpedicel setose basally, length (from bulbous base) 0.26 mm, ratio of L/W_{max} = 4.4 (Fig. 9D). Thorax black, 0.67 mm long, wing length 2.0 mm, width 0.94 mm, lw/ww = 2.14, wing area 1.5 mm^2, TAL = 2.5, M_2/d = 1.68, M_4 ratio = 0.4, length of cell br > cell bm > cell cua, vein CuA recurved and confluent with underside of cell cua (Fig. 9B, C). Hind femur pennate with scales 0.13 mm long (Figs 9A, 10B) ventrally, 0.75 mm long, 0.17 mm wide (scales not included); hind tibia approximately 0.68 mm long, 0.13 mm wide, with shorter, narrower scales ventrally; hind tarsus 0.87 mm long, 63 µm wide (T1), mid femur and tibia both narrow and without scales; all legs dark reddish in color. Abdomen brown, 1.86 mm in length, cerci 0.16 mm long (Fig. 9D).

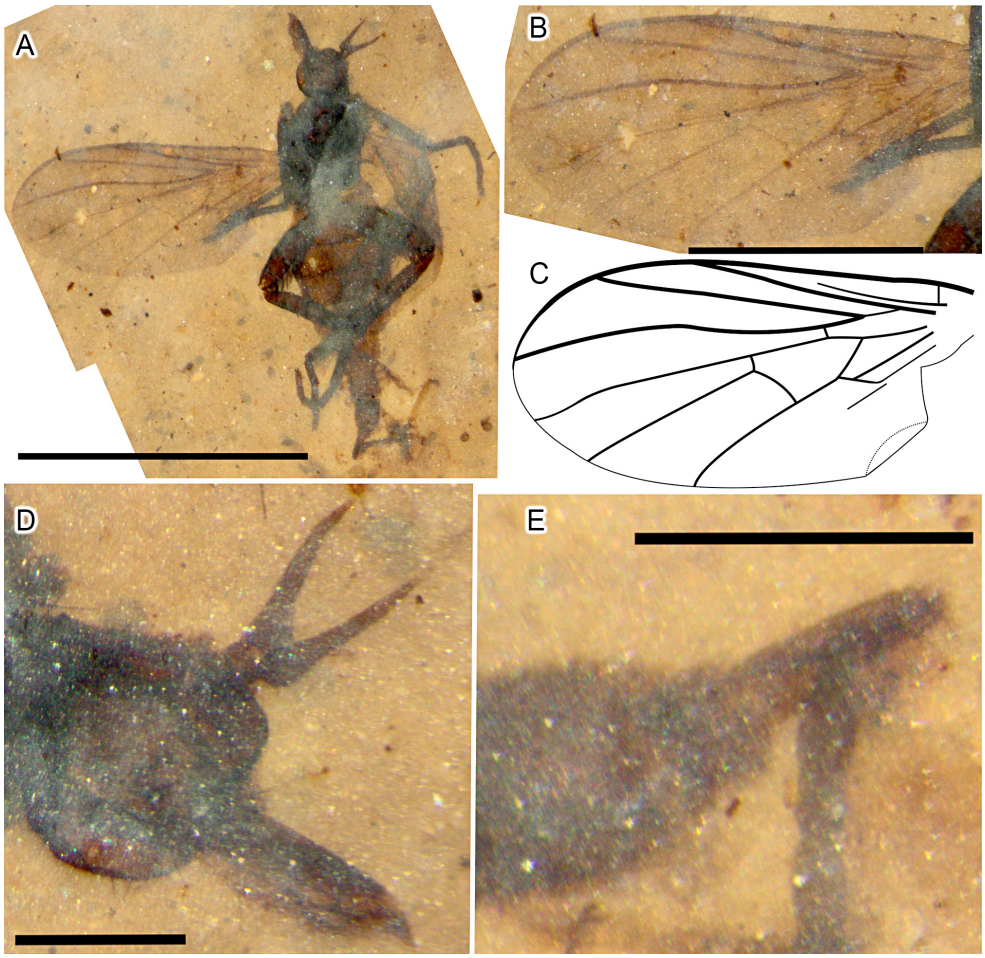

FIGURE 9. *Rhamphomyia pennipes* **sp. nov.**, female, USNM 620447. **A**, Habitus. **B**, Left wing. **C**, Drawing of wing. **D**, Head, antennae and proboscis. **E**, Terminalia. Scale bars = 2.0 mm (**A**), 1.0 mm (**B**), 0.25 mm (**D**, **E**).

Key to ornamented female Empidini of the Eocene

1 Modified sexual features present 2
– Modified sexual features absent .....(not treated here)
2 R_{4+5} forked 3
– R_{4+5} not forked 5
3 Tibiae without pennate scales.....*Empis mala* Meunier
– One or more tibiae with pennate scales 4
4 Pennate scales restricted to hind tibiae; body length 7 mm.. .....*E. malefica* Meunier
– Pennate scales present on both mid and hind tibiae; body length 2.25 mm..... *E. personata* Meunier
5 Wings darkly pigmented and enlarged (Figs 1A, B, 6A, 7A, B, 11); legs without pennate scales 6
– Wings not darkly pigmented; one or more legs with pennate scales (Figs 3B, 4D, 10A, B)..... 7
6 Wings suboval in shape (Figs 6A, 7A, B) .... *Rhamphomyia kitadai* **sp. nov.**
– Wings not suboval (Fig. 1A, B)..... .....*R. brunnipennis* **sp. nov.**
7 Hind basitarsus fringed with pennate scales..... 8
– Hind basitarsus not fringed with pennate scales..... 9
8 Fore tarsomere 1 longer than remaining tarsomeres combined (Fig. 3B)..... *R. decens* **sp. nov.**
– Fore tarsomere 1 shorter than remaining tarsomeres combined ..... *R. ablata* Meunier
9 Mid tibiae with pennate scales .....*R. media* Meunier
– Mid tibiae without pennate scales 10
10 Hind femora without pennate scales; body length ≥ 4.5 mm..... 11
– Hind femora with pennate scales; body length ≤ 3 mm 12
11 Length of hind tibial pennate scales longer than width of tibia..... *R. infernalis* Melander
– Length of hind tibial pennate scales subequal to width of tibia.....*R. interita* Melander
12 Body length/wing length > 1 13
– Body length/wing length < 1 14
13 Terminal abdominal segments short, 2.4 mm in length..... .....*R. enena* Cockerell
– Terminal abdominal segments long, 4.3 mm in length..... .....*R. pennipes* **sp. nov.**
14 Hind tibiae with long pennate scales.....*R. obtusa* Meunier
– Hind tibia without pennate scales..... *R. insolita* Meunier

Discussion

Both female sexual ornamentation and male nuptial gift-giving behavior in Empidinae are driven by the fact that, in many species, females do not hunt and a gift of prey from the male is their only source of nutrition as

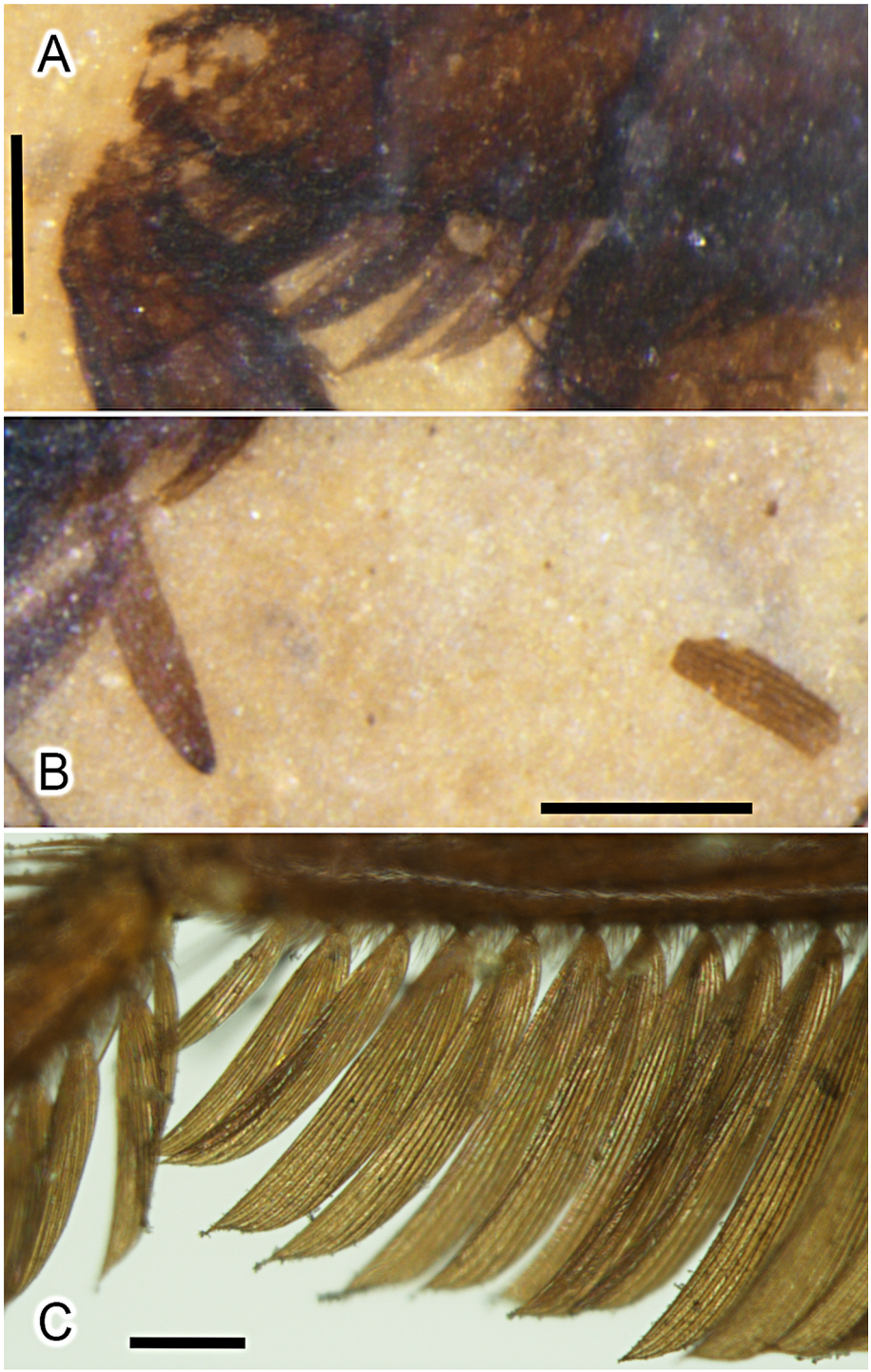

FIGURE 10. Comparison of fossil and extant pennate leg scales. **A**, Pennate scales of ventral side of hind femur of *Rhamphomyia pennipes* **sp. nov. B**, Pennate scales (loose), presumably from ventral aspect of hind femur of *R. decens* **sp. nov. C**, Pennate scales on right mid tibia of *R. fumosa* (extant). Scale bars = 0.1 mm

an adult (Svensson *et al*., 1990; Vahed, 1998; Gwynne, 2008; Sinclair *et al*., 2013). Nuptial gift-giving behavior is at least 100 million years old as indicated by the recent improbable discovery of a male of the Cretaceous species *Alavesia lanceolata* Sinclair & Grimaldi (Diptera: Empidoidea: Atelestidae) carrying an empty shell as a nuptial gift (Tang *et al*., 2022). However, existence of various types of nuptial gifts suggests that gift-giving behavior is even older. Nuptial gifts can take the form of freshly captured prey, either bare or wrapped in a balloon-like shell composed of either mucosal secretions or silk (secreted by glands on fore tarsomere 1 of some species [Young & Merritt, 2003]), mucosal or silk-derived shells that contain inedible detritus and mucosal or silk-derived

shells that are empty (reviewed in Tang *et al*., 2022). This variety of gift structures has elicited speculation as to their evolution and appearance over time (Kessel, 1955; Svensson & Petersson, 1987; Daugeron, 1997). One possible scenario starts with bare unencapsulated prey as the oldest type of nuptial gift, followed by encapsulated prey—that takes longer to be consumed and therefore prolongs insemination—and culminates with shells that contain either more easily obtained detritus, albeit of negligible nutritional value, instead of prey, or simply empty shells. If this sequence is correct, the use of bare prey must have occurred much earlier than the specimen carrying an empty shell described by Tang *et al*. (2022).

If we assume that female ornamentation developed as a strategy to attract males carrying nutritional gifts, its evolution must have been a more recent series of events as different ornamentation strategies appeared independently and at different times. Empidine female sexual ornamentation is both varied and complex. Pennation can be restricted to the hind legs, or it can occur on all legs—that is, to the hind femora only or to all legs and all leg segments (Cumming, 1994). Scales can be relatively short or, as in *Empis jacobsoni* Meijere, very long, over three times the width of the associated leg segment itself (Daugeron & Grootaert, 2005: fig. 26). Interestingly, *Empis jacobsoni* has scales along the lateral margin of its abdomen as well as on its legs (Daugeron & Grootaert, 2005). Wings can be either darkly pigmented, enlarged or both (Hunter & Bussière, 2019; Murray *et al*., 2022). Some empidine species have a single eversible abdominal sac (*e.g*., *Rhamphomyia* (*Calorhamphomyia*) sp.) while other species have multiple eversible sacs (*e.g*., three pair between segments 2–6 in *Rhamphomyia longicauda* Loew) (Cumming, 1994). Single species can also have more than one type of ornamentation. For example, *Rhamphomyia fumosa* and *R. longicauda* have both pennate legs and eversible sacs, while *Empis aestiva* Loew, *E. nigripes* Fabricius and *E. longiseta* Daugeron & Grootaert have both darkly pigments wings and pennate legs (Daugeron & Grootaert, 2005; Murray *et al*., 2022).

The discovery of nuptial gift-giving nearly 100 million-years-ago (Tang *et al*., 2022) presents a conundrum in that the relict family Atelestidae is sister to all remaining families of Empidoidea, all of which—with the single exception of Empididae—have no record, extant or extinct, of female sexual ornamentation (Cumming, 1994; Tang *et al*., 2022). There is then a huge void in the fossil record. We can ask when these ornaments first appeared and in what order. Did the least effective ornament appear first; did the more seemingly complex ornament, inflatable abdominal sacs, appear more recently? Was the transition from leg setae to scales an evolutionarily slow, step-like process with pennate scales first appearing in a relatively narrow form and gradually becoming wider? The same questions can be asked about wing size and pigmentation. In extant Empidinae, different species can have wings that are enlarged and hyaline, darkly pigmented of normal size or both enlarged and pigmented or even enlarged and patterned wings.

The current fossil record, which has a gap of nearly 50 million years between the nuptial gift-giving specimen *Alavesia lanceolata* and *Rhamphomyia enena*, the oldest example of female sexual ornamentation, has little to say about these questions. The oldest fossil of the superfamily Empidoidea, *Protoreogeton admirabilis* Mostovski, is approximately 170 Ma (Mostovski, 1999); there are an additional two described genera and six specimens of the family Empididae from the Jurassic and ten specimens, including eight described genera, from the Cretaceous (PBDB, 2023). Of these, three, *Empis orapensis* Waters, *Turonempis styx* Grimaldi & Cumming and *Emplita casei* Grimaldi & Cumming, have been assigned to the subfamily Empidinae (Waters, 1989; Grimaldi & Cumming, 1999). None of the Cretaceous and Jurassic specimens display any type of sexual ornamentation (*Empis orapensis* is a male). It is interesting to note that the hugely productive Cretaceous site in Myanmar has produced no specimens of Empididae.

Table 1 lists the 14 known female fossil species of Empididae that display ornamentation, including the four species described herein. Three of these belong to *Empis*—all in Baltic amber—and 11 (counting the four new species from the Kishenehn described herein) are in *Rhamphomyia.* Of these latter eleven, four are in Baltic amber, two are from the Florissant and one, *Rhamphomyia enena* is from the Green River. In all fifteen cases, the preserved ornamentation consists of pennate legs. The first and only species with enlarged and/or darkly pigmented wings, described herein, are approximately 46 million-years-old; inflatable abdominal sacs have no fossil record. It is of interest to note that some extant empidine species display more than one type of ornamentation (*e.g*., both pennate legs and inflatable abdominal sacs [*Hilara luteolimbata* Collin]).

Pennate legs

Females of the extant species *Rhamphomyia sociabilis* (Williston) have pennate legs, but rather than being aligned along the perimeter of the abdomen, the legs hang below the body of the fly. Funk & Tallamy (2000) have suggested that this behavior represents an ancestral step in the evolution of empidine sexual display. Empidine leg scales are modified setae and common in many insects, most famously in Lepidoptera (Winterton, 2009). They are, however, relatively rare in Diptera although exceptions exist (*e.g*., mosquitos). The complexity of empidine scales, which, in addition to striations, have pedicels and sockets much larger than those of the setae

TABLE 1. The fossil record of sexual display in female Empidini (Diptera: Empididae: Empidinae).

Taxon	Locality	Reference	Ornamentation	Descriptions
Empis carbonum	Miocene Eger graben brown coal	Germar, 1837		No mention of leg morphology
Empis florissantana	Florissant	Cockerell, 1915		Wings hyaline, except for a brown stigmatic cloud
Empis infossa	Florissant	Melander, 1949		Lightly infumated wings; legs without bristles visible except apical spurs of tibiae, hairs microscopic
Empis mala	Baltic amber	Meunier, 1908	Present	Upper half of hind femur with about a dozen scales; tibia without scales, ciliated
Empis malefica	Baltic amber	Meunier, 1908	Present	Hind femur and tibia fringed (with scales)
Empis miocenica	Florissant	Cockerell, 1915		Wings reddish with very dilute stigmatal cloud; hind femur with row of short stiff spiniform bristles
Empis mordax	Baltic amber	Meunier, 1908		Hind femora and tibiae quite densely and fairly evenly ciliated
Empis morosella	Baltic amber	Meunier, 1908		Hind femora and tibiae of female shortly ciliate, tibiae adorned with a few fairly long cilia
Empis perdita	Florissant	Cockerell, 1916a		Wing with apical and costal apical region faintly dusky; hind femora not incrassate, thinly clothed with bristles
Empis personata	Baltic amber	Meunier, 1908	Present	Femora and mid tibiae fringed (with scales), femora and hind tibiae slightly more heavily feathered than on mid legs.
Empis poeppigi	Baltic amber	Giebel, 1856		Legs thin, not hairy
Empis (*Acallomyia*) *probolaea*	Florissant	Melander, 1949		Legs slender, simple; wings nearly hyaline
Empis spinifera	Rott	Statz, 1940		Wings hyaline; double row of comb-like spines on distal undersides of mid and hind legs
Empis umbonata	Rott	Statz, 1940		Wings light brown; legs similar to male
Progloma rohweri	Florissant	James, 1937		Legs with brown pile; wings hyaline
Rhamphomyia ablata	Baltic amber	Meunier, 1908	Present	Tibiae with scales, hind tarsomere 1 quite long fringed on outside
Rhamphomyia angusta	Baltic amber	Meunier, 1908		Hind tibiae adorned with a few cilia longer than the others
Rhamphomyia brunnipennis sp. nov.	Kishenehn	Greenwalt & Sinclair, this paper	Present	Oval & darkly pigmented wings
Rhamphomyia corrupta	Baltic amber	Meunier, 1908		No information provided
Rhamphomyia craterae	Florissant	Melander, 1949		Wings with slight flavescent tinge; hind femora with some setae beneath, hind tibiae with at least one seta
Rhamphomyia crinitarsis	Baltic amber	Meunier, 1908		Hairy hind femora and tibiae of female slightly less densely ciliated than in male.

.....continued on the next page

TABLE 1 (Continued)

Taxon	Locality	Reference	Ornamentation	Descriptions
Rhamphomyia decens	Kishenehn	Greenwalt & Sinclair, this paper	Present	All femora and tibiae and hind tarsomere 1 pennate
Rhamphomyia enena	Green River	Cockerell, 1921	Present	Wings clear to very slightly light brown; hind femur and tibia with scales
Rhamphomyia errabunda	Baltic amber	Meunier, 1908		Hind tibiae fairly regularly ciliate
Rhamphomyia fossa	Florissant	Melander, 1949		Wings moderately infumate; legs without evident bristles
Rhamphomyia infernalis	Florissant	Melander, 1949	Present	Wings subhyaline; hind tibiae enlarged. All femora with course short hairs, hind tibiae with fringe, the extensor edge with close narrow scales
Rhamphomyia insolita	Baltic amber	Meunier, 1908	Present	Hind femora and tibiae with scales
Rhamphomyia interita	Florissant	Melander, 1949	Present	Wings probably hyaline; hind tibiae with fringes equal to diameter of tibiae
Rhamphomyia kitadai sp. nov.	Kishenehn	Greenwalt & Sinclair, this paper	Present	Darkly pigmented wings
Rhamphomyia latipennata	Rott	Statz, 1940		Wings hyaline; legs long and slender, fairly densely haired, without scales
Rhamphomyia media	Baltic amber	Meunier, 1908	Present	Femora and mid and hind tibiae fringed
Rhamphomyia morticina	Florissant	Melander, 1949		Legs without scales
Rhamphomyia obtusa	Baltic amber	Meunier, 1908	Present	Hind femora furnished with striated fringed parts (scales), hind tibiae somewhat fringed
Rhamphomyia pennipes sp. nov.	Kishenehn	Greenwalt & Sinclair, this paper	Present	Hind femora and tibiae pennate
Rhamphomyia rottensis	Rott	Statz, 1940		Wings very slightly dusky, legs slender, black and hairy
Rhamphomyia sepulta	Florissant	Cockerell, 1916b		Female? Wings brownish

from which they were derived (Fig. 10C), suggests that their evolution was a complex multi-step process. As such, the process should have a fossil record. In other insects (*e.g*., Lepidoptera and their ancestors), important strides in our understanding of the evolution of the scales have been made (Zhang *et al*., 2018; Wang *et al*., 2022).

Although no studies of the relative lengths and widths of empidine pennate leg scales have been published, cursory observation of extant species indicates that the lengths and widths of empidine pennate scales vary with the size of the fly (personal observation). The scales on the pennate legs of *R. enena* are poorly preserved and their widths and lengths cannot be determined. Scales of *R. decens* **sp. nov.** and *R. pennipes* **sp. nov.** are better preserved. A scale on the hind femur of *R. pennipes* **sp. nov.** measures 26 μm wide × 132 μm long (Fig. 10A) and a scale on the hind femur of *R. decens* measures 28 μm wide × 155 μm long (Fig. 10B). However, scales on one segment of a leg can vary in size. In the extant *R. fumosa*, a medial scale on the mid tibia measures 68 μm × 439 μm and another, more basal scale, measures 28 μm × 186 μm (Fig. 10C). The scales are attenuated at the apex and have longitudinal striations, the numbers of which vary with scale size; scales on the mid tibia of *R. fumosa* contained 5 to 12 striations (Fig. 10C). The leg scales of *Empis personata* Meunier, preserved in Baltic amber,

were figured with approximately 5 to 10 longitudinal striations (Meunier, 1908). Scales from the fossil species *R. pennipes* **sp. nov.** and *R. decens* **sp. nov.** also exhibit a striated structure although they number only four in each of two different scales from *R. pennipes* **sp. nov.** (Fig. 10B).

Enlarged and/or pigmented wings

The female wing of *Empis borealis* Linnaeus (Fig. 11F) is an archetypal example of an enlarged ornamental empidine wing. It has an area to TAL ratio (A/TAL) of 4.4, a value 2 to 5 times as large as that of several unornamented extant females of species randomly selected from the literature, *Rhamphomyia fortisetosa* Saigusa (2.7) and *R. aquila* Akbar *et al*. (0.9) (Fig. 11A, B, respectively) and *R. chillcottiana* Saigusa (2.4) and *R. arakawae* Matsumura (2.2) (Saigusa, 2012; Akbar *et al*., 2022). The shape of the wing of *E. borealis* is atypical in that its height is essentially the same as its length (Fig. 11F). Svensson & Petersson (1987) demonstrated that, while wing length was 15% greater in females of *E. borealis* relative to males, the area of females' wings averaged 160% that

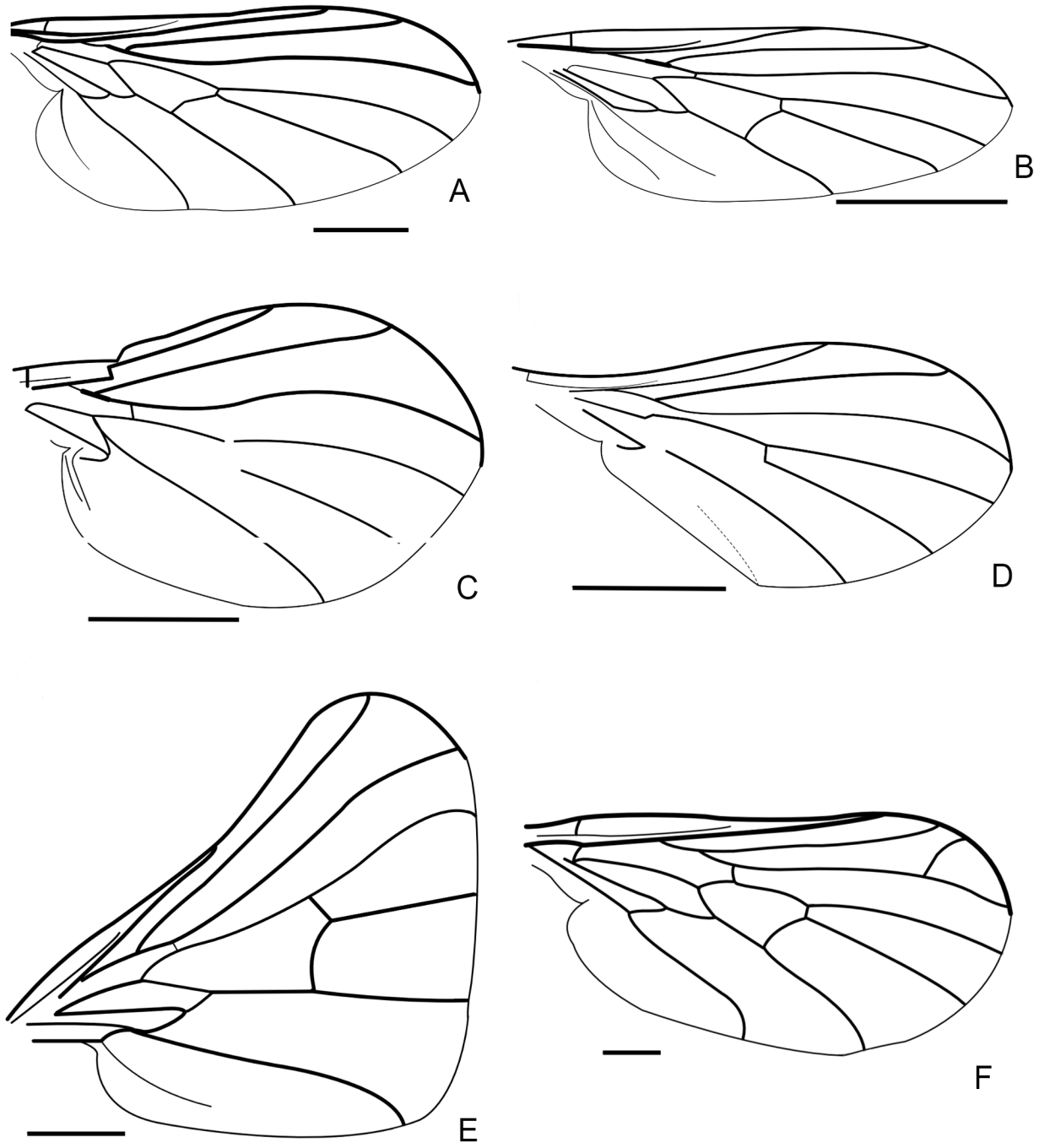

FIGURE 11. Comparison of the sizes and shapes of wings of female Empidini. **A**, *Rhamphomyia fortisetosa*. **B**, *Rhamphomyia aquila*. **C**, *Rhamphomyia brunnipennis* **sp. nov. D**, *Rhamphomyia kitadai* **sp. nov. E**, *Rhamphomyia marginata*. **F**, *Empis borealis*. Drawings not to scale; Scale bars = 1.0 mm.

of males. This suggests that a relative increase in wing height is the major driver of increased wing area.

The wing area to TAL ratios of females of the Eocene *R. kitadai* **sp. nov.** (holotype) and *R. brunnipennis* **sp. nov.** are 0.9 and 1.3, respectively. Although the sizes (A/TAL) of their wings are not significantly enlarged relative to unornamented species of the subfamily, their shapes are distinctly different. Figures 11C and D depict wings that are distinctly rounded apically or oval in shape. It is impossible to know if changes in shape preceded the appearance of enlarged wings. The presence of darkened wings in the absence of wing enlargement is known in a number of extant empidine females, some of which have no other type of ornamentation (*e.g.*, *Empis livida* Linnaeus), while others have pennate legs (*e.g.*, *E. aestiva* and *E. nigripes*) (Murray *et al*., 2022—it should be noted that Murray *et al*. uses the phrase "wing color" in place of darkened and, as in *E. livida*, the color can be quite light).

Wings of female *Rhamphomyia marginata* (Fabricius) are patterned, with dark pigment only present at the edges of the wing, concentrated at the apical margin. Such patterns are atypical however as pigmentation in extant female empidine wings often covers the entire wing, as in the enlarged wings of *Empis borealis*. The darkened wings of the two Eocene species described here all have the apical 75%–85% of the wing uniformly pigmented (Figs 1B, 8A).

Evolution of Empidine ornamentation

The superfamily Empidoidea consists of up to nine families, including Atelestidae—with its Cretaceous specimen of nuptial gift giving—as sister to the remaining families, and greater than 13,000 extant species (Pape *et al*., 2011; Wahlberg & Johanson, 2018; Sinclair *et al*., 2023). Empididae itself consists of at least three subfamilies and approximately 3,500 species, with the empidine genera *Empis*, with 850 described species, *Rhamphomyia*, with 646 species, and *Hilara*, with 533 species, comprising 60 percent of the diversity of the dipteran family (CoL, 2022). These genera are distributed worldwide and contain essentially all known examples of female empidid sexual display (Cumming, 1994; Tang *et al*., 2022). *Empis* and *Rhamphomyia* have historically been differentiated by the branched R_{4+5} in *Empis*, but morphological studies and recent molecular studies have indicated that both are paraphyletic and perhaps constitute a single genus (Barták, 1982; Murray *et al*., 2020; Rhodén & Wahlberg, 2020).

Several first appearance estimates for the evolution of the various clades of these flies have been made. The Empidoidea have been estimated to have first appeared approximately 167, 150 and 147 Ma; the Empididae and Empidinae approximately 140 and 123 Ma, respectively (Grimaldi & Engel, 2005; Wiegmann *et al*., 2011; Turner, 2012). The oldest fossils of the Empididae are from the middle Jurassic while the oldest representatives of Empidinae date to the middle Cretaceous with three specimens from 93 Ma (assigned to the genus *Empis*) and 90–94 Ma (Waters, 1989; Grimaldi & Engel, 1999; PBDB, 2023). The fossil record of female sexual ornamentation consists of 14 species; the oldest record of pennate legs is *Rhamphomyia enena*, from 52 Ma while the oldest record of enlarged and/or darkened wings is approximately 46 Ma. The gap of 40 million years assuredly contains evidence needed to better understand the evolution of the phenomenon of female sexual display in Empididae. Existing collections of amber inclusions from New Jersey (90–94 Ma), Canada (73–83 Ma) and Myanmar (99 Ma) are obvious sources of such evidence. The possibility that informative fossils may come from other clades within the superfamily is also a possibility.

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