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Two Eocene species of *Culiseta* (Diptera: Culicidae) from the Kishenehn Formation in Montana

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Abstract

Culiseta kishenehn, **sp. n.** and *Cs. lemniscata*, **sp. n.** (Diptera: Culicidae: Culisetini) are described from compression fossils from the 46 million year old Kishenehn shale deposits in Montana, USA. The new species appear to share features with extant species of subgenera *Climacura* and *Culicella*, respectively. The antiquity of *Culiseta* is examined and previously described Eocene fossil species are discussed. *Eoaedes* **gen. n.** and *Aetheapnomyia* **gen. n.** are established for *Aedes damzeni* Podėnas and *Ae. hoffeinsorum* Szadziewski, two Eocene fossil species in Baltic amber.

Key words: *Aetheapnomyia* gen. n., compression fossils, *Culiseta kishenehn* sp. n., *Cs. lemniscata* sp. n., *Eoaedes* gen. n., mosquitoes

Introduction

Family Culicidae (Diptera) includes 3,523 extant species classified in 111 genera (including the 80 genera of tribe Aedini recognized in the phylogenetic classification of Reinert *et al*., 2009) (Harbach, 2012). Fossil Culicidae have been described from amber inclusions (11 species) and compression/impressions (12 species) from localities in Canada, Dominican Republic, England, Germany, France, Mexico, Myanmar, Poland and the United States. Twenty-one of the fossil species are from the Tertiary, including species of *Anopheles* Meigen, *Culex* Linnaeus, *Mansonia* Blanchard, *Toxorhynchites* Theobald and two extinct genera, and two are from the Cretaceous. The discovery of the two Cretaceous species confirms Edwards' (1923) view that Culicidae must have originated in the Mesozoic. The oldest fossil, *Burmaculex antiquus* Borkent & Grimaldi, is in Burmese amber from the mid-Cretaceous (89.3–99.6 million years ago, Mya) and the second oldest fossil, *Paleoculicis minutus* Poinar, Zavortink, Pike & Johnston, is in Canadian amber from the Late (Upper) Cretaceous (66.0–100.5 Mya). Ten of the Tertiary species are from the Oligocene (23.0–33.9 Mya; 5 Late Oligocene 23.0–28.1 Mya), nine from the Eocene (33.9–58.0 Mya; 2 Late Eocene 33.9–41.3 Mya, 2 Early Eocene 41.3–56.0 Mya), one from the Early Miocene to Late Eocene (13.8–41.3 Mya) and one from the Early Miocene to Late Oligocene (13.8–33.9 Mya). The Eocene fossil species are placed in two or three extant genera, *Anopheles* (1 species), *Culex* (4 species) and perhaps *Toxorhynchites* (1 species), and four species that are doubtfully assigned to the extant genus *Aedes* Meigen (Harbach, 2012).

Two Eocene species of genus *Culiseta* Felt are described here from compression fossils discovered in shale deposits of the Kishenehn Basin (46.2 ±0.4 Mya) in North America. The depositional environment of the Kishenehn Basin 46 Mya was a large shallow body of water, both lacustrine and paludal. Data from several studies suggest that the climate of the Kishenehn Basin 46 Mya was wet subtropical to tropical: (1) Approximately 10 million years after the higher temperatures of the Paleocene-Eocene Thermal Maximum, the mean annual temperature for what is now northern Montana was approximately 15°C higher than it is now (Wolfe, 1995). (2) The early arboreal primate *Tarkadectes montanensis*, originally described from the Coal Creek member (McKenna, 1990), was recently assigned to the extinct family Omomyidae (Ni *et al*., 2010). Most closely related to the Omomyidae are the insectivorous Tarsiidae, extant species of which are restricted to islands of Southeast Asia

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(Groves & Shekelle, 2010). (3) The molluscan fauna of the Kishenehn Formation is divided into four different successional groups, the first exemplified by *Gastrocopta miniscula*. *Gastrocopta pellucida*, selected as the extant analog of *G. miniscula*, lives in an environment characterized by a mean annual temperature of 25–27°C (Pierce & Constenius, 2001). Thus, mosquitoes that existed in the Nearctic Region during the Eocene flourished in a climate that was considerably warmer than it is today, and that fauna is likely to be more closely related to species now distributed mostly in the tropics and subtropics.

As Huber & Greenwalt (2011) pointed out, specimens preserved as compression fossils are generally less informative morphologically than specimens preserved in amber. Nevertheless, as is evident from the Kishenehn fossils described here, "they can be diagnosed moderately well and differentiated with reasonable certainty from each other and from other extinct and extant genera". The two Eocene species described below are the first fossil species of *Culiseta* discovered thus far.

Materials and methods

Ten specimens of fossil Culicidae (5 females; 5 males) were collected in August, 2009 (USNM numbers 546534 and 546535 [Kishenehn numbers 20093.1 and 30294.5 respectively]) and August, 2011 (USNM numbers 546528–546533, 547065 and 547066 [Kishenehn numbers 505.1, 610.4, 624.1, 635.3, 686.1, 693.1, 30542.1 and 30624.1 respectively]) at three sites: Dakin (W 113° 42.173¢, N 48° 23.476¢) (USNM numbers 546535, 547065 and 547066 [Kishenehn numbers 30294.5, 30542.1 and 30624.1]), Disbrow Creek (W 113° 40.999¢, N 48° 22.572¢) (USNM number 546534 [Kishenehn number 20093.1]) and Constenius Park (W 113° 42.085¢, N 48° 23.517¢) (USNM numbers 546528–546533 [Kishenehn numbers 505.1, 610.4, 624.1, 635.3, 686.1 and 693.1 respectively]). All three collection sites contain exposures of the middle sequence of the Coal Creek member of the Kishenehn Formation exposed along the Middle Fork of the Flathead River in northwestern Montana between Paola and Coal Creeks. The middle sequence of the Coal Creek member has been estimated to be 46.2 ±0.4 million years old (Lutetian) by $^{40}Ar/^{39}Ar$ analysis and 43.5 ±4.9 million years old by fission-track analysis (Constenius, 1996). These dates are supported by biostratigraphic correlations with mammalian and molluscan fossils as well as palynology (Constenius *et al*., 1989; Pierce & Constenius, 2001).

Fossils were immersed in 95% ethanol for examination and photography. 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, Maryland) was used to capture and record the images and measurements. The anatomical terminology and abbreviations of Harbach & Knight (1980, 1982), revised and updated by Harbach (2012), are used for the descriptions. The descriptions are based on examination of all available specimens, all of which have various missing or obscured body parts and structures. The fossils are deposited in the National Museum of Natural History, Washington, D.C. The ages indicated for mosquito fossils follow the geological timescale determined by the International Commission on Stratigraphy (http://www.stratigraphy.org). These ages generally differ slightly from those reported in the literature on mosquito fossils.

Taxonomy

Culiseta kishenehn, sp. n.

(Figs 1, 2, 4A)

Adults. Darkly ornamented mosquitoes, maxillary palpus, proboscis, legs (except ventral area of femora), wing and abdominal terga dark-scaled; proboscis slender, longer than forefemur; cell R_2 longer than vein R_{2+3}, tibiae and tarsi dark-scaled; base of hindcoxa below base of mesomeron; pulvilli absent or inconspicuous.

Female. Head: Ornamentation of head capsule not evident; antenna 1.6–1.7 mm, about 0.7 length of proboscis; maxillary palpus 0.3–0.5 mm, 0.15−0.20 length of proboscis, with 4 palpomeres; proboscis 2.2−2.4 mm, 1.3−1.5 length of forefemur, slightly to moderately bent ventrad (appearing straight in ventral view, specimen no. USNM 547066). *Thorax*: Black, ornamentation obscured. *Legs*: Femora without knee spots; forefemur 1.6–1.9 mm, 0.7–0.8 length of proboscis; tibiae slightly swollen distally; ungues simple, fore- and midungues relatively large,

equal, hindungues smaller, equal. *Wing* (Fig. 4A): Length 3.1–3.7 mm (mean 3.3 mm); base of subcosta with sparse(?) setae (radial setae of Maslov, 1989); distal half of wing with outstanding linear scales on most veins; vein R_2 longer than vein R_{2+3} (R_2/R_{2+3} = 1.7–2.0); base of vein M_{3+4} intersects M_{1+2} proximal to intersection of mediocubital crossvein with M_{1+2}; anal vein (vein 1A) terminates well beyond intersection of mediocubital crossvein and cubitus. *Abdomen*: Apically rounded; terga entirely dark-scaled, no evidence of basolateral pale patches. *Genitalia*: Cerci short, rounded and scarcely visible; 3 spermathecal capsules.

*Male***.** Essentially as female. *Head*: Antenna about 0.7 length of proboscis; flagellomeres 1–11 each with whorl of very long dense setae, flagellomeres 12 and 13 very long, their combined length greater than total length of preceding flagellomeres; maxillary palpus longer than proboscis (1.1 times as long), comprised of 5 palpomeres, palpomeres 2 and 3 ankylosed, long, about 0.75 length of proboscis, palpomere 3 slightly swollen, bearing setae apically, palpomeres 4 and 5 not noticeably swollen, generally projecting straight forwards or turned slightly upwards, palpomere 4 and base of palpomere 5 with numerous long setae, remainder of palpomere 5 with some relatively short setae; proboscis about 1.4 length of forefemur. *Legs*: Ungues of fore- and midlegs enlarged, larger anterior unguis with proximal tooth; hindungues small, equal. *Abdomen*: Terga with well-developed setae along posterior margin. *Genitalia*: Prominent; gonocoxite elongate, relatively stout basally, gradually narrower toward apex, with crescentiform (ridge-like) basal mesal lobe (basal lobe of authors, gonofurca of Maslov, 1989) apparently bearing row(s) of setae on crest, no distinct apicodorsal lobe (apical lobe of authors); gonostylus borne at apex of gonocoxite, rather long and narrow, undivided; paraprocts of proctiger elongate, heavily sclerotized, with strong apical denticle.

Egg, larva and pupa. Unknown.

Etymology. The Kishenehn Formation is named for Kishenehn Creek. Kishenehn (American spelling) is a Kutenai Native American word meaning “no good”. Why the Kutenai adopted this name for the creek is unknown. The specific name *kishenehn* is understood to be masculine, but the evidence for usage as either a noun or an adjective is not decisive; consequently, it is regarded here to be a noun in apposition to the generic name of *Culiseta*, which is feminine.

Systematics. In view of the importance of larval characters for recognizing the subgenera of *Culiseta* (Edwards, 1932; Dobrotworsky, 1954, 1960, 1971), it is not possible to place *Cs. kishenehn* in an extant subgenus. The weakly produced basal mesal lobe of the male genitalia is shared with species of subgenera *Culiseta*, *Climacura* Howard, Dyar & Knab and *Culicella* Felt. The origin of vein M_{3+4} proximal to the radiomedial crossvein (Fig. 4A,B), the entirely dark-scaled abdominal terga and the absence of an apicodorsal lobe on the gonocoxite of the male preclude the species from being placed in subgenus *Culiseta*, species which have the base of M_{3+4} more or less in line with the radiomedial crossvein, banded abdominal terga and an apicodorsal lobe on the gonocoxite. The distal position of the radiomedial crossvein relative to the origin of vein M_{3+4} and the absence of an apicodorsal lobe on the gonocoxite are characteristics of subgenera *Climacura* and *Culicella*. Subgenus *Climacura* includes five species in different parts of the world: *Cs. antipodea* Dobrotworsky in southeastern Australia, the type species *Cs. melanura* (Coquillett) in eastern North America, *Cs. tonnoiri* (Edwards) and *Cs. novaezealandiae* Pillai in New Zealand, and *Cs. marchettei* Garcia, Jeffery & Rudnick in Southeast Asia. *Culiseta kishenehn* resembles these species, except the last one, in having entirely dark-scaled tarsi and abdominal terga, and also resembles *Cs. melanura* in having dark-scaled maxillary palpi, which are longer than the proboscis in males. It is not certain, but *Cs. kishenehn* seems to further resemble species of subgenus *Climacura* in having few subcostal setae (Dobrotworsky, 1971). Subgenus *Culicella* includes 14 species with distributions in Australia (seven species), North America (one species) and the Palaearctic Region (six species). Most of the species have banded tarsi and abdominal terga (three Australian species have unbanded terga and two of these have unbanded tarsi), but in most respects *Cs. kishenehn* seems to be more similar to species of subgenus *Climacura*. Considering the North American provenance of *Cs. kishenehn* and *Cs. melanura*, their close similarity in adult habitus is unlikely to be due to convergence.

Type series. Holotype male (USNM no. 546528; Kishenehn no. 505.1), allotype female (USNM no. 546529, Kishenehn no. 610.4), paratypes males (USNM nos. 546530–546533, Kishenehn nos. 624.1, 635.3, 686.1 and 693.1 respectively), Constenius Park (W 113° 42.085¢, N 48° 23.517¢), paratype female (USNM no. 546534, Kishenehn nos. 20093.1), Disbrow Creek (W 113° 40.999¢, N 48° 22.572¢) and paratype female (USNM no. 547066, Kishenehn no. 30624.1), Dakin (W 113° 42.173¢, N 48° 23.476¢), Kishenehn Formation, Montana, USA.

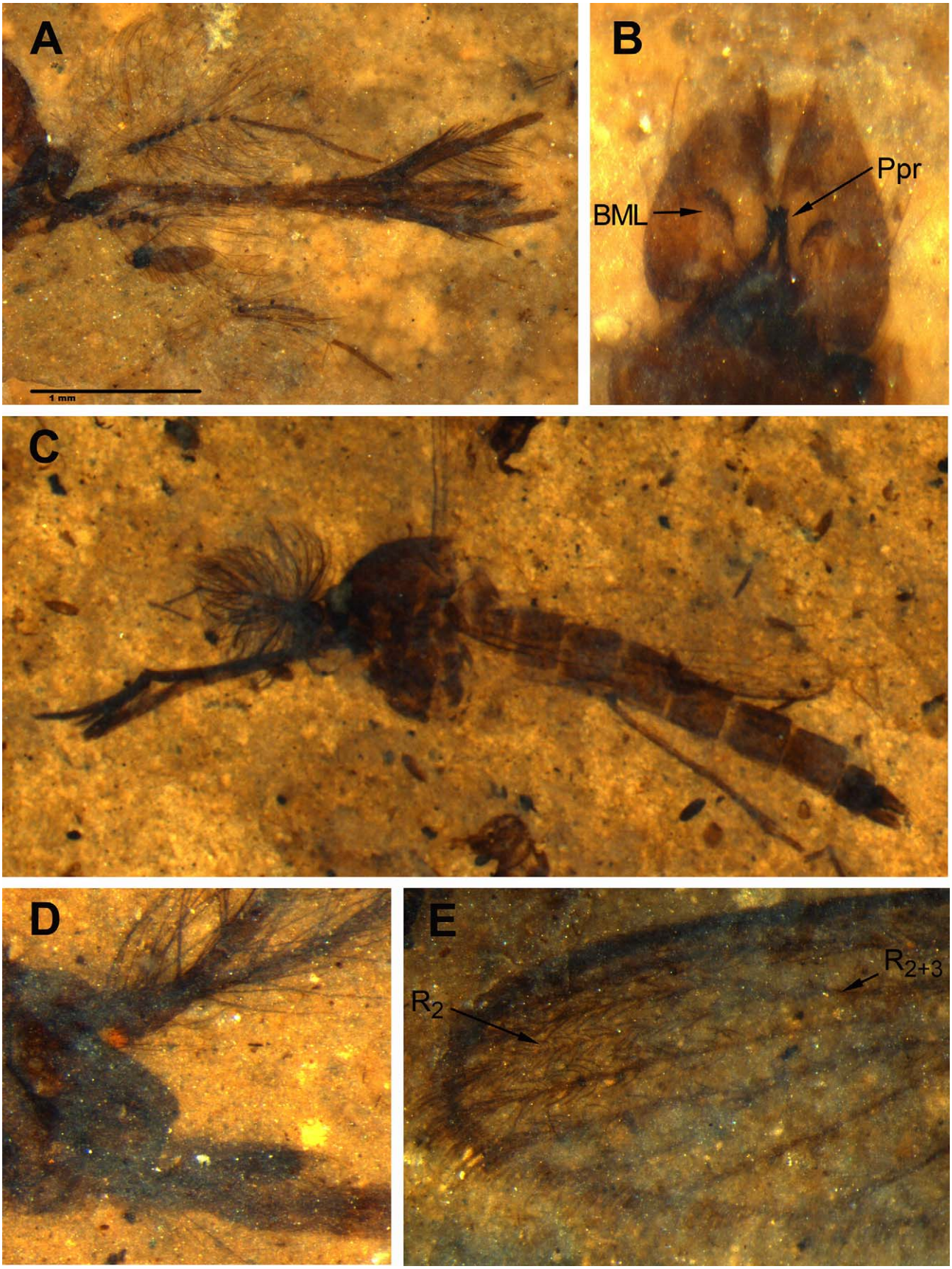

FIGURE 1. *Culiseta kishenehn*, sp. n. A,B. Holotype male (USNM 546528), (A) head and its appendages, (B) genitalia (tergal aspect). C. Paratype male (USNM 546530), body, maxillary palpi, proboscis and abdominal terga entirely dark-scaled. D. Paratype female (USNM 546534), head with short maxillary palpus. E. Allotype female (USNM 546529), distal part of left wing (dorsal) showing the projecting linear scales and long cell R_2. BML = basal dorsomesal lobe; Ppr = paraproct; R_2 = cell R_2; R_{2+3} = vein R_{2+3}.

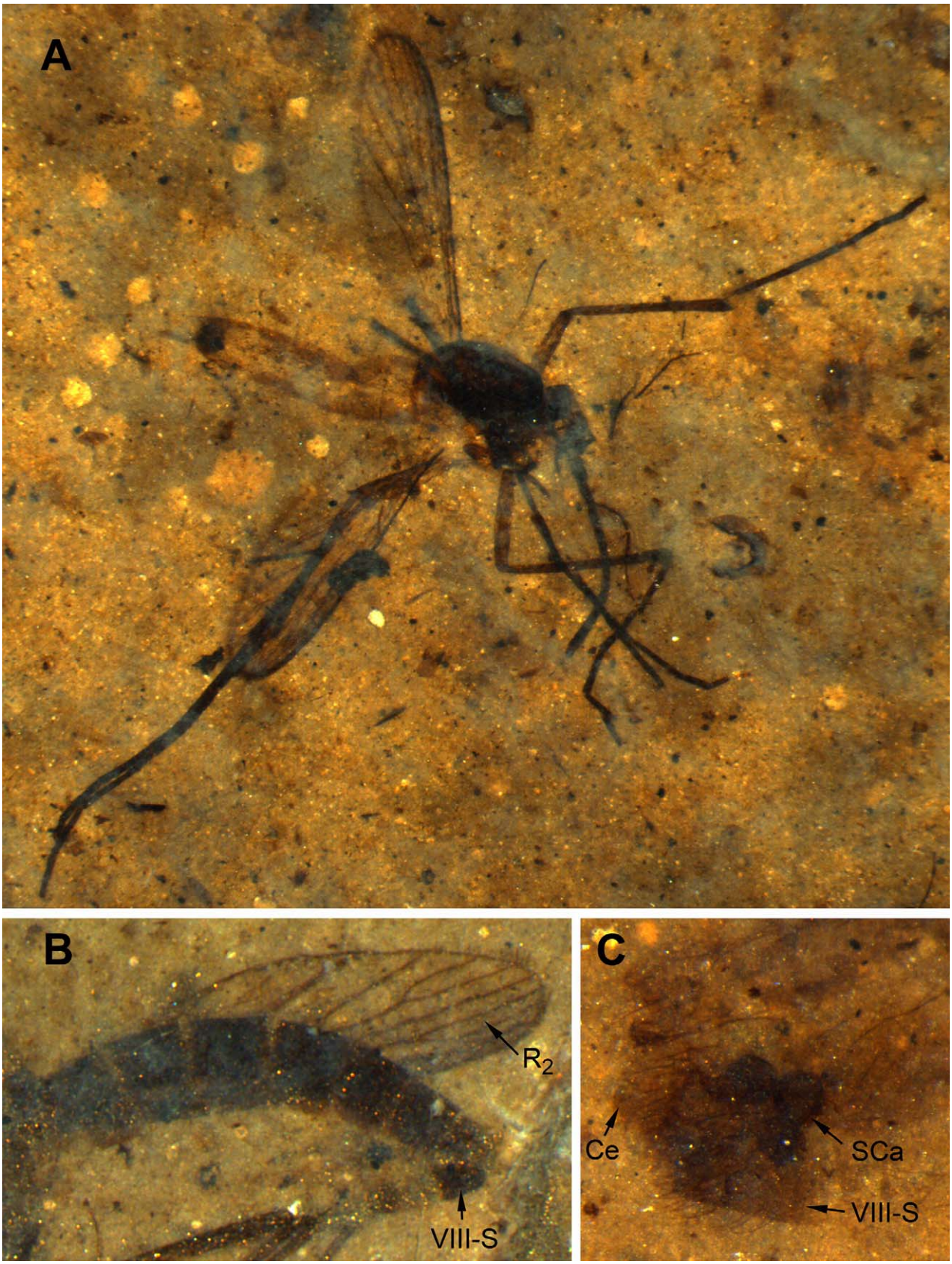

FIGURE 2. *Culiseta kishenehn*, sp. n. A. Allotype female (USNM 546529), habitus, appendages of head and thorax entirely dark-scaled (abdomen poorly preserved). B. Paratype female (USNM 547066), abdomen (left side) and right wing (ventral), terga and wing entirely dark-scaled, long cell R_2, apex of abdomen blunt. C. Paratype female (USNM 546534), apex of abdomen showing the short cercus (partially obstructed by tergum VIII) and three spermathecal capsules. Ce = cercus; R_2 = cell R_2; SCa = spermathecal capsule; VIII-S = sternum VIII.

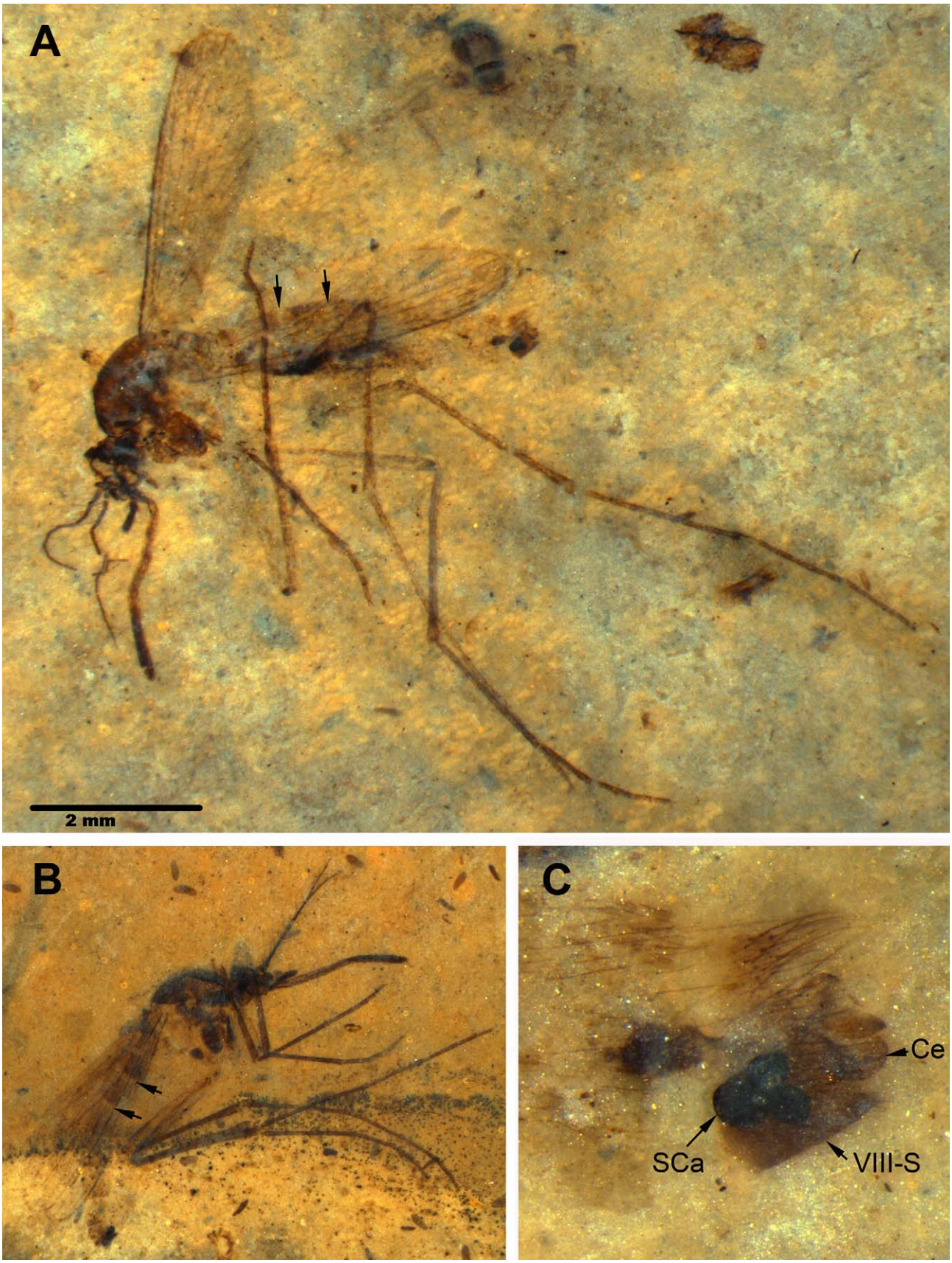

FIGURE 3. *Culiseta lemniscata*, sp. n. A,B. Holotype female (USNM 547065) and paratype female (USNM 546535) respectively, habitus, proximal portion of proboscis pale, legs and wings dark-scaled, abdominal terga with basal pale bands (arrows). C. Same as A, apex of abdomen showing the short cerci and three (indistinct) spermathecal capsules. Ce = cercus; SCa = spermathecal capsule; VIII-S = sternum VIII.

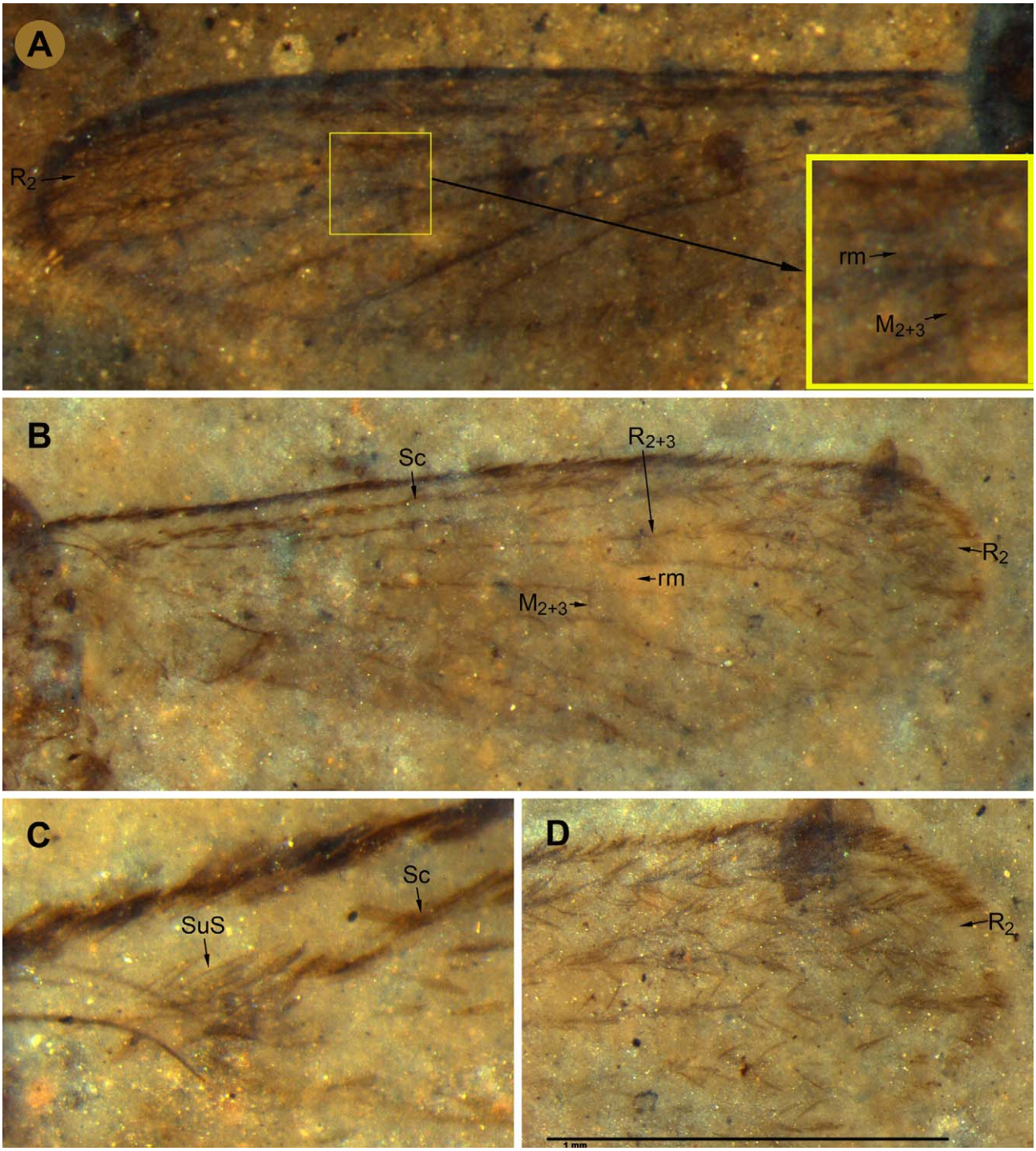

FIGURE 4. A. *Culiseta kishenehn*, sp. n. Left wing of allotype female (USNM 546529). B–D. *Culiseta lemniscata*, sp. n. B. Right wing (dorsal) of holotype female ((USNM 547065). C,D. Same as B, (C) base of wing showing subcostal setae (actually on ventral surface), (D) distal portion of wing showing narrow semi-erect fusiform scales on post-costal veins. M_{2+3} = vein M_{2+3}; rm = radiomedial crossvein; R_2 = cell R_2; R_{2+3} = vein R_{2+3}; Sc = subcosta; SuS = subcostal setae.

***Culiseta lemniscata*, sp. n.**
(Figs 3, 4B,C)

*Female***.** Similar to *Cs. kishenehn* but generally paler in overall habitus; maxillary palpus, wing, tibiae and tarsi entirely dark-scaled; differing as follows. *Head*: Ornamentation of head capsule not evident; antenna 2.0–2.2 mm, about 0.8 length of proboscis, flagellomeres 1–3 slightly thicker and gradually tapering to width of distal

flagellomeres; maxillary palpus with 4 palpomeres and possibly a fifth minute palpomere, length 0.5 mm, 0.20 length of proboscis; proboscis slender, longer than forefemur, length 2.5–2.7 mm, 1.3−1.5 length of forefemur, bent ventrad, dark-scaled with lighter scaling on proximal 0.6, slightly swollen before labella. *Thorax*: Dark, ornamentation obscured; mesonotum rather strongly arched. *Legs*: Base of hindcoxa below base of mesomeron; femora without knee spots; forefemur 1.8−2.0 mm, 0.7−0.8 length of proboscis; hindfemur pale ventrally to near apex; tibiae slightly swollen distally; foretibia and foretarsomere 1 with complete anteroventral and posteroventral rows of prominent setae (evident from large alveoli); foretarsomere 1 nearly as long as foretarsomeres 2–5 combined; ungues of all legs equal, simple; pulvilli absent or inconspicuous. *Wing* (Fig. 4B–D): Length 3.9 mm; base of subcosta with numerous conspicuous setae, distal half of wing with semi-erect narrow fusiform scales on all veins except costa; cell R_2 longer than vein R_{2+3} (R_2/R_{2+3} = 1.6–1.7); base of vein M_{3+4} proximal to mediocubital crossvein; vein CuP distinct from vein CuA; anal vein (vein 1A) terminates well beyond intersection of mediocubital crossvein and cubitus. *Abdomen*: Apex rounded; terga with basal pale bands. *Genitalia*: Cerci short and rounded; 3 spermathecal capsules.

*Male, egg, larva and pupa***.** Unknown.

Etymology. The specific name *lemniscata* is a Latin adjective (feminine form of the masculine *lemniscatus*) meaning “ribboned” or “adorned with ribbons”. The name refers to the pale banding of the abdominal terga.

Systematics. *Culiseta lemniscata*, like *Cs. kishenehn*, cannot be placed in an extant subgenus of *Culiseta* based solely on adult characters. The distal position of the radiomedial crossvein relative to the origin of vein M_{3+4} (Fig. 4B), as noted above, is characteristic of subgenera *Climacura* and *Culicella*. The numerous subcostal setae (Fig. 4C) and banded abdominal terga (Fig. 3) indicate a closer relationship with species of subgenus *Culicella* than to species of *Climacura*. In fact, the female of *Cs. lemniscata* keys to *Culicella* in Dobrotworsky’s (1971) key to the world subgenera of *Culiseta*.

Type series. Holotype female (USNM no. 547065, Kishenehn no. 30542.1) and paratype female (USNM no. 546535, Kishenehn no. 30294.5), Dakin (W 113° 42.173¢, N 48° 23.476¢), Kishenehn Formation, Montana, USA.

Discussion

Fossil records can provide insights into anatomical diversification, historical biogeography and the antiquity of taxa. Edwards (1923) surmized that “The origin and phylogenetic history of the Culicidae must go back to well into the Mesozoic Era” (~66.0 Mya). From divergence times based on sequence data for nuclear protein-coding genes and fossil calibration points, it appears that major culicid lineages date to the Early (Lower) Cretaceous (100.5–145.0 Mya), and genus *Culiseta* may have appeared as early as 191.0 Mya (CL = 154.7–218.8 Mya) during the Middle Jurassic (Reidenbach *et al*., 2009). Extant species of *Culiseta* exhibit generalized features that indicate the genus is a primitive lineage of subfamily Culicinae (Edwards, 1932; Belkin, 1962; Marks, 1968). *Culiseta* may be what paleontologists refer to as a “stem group” (Smith, 1994), a paraphyletic or polyphyletic assemblage of species that share features of extinct taxa. The spotted distribution of the “living fossil” species of *Culiseta* suggests that their extinct relatives (primitive lineage) may have existed before the separation of Pangaea during the Late Paleozoic and Early Mesozoic Eras from about 300–200 Mya.

A number of fossil species have been assigned to Culicidae since the beginning of binomial nomenclature, but only 23 can be placed in the family with confidence. The oldest fossil, *Burmaculex antiquus* from the mid-Cretaceous (89.3–99.6 Mya), bears several plesiomorphic features, including a relatively short proboscis, which suggest it is a stem-group mosquito that is intermediate between extant mosquitoes and other midges. In fact, the phylogenetic analysis of morphological data conducted by Borkent & Grimaldi (2004) indicates that *Burmaculex* is the sister group of all other fossil and modern mosquitoes. Morphological features of the second oldest fossil, *Paleoculicis minutus* from the Late Cretaceous (66.0–100.5 Mya) indicate that *Paleoculicis* shares a closer affinity with culicine than anopheline mosquitoes, which suggests that this ancestral lineage is younger than the lineage that gave rise to subfamily Anophelinae. *Anopheles dominicanus* Zavortink & Poinar and *Anopheles*? *rottensis* Statz are the only fossil anopheline mosquitoes. The former is in Dominican amber from the Late Eocene (33.9–41.3 Mya) and the latter is a compression fossil from the Late Oligocene of Germany (13.8–33.9 Mya).

The new fossil species described above are from the Middle Eocene (41.3–47.8 Mya); hence, they are older than the two previously described species from the Late Eocene (33.9–41.3 Mya): *Anopheles dominicanus* and

Culex erikae Szadziewski & Szadziewska (Baltic amber). They are also older than *Culex malariager* Poinar (Dominican amber) from the Early Miocene to Late Eocene (13.8–41.3 Mya) and *Toxorhynchites mexicanus* Zavortink & Poinar (Mexican amber) from the Early Miocene to Late Oligocene (13.8–33.9 Mya). Seven other Eocene species have been described. These include *Culex damnatorum* Scudder (Green River, Wyoming, Early Eocene, compression/impression), *Culex pipiens* Linnaeus (an extant species in Baltic amber), *Culex winchesteri* Cockerell (Cathedral Bluffs, Colorado, Early Eocene, compression/impression) and four species placed in the extant genus *Aedes* (broad traditional sense).

According to Edwards (1923), *Culex damnatorum* is "Evidently a Culicine [*sic*] mosquito; perhaps a true *Culex*, but it cannot be definitely assigned to that genus on the information available". Cockerell (1919) named *Culex winchesteri* from "a female with short maxillary palpi (about 0.4 mm), distinctly curved proboscis (3 mm) and an abdomen "like that of true *Culex*, obtuse at the end, not tapering as in *Aedes*". No further information is given, but it is possible, perhaps likely, that this fossil species belongs to genus *Culiseta*, even though it is older (49.0–54.8 million years old) than the two new species described here.

The four Eocene mosquitoes described as species of *Aedes* are in Baltic amber. Three of these species, *Ae. damzeni* Szadziewski, *Ae. hoffeinsorum* Szadziewski and *Ae. serafini* Szadziewski, were described as species of the extant subgenus *Finlaya* Theobald (broad traditional sense) (Szadziewski, 1998) and the fourth, *Ae. perkunas* Podėnas, was regarded as "most probably" belonging to that subgenus (Podėnas, 1999). These species are certainly culicine mosquitoes, but they cannot be assigned to an extant genus of Aedini based on the available information. The absence of spotted wings in these species precludes them from being included in genus *Finlaya* (restricted sense of Reinert *et al*., 2009).

The claspettes of the holotype male of *Ae. damzeni* are elongate with an apical sickle-like appendage as in extant *Ochlerotatus* Lynch Arribálzaga, but the proctiger is said to be "barely visible" and what appears to be the aedeagus (Szadziewski, 1998: fig. 3b,c) bears a closer resemblance to the aedeagus of members of the *Aedes* group of genera, e.g. *Aedimorphus* Theobald, than to members of the *Ochlerotatus* group. Szadziewski (1998) did not describe the ornamentation of this species, but his photograph of the holotype (fig. 5b) shows that it is a darkly ornamented species. However, in addition to features of the male genitalia, the species differs markedly from extant Aedini in having a short fifth palpomere (about 0.4 the length of palpomere 4) and a prominent setose lobe borne ventrally at the base of foretarsomere 5. Based on these distinctions and other information contained in the descriptions and illustrations of Szadziewski (1998) and Podėnas (1999), *Ae. damzeni* cannot be assigned to a currently recognized genus (extinct or extant) of Aedini; hence, *Eoaedes* **gen. n.** is hereby proposed for this fossil species. The name is derived from the Greek *eos* (dawn, morning, early, east) and *Aedes*, an extant genus. The gender is masculine.

The type specimen of *Ae. hoffeinsorum* is a male with short maxillary palpi, shorter than the proboscis, a greatly reduced palpomere 5 (about 0.3 length of palpomere 4), proboscis noticeably swollen distally, vein R_2 of the wing much shorter than vein R_{2+3} and the fore- and midungues borne well before the apex of the fifth tarsomere, unique features which suggest that this species does not belong to a currently recognized genus of Aedini. The genitalia of the specimen (illustrated but not described) bear some resemblance to those of certain members of the *Ochlerotatus* group of genera, e.g. *Acartomyia mariae* (Sergent & Sergent), but this only supports the tribal placement of the species. Based on the combination of unusual characters noted here and the likelihood that re-examination of the specimen will reveal additional distinctive characters not mentioned in Szadziewski's (1998) brief description, *Aetheapnomyia* **gen. n.** is proposed here for the fossil species originally named *Aedes hoffeinsorum*. The name is derived from the Greek *aethes* (unusual, strange), *apnoos* (dead) and *myia* (fly). The gender is feminine.

The presence of postspiracular setae and claspettes with blade-like apical filaments (Szadziewski, 1998) clearly place the holotype male of *Ae. serafini* within Aedini. Other than these features, the description of the specimen only includes some measurements of head and thoracic appendages and characteristics of the ungues. In the absence of more detailed information, it is not possible to ascertain the affinities and generic placement of this species.

Podėnas (1999) described *Ae. perkunas* from a male that is missing its genitalia. The specimen is darkly ornamented, the maxillary palpi are developed as they are in many Aedini, the larger unguis of the fore- and midlegs bears a median tooth and midtarsomere 4 is expanded ventrally toward the apex. The thoracic pleura are partially obscured and distal parts of the wings are twisted. The specimen could be allied with extant species of *Ochlerotatus*, but we are loath to relegate it to that genus in the absence of genital and wing characters.

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References

Belkin, J.N. 1962. *The mosquitoes of the South Pacific* (*Diptera, Culicidae*). Volumes 1 and 2. University of California Press, Berkeley and Los Angeles.

Borkent, A. & Grimaldi, D.A. (2004) The earliest fossil mosquito (Diptera: Culicidae), in mid-Cretaceous amber. *Annals of the Entomological Society of America*, 97, 882–888.

Cockerell, T.D.A. (1919) The oldest mosquitoes. *Nature*, 103, 43–46.

Constenius, K.N. (1996) Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. *Geological Society of America Bulletin*, 108, 20–39.

Constenius, K.N., Dawson, M.R., Pierce, H.G., Walter, R.C. & Wilson, M.V.H. (1989) Reconnaissance paleontologic study of the Kishenehn Formation, northwestern Montana and southeastern British Columbia, pp. 189–203. *In*: French, D.E. & Grabb, R.F. (Eds), *1989 Field Conference Guidebook: Montana Centennial Edition*, Vol. 1. Geological Resources of Montana.

Dobrotworsky, N.V. (1954) The genus *Theobaldia* (Diptera, Culicidae) in Victoria. *Proceedings of the Linnean Society of New South Wales*, 76, 65–78.

Dobrotworsky, N.V. (1960) The genus *Theobaldia* (Diptera, Culicidae) in Victoria. II. *Proceedings of the Linnean Society of New South Wales*, 85, 240–247.

Dobrotworsky, N.V. (1971) Contributions to the mosquito fauna of Southeast Asia. X. The genus *Culiseta* Felt in Southeast Asia. *Contributions of the American Entomological Institute*, 7(3), 38–61.

Edwards, F.W. (1923) Oligocene mosquitoes in the British Museum; with a summary of our present knowledge concerning fossil Culicidae. *Quarterly Journal of the Geological Society of London*, 79, 139–155, 1 pl.

Edwards, F.W. (1932) *Genera Insectorum. Diptera, Fam. Culicidae*. Fascicle 194. Desmet-Verteneuil, Brussels.

Groves, C. & Shekelle, M. (2010) The genera and species of Tarsiidae. *International Journal of Primatology*, 31, 1071–1082.

Harbach, R.E. (2012) Mosquito Taxonomic Inventory, http://mosquito-taxonomic-inventory.info/, accessed on 1 July 2012.

Harbach, R. E. & Knight, K. L. (1980) *Taxonomists' glossary of mosquito anatomy.* Marlton, New Jersey: Plexus Publishing.

Harbach, R. E. & Knight, K. L. (1982) Corrections and additions to *Taxonomists' glossary of mosquito anatomy. Mosquito Systematics* (for 1981), 13, 201–217.

Huber, J.T. & Greenwalt, D. (2011) Compression fossil Mymaridae (Hymenoptera) from Kishenehn oil shales, with description of two new genera and review of Tertiary amber genera. *ZooKeys*, 130, 473–494.

Marks, E.N. (1968) Northern records of the genus *Culiseta* Felt in Australia with the description of a new species (Diptera: Culicidae). *Journal of the Australian Entomological Society*, 7, 43–56.

Maslov, A.V. (1989) *Blood-sucking mosquitoes of the subtribe Culisetina* (*Diptera, Culicidae*) *in world fauna*. Smithsonian Institution Libraries and the National Science Foundation, Washington, D.C.

McKenna, M.C. (1990) Plagiomenids (Mammalia: ?Dermoptera) from the Oligocene of Oregon, Montana and South Dakota, and Middle Eocene of northwestern Wyoming, pp. 211–234. *In*: Brown, T.M. & Rose, K.D. (Eds), *Dawn of the age of mammals in the northern part of the Rocky Mountain interior, North America*. Special paper 243, Geological Society of America, Boulder, Colorado.

Ni, X., Meng, J., Beard, K.C., Gebo, D.L., Wang, Y. & Li, C. (2010) A new tarkadectine primate from the Eocene of Inner Mongolia, China: phylogenetic and biogeographic implications. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 277, 247–256.

Pierce, H.G. & Constenius, K.N. (2001) Late Eocene – Oligocene nonmarine mollusks of the northern Kishenehn Basin, Montana and British Columbia. *Annals of the Carnegie Museum*, 70, 1–112.

Podėnas, S. (1999) New species of fossil mosquitoes (Diptera, Culicidae) from the Baltic amber. *Acta Zoologica Lituanica*, 9, 111–114.

Reidenbach, K.R., Cook, S., Bertone, M.A., Harbach, R.E., Wiegmann, B.M. & Besansky, N.J. (2009) Phylogenetic analysis and temporal diversification of mosquitoes (Diptera: Culicidae) based on nuclear genes and morphology. *BMC Evolutionary Biology*, 9, 298.

Reinert, J.F., Harbach, R.E. & Kitching, I.J. (2009) Phylogeny and classification of tribe Aedini (Diptera: Culicidae). *Zoological Journal of the Linnean Society*, 157, 700–794 + 2 online appendices.

Smith, A.B.1994. *Systematics and the fossil record: Documenting evolutionary patterns*. Blackwell Scientific Publications, Oxford.

Szadziewski, R. (1998) New mosquitoes from Baltic amber (Diptera: Culicidae). *Polskie Pismo Entomologiczne*, 67, 233–244.

Wolfe, J.A. (1995) Paleoclimatic estimates from Tertiary leaf assemblages. *Annual Review of Earth and Planetary Sciences*, 23, 119–142.