

The first fossil New World Dixidae with a critical discussion of generic definitions

Dale E. Greenwalt and John K. Moulton

ABSTRACT

Four new fossil species of the dipteran family Dixidae, including the first fossil specimens of females in this family, are described from the Middle Eocene Kishenehn Formation oil shales of northwestern Montana. These new species, *Dixella intacta* sp. nov., *D. eomarginata* sp. nov., *D. spinilobata* sp. nov. and *D. curvistyla* sp. nov., are the first fossils of Dixidae to be described from the New World. The morphological bases of all generic assignments of extant and extinct dixids are critically reviewed, and new data on wing venation pattern variability in extant Dixidae are presented. It is concluded that it is impossible to distinguish between adults of the two major genera, *Dixa* and *Dixella*, based solely on wing venation. Given the lack of distinguishing features, the names of the two Cenozoic species that consist only of a single wing, *Dixa priscula* and *D. cimbrica*, are declared *nomina dubia* and the fossils are assigned to Dixidae *incertae sedis*.

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INTRODUCTION

Meniscus midges (Diptera: Culicomorpha: Culicoidea: Dixidae Schiner, 1868) constitute a very small family of 197 species (184 extant) in nine genera (Pape et al., 2011) (Tables 1 and 2). Historically, Dixidae have been considered to be the sister taxon to the other Culicoidea (Ross, 1951), and this concept is supported by both biochemical (Rao and Rai, 1987, 1990) and phylogenetic studies in which Dixidae is the sister group to

Corethrellidae + (Culicidae + Chaoboridae) (Wood and Borkent, 1989; Oosterbroek and Courtney, 1995; Saether, 2000; Bertone et al., 2008; Woodley et al., 2009; Wiegmann et al., 2011; Borkent, 2012). A divergence time estimate of approximately 190 Ma, calculated from nuclear gene sequence data, appears conservative given the report of dixid fossils from the lowermost Jurassic (Lukashevich, 1996; Bertone et al., 2008). Fossil Chironomidae have been reported from the 202 Ma Lilstock Formation, Gloucestershire, UK

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TABLE 1. Extant genera of the family Dixidae.

Name	Number of species	Geographical distribution
<i>Asiodixa</i> Papp et al., 2006	2	Thailand
<i>Dixa</i> Meigen, 1818	106	World-wide except Antarctica
<i>Dixella</i> Dyar & Shannon, 1924	64	World-wide except Antarctica
<i>Meringodixa</i> Nowell, 1951	1	North America
<i>Mesodixa</i> Belkin, Heinemann & Page, 1970	1	Jamaica
<i>Metadixa</i> Peters and Savary, 1994	1	Philippines
<i>Neodixa</i> Tonnoir, 1924	1	New Zealand
<i>Nothodixa</i> Edwards, 1930	10	Australia, Chile & New Zealand

TABLE 2. Fossils of the family Dixidae.

Name	Age	Lithology	Formation/Location	Reference
<i>Dixidae incertae sedis</i> (<i>Dixa priscula</i> Cockerell, 1921. <i>Nomen dubium</i>)	Oligocene	Marl	Bouldnor Formation, U. K.	Cockerell, 1921
<i>Dixidae incertae sedis</i> (<i>Dixa cimbrica</i> Ansoerge, 1992. <i>Nomen dubium</i>)	Paleocene/ Eocene	Clayey diatomite	The Fur Formation, Denmark	Ansoerge, 1992
<i>Dixa minuta</i>	Late Eocene	Amber	The Baltic region (Europe)	Meunier, 1906
<i>Dixa tertiaria</i> (<i>Dixa hyalipennis</i> Theobald, 1937)	Oligocene	Marl	The d'Aix Formation, France	Meunier, 1915; Theobald, 1937
<i>Dixella distans</i>	Late Eocene	Amber	The Baltic region (Europe)	Hennig, 1966
<i>Dixella filliforceps</i>	Late Eocene	Amber	The Baltic region (Europe)	Hennig, 1966
<i>Dixella intacta</i>	Middle Eocene	Oil shale	Kishenehn Formation, U.S.A.	Greenwalt & Moulton, 2016*
<i>Dixella eomarginata</i>	Middle Eocene	Oil shale	Kishenehn Formation, U.S.A.	Greenwalt & Moulton, 2016*
<i>Dixella spinilobata</i>	Middle Eocene	Oil shale	Kishenehn Formation, U.S.A.	Greenwalt & Moulton, 2016*
<i>Dixella curvistyla</i>	Middle Eocene	Oil shale	Kishenehn Formation, U.S.A.	Greenwalt & Moulton, 2016*
<i>Dixella succinea</i>	Late Eocene	Amber	The Baltic region (Europe)	Meunier, 1906
<i>Eucorethrina convexa</i>	Late Jurassic	Shale	The Itat Formation, Siberia	Lukashevich, 1996
<i>Eucorethrina flexa</i>	Middle Jurassic	Shale	The Itat Formation, Siberia	Kalugina & Kovalev, 1985
<i>Eucorethrina westwoodi</i>	Early Cretaceous	Shale	Durlston & Lulworth Formations, U.K.	Lukasevich et al., 2001
? <i>Syndixa liasina</i>	Middle Jurassic	Shale	Dzhil Formation, Kyrgyzstan	Lukashevich, 1996
<i>Syndixa mollis</i>	Middle Jurassic	Shale	The Itat Formation, Siberia	Lukashevich, 1996
<i>Syndixa sibirica</i>	Early Jurassic	Shale	The Itat Formation, Siberia	Lukashevich, 1996

*This study

(Krzeminski and Jarzembowski, 1999), Chaoboridae from the 161–156 Ma Ichetuy Formation (Kalugina, 1985) and unidentified Culicomorpha from the 220 Ma Cow Branch Formation in Virginia, USA (Blagoderov et al., 2007 but see Borkent, 2012 for reservations about assignment to the infraorder). A recent estimate places the divergence of the Culicomorpha at approximately 225 Ma (Wiegmann et al., 2011). No phylogenetic work, either morphological or molecular, has been done, at the intrafamilial level, on the family Dixidae.

The Mesozoic Dixidae (Table 2) consist of six species, all of which are based on isolated wings, in the two extinct genera *Eucorethrina* Kalugina, 1985 and *Syndixa* Lukashevich, 1996 (Kalugina, 1985; Lukashevich, 1996). None of the six species exhibits the strongly arched R_{2+3} vein that is the only recognized synapomorphy of the recent adult members of the family (Peters and Cook, 1966). Note that the holotype of *E. westwoodi* Lukashevich, Coram and Jarzembowski, 2001 has a slightly arched R_{2+3} while R_{2+3} in its figured paratype is straight (Lukashevich et al., 2001). The wing venation of *Eucorethrina* is otherwise very similar to that of extant genera; criteria in the original diagnosis by Kalugina (1985) such as Sc proximal to r-m and A_1 proximal to the bifurcation of Cu are plesiomorphies commonly encountered in extant Dixidae and other Diptera. R_1 and R_2 converging at the wing margin, another criterion of the original diagnosis, is uncommon in extant Dixidae although it, and all other criteria in the original diagnosis, are found in *Nothodixa* Edwards, 1930 (Belkin, 1968). The convergence of R_1 and R_2 is not found in some specimens of *Eucorethrina* figured by Lukashevich (1996). Lukashevich et al. (2001) amended the diagnosis of *Eucorethrina* to Sc ending distal to Rs origin and the apex of R_1 equidistant from the apices of C and R_2 . Again however, *Eucorethrina flexa* Kalugina, 1985, as figured by Kalugina (1985) and *Eucorethrina westwoodi* as figured by Lukashevich et al. (2001), have Sc only slightly distad of the Rs origin, a configuration also found in the extant species *Dixella shannoni* Lane, 1942 and *D. hernandezii* Chaverri and Borkent, 2007. The criterion apex of R_1 equidistant from the apices of C and R_2 , which is figured but not commented on by Kalugina (1985), appears to be unique to *Eucorethrina*; in all extant Dixidae, R_1 is closer to C. The venation of the extinct genus *Syndixa* is indistinguishable from that of *Eucorethrina* but for the defining fusion of R_2 with R_1 . Three different species of *Syndixa* have been established, with two of the three based on a

single specimen. Given the fusion of R_1 and R_2 , “like in Chironomoidea,” Lukashevich (1996) has suggested that “*Syndixa* could be related to ancestors of the Chironomoidea.” If this is indeed the case, inclusion of *Syndixa* in Dixidae renders this family paraphyletic.

Of the seven previously described Cenozoic fossil species, four are inclusions in Baltic amber and three species are compression fossils found in Denmark, France, and England. These specimens are discussed in greater detail below. All extant members of the family are restricted to wet environments such as streams, lakes, swamps, etc. (Belkin, 1968). The larvae require free standing water to feed and swim. None of the Dixidae is known to be of economic or medical/veterinary importance; as a result very little is known about the biology of most species despite their earlier inclusion, as a subfamily, in the Culicidae (Peters, 1981). The classification of the extant Dixidae has been referred to as “chaotic” and “confused,” and classification of the Dixidae has long been known to be in need of major revision (Belkin, 1968; Belkin et al., 1970, Chaverri and Borkent, 2007). The largest genera, *Dixa* Meigen, 1818 and *Dixella* Dyar and Shannon, 1924, which contain more than 90% of extant Dixidae (Table 1), have been assumed to be polyphyletic (Belkin, 1968). In the present study, the generic assignments of the Eocene fossil dixids are reviewed, and data are presented to further document wing venation variability and the inability to discriminate between the major genera based solely on wing venation.

The oil shale of the Coal Creek Member of the Kishenehn Formation, dated to the Middle Eocene (approximately 46 Ma), was shown to contain fossil insects a quarter of a century ago (Constenius et al., 1989). However, extensive collection from exposures of the Coal Creek member has only recently taken place. An apparent taphonomic bias towards the preservation of particularly small insects has permitted recent descriptions of the first compression fossils of Mymaridae (Hymenoptera: Chalcidoidea), *Culiseta* Felt, 1904 (Diptera: Culicidae) and specimens of the smallest of all beetles (Coleoptera: Ptiliidae) from the Kishenehn Formation (Huber and Greenwalt, 2011; Harbach and Greenwalt, 2012; Shockley and Greenwalt, 2013). The environment that existed when the Kishenehn sediments were deposited was seasonal subtropical/tropical. Sediments formed in a shallow near-shore environment that exhibited little or no water flow (Greenwalt et al., 2015).

MATERIALS AND METHODS

Specimens described herein as new species were collected from the Deep Ford, Dakin, and Disbrow Creek sites on the Middle Fork of the Flathead River in northwestern Montana between 2009 and 2012 in accordance with USFS Authorization HUN281. Exposures there are from the middle sequence of the Coal Creek member of the Kishenehn Formation, which has been estimated to be 46.2 ± 0.4 Ma by $^{40}\text{Ar}/^{39}\text{Ar}$ 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. Fossils were immersed in 95% ethanol for examination and photography. Measurements were made with the Image-Pro Plus 7.0 software. Venational terminology is from McAlpine (1981). Ratios R_2/M_2 , M_2/M_1 , M_2/M_{1+2} , and R_{2+3}/R_3 , are those defined by Peters and Cook (1966). *Dixa priscula* Cockerell, 1921 (specimen # H.708) was examined at the Natural History Museum, London. Abbreviations used are F = flagellomere; L = Latin; L/W = length to width ratio; Ma = million years ago; MSC = Museum Support Center of the Smithsonian Institution's National Museum of Natural History, Suitland, MD; NHM = Natural History Museum, London; NMNH = National Museum of Natural History, Washington DC; WRBU = Walter Reed Biosystematics Unit.

Representatives of seven extant genera and all extinct species (116 total species, Appendix 1) were scored for 13 characters of the wings, mostly those of venation. Characters (Appendix 2) were coded as binary or multistate; if a particular character state could not be determined, a dash (-) was entered in the matrix to indicate missing data. Elimination of characters found only in extinct genera and extant genera other than *Dixa* and *Dixella* resulted in a subset of seven of the 13 characters (characters 1–6 and 9 in Appendix 2) that were then used in the comparative analysis of wing venation variability. The comparative analysis was confined to the 91 extant species of the two genera *Dixa* and *Dixella* listed in Appendix 1. Forty-nine species of *Dixa* and *Dixella* were accessed from collection at the Walter Reed Biosystematics Unit (WRBU) of the Smithsonian Institution's Museum Support Center (MSC) in Suitland, MD. When more than a single specimen was examined (for example in the study of intraspecific variability), they were selected at random. Data for an additional 65 species, not including *Dixa priscula* and

the four new species described herein, were obtained from holotype descriptions available in the literature. In an attempt to document intraspecific venation pattern variability, seven species were selected at random from specimens housed at the WRBU from among those that had a minimum of 10 specimens/species. Between three and 16 randomly selected specimens were examined per species. Generic assignments are based on the original literature and specimen labels. The purpose of these analyses was simply to determine and document the degree of variability of these seven characters either between the two major genera of the family, *Dixa* and *Dixella*, or within a single species. Given the high degree of variability observed in this study, a phylogenetic analysis of the data was deemed futile and unproductive and was not attempted.

RESULTS

Systematic Palaeontology

Order DIPTERA Linnaeus, 1758

Family DIXIDAE Schiner, 1868

Genus *DIXELLA* Dyar and Shannon, 1924

Type species. *Dixella lirio* Dyar and Shannon, 1924

Dixella intacta Greenwalt and Moulton, new species

Figures 1, 2, 3.1, 4.1, 5

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Etymology. The specific epithet is Latin for "untouched", an indication of the intact nature of this fossil.

Holotype. *Dixella intacta* Greenwalt and Moulton, female; NMNH, USNM 546204.

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

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

Differential Diagnosis. Distinguished from all other fossil Dixidae based on the presence of one or more of the following character states: distinct stylized spade-shaped cercus (similar to *Dixa brevis* Garrett, 1924), first flagellomere very slightly fusiform, antenna length much more than combined lengths of head and thorax, wing length/body length ratio equal to one, and apex of R_1 closer to C than to R_2 .

Description. Adult female (Figure 1), body length 4.5 mm.

Head. Black. Eyes dichoptic, large, oval with dorsal-ventral height (0.45 mm) greater than width



FIGURE 1. Habitus of *Dixia intacta*, holotype. Scale bar equals 3 mm.

(0.40 mm). Eyes separated by 0.12 mm. Maxillary palpus not visible. Antenna brown, 2.4 mm in length (Figure 2.1). Scape barely visible, small, approximately 40 μm in width. Pedicel subspherical, 104 μm wide, 118 μm long. Antenna with 14 flagellomeres, each setose. F1 very slightly fusiform, 40 μm wide; F2–F4 widths gradually decrease to 30 μm . F5 (22 μm) more slender than F4. F5, subsequent flagellomere widths gradually decrease to 7 μm at F14. Flagellomere lengths/widths (in mm) as follows: F1 (0.30/0.04), F2 (0.12/0.04), F3 (0.16/0.03), F4 (0.17/0.03), F5 (0.23/0.02), F6 (0.20/0.02), F7 (0.19/0.02), F8 (0.190/0.01), F9 (0.18/0.01), F10 (0.15/0.01), F11 (0.13/0.01), F12 (0.12/0.01), F13 (0.12/0.01), F14 (0.13/0.01).

Thorax. Length 1.3 mm. Dark brown medial, lateral vittae covering most of scutum except for posteromedial portion and four medial light brown spots connecting medial, lateral vittae (Figure 2.2). Scutellum yellow. Acrostichal setae at lateral margin of medial vitta. Setae present along posterior margin of scutellum, lateral surface of mediotergite.

Wings. Length 4.28 mm, width 1.37 mm (Figure 3.1). L/W ratio = 3.12. Vein R_{2+3} arched. Sc apex even with Rs origin. Crossvein r-m single vein-

width distal to Rs bifurcation, slightly sigmoidal. Crossvein m-cu even with posterior point of r-m. A1 apex slightly basal to Cu bifurcation, distal to Sc apex and Rs origin. R_{2+3} bifurcation basal to M bifurcation. Length ratios R_2/M_2 , M_2/M_1 , M_2/M_{1+2} , R_{2+3}/R_3 = 2.6, 0.61, 0.54, 0.49, respectively. Vein CuP present. Wing surface covered with microtrichiae; veins, margin of wing with spiniform setae 55 ± 15 μm in length. Haltere dark brown, length 0.59 mm with setae on anterior margin of proximal end, knob; knob spherical, diameter 155 μm ; base black.

Legs. All legs setose; hind tibia expanded distally. Foreleg femur, tibia, 5 tarsomeres lengths 1.38, 1.32, 0.9, 0.36, 0.23, 0.12, 0.14 mm, respectively. Midleg femur, tibia, 5 tarsomeres lengths 1.74, 1.58, 0.76, 0.42, 0.27, 0.14, 0.15 mm, respectively. Hind leg femur, tibia, 5 tarsal segments lengths 1.8, 1.83, 1.52, 0.53, 0.34, 0.18, 0.13 mm, respectively. Claws without teeth (Figure 4.1).

Abdomen and genitalia. Abdomen brown, setose, length 2.84 mm (not including cercus); sternite 8, tergite 9 dark brown/black, more heavily setose than anterior portion of abdomen. With single sclerotized spermatheca, spherical, 0.17 mm in diame-

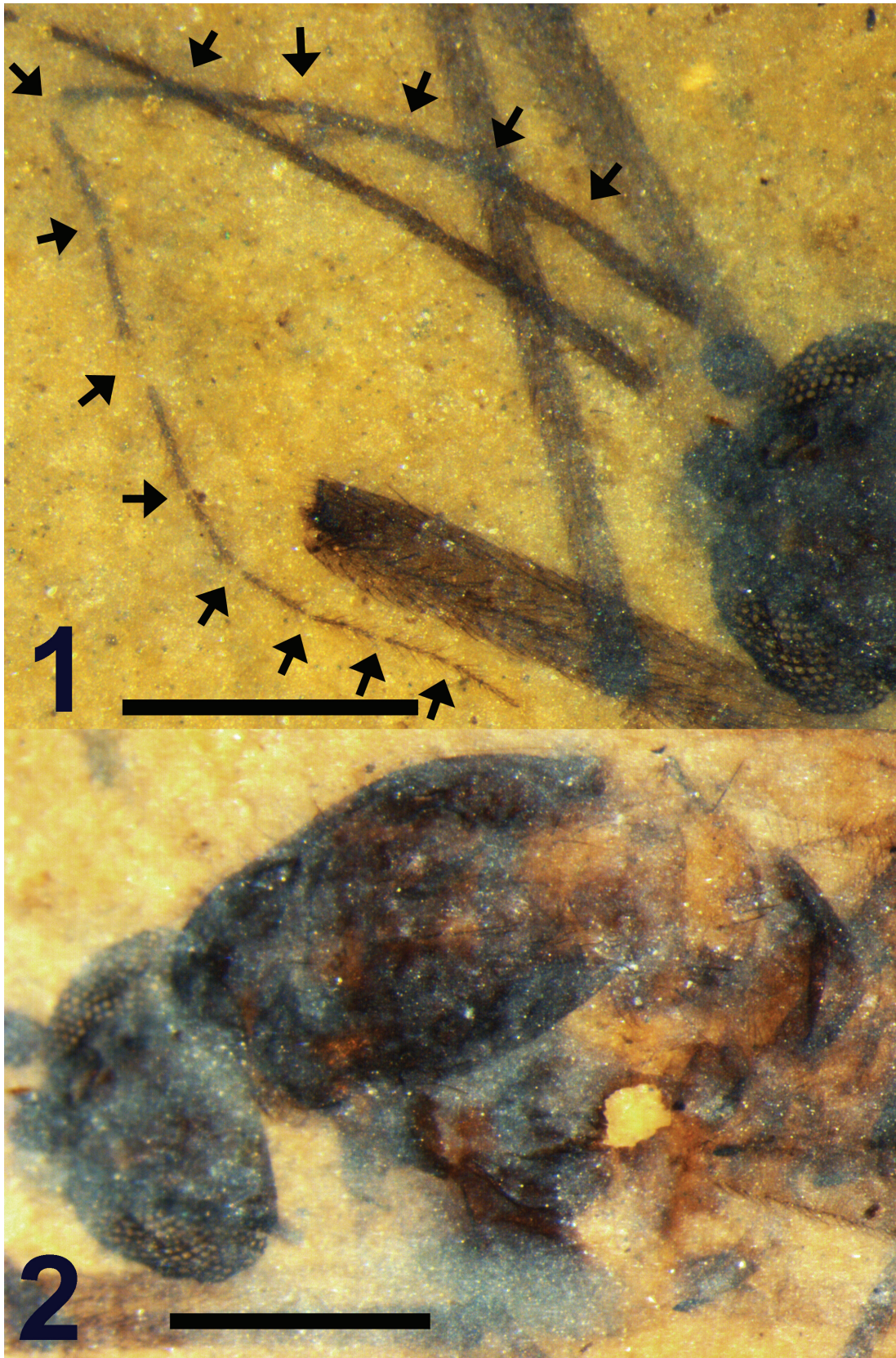


FIGURE 2. Morphological features of *Dixia intacta*. **1**, Antennae with individual flagellomeres delineated; **2**, Dorsal aspect of the thorax. Scale bars equal 0.5 mm for both figures.

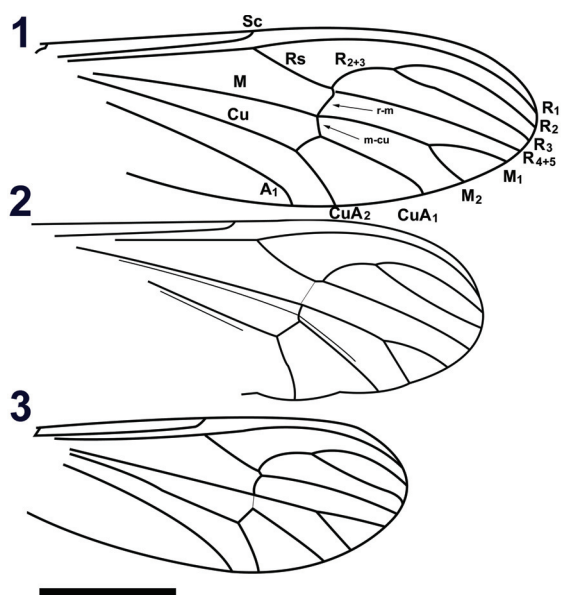


FIGURE 3. Line drawings of wings. **1**, *Dixella intacta*; **2**, *D. eomarginata*; **3**, *D. curvistyla*. Wing venation is from McAlpine (1981). Scale bar equals 1 mm.

ter. Cercus black, setose, shaped like stylized spade, length 0.12 mm (Figure 5).

Male unknown.

Dixella eomarginata Greenwalt and Moulton, new species

Figures 3.2, 6, 7

zoobank.org/0EC67728-2799-4615-B318-3723C944DE99

Etymology. The specific epithet is a combination of the Greek term *eos*, meaning dawn, and the specific epithet *marginata*, indicating similarity of the shape of the posterior margin of the wing with that of the extant *Dixella marginata* Loew, 1863.

Holotype. *Dixella eomarginata* Greenwalt and Moulton, female; NMNH, USNM 553521.

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

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

Differential Diagnosis. Distinguished from all other fossil Dixidae based on the presence of the following character states: wing emarginate between CuA1 and CuA2, wing length to body length ratio equal to 0.91, R₁ closer to C than R₂.

Description. Adult female (Figure 6), body length 3.8 mm.

Head. Black. Eyes dichoptic, spherical, diameter 0.26 mm, 0.12 mm. Maxillary palps not visible. Antennae not preserved intact, contiguous flagellomeres present, brown, filiform. Pedicel light brown, longer than wide. One maxillary palp present, poorly preserved, length 0.5 mm; length terminal segment 0.179 mm.

Thorax. Lateral view. Length 1.03 mm, black; lateral vittae absent; scutellum brown. Thoracic setae not visible.

Wings. Length 3.46 mm (measured from base of humeral crossvein), width 1.18 mm (Figures 3.2, 7.1). L/W ratio = 2.93. Vein R₂₊₃ arched. Vein Sc apex basal to origin of Rs (1.4 times distance between C, R₁). Crossvein r-m basal to Rs bifurcation. Crossvein m-cu very lightly sclerotized, apex just distal to r-m terminus. A₁ apex poorly preserved, basal to Cu bifurcation, distal to Sc apex. R₂₊₃ bifurcation significantly basal to M bifurcation. Ratios R₂/M₂, M₂/M₁, M₂/M₁₊₂, R₂₊₃/R₃ = 2.37, 0.71, 0.55, 0.44, respectively. Wing veins, margin with thin setae, length ≤ 20 μm. Wing posterior margin emarginate between CuA₁, CuA₂. Prominent false vein (?) between M, Cu continues between M₁₊₂,

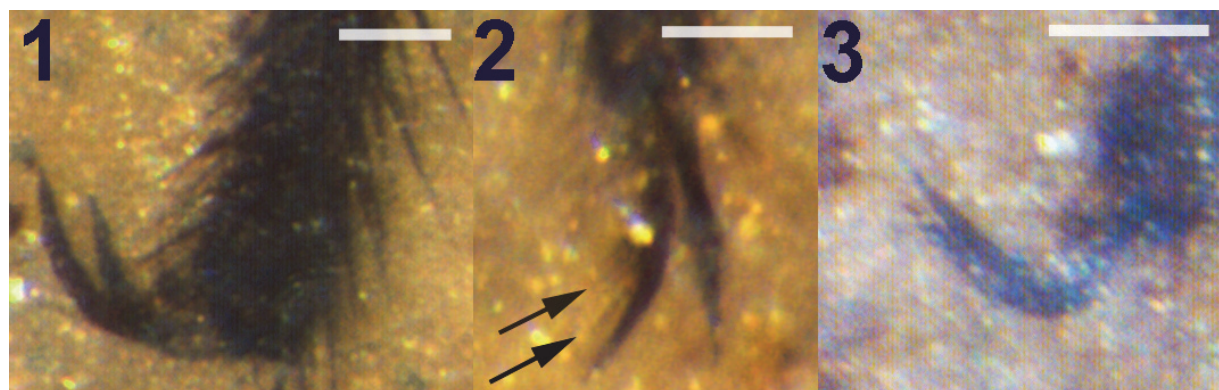


FIGURE 4. Tarsal claw teeth of the Kishenehn *Dixella*. **1**, *Dixella intacta* left metatarsal claw; **2**, *D. curvistyla* left metatarsal claw; **3**, *D. spinilobata* right metatarsal claw. Arrows point to teeth. Scale bars equals 50 μm.

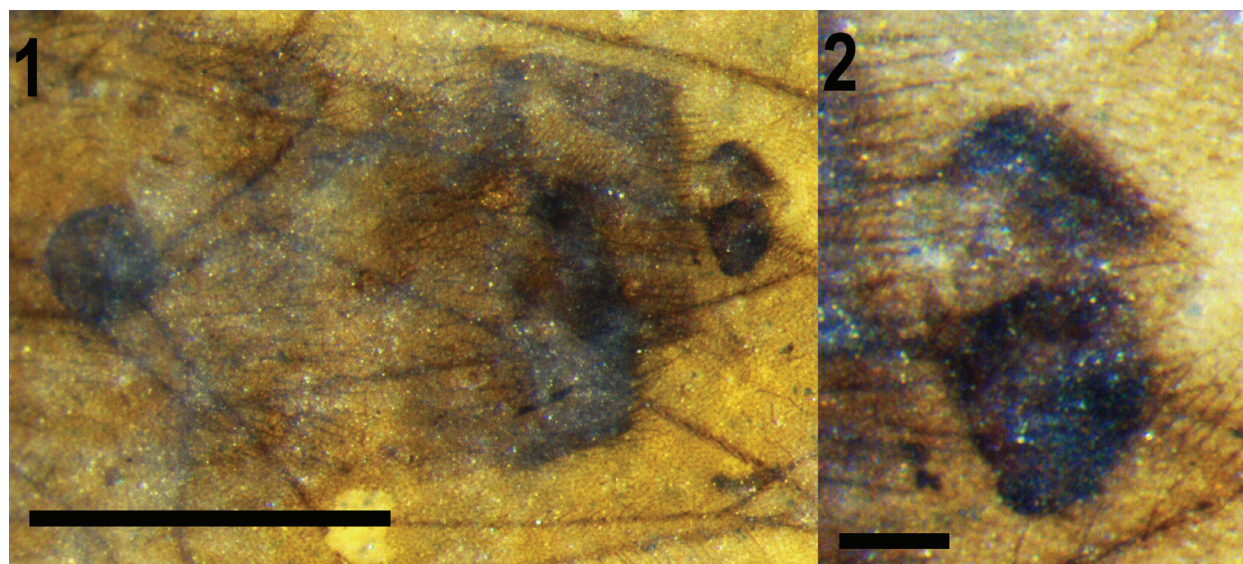


FIGURE 5. The terminalia of *Dixella intacta*. **1**, Posterior portion of abdomen including the spermatheca; **2**, Cerci. Scale bars equal 0.5 mm (1) and 0.05 mm (2).

CuA₁ (not present in the right wing). Haltere brown, length 0.53 mm long, knob oval, width 144 μ m, length wide 207 μ m.

Legs. All legs setose; metatibia expanded distally. Foreleg femur, tibia, tarsus lengths 1.28, 1.29, 1.65 mm, respectively. Midleg femur, tibia, tarsus lengths 1.71, 1.40, 1.78 mm, respectively. Hind leg femur, tibia, tarsus lengths 1.65, 1.56, 2.22 mm, respectively. Metapretarsal claws not preserved sufficiently to determine presence, absence of teeth.

Abdomen and genitalia. Abdomen light brown, length 2.66 mm (not including cerci). Segment 7 with single sclerotized spermatheca, oval, 154 μ m x 115 μ m. Tergite 9, posterior edge sternite 8 dark brown/black, more heavily setose than anterior portions of abdomen. Cerci dorsally situated, brown, setose, length 0.12 mm (Figure 7.2). Posterior margin sternite 8 lined by numerous setae approximately 35 μ m long, Cerci, tergite 9 with several setae 70 μ m or longer. Sternite 9 bulbous, protruding just below cerci.

Male unknown.

Dixella curvistyla Greenwalt and Moulton, new species

Figures 3.3, 4.2, 8, 9

zoobank.org/716DBCD1-3920-42D3-949D-BEC02984A27F

Etymology. The specific epithet is derived from a combination of the terms *curvi* (L) meaning curved and *stylus* (L) meaning stalk or pike, and denotes the sharply curved gonostylus of this species.

Holotype. *Dixella curvistyla* Greenwalt and Moulton, male; NMNH, USNM 546860.

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

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

Differential Diagnosis. Distinguished from the three previously described Eocene fossil *Dixella* based on wing width (1.32 mm vs. 0.56 in *D. distans* Hennig, 1966), length of flagellomere F1 (0.234 mm vs. 0.415 mm in *D. succinea* Meunier, 1906) and form of the gonostylus (very long and narrow in *D. filiforceps* Hennig, 1966).

Description. Adult male (Figure 8), body length 3.36 mm.

Head. Black. Eyes dichoptic, large, oblong, width 0.186 mm, length 0.284 mm. Three prominent setae at lateral margin of eye. Maxillary palp length 0.34 mm, two basal segments wider than long (31 x 41 μ m); segments three and four 42 and 54 μ m long, respectively, both 35 μ m wide; terminal segment length 0.169 mm, width 21 μ m, terminus with several short setae (Figure 9.1). Most distal flagellomeres missing (Figure 9.1). Scape black, large, subspherical, 72 μ m in diameter. Pedicel black, globular, diameter 0.1 mm. Flagellomeres setose, light brown. F1 cylindrical, diameter 32 μ m, length 0.23 mm. F2–F4 gradually decreasing in diameter.

Thorax. Lateral view. Black, length 1.08 mm, no setae apparent.

Wings. Length 2.89 mm (measured from base of the humeral crossvein), 1.17 mm wide. L/W ratio = 2.47. Vein R₂₊₃ arched (Figure 3.3). Vein Sc apex



FIGURE 6. Habitus of *Dixella eomarginata*, holotype. Scale bar equals 3 mm.

even with Rs origin. Crossvein r-m distal to Rs bifurcation. Crossvein m-cu even with r-m apex, less heavily pigmented than r-m. A1 apex slightly basal to Cu bifurcation, distal to Sc apex, Rs origin. R_{2+3} bifurcation even with M bifurcation. Ratios R_2/M_2 , M_2/M_1 , M_2/M_{1+2} , R_{2+3}/R_3 = 2.03, 0.70, 0.75, 0.52, respectively. Wing surface infuscate; veins, except M, Cu, margin of wing covered with setae. Haltere dark brown, length 0.48 mm; knob oblong, diameter 119 μ m.

Legs. All legs setose, brown. At least two legs, including left hind leg, with tarsal claws with four observable teeth (Figure 4.2). All legs mostly disarticulated; mid and hind tarsi identification based on swollen apical portion of metatibia, combined fragment lengths. The foreleg femur, tibia lengths 1.08

and 1.0 mm, respectively. Midleg femur, tibia, tarsus lengths 1.50, 1.13 mm, 1.70 mm, respectively. Hind leg femur, tibia, and tarsus lengths 1.30, 1.26, 1.9 mm, respectively.

Abdomen and genitalia. Abdomen brown, setose, length 2.35 mm (including genitalia). Anterior half of abdomen with light bands of varying widths wherein setae are absent or reduced. Sternite 9 posterior margin with numerous setae. Gonocoxite length 220 μ m, apical lobe length 79 μ m, width 24 μ m (Figure 9.2), distal margin with several prominent setae, each about 10 μ m in length. Gonostylus length 158 μ m, very broad, base 79 μ m, midpoint 54 μ m, bent approximately 75 degrees at midpoint, tapering to very fine point.

Female unknown.

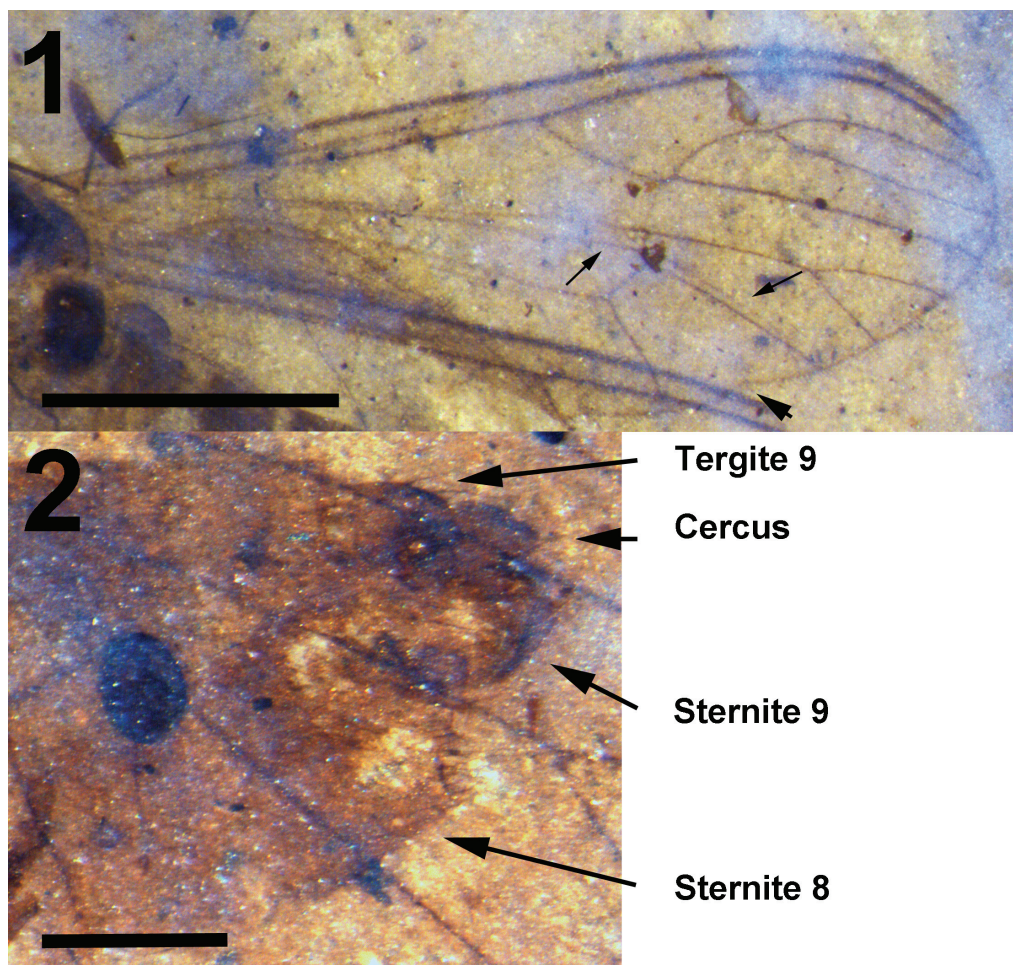


FIGURE 7. Morphological features of *Dixia eomarginata*. **1**, Wing with an emarginate posterior margin (arrowhead); arrows denote an apparent false vein posterior to vein M. **2**, Terminalia. Scale bars equal 1.0 mm (1) and 0.25 mm (2).

Dixella spinilobata Greenwalt and Moulton, new species

Figures 4.3, 10, 11

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Etymology. The specific epithet is derived from a combination of the terms *spinosa* (L) meaning spiny and *lobata* (L) meaning lobed and refers to the spiniform shape of both the apical lobe and the tip of the basal lobe of the gonocoxite.

Holotype. *Dixella spinilobata* Greenwalt and Moulton, male; NMNH, USNM 553522.

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

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

Differential Diagnosis. Distinguished from all other known fossil Dixidae based on one or more of the following characters: first flagellomere filliform, wing length to body length ratio equal to 0.95,

R_1 much closer to C than R_2 , antennal length (0.61 of its total body length), size of the gonocoxite and shape of the gonostylus.

Description. Adult male (Figure 10), body length 3.5 mm.

Head. Black; eyes dichoptic, large, spherical, diameter 0.222 mm. Maxillary palps long, length 0.34 mm, basal most segments not visible; segments four and five 88 x 40 and 230 x 27 μ m (length x width), respectively. Antenna brown, relatively long (2.12 mm; Figure 10), thin. Scape and pedicel poorly resolved, pedicel spherical, 73 μ m in diameter. Both F1 apparently filiform although partially covered by foreleg; dimensions unknown. Widths F2–F14 gradually decreasing. All flagellomeres setose.

Thorax. Length 0.95 mm, black with dark brown medial, lateral vittae covering scutellum; scutellum light brown. Setae absent.



FIGURE 8. Habitus of *Dixella curvistyla*, holotype. Scale bar equals 3 mm.

Wings. Length 3.32 mm, width 1.08 mm. L/W ratio = 3.07. R1 very close to costal vein; vein R_{2+3} arched. Vein Sc apex basal to Rs origin (by distance 1.5 x distance separating C, R1). Ratio R_{2+3}/R_3 0.59. Wing surface covered with microtrichae; veins, margin covered with long setae approximately 59 μm in length. Haltere dark brown, length 0.55 mm, knob elongate 114 μm x 256 μm .

Legs. All legs setose; hind tibia expanded distally. Foreleg femur, tibia, tarsus lengths 1.26, 1.07, 1.69 mm, respectively. Midleg femur, tibia, tarsus lengths 1.66, 1.42, 1.78 mm, respectively. Hind leg femur, tibia, tarsus lengths 1.56, 1.58, 2.0 mm, respectively; hind leg claws without apparent teeth (Figure 4.3).

Abdomen and genitalia. Abdomen brown, setose, length 2.84 mm (including terminalia). Sternite 8, tergite 9 dark brown/black, more heavily setose. Terminalia width (at widest point of two gonocoxites) 0.419 mm, each gonocoxite approximately 0.202 mm long and 0.139 mm wide; gonostylus elongate, length 0.179 mm, width 43 μm (Figures 11.1, 11.2). Gonocoxite apex with possibly two or

three spiniform structures, the largest and basal-most 63 μm long, 15 μm wide at base, not preserved/visible on right gonocoxite. Gonocoxite with large basal lobe, tip spiniform.

Female unknown.

Remarks

Given the demonstrably unreliable criteria for identification of adult Dixidae at the generic level (see Discussion), the option of designating the four fossil specimens described herein as “Dixidae *incertae sedis*” was considered. However, given 1) our desire to distinguish these four species from all fossil dixids described previously and 2) the observation that designations such as “Genus *incertae sedis*” or “Genus indeterminate” are often not recorded in commonly used databases, a generic designation has been provided. The four new species described herein are assigned to the genus *Dixella*, not necessarily based on morphological criteria, but rather on the near-shore lacustrine environment in which they lived and were deposited (Greenwalt et al., 2015; see Discussion). This

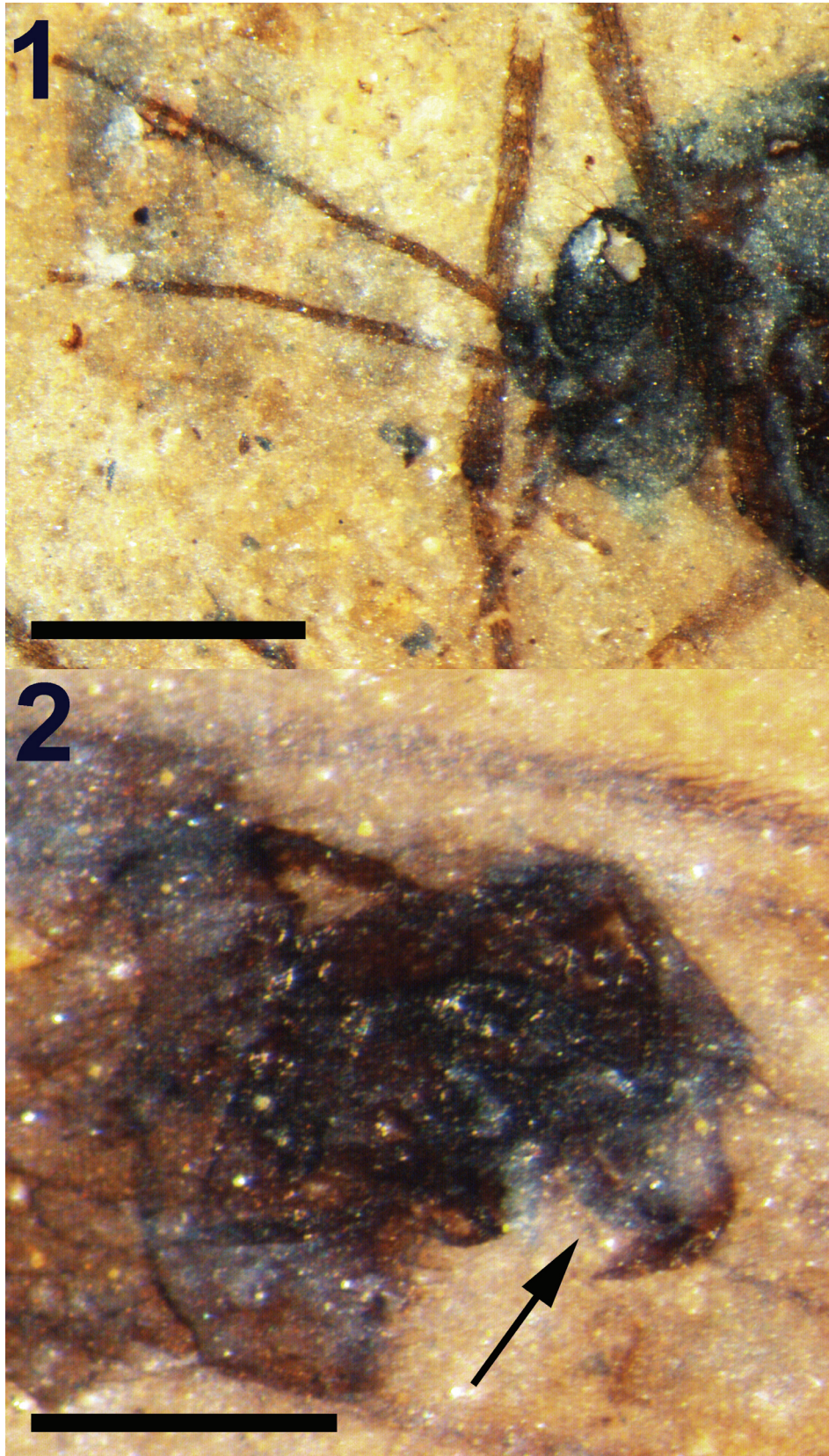


FIGURE 9. Morphological features of *Dixella curvistyla*. **1**, Head and antennae; **2**, Terminalia. The arrow points to the apical lobe of the gonocoxite. Scale bars equal 0.5 mm (**1**) and 0.2 mm (**2**).



FIGURE 10. Habitus of *Dixella spinilobata*, holotype. Scale bar equals 3 mm.

of course presumes that genus-specific ecological niches (fast-flowing waters in the mid-stream of waterways or water falls [*Dixa*] vs. still waters of near-shore lake or pond environments [*Dixella*] [Nowell, 1951]) had already been established 46 Ma. Specific characteristics, in various combinations, used to distinguish the four fossil Nearctic species from all other dixid genera both extant and extinct, other than *Dixa* and *Dixella*, are as follows (with number of species given in parentheses): *Syndixa* (3): R_2 fused with R_1 (Lukashevich, 1996); *Eucorethrina* (3): R_1 equidistant from C and R_3 (R_2 in Peters and Cook [1966]) and Sc ending distad of Rs origin (Lukashevich, 1996); *Asiodixa* Papp et al., 2006 (2): small size (wings 2.0–2.5 mm) and Sc ending substantially before the Rs origin, Rs sigmoidal, F1 of male with a ventromedial dilation (Papp et al., 2006); *Neodixa* Tonnoir, 1924 (1): R_{2+3} unbranched (Belkin, 1968); *Nothodixa* (10): first flagellomere oval, its length equal to or less than 2.5x its width (Belkin, 1968); *Metadixa* Peters and Savary, 1994 (1): known only from a single larval specimen (Peters and Savary, 1994); *Mesodixa* Belkin et al., 1970 (1): F1 longer than F2 + F3, gonostylus longer than gonocoxite, curved, spinose and small size (wing 2.5 mm) (Belkin et al., 1970);

Meringodixa Nowell, 1951 (1): large spatulate ventral process of gonocoxite, F1 fusiform and 6x as long as wide, head and thorax brown and brownish yellow, respectively, stem of haltere yellow and dorsum of abdomen black (Nowell, 1951).

The Cenozoic dixids consist of nine species including the four described herein as well as two designated as *incertae sedis* (Table 2). A comparison between these is impeded by deficiencies in the published descriptions of the European fossils. Both *Dixa priscula* and *D. cimbrica* Ansorge, 1992 were described from isolated wings and, given the variability in wing venation in this family, can only be identified as members of the family Dixidae (see below). *Dixa tertiaria* Meunier, 1915 was originally described as a member of the family Limoniidae and, although the fossil is of an intact adult, no relevant information was provided other than a very low-resolution photograph and scale bar (Meunier, 1915). Theobald (1937) described *Dixa hyalipennis* Theobald, 1937 as having venation identical to *D. tertiaria* and synonymized the two species; Evenhuis (1994) synonymized both under *D. tertiaria*. However, comparison of Theobald's figure and Meunier's photograph clearly shows numerous differences in wing venation. Theobald's depiction of

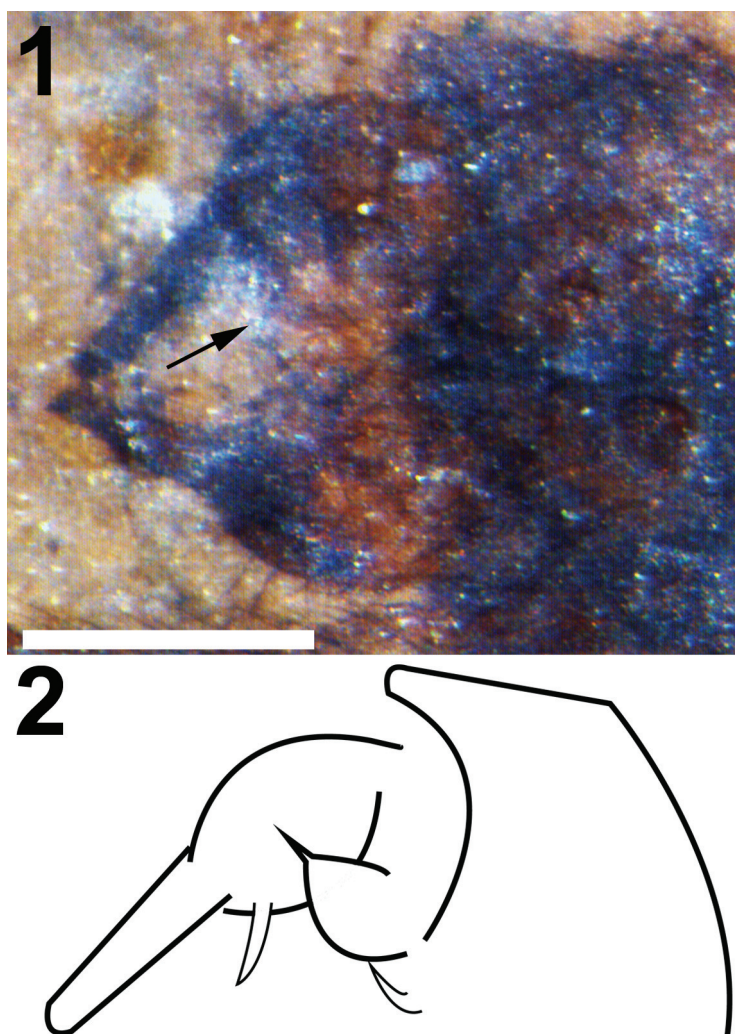


FIGURE 11. Morphological features of *Dixella spinilobata*. **1**, Photograph of the terminalia; spiniform apical lobe marked with an arrow; **2**, Line drawing of a partial reconstruction of the right portion of the terminalia (dorsal view). Scale bar equals 0.25 mm.

the first abscissa of CuA₁ portrays a vein unlike that in any other species of dixid; the distal half of this vein segment is parallel with vein M and forms a smooth continuous curve with the distal portion of CuA₁. Meunier's photograph depicts the first abscissa of CuA₁ as straight and at a distinct angle to the second abscissa, in a fashion similar to all other dixids. Descriptions of genitalia are not provided and, in fact, neither specimen is identified as to its sex. Similarly, the genitalia of *Dixa succinea* were not visible in the original specimen described by Meunier (1906) although it was described as male (mistakenly identified as female in the figure legend). Because the type specimen of *Dixa succinea* has been lost, Hennig (1966) designated and described a neotype and figured its genitalia as well as those of *Dixella filiforceps*, *D. distans* and

Dixa minuta Meunier, 1906, all males. Unfortunately, Hennig's descriptions of *Dixa succinea*, *Dixella filiforceps* and *D. distans* were otherwise purposefully very brief – no measurements were made – as he believed that “A detailed description of this and the following species would have little meaning. In order to clarify their position within the Paradixinae (*Dixella*), the extant species must first be carefully worked through.”

All four of the Nearctic fossil dixids are distinguished from *Dixa minuta* and *Dixella distans* in that these specimens, both Baltic amber inclusions, are much smaller in size with wing widths less than 0.6 mm (Cockerell, 1921; Hennig, 1966). Although both *Dixa priscula* and *Dixa cimbrica* are herein declared *nomina dubia* (See Discussion), differences in venation between them and the four

Nearctic fossils are as follows: *Dixa cimbrica* differs from *Dixella eomarginata* in that Sc originates at the origin of Rs, Rs forks basal of r-m, and m-cu originates basal of r-m; from *Dixella spinilobata* in that Sc originates at the origin of Rs; from *Dixella curvistyla* in that M_{1+2} is longer than M_1 , and m-cu originates basal of r-m; from *Dixella intacta* in that m-cu originates basal of r-m. *Dixa priscula* differs from *Dixella eomarginata* in that Sc originates basal of Rs, and m-cu originates basal of r-m; from *Dixella spinilobata* in that Sc originates basal of the origin of Rs; from *Dixella curvistyla* in that M_{1+2} is longer than M_1 , m-cu originates basal of r-m, and Sc originates basal of the origin of Rs; from *Dixella intacta* in that m-cu originates basal of r-m and Sc originates basal of the origin of Rs.

Dixella eomarginata and *D. intacta* differ from all other fossil dixids in being female. *Dixella eomarginata* differs from all other fossil dixids in having the posterior margin of the wing slightly emarginate between CuA1 and CuA2 – similar to the extant *Dixella marginata*. The prominent apparent false vein between M and Cu that continues between M_{1+2} and CuA₁ in the left wing of *D. eomarginata* may be an artifact, possibly a result of partial delamination of the wing; it does not appear in the right wing. This character is not common in the ‘Nematocera’ but it is found, between M_2 and CuA₁, in both Scatopsidae (*Coboldia* Melander, 1916) and several genera of Simuliidae (McAlpine et al., 1981). A false vein parallel to and just posterior of Cu and CuA₂ was described in *Dixa appalachiensis* (Moulton, 2016). While the male of *Dixella marginata* lacks the emarginate (excavate) wing margin of the female (Peters and Cook, 1966), there is no evidence for or against *Dixella eomarginata* being conspecific with either *D. curvistyla* or *D. spinilobata*. The body and wing lengths of *Dixella intacta* are 34% and 48% longer than those of *D. curvistyla* and 29% longer than *D. spinilobata*, respectively. Males and females of a given species can vary in size, females commonly with larger wing and body lengths, but the relationship is not consistent (e.g., wing lengths in males of both *Dixella fraxina* Taber, 2010 and *D. indiana* Dyar, 1925 are often larger than in the female) (Takahasi, 1958; Peters and Cook, 1966; Taber, 2010). Because wing and body lengths within a single sex of a species can vary as much as 50% (Takahasi, 1958; Peters and Cook, 1966), differences in wing and body lengths alone do not preclude *Dixella intacta* from a conspecific relationship with *D. spinilobata* or *D. curvistyla*. However, given the absence of any analysis of female genitalia relative

to the definition of the genera *Dixa* and *Dixella*, the variability in wing venation patterns between these two genera and within individual species (see below and Discussion), and the dearth of morphological detail available for the European fossils, it would be speculative to depict *Dixella intacta* as congeneric with any other known fossil male dixid.

The male Nearctic fossil species, *Dixella curvistyla* and *D. spinilobata*, are distinguished from those of *D. succinea*, *D. filiforceps*, and *D. distans* based on the shape of the gonocoxite and gonostylus. The gonocoxite of *D. succinea* is short relative to the gonostylus, the latter tapered distally with the terminal quarter of the stylus bent at a right angle to the base, approximately 150 µm long and less than 20 µm wide at mid-length. The apical lobe of the gonocoxite is long and narrow (about 75 µm x 10 µm). The gonostylus of *D. filiforceps* is very long and narrow (approximately 225 µm long and less than 20 µm wide), slightly widened at the end, and smoothly curved such that the distal half is at a right angle to the base. The apical lobe of the gonocoxite is long and narrow (about 10 µm x < 10 µm). The gonocoxite of *D. distans* is short relative to the gonostylus and, like *D. filiforceps*, the gonostylus is long and narrow (approximately 125 µm long x 20 µm wide) and smoothly curved. Unlike in *D. filiforceps*, the gonostylus is tapered to an asymmetrical point at the end. The apical lobe of the gonocoxite is long and narrow (about 75 µm x < 10 µm). These characteristics contrast with *D. curvistyla* in which the gonostylus is relatively short and wide (approximately 158 µm x 79 µm at its base) and bent at a near right angle and the apical lobe of the gonocoxite is quite wide (approximately 24 µm). In contrast, *D. spinilobata* has a straight and relatively wider rectangular gonostylus (179 µm x 43 µm) with a relatively shorter apical lobe (0.35 x the length of the gonostylus vs. ratios of 0.5–0.6 for the three specimens described by Hennig (1966)).

Dixa tertiaria is problematic in that the original description (Meunier, 1915) is essentially devoid of useful information and no redescription has so far been produced. A photograph and a scale bar is provided and enables body (3.2 mm) and wing (2.8–3.2 mm) lengths to be determined, albeit with a degree of uncertainty. These measurements contrast with those of Theobald (1937), who described *Dixa hyalipennis* with a body length significantly shorter than the wing length (3.7 mm and 4.2 mm respectively). All of the Nearctic fossils have body/wing length ratios greater than one. As described above, the very peculiar morphology of vein CuA1,

as figured by Theobald (1937), also differentiates these two specimens. Without examination of the actual specimens, it is impossible to accurately compare them with the Nearctic dixids.

It is difficult to compare *Dixella intacta* and *D. eomarginata* with extant dixids of the genera *Dixa* and *Dixella* as there exists neither detailed nor extensive studies of female genitalia with respect to the taxonomy of these two genera. Some keys to females of this family exist (e.g., Disney, 1975 - which does not use genitalic characters to distinguish between genera) but they are of limited use. The structure of the genitalia of *D. intacta* is very similar to that of *Dixa brevis* as figured by Nowell (1951). The very broad and acutely curved gonostylus of *Dixella curvistyla* resembles that of *Dixa formosana* Papp, 2007 although the latter has a very short apical lobe on the gonocoxite (Papp, 2007). *Dixa neohegemonica*, with a sickle/finger-shaped gonostylal apex, also resembles *D. curvistyla* (Moulton, personal obs.); note that this structure is figured as straight in Peters and Cook (1966). The genitalic morphology of *Dixella spinilobata* is unique amongst extant members of this

family although the gonostylus of *Dixa pollex* Nowell, 1980 also has a small projection near its distal terminus (Nowell, 1980). A key to all fossils of the family Dixidae, with the exception of *Dixa cimbrica*, *D. priscula* and *D. tertiaria*, which either consist only of a wing or are too poorly described to provide the data required for inclusion in a key, is provided here so as to facilitate identification of new fossil specimens.

See *Key to the fossil species of Dixidae* below.

Wing Venation Pattern Variability

Examination of the 35 different character states for vein position within extant Dixidae reveals that in only 10 instances are specific character states present in one genus and not the other. For example, state "3" for the position of the terminus of A_1 relative to the origin of Rs is not present in extant *Dixella*. However, this character state exists in extant *Dixa* in only one of the 50 species examined. In fact, in each of the 10 cases, the character state is rare in the other genus, occurring only once or twice. Therefore, no single character

Key to the fossil species of Dixidae

1a.	R_{2+3} not strongly arched	2
1b.	R_{2+3} strongly arched	6
2a.	R_1 fused with R_2	<i>Syndixa</i> 3
2b.	R_1 not fused with R_2	<i>Eucoethrina</i> 5
3a.	r-m and m-cu crossveins in-line	4
3b.	m-cu distal of r-m	? <i>Syndixa liasina</i>
4a.	R_{2+3} short, $< \frac{1}{4}$ length of $R_{2+3} + R_2$	<i>Syndixa mollis</i>
4b.	R_{2+3} subequal to R_2	<i>Syndixa sibirica</i>
5a.	Length of Sc relative to wing length (h – apex) < 0.45	<i>Eucoethrina westwoodi</i>
5b.	Length of Sc relative to wing length (h – apex) $> 0.45 \leq 0.50$	<i>Eucoethrina flexa</i>
5c.	Length of Sc relative to wing length (h – apex) ≥ 0.50	<i>Eucoethrina convexa</i>
6a.	Wing width < 0.6 mm.	7
6b.	Wing width > 1.0 mm.	8
7a.	Gonostylus stout, divided apically	<i>Dixella minuta</i>
7b.	Gonostylus long, slender, not divided apically	<i>Dixella distans</i>
8a.	Female	9
8b.	Male	10
9a.	Wing margin emarginated between CuA_1 and CuA_2	<i>Dixella eomarginata</i>
9b.	Wing margin not emarginated	<i>Dixella intacta</i>
10a.	Gonostylus bent at about right angle apically	11
10b.	Gonostylus not bent apically	12
11a.	Gonostylus stout, with broad base	<i>Dixella curvistyla</i>
11b.	Gonostylus long, slender	<i>Dixella succinea</i>
12a.	Gonostylus moderately long, $L/W < 5$	<i>Dixella spinilobata</i>
12b.	Gonostylus very long, slender, $L/W > 10$	<i>Dixella filiforceps</i>

state is characteristic of (i.e., both universally present in and restricted to) either genus. Similarly, while there are combinations of specific character states that occur in only one of the two genera, they occur only rarely (e.g., the *Dixa aliciae* Johannsen, 1924 pattern occurs only once within the 50 extant *Dixa* species examined). There are also instances in which a specific character state or combination of character states is much more likely to occur in one genus. For example, the character state combination m-cu/r-m as “4” and r-m/Rs as “2” is 2-fold more common in *Dixa* than *Dixella*, but occurs in less than one in four of the *Dixa* species examined. Similarly the position of the bifurcation of R2+3 relative to that of M is three times more likely to be “3” or “4” in *Dixa* than in *Dixella*, but that combination occurs in a minority of the *Dixa* species. When the statistically most common combination of character states for each character is calculated for each genus, they are essentially identical: 0, 4/2, 4, 4, 4, 0, 4/0 for *Dixa*, and 0, 4, 4, 4, 4, 0, 0 for *Dixella*. Obviously, however, in order for a character state to define a clade, in this case either *Dixa* or *Dixella*, that character state must not simply occur once or even statistically most commonly, it must be invariant within that genus. Given these data and the fact that an examination of the holotype of *Dixa priscula* clearly shows that, in contrast to Cockerell’s original description, the crossveins r-m and m-cu are not preserved, *D. priscula* is reassigned to Dixidae *incertae sedis*. Similarly, although the venation pattern (2, 4, 0, 4, 4, 2, 0) of *Dixa cimbrica* is unique relative to the 92 species examined in the current study, it too is reassigned to Dixidae *incertae sedis*.

Figure 12.1-8 depict four examples of intraspecific venation pattern variability. A total of seven different species were examined: photographs of wings from different individuals of *Dixa nova* Walker, 1848 (Now classified as *Dixella* [Pape and Thompson, 2013]), *Dixa terna* Loew, 1863, *D. rathymy* Dyar and Shannon, 1924 and *Dixella obscura* Loew, 1849, for which 16, 14, seven and four specimens were examined, respectively, are shown. *Dixella torrentia* Lane, 1939 and *D. solomonis* Belkin, 1962, for which six and seven specimens were examined, respectively, displayed variability but to a degree less than that found in the figured species. *Dixella cornuta* Johannsen, 1923, for which only six specimens were examined, exhibited no variability. For four of the seven species examined, all specimens were from the same locality. Specimens of *Dixa terna* were from Pennsylvania and Virginia, *Dixella obscura* from

Arizona and Alaska and *Dixella cornuta* from Delaware and Idaho. In all four figured species, the relative position of the crossvein r-m varies from even (2) to apical (4) of the Rs fork. The relative position of Sc differs in two of the four figured species, ranging from even to basal relative to the origin of Rs in *Dixella obscura* and from apical to basal in *Dixa rathymy*. The position of m-cu relative to r-m is apical in one of the two specimens of *Dixella obscura* and basal in the other.

DISCUSSION

The current unsatisfactory state of dixid taxonomy appears to be due to several factors: 1) as Belkin (1968) states, “Speciation has been accompanied by very few and minor changes in the general external characters of the adults.”, 2) a large degree of both interspecific and intraspecific variability (Peus, 1936; Peters and Cook, 1966; Disney, 1975), and 3) choices of seemingly superficial criteria for the definition of genera (Takahashi, 1958; Hennig, 1966; Borkent, 2009). As a result, the generic assignment of fossil species within the family Dixidae is a challenge. Several keys to extant dixids exist but they are geographically restricted, out-of-date, or both (Nowell, 1951; Takahashi, 1958; Peters and Cook, 1966; Nowell, 1980). The Nearctic species were last treated by Peters and Cook (1966); dixids of Asia were keyed by Nowell (1980), although the 10 species from Japan described by Takahashi (1958) were not included. Numerous species of this family have been described from the tropics of both America and Asia in the last decade and we can assume that many more await discovery (Papp et al., 2006; Chaverri and Borkent, 2007; Papp, 2007; Taber, 2010). The most robust morphological characters for differentiation between *Dixa* and *Dixella* appear to be those of the larval stage (Nowell, 1951; Belkin, 1968; Disney, 1975), and keys have been devised that separate these genera based on character states of the immature stages (Edwards, 1932; Johannsen, 1933; Smith, 1938; Belkin, 1968; Disney, 1975). The necessity to identify the dixid imago has led to a reliance on what has been termed uninformative characters (Takahasi, 1958; Belkin, 1968); their weaknesses in generic and suprageneric classification, as used in the literature, are discussed in detail here.

Tonnoir (1924), in his original differentiation of *Dixa* and *Paradixa* Tonnoir, 1924 (now *Dixella*), defined *Paradixa*, in part, as having crossvein r-m at or distal to the fork of Rs. However, as long ago as 1923, Johannsen described intraspecific varia-

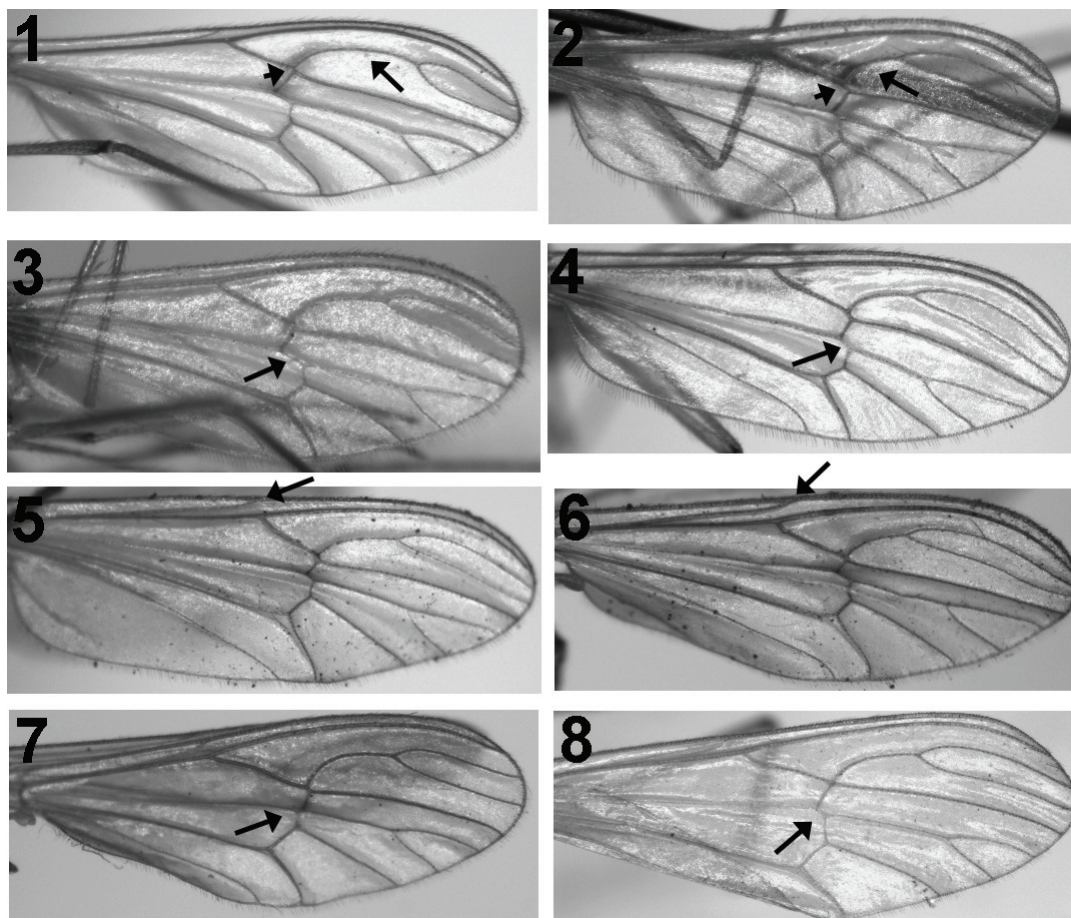


FIGURE 12. Intraspecific wing venation pattern variability in Dixidae. **1-2,** Wings from two different individuals of *Dixella nova* (USNM01193745, USNM01193785, ♀, ♂, respectively; NY). **3-4,** Wings from two different individuals of *Dixia terna* (USNM01193791, USNM01193792, ♂, ♂, respectively; PA & VA). **5-6,** Wings from two different individuals of *Dixia rhathyme* (USNM01193798, USNM01193868, ?, ♀, respectively; CA). **7-8,** Wings from two different individuals of *Dixella obscura* (USNM01193908, USNM01193974, ?, ♀, respectively; AZ & AK). Collection localities are in parentheses. Arrows and arrowheads denote specific points of variation. Abbreviations: AK = Alaska, AZ = Arizona, CA = California, NY = New York, PA = Pennsylvania, VA = Virginia, USA.

bility in the wing venation of two species of dixids. Peus (1936) also detailed significant variation in the wing venation patterns of members of this family. Locality-specific differences in the position of crossvein m-cu were noted in *Dixia pyrenaica* Seguy, 1921 (Now classified as *Dixella* [Pape and Thompson, 2013]), and differences in the positions of both m-cu and r-m were documented in specimens of *Dixia laeta* Loew, 1849 (Now classified as *Dixella* [Pape and Thompson, 2013]), from the same locality; minor differences were found in the two wings of a single specimen. Variability in the venation pattern of *Dixia filicornis* Edwards, 1926 (Now classified as *Dixella* [Pape and Thompson, 2013]), was also observed. Peus (1936) concluded that wing veins were “wertlos und unbrauchbar”

(worthless and unusable) in species-level identifications. This may be an overstatement, however, as not all dixid species exhibit the same degree of variability. Nevertheless, Disney (1975) documented intraspecific variability in venation patterns in *Dixella attica* Pandazis, 1933 and *D. autumnalis* Meigen, 1838 with, for example, crossvein r-m basad of the bifurcation of Rs in one individual and apical in another. Disney, like Peus, also demonstrated variability in wings from the same individual. In Peters and Cook’s (1966) revision of the Nearctic Dixidae, 23 species of *Dixia* and 18 species of *Dixella* were examined. Although the positions of the various veins were not extensively studied, their lengths were. In three of 23 *Dixia* species, the length of R_{2+3} varied by a factor greater

than 2 amongst individuals of the same species. Such huge intraspecific differences were also found in one species of *Dixella*. The length of M_{3+4} varied by more than twofold within several other species of *Dixella*; differences of $\pm 25\%$ were common.

Statements by Cockerell (1921) that *Dixa priscula*'s "venation is typical for *Dixa*," Ansorge (1992) that "Typical Dixidae (with) m-cu crossvein located proximal to the r-m crossvein" and Hennig (1966) that "the location (basal to the bifurcation of Rs) of the crossvein r-m of (*Dixa*) *minuta* is not an entirely random feature," are inaccurate. Although Cockerell's statement must be taken in historical context – *Nothodixa* was the only genus other than *Dixa* recognized in 1921, the point is that *Dixa*- and *Dixella*-specific venation patterns do not appear to exist. In contrast to the statements of Ansorge and Hennig, r-m basal to the bifurcation of Rs is more than twice as likely to occur in *Dixella* than *Dixa* and m-cu basal to r-m was found in only 11.5% of the *Dixa* and *Dixella* species examined in the present study. The data from the comparative study reported here demonstrate that there is no single wing venation character or combination of characters that is unique to either genus (Appendix 3). The very small numbers of specimens that had to be examined in order to establish even intraspecific pattern variation underlines the predominance of this phenomenon. Given these data and the fact that an examination of the holotype of *Dixa priscula* clearly shows that, in contrast to Cockerell's original description, the crossveins r-m and m-cu are not preserved, *D. priscula* is reassigned to Dixidae *incertae sedis*. Similarly, although the venation pattern of *Dixa cimbrica* (2, 4, 0, 4, 4, 2, 0 [Appendix 3]) is unique relative to those examined in the current study, it too can not be assigned to genus and is reassigned to Dixidae *incertae sedis*.

Although these data were not generated by a formal cladistic study, they provide conclusive documentation of the symplesiomorphic nature of venation-based character states within the genera *Dixa* and *Dixella*. These data then form the basis of our conclusion that generic assignments cannot be made on venation-based character states. The comprehensive cladistic analysis required to establish or reject the validity of these two genera, while beyond the scope of the current study, is essential to our understanding of the organization of the family. If character states that accurately define genera within the family can be established, the question of the utility of wing venation patterns at the generic level will have to be reexamined.

Use of the size and form of the antennae was introduced by Tonnoir (1924) and Garrett (1924) and persists today in differentiation of the two major genera, *Dixa* and *Dixella*; species of *Dixa* are usually described as having a fusiform first flagellomere (F1) while those of *Dixella* have a cylindrical F1. However, published descriptions, in reference to both F1 and all flagellomeres, differ substantially, as exemplified by the following examples. For *Dixa*: "flagellar segments distinct," F1 "fusiform, much thicker medially than basally or apically," F1 "slightly fusiform"; F1 "swollen while the other basal segments . . . at least slightly fusiform if not swollen," F1 "cylindrical, slightly fusiform," F1 "terete" (cylindrical, tapering at both ends), "flagellar segments narrow and cylindrical" (subgenus *Dixella* sensu Nowell, 1980), F1 "somewhat fusiform (i.e., not strictly cylindrical)." For *Dixella*: F1 "cylindrical, rarely slightly fusiform," "flagellar segments all elongate, cylindrical," F1 "elongate, cylindrical and no segments fusiform," "all segments of flagellum elongated, filiform and scarcely distinguishable from one another," F1 "elongate fusiform rather than strictly cylindrical" (*Dixella* sensu Nowell, 1951), F1 "slightly fusiform so that flagellar segments are distinct" (Nowell, 1951; Peters and Cook, 1966; Belkin, 1968; Disney, 1975; Nowell, 1980; Peters, 1992, 1993; Papp, 2007). Difficulty in interpretation of this character state has led to its abandonment by some authors. Takahashi (1958) identified 10 new species of the genus *Dixa*, four of which were described as having F1 cylindrical. In the same study, the F1 of *Dixella subobscura* Takahashi, 1958 was described as "somewhat widened before the middle."

The ratio of F1 length/width and the total length of the antenna have also been widely used. For example, Nowell (1951) described *Dixa* with F1 "about three to four times as long as broad, rarely less or more" and *Paradixa* and *Dixella* (both now as *Dixella*) with F1 "at least five times as long as broad" or "about six times as broad," respectively. In his key to Oriental species, Nowell (1980) described *Dixa* with F1 four to six times as long as broad and three species that are currently classified as *Dixella* as having F1 10 to 15 times as long as broad. Takahashi (1958) described 10 species of *Dixa* with F1 length/width ratios of 4.5 to 10 (6/10 with the ratio ≥ 7) and a ratio of about 5 for *Dixella subobscura*. Chaverri and Borkent (2007) recently described 10 new species of *Dixella* and, in the six species for which measurement could be made (from figure 1), the F1 length to width ratio

varied from 6.75 to 9.1. Peters (1993) described *Dixa dolichostyla* Peters, 1993 with a F1 length/width ratio of 8, while Papp (2007) described *Dixa foldvarii* Papp, 2007 with this ratio equal to 7.5 to 8 and “i.e., between the realms of *Dixa* and *Dixella*.” Takahashi concluded that this particular “character does not divide accurately the (*Dixa* and *Dixella*) groups.” Similarly, the total lengths of the antennae have failed to enable a clear discrimination between *Dixa* and *Dixella*. Nowell (1951) described *Dixa* as having “antennae moderately long, scarcely longer than the thorax” and *Paradixa* with elongate antennae or antennae “nearly as long as the body.” Belkin (1968), in a key to the Culicoidea of New Zealand, characterized the antennae of *Paradixa* as 1.5 times as long as the head and thorax combined. Peters and Cook (1966) described *Dixella indiana* with antennae about 2/3 the length of the wing (total body lengths were not provided) and later, Peters (1993) described *Dixa dolichostyla* as having antennae 2.3 times the length of the thorax. When applied to *Dixella intacta*, the criteria provided in the three preceding studies give antenna/body length ratios of 0.52, 0.65 and 0.65, respectively. It appears that, within Dixidae, F1 and total antennal length and flagellomere shape are both continua with no defining boundaries.

Details of the structure of pretarsal claws have also been used in the classification of the Dixidae (Nowell, 1951; Peters and Cook, 1966; Belkin, 1968; Belkin et al., 1970; Peters, 1981, 1993; Chaverri and Borkent, 2007; Tabor, 2010). Numerous studies have documented sexual dimorphism relative to claw structure; pretarsal claws of females are smaller than those of males and have basal combs composed of variable numbers of short and/or long teeth as well as what has been termed spicules on the lateral surfaces of the claws. The pretarsal claws of males have basal combs that are often smaller than those of females, as well as external spicules. Unique to the pretarsal claws of males, however, are teeth, sometimes described as pectinate, on the venter or ventral (concave) surface of the claw. These ventral teeth have been reported to vary in number from zero to as many as seven per claw. The pretarsal claws of both males and females of the genera *Dixa*, *Mesodixa*, *Nothodixa*, and *Dixella* have been figured in several studies (Nowell, 1951; Belkin, 1968; Belkin et al., 1970; Chaverri and Borkent, 2007; Tabor, 2010). Nowell (1951) described male *Dixa* as with long fine teeth on fore- and midpretarsal claws and male *Dixella* as with short fine teeth on all legs. Peters and Cook (1966) later described *Dixa* with

hind leg pretarsal claws of males frequently without ventral teeth and male *Dixella* hind leg tarsi as frequently with ventral teeth. Peter and Cook’s key twice used the symbol ♀ in describing pretarsal claws where ♂ was intended (key to genera, couplets 1 and 2). Of the 20 species of *Dixa* for which they described the hind leg pretarsal claws, three species were described as having “very small”, “short, weak,” or “moderately long” ventral teeth and three species had “long ventral teeth”; in the remaining 16 species, the metatarsal claws were “simple” (without teeth). Of the 15 species of *Dixella* for which descriptions of the hind leg pretarsal claws were given, three species had simple claws and a fourth was without “prominent teeth.” Peters (1981) amended his description of *Dixa* to hind leg pretarsal claws ± ventral teeth and in 1993, described *Dixa dolichostyla* as having four long teeth on the pro- and middle leg tarsi but only “with a few weak hairs” on the ventral aspect of the hind leg pretarsal claws. Belkin (1968) described the genus *Nothodixa* with all claws pectinate (4–5 teeth per claw) and the genus *Dixella* (with four species in New Zealand) with pro- and middle leg pretarsal claws pectinate but the hind leg tarsal claw either simple or with a single tooth. He figured *Dixella neozelandica* Tonnoir, 1924 with 4, 2, and 1 teeth on the pro-, meso-, and hind leg pretarsal claws, respectively. Belkin et al. (1970) described the male of *Mesodixa biambulacra* Belkin, Heinemann, and Page, 1970 with four to five teeth on all pretarsal claws and the male of *Dixella scitula* Belkin, Heinemann and Page, 1970 with three to four moderately long teeth on all legs. Peters (1992) described a specimen of *Dixa orientalae* Peters, 1992 with three to four hind leg pretarsal teeth. More recently, Chaverri and Borkent (2007) figured the pretarsal claws of the males of 10 species of *Dixella* and depicted metatarsal claws with from zero to as many as three ventral teeth. In some species, the teeth do not originate strictly ventrally but subventrally/laterally and, in such cases are usually smaller in diameter. *Dixella jironi* Chaverri and Borkent, 2007 has a single short tooth at the distal base of the claw but the ventral aspect of the claw itself has no teeth. This same study also documented significant variation in the number of teeth on the two claws of a single pretarsus. Taber (2010) figured *Dixella fraxina* with five long ventral teeth on all pretarsi of the male. It appears obvious that, while there may be a tendency towards fewer hind leg pretarsal ventral teeth in male *Dixa* relative to *Dixella*, the relationship is not invariant and does not provide an accurate basis for classification.

In his generic and suprageneric keys, Nowell (1951) did not utilize genitalic features. However, in descriptions of individual genera, species of *Dixa* were characterized as either without an apical lobe of the gonocoxite or with a short apical lobe, *Nothodixa* as without a prominent apical lobe, *Paradixa* as with a long apical lobe “usually half as long as the style or longer” and *Dixella* with a “moderately long apical (lobe).” Peters’ (1981) key characterized *Dixella* as with an apical lobe greater or equal to the length of the gonostylus and *Dixa* as with an apical lobe less than half the length of the gonostylus. Numerous additional descriptions of species of *Dixa* and *Dixella* suggest that the relative lengths of the apical lobe of the gonocoxite and the gonostylus accurately define the two genera (Belkin et al., 1970; Nowell, 1980; Peters, 1993; Chaverri and Borkent, 2007; Papp, 2007). However, exceptions have been reported. Belkin (1968) described three species of *Dixella* (*D. harrisi* Tonnoir, 1925, *D. neozelandica*, and *D. fuscinervis* Tonnoir, 1924) as having “short” or “very short” apical lobes with lengths less than half that of the gonostylus. Disney (1975) described *Dixella corensis* Peters, 1992 with an apical lobe less than half the length of the gonostylus. Of the 11 species described by Takahasi (1958), there was a single exception, *Dixa longistyla* Takahashi, 1958, which was described with a “dorsal process relatively long.” Peus (1936) figured both *Dixa borealis* Martini, 1929 and *D. pyrenaica* with apical lobes greater than half the length of the gonostylus. *Dixa pyrenaica*, however, was subsequently synonymized with *Dixella obscura* (Pape and Thompson, 2013). Tabor (2010) described *Dixella fraxina* with “the digitate extension of the apical lobe less than half the length of the (gonostyle).” However, if the length is taken from the base of the lobe, the apical lobe of *D. fraxina* is greater than that of the gonostylus. Belkin (1968), in reviewing the morphology of the male genitalia, stated that the “superficial details of . . . the sidepiece (gonocoxite) and clasper (gonostylus) . . . show excellent diagnostic features” but this at the species level. Disney (1975), in describing the British Dixidae, reared each of the 14 endemic species and produced keys for both male and female imago, the larvae and the pupae. In his key, the primary character used in the differentiation of the male adults (six *Dixa* and eight *Dixella*) was the length of the apical lobe of the gonocoxite relative to that of the gonostylus. However, the variability cited in the discussion above suggests that, until the exceptions described in the literature are re-examined and

many other species in both *Dixa* and *Dixella* are reared, Disney’s limited study cannot be extrapolated to the genera of the world.

Individual character states based on wing venation and antennal, genital and metapretarsal morphology are homoplastic and do not separate the dixids into natural divisions. Hennig (1966) voiced similar concerns, purposefully limiting his descriptions of *Dixa succinea*, *Dixella filiforceps* and *D. distans*. Takahasi (1958) referred to his key to the Dixidae of Japan as “artificial.” Despite well-documented variability in all of the adult characters used to define *Dixa* and *Dixella* and the numerous admonitions by essentially all of the leading dixid taxonomists that these two genera are problematic, the designation of new species, in the absence of study of both larvae and adult specimens, continues. It should be noted that Takahashi’s *Dixa obtusa* Takahashi, 1958 should be placed in the genus *Dixella* (T. Saigusa, unpublished observations) based on larval morphology; this same observation is supported by molecular data (J.K. Moulton, unpublished data). The morphology of immature stages has been described by a number of investigators, but the number of species involved is very limited (Edwards, 1932; Johannsen, 1933; Smith, 1938; Nowell, 1951; Belkin, 1962, 1968; Brundin, 1966; Belkin et al., 1970; Disney, 1975; Borkent, 2012). For example, Borkent (2012), in a search of the literature for detailed descriptions of dixid pupae, found only seven, only one of which was genus *Dixa*. Larval and/or pupal synapomorphies specific to redefined *Dixa* and *Dixella*, should be a major thrust of future morphology-based research. The two major genera within Dixidae, as currently defined in the literature, are obviously not monophyletic. Detailed cladistic analyses that utilize both morphological and molecular data, along with expanded studies of larval and pupal morphology, are required to establish whether or not any natural monophyletic subdivisions exist within the family.

Nowell (1951) recognized that the major genera *Dixa* and *Dixella* could be differentiated based on their respective habitat: *Dixa*, never found in quiet pools of water, preferring the fast flowing water of the middle of streams and waterfalls and *Dixella*, found in both the quiet waters of ponds and lake edges as well as fast-flowing streams. Nowell qualified the latter, however, in stating that when *Dixella* reside in streams and rivers, they are at the water line (e.g., moving up and down on vegetation). Håland (2009) reported a rare exception with the collection of a single specimen of *Dixa nebu-*

Iosa Meigen, 1830 from a small lake. In reality this habitat distinction is not clear-cut. For instance, *Dixa fluvica* prefers slow flowing watercress-choked springs (almost ditches) and *Dixella cornuta* and *Dixa pseudindiana* occur in streams and rivers, respectively (Moulton, personal obs.). Although the four new fossil species of *Dixella* were collected at three different sites, all of the sites had shallow near-shore depositional environments (Greenwalt et al., 2015).

Fossil Dixidae are essential tools in our understanding of the phylogeny and evolution of this and related families. Other fossil Dixidae await description. Grimaldi and Engel (2005) and Haenni (2003) have reported specimens in Eocene Baltic amber and Dixidae in Miocene Dominican and Eocene Rovno amber have also been reported (Poinar, 1992; Perkovsky et al., 2010). Meniscus midges have also been reported from the Eocene Fossil Butte Member of the Green River Formation (Grande, 2013). A single specimen of an adult dixid has been reported from the Cretaceous Koonwarra fossil bed in Victoria, Australia (Jell and Duncan, 1986). Description of this latter specimen is of particular interest given that all described fossil Dixidae are from the Holarctic region. The Koonwarra bed has been dated to 116 ± 5 Ma (Drinnan and Chambers, 1986) so it would be of interest to compare and contrast the Australian dixid with the only other fossil dixid from the Cretaceous, *Eucoerithrina westwoodi*.

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APPENDIX 1.

Taxa examined in wing venation variability analysis. † denotes an extinct taxon.

Taxon	Reference/Depository
<i>Asiodixa pura</i>	Papp et al., 2006
<i>Asiodixa maculosa</i>	Papp et al., 2006
<i>Dixa aliciae</i>	WRBU
<i>Dixa babai</i>	Takahashi, 1958
<i>Dixa brevis</i>	WRBU
<i>Dixa californica</i>	WRBU
<i>Dixa camerounensis</i>	WRBU
<i>Dixa cimbrica</i> †	Ansorge, 1992
<i>Dixa clavata</i>	WRBU
<i>Dixa dilatata</i>	WRBU
<i>Dixa dyari</i>	WRBU
<i>Dixa fluvica</i>	WRBU
<i>Dixa fusca</i>	WRBU
<i>Dixa hegemonica</i>	WRBU
<i>Dixa hikosana</i>	Takahashi, 1958
<i>Dixa hoffmani</i>	WRBU
<i>Dixa inextricata</i>	WRBU
<i>Dixa johannseni</i>	WRBU
<i>Dixa kaplani</i>	Wagner et al., 1991/1992
<i>Dixa kyushuensis</i>	Takahashi, 1958
<i>Dixa lobata</i>	WRBU
<i>Dixa lobatus</i>	WRBU
<i>Dixa longistyla</i>	Takahashi, 1958
<i>Dixa lunata</i>	WRBU
<i>Dixa maculata</i>	WRBU
<i>Dixa melanderi</i>	WRBU
<i>Dixa minuta</i> †	Hennig, 1966
<i>Dixa minutiformis</i>	Takahashi, 1958
<i>Dixa modesta</i>	Johannsen, 1923
<i>Dixa modesto</i>	WRBU
<i>Dixa naevia</i>	WRBU
<i>Dixa nebulosa</i>	WRBU
<i>Dixa neoaliciae</i>	WRBU
<i>Dixa neohegemonica</i>	WRBU
<i>Dixa nipponica</i>	Takahashi, 1958
<i>Dixa notata</i>	WRBU
<i>Dixa nova</i>	Peters, 1981
<i>Dixa nubilipennis</i>	WRBU
<i>Dixa obtusa</i>	Takahashi, 1958
<i>Dixa orientale</i>	WRBU
<i>Dixa priscula</i> †	Cockerell, 1921
<i>Dixa puberula</i>	Disney, 1975
<i>Dixa punctata</i>	Wagner et al., 1991/1992

Taxon	Reference/Depository
<i>Dixa rathyme</i>	WRBU
<i>Dixa serrata</i>	WRBU
<i>Dixa serrifera</i>	WRBU
<i>Dixa similis</i>	WRBU
<i>Dixa spiralis</i>	WRBU
<i>Dixa stuckenbergi</i>	WRBU
<i>Dixa submaculata</i>	WRBU
<i>Dixa subobscura</i>	Takahashi, 1958
<i>Dixa terna</i>	WRBU
<i>Dixa tertiarif</i>	Theobald, 1937
<i>Dixa trilineata</i>	Takahashi, 1958
<i>Dixa xavia</i>	WRBU
<i>Dixa yamatona</i>	Takahashi, 1958
<i>Dixella aegyptiaca</i>	Wagner et al., 1991/1992
<i>Dixella aestivalis</i>	WRBU
<i>Dixella amphibia</i>	Disney, 1975
<i>Dixella attica</i>	Wagner et al., 1991/1992
<i>Dixella aurora</i>	WRBU
<i>Dixella autumnalis</i>	WRBU
<i>Dixella corensis</i>	Peters, 1992
<i>Dixella cornuta</i>	WRBU
<i>Dixella curvistyla</i>	This study
<i>Dixella deltoura</i>	WRBU
<i>Dixella distans</i>	Hennig, 1966
<i>Dixella eomarginata</i>	This study
<i>Dixella fernandezae</i>	Chaverri and Borkent, 2007
<i>Dixella filicornis</i>	Disney, 1975
<i>Dixella filiforceps</i>	Hennig, 1966
<i>Dixella fraxina</i>	Taber, 2010
<i>Dixella fuscifrons</i>	Wagner et al., 1991/1992
<i>Dixella fuscinervis</i>	WRBU
<i>Dixella golanensis</i>	Wagner et al., 1991/1992
<i>Dixella hansonii</i>	Chaverri and Borkent, 2007
<i>Dixella hernandezi</i>	Chaverri and Borkent, 2007
<i>Dixella indiana</i>	Peters and Cook, 1966
<i>Dixella intacta</i>	This study
<i>Dixella israelis</i>	Wagner et al., 1991/1992
<i>Dixella jironi</i>	Chaverri and Borkent, 2007
<i>Dixella laeta</i>	Peus, 1936
<i>Dixella limai</i>	WRBU
<i>Dixella lobata</i>	Chaverri and Borkent, 2007
<i>Dixella maculata</i>	Chaverri and Borkent, 2007
<i>Dixella martini</i>	WRBU
<i>Dixella neozelandica</i>	Belkin, 1968
<i>Dixella nixiae</i>	Peters, 1980
<i>Dixella obscura</i>	WRBU

Taxon	Reference/Depository
<i>Dixella pollex</i>	Nowell, 1980
<i>Dixella pyrenaica</i>	Peus, 1936
<i>Dixella scitula</i>	Belkin et al., 1970
<i>Dixella serotina</i>	Disney, 1975
<i>Dixella shannoni</i>	Chaverri and Borkent, 2007
<i>Dixella solomonis</i>	WRBU
<i>Dixella spinilobata</i> †	This study
<i>Dixella succinea</i> †	Hennig, 1966
<i>Dixella suzukii</i>	Chaverri and Borkent, 2007
<i>Dixella techana</i>	WRBU
<i>Dixella torrential</i>	WRBU
<i>Dixella trinitensis</i>	WRBU
<i>Dixella venezulensis</i>	Chaverri and Borkent, 2007
<i>Dixella vespertina</i>	WRBU
<i>Dixella woodi</i>	Chaverri and Borkent, 2007
<i>Eucorethrina convexa</i> †	Lukashevich, 1996
<i>Eucorethrina flexa</i> †	Kalugina, 1985, Lukashevich, 1996
<i>Eucorethrina westwoodi</i> †	Lukashevich et al., 2001
<i>Meringodixa chalonensis</i>	Nowell, 1951
<i>Mesodixa biambulacra</i>	Belkin et al., 1970
<i>Neodixa minuta</i>	Belkin, 1962
<i>Nothodixa campbelli</i>	Belkin, 1968
<i>Nothodixa otagensis</i>	Belkin, 1962
<i>Nothodixa septentrionalis</i>	Belkin, 1962
<i>Nothodixa philpotti</i>	Belkin, 1962
<i>Syndixa mollis</i> †	Lukashevich, 1996
<i>Syndixa sibirica</i> †	Lukashevich, 1996

APPENDIX 2.

Character states used in the analysis of fossil and extant dipterid wing venation.

1. Vein Sc apex relative to the origin of Rs: basal [$>2X$ vein width] (0); subbasal [$<2X$ vein width] (1); even (2); subapical [$<2X$ vein width] (3); apical [$>2X$ vein width] (4).
2. Crossvein r-m origin relative to the bifurcation of Rs: basal (0); subbasal [$<2X$ vein width] (1); even (2); subapical [$<2X$ vein width] (3); apical (4).
3. Crossvein m-cu origin relative to the terminus of r-m: basal (0); subbasal [$<2X$ vein width] (1); even (2); subapical [$<2X$ vein width] (3); apical (4).
4. Vein A_1 terminus relative to the origin of Rs: basal (0); subbasal [$<2X$ vein width] (1); even (2); subapical [$<2X$ vein width] (3); apical (4).
5. Vein A_1 terminus relative to Sc terminus: basal (0); subbasal [$<2X$ vein width] (1); even with (2); subapical [$<2X$ vein width] (3); apical (4).
6. Vein A_1 terminus relative to the bifurcation of Cu: basal (0); subbasal [$<2X$ vein width] (1); even (2); subapical [$<2X$ vein width] (3); apical (4).
7. Vein R_{2+3} : branched (0); unbranched (1).
8. R_{2+3} curvature: straight or very slightly arched (0); strongly arched (1).
9. Vein R_{2+3} branch relative to the bifurcation of M: basal (0); subbasal [$<2X$ vein width] basal (1); even (2); subapical [$<2X$ vein width] (3); apical (4).
10. Vein R_1 : fused to C far basal (near $3/4$ wing length) of wing apex (0); closer to C than R_2 and fused near wing apex (1); equidistant to C and R_2 and fused near wing apex (2).
11. Vein R_2 : not fused with R_1 (0); fused with R_1 (1).
12. Rs: straight (0); sigmoidal (1).
13. Wing length/width: <2.5 (0); $2.5 - 3$ (1); $>3 <4$ (2) >4 (3).

APPENDIX 3.

Morphological data matrix (Dixidae wing and venation characters only).

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dixa aliciae</i>	2	1	2	2	2	0	0	1	4	1	0	0	-
<i>Dixa babai</i>	0	-	4	4	4	0	0	1	0	1	0	0	1
<i>Dixa brevis</i>	2	4	4	4	4	0	0	1	0	1	0	0	0
<i>Dixa californica</i>	3	2	4	4	4	0	0	1	2	1	0	0	-
<i>Dixa camerounensis</i>	0	4	4	2	4	0	0	1	0	1	0	0	-
<i>Dixa clavata</i>	2	3	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa dilatata</i>	0	3	4	4	4	0	0	1	3	1	0	0	-
<i>Dixa dyari</i>	0	2	4	4	4	0	0	1	4	1	0	0	-
<i>Dixa fluvica</i>	1	2	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa fusca</i>	0	3	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa hegemonica</i>	1	3	4	4	4	0	0	1	2	1	0	0	-
<i>Dixa hikosana</i>	0	-	4	4	4	0	0	1	0	1	0	0	1
<i>Dixa hoffmani</i>	0	2	0	4	4	0	0	1	4	1	0	0	-
<i>Dixa inextricata</i>	2	2	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa johannseni</i>	4	2	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa kaplani</i>	0	2	0	2	4	0	0	1	3	1	0	0	1
<i>Dixa kyushuensis</i>	0	2	4	4	4	0	0	1	4	1	0	0	1
<i>Dixa lobata</i>	4	2	4	4	4	2	0	1	0	1	0	0	-
<i>Dixa lobatus</i>	2	4	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa longistyla</i>	0	0	4	0	4	0	0	1	4	1	0	0	1
<i>Dixa lunata</i>	0	4	4	4	4	0	0	1	4	1	0	0	-
<i>Dixa maculata</i>	0	4	4	4	4	0	0	1	4	1	0	0	-
<i>Dixa melanderi</i>	2	4	4	4	4	0	0	1	4	1	0	0	-
<i>Dixa minutiformis</i>	0	3	4	4	4	2	0	1	0	1	0	0	1
<i>Dixa modesta</i>	0	4	4	2	4	0	0	1	0	1	0	0	2
<i>Dixa modesto</i>	0	4	4	4	3	0	0	1	4	1	0	0	-
<i>Dixa naevia</i>	2	2	4	4	4	0	0	1	4	1	0	0	-
<i>Dixa nebulosi</i>	0	2	4	4	4	0	0	1	2	1	0	0	-
<i>Dixa neoaliciae</i>	0	0	0	4	4	1	0	1	4	1	0	0	-
<i>Dixa neohegemonica</i>	0	4	4	4	4	0	0	1	2	1	0	0	-
<i>Dixa nipponica</i>	0	-	4	4	0	0	0	1	4	1	0	0	1
<i>Dixa notata</i>	0	4	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa nubilipennis</i>	0	4	4	2	4	0	0	1	0	1	0	0	-
<i>Dixa obtusa</i>	0	-	4	4	4	0	0	1	0	1	0	0	1
<i>Dixa orientale</i>	4	3	4	4	4	0	0	1	4	1	0	0	-
<i>Dixa puberula</i>	1	3	4	4	4	1	0	1	2	1	0	0	1
<i>Dixa punctata</i>	0	2	0	2	4	0	0	1	2	1	0	0	2
<i>Dixa rhathyme</i>	2	3	4	4	4	1	0	1	1	1	0	0	-
<i>Dixa serrata</i>	0	2	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa serrifera</i>	0	4	4	3	4	0	0	1	3	1	0	0	-
<i>Dixa similis</i>	0	4	4	4	4	0	0	1	2	1	0	0	-
<i>Dixa spiralis</i>	0	0	4	2	4	0	0	1	0	1	0	0	-

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dixa stuckenbergi</i>	0	0	4	1	4	0	0	1	4	1	0	0	-
<i>Dixa submaculata</i>	1	3	4	4	4	0	0	1	4	1	0	0	-
<i>Dixa subobscura</i>	0	0	4	4	4	0	0	1	0	1	0	0	1
<i>Dixa terna</i>	0	3	4	4	4	0	0	1	0	1	0	0	-
<i>Dixa trilineata</i>	0	-	4	4	4	2	0	1	4	1	0	0	1
<i>Dixa xavia</i>	0	4	4	4	4	0	0	1	4	1	0	0	-
<i>Dixa yamatona</i>	0	-	4	4	4	1	0	1	2	1	0	0	1
<i>Dixa priscula</i>	0	2	0	4	4	0	0	1	0	1	0	0	2
<i>Dixa cimbrica</i>	1	4	0	4	4	2	0	1	4	1	0	0	0
<i>Dixa minuta</i>	0	0	2	-	-	-	0	1	4	1	0	0	1
<i>Dixa tertiaria</i>	0	0	1	3	4	1	0	1	4	1	0	0	2
<i>Dixella aegyptiaca</i>	0	1	4	4	4	0	0	1	2	1	0	0	2
<i>Dixella aestivalis</i>	0	0	4	4	4	0	0	1	0	1	0	0	-
<i>Dixella amphibia</i>	2	4	4	4	4	0	0	1	1	1	0	0	1
<i>Dixella attica</i>	3	2	4	4	4	0	0	1	4	1	0	0	0
<i>Dixella aurora</i>	0	4	3	4	4	0	0	1	0	1	0	0	-
<i>Dixella autumnalis</i>	0	2	4	4	4	0	0	1	0	1	0	0	-
<i>Dixella corensis</i>	0	2	4	4	4	0	0	1	1	1	0	0	-
<i>Dixella cornuta</i>	1	2	4	4	4	0	0	1	0	1	0	0	-
<i>Dixella deltoura</i>	0	2	-	4	4	0	0	1	0	1	0	0	-
<i>Dixella fernandezae</i>	0	0	3	4	4	0	0	1	0	1	0	0	1
<i>Dixella filicornis</i>	0	0	4	4	4	2	0	1	1	1	0	0	0
<i>Dixella fraxina</i>	0	3	4	4	4	0	0	1	0	1	0	0	1
<i>Dixella fuscifrons</i>	0	4	4	4	4	0	0	1	0	1	0	0	1
<i>Dixella fuscinervis</i>	4	4	4	4	4	0	0	1	0	1	0	0	-
<i>Dixella golanensis</i>	2	4	4	4	4	2	0	1	4	1	0	0	1
<i>Dixella hansonii</i>	0	0	2	4	4	0	0	1	1	1	0	0	1
<i>Dixella hernandezii</i>	4	4	2	4	3	0	0	1	1	1	0	0	1
<i>Dixella indiana</i>	0	4	4	4	4	0	0	1	0	1	0	0	2
<i>Dixella israelis</i>	0	4	4	4	4	4	0	1	0	1	0	0	2
<i>Dixella jironi</i>	0	2	2	4	4	0	0	1	0	1	0	0	1
<i>Dixella laeta</i>	4	0	4	4	4	0	0	1	2	1	0	0	-
<i>Dixella limai</i>	0	2	0	4	4	0	0	1	0	1	0	0	-
<i>Dixella lobata</i>	0	2	2	4	4	0	0	1	-	1	0	0	1
<i>Dixella maculata</i>	4	2	4	2	0	0	0	1	2	1	0	0	1
<i>Dixella martini</i>	0	4	4	4	4	0	0	1	4	1	0	0	-
<i>Dixella neozelandica</i>	1	4	4	4	4	0	0	1	0	1	0	0	2
<i>Dixella nixiae</i>	0	2	1	4	4	0	0	1	4	1	0	0	1
<i>Dixa nova</i>	4	3	4	4	4	0	0	1	4	1	0	0	2
<i>Dixella obscura</i>	0	4	4	4	4	0	0	1	0	1	0	0	-
<i>Dixella pollex</i>	0	4	4	0	4	0	0	1	2	1	0	0	1
<i>Dixella pyrenaica</i>	0	0	4	4	4	2	0	1	4	1	0	0	-
<i>Dixella scitula</i>	2	4	0	4	4	0	0	1	0	1	0	0	2
<i>Dixella serotina</i>	0	3	4	4	4	1	0	1	0	1	0	0	1
<i>Dixella shannoni</i>	4	0	2	4	0	0	0	1	0	1	0	0	1
<i>Dixella solomonis</i>	2	0	4	4	4	0	0	1	2	1	0	0	-

GREENWALT & MOULTON: NEW WORLD FOSSIL DIXIDAE

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dixella suzukii</i>	0	2	0	4	4	0	0	1	2	1	0	0	1
<i>Dixella techana</i>	0	4	0	4	4	0	0	1	3	1	0	0	-
<i>Dixella torrentia</i>	0	2	0	4	4	4	0	1	0	1	0	0	-
<i>Dixella trinitensis</i>	0	0	4	0	4	0	0	1	4	1	0	0	-
<i>Dixella venezulensis</i>	0	0	4	4	4	0	0	1	0	1	0	0	1
<i>Dixella vespertina</i>	1	3	2	4	4	0	0	1	0	1	0	0	-
<i>Dixella woodi</i>	2	0	4	4	4	0	0	1	0	1	0	0	1
<i>Dixella spinilobata</i>	0	-	-	-	-	-	0	1	-	1	0	0	2
<i>Dixella eomarginata</i>	2	3	2	4	4	0	0	1	1	1	0	0	1
<i>Dixella curvistyla</i>	0	0	3	-	-	-	0	1	0	1	0	0	0
<i>Dixella intacta</i>	2	3	2	0	0	0	0	1	0	1	0	0	2
<i>Dixella distans</i>	0	3	4	4	4	4	0	1	4	1	0	0	-
<i>Dixella filiforceps</i>	0	2	3	4	4	2	0	1	4	1	0	0	-
<i>Dixella succinea</i>	0	2	4	4	4	1	0	1	4	1	0	0	1
<i>Mesodixa biambulacra</i>	1	2	3	4	4	0	0	1	2	1	0	0	1
<i>Meringodixa chalonensis</i>	2	4	4	4	4	1	0	1	2	1	0	0	1
<i>Neodixa minuta</i>	0	0	4	4	4	0	1	1	0	1	0	0	1
<i>Asiodixa pura</i>	0	0	3	2	4	0	0	1	0	1	0	1	0
<i>Asiodixa maculosa</i>	0	0	4	0	4	0	0	1	0	1	0	1	1
<i>Nothodixa campbelli</i>	0	0	4	4	4	0	0	1	4	1	0	0	0
<i>Nothodixa otagensis</i>	0	0	4	4	4	2	0	1	4	1	0	0	1
<i>Nothodixa septentrionalis</i>	0	0	4	4	4	0	0	1	1	1	0	0	0
<i>Nothodixa philpotti</i>	0	0	4	0	4	0	0	1	4	1	0	0	0
<i>Eucorethrina convexa</i>	4	4	2	4	3	0	0	0	0	2	0	0	0
<i>Eucorethrina flexa</i>	3	4	2	1	0	0	0	0	0	2	0	0	1
<i>Eucorethrina westwoodi</i>	4	4	2	4	2	0	0	0	0	2	0	0	0
<i>Syndixa mollis</i>	4	4	2	4	3	4	0	0	0	-	1	0	0
<i>Syndixa sibirica</i>	4	4	2	4	1	4	0	0	0	-	1	0	1