Zootaxa 3887 (2): 138–156
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3887.2.2
http://zoobank.org/urn:lsid:zoobank.org:pub:D9275063-BD74-498E-B504-1421B50114A5

A re-description of the fossil damselfly *Eolestes syntheticus* Cockerell, 1940 (Odonata: Zygoptera: Eolestidae n. fam.) with description of new taxa from the Eocene of North America

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Abstract

The enigmatic species *Eolestes syntheticus* Cockerell, 1940, from the Early Eocene of North America, previously attributed to the lestoid family Synlestidae, is re-examined in light of the discovery of new material from the Middle Eocene Kishenehn Formation in northwestern Montana. *E. syntheticus* and a new species, *Eolestes ramosus* **sp. n.**, are attributed to a new family Eolestidae **fam. n.**. In addition, a new genus and species very closely related to Lestidae but assigned to family unknown, *Lutetialestes uniformis* **sp. n.**, is described from the Kishenehn Formation.

Key words: taxonomy, fossil insects, Lestoidea, Middle Eocene, Montana, Kishenehn Formation, Green River Formation

Introduction

Damselflies (suborder Zygoptera) constitute approximately half of all Odonata with about 3,000 described extant species as of 2014 (Schorr & Paulson, 2014). The suborder has repeatedly been demonstrated to be monophyletic, in both molecular and morphological analyses (Bechly, 1996; Rehn, 2003; Bybee *et al.*, 2008; Carle *et al.*, 2008; Dumont *et al.*, 2010; Dijkstra *et al.*, 2014). Trueman (1996, 2007) however has argued to the contrary in proposing that Zygoptera is paraphyletic and ancestral to all other modern odonates. Within the suborder, the basal superfamily Lestoidea *sensu* Dijkstra *et al.* (2013) (= Lestomorpha *sensu* Bechly, 1996) appears to be the sister group to all other Zygoptera and has been shown to be monophyletic. The phylogenetic relationships of the constituent families of Lestoidea, the monotypic Hemiphlebiidae and Chorismagrionidae, Perilestidae, Synlestidae, Megalestidae and Lestidae, are still a matter of much discussion (Bybee *et al.*, 2008; Carle *et al.*, 2008; Dumont *et al.*, 2010; Davies *et al.*, 2011; Dijkstra *et al.*, 2014).

The fossil record of Lestoidea is relatively poor. In an extensive review of the extinct members of the superfamily, defined then as including the additional extant family Megapodagrionidae and the extinct families Sieblosiidae and Pseudolestidae, Nel & Paicheler (1994) listed a total of 74 fossil species and/or specimens although approximately a third of them were of "uncertain systematic position" due largely to their fragmentary condition. Sixteen described species and 14 specimens not assigned to a species belonged to the family Lestidae. No fossils of Perilestidae existed and only one, *Eolestes syntheticus*, was assigned to Synlestidae.

Subsequent to Nel and Paicheler's review, many additional fossil species of Lestoidea have been described. Five new genera of Hemiphlebiidae, all from the early Cretaceous when this family is thought to have been widespread, have been described (Bechly 1998; Jarzembowski *et al.* 1998; Vasilenko 2005; Lak *et al.* 2009). Three new extinct monotypic families, Cretacoenagrionidae, Priscalestidae, and Austroperilestidae have been assigned to Lestoidea (Bechly 1995; Wappler & Petrulevicius 2007; Petrulevicius & Nel 2005) and three new extinct monotypic genera, *Cretalestes*, *Libanolestes*, and *Promegalestes*, assigned to either ?Lestoidea or Lestoidea, but

Accepted by D. Paulson: 23 Oct. 2014; published: 24 Nov. 2014

not to a family, have also been described since Nel and Paicheler's review (Jarzembowski *et al.* 1998; Petrulevicius & Nel 2004; Azar *et al.* 2010). In several cases, new species and specimens have been attributed to existing lestoid families. Within Lestidae, *Lestes brisaci, Sympecma ribesalbesensis*, and a new specimen of *Lestes regina* were described by Nel *et al.* (1997), Penalver *et al.* (1996), and Nel & Jarzembowski (1999) respectively, while unnamed specimens of *Lestes* were described by Riou & Nel (1995) and Penalver *et al.* (1996). Vasilenko (2005) described *Gaurimacia sophiae* and assigned it to Synlestidae. Bechly & Wichard (2008) documented the presence of larval and adult specimens of Synlestidae in Eocene Baltic amber.

Eolestes syntheticus was described by Cockerell (1940) as having characteristics similar to *Archilestes*, *Hypolestes*, and *Megalestes*, and was included within Synlestidae by Nel & Paicheler (1994). Fraser (1945), while correcting Cockerell's inadvertently incorrect vein designations, himself misidentified a longitudinal supplementary sector in the cubital field of *E. syntheticus* as CuA. His subsequent incorrect identification of "a branching of the anal vein" (CuA) led him to propose *E. syntheticus* as an intermediate in the evolution of the Calopterygoidea and led him to predict that a re-inspection of *E. syntheticus* would reveal supplementary antenodal crossveins. Fisher (1974) speculated that *E. syntheticus* was transitional between *Megalestes* and Sieblosiidae. All of these authors noted the two longitudinal supplementary sectors and the broad cubital field (the area between MP and CuA in our notation) that most distinguishes *E. syntheticus*. We herein re-describe this specimen, along with a new specimen of this species from the 46 Ma Kishenehn Formation of northwestern Montana, and assign it to the new family Eolestidae. In addition, we describe two additional specimens recently collected from Kishenehn Formation as *Eolestes ramosus* **n. sp.** and *Lutetialestes uniformis* **n. gen.**, **n. sp.**

Material and methods

The specimens of *Eolestes ramosus* (USNM 559047), *Eolestes syntheticus* (USNM 559049), and *Lutetialestes uniformis* (USNM 559048) were collected from the Spring and Disbrow Creek sites on the Middle Fork of the Flathead River in northwestern Montana by DEG in 2011. 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}Ar/^{39}Ar analysis and 43.5 +/- 4.9 Ma by fission-track analysis (Constenius, 1996). The holotype specimen of *Eolestes syntheticus* (University of Colorado Museum # 19170) was obtained on loan from the University of Colorado Museum, Boulder, CO. The Kishenehn specimens were immersed in 95% ethanol for examination and photographed using an Olympus SZX12 microscope, DP-25 camera and DPM imaging software. The holotype specimen of *Eolestes syntheticus* was photographed dry. Measurements were taken with cellSens Standard 1.6 software (Olympus Corporation). Specimens examined from the NMNH Entomology collections include *Lestes simulans* (343719), *L. paulistus* (390021), *L. bipupillatus* (387908), *Austrolestes aleison* (349627), *A. analis* (349632), *A. colensonis* (349646) *A. cingulatus* (349642), *Orolestes octomaculatus* (828096), *Sympecma paedisca* (349831), *Megalestes chengi* (360340), *M. distans* (360343), *M. heros* (360358), *M. kurahashii* (360359), *M. major* (360260), and *M. micans* (827015). *Megalestes irma* (BMNH(E) 1201796) was photographed and examined at the NHM, London. The wing venation nomenclature of Riek & Kukalová-Peck (1984) as modified by Nel *et al.* (1993) and Bechly (1995, 1996) was used throughout this study.

Abbreviations used in the figures: RA = radius anterior, RA & RP = common basal stem of radius anterior and radius posterior; RP' = common stem of radius posterior 1 and radius posterior 2; M & Cu = common stem of media and cubitus; CuP = vestige of cubitus posterior; AA' = first branch of anal vein separating from hind margin; AA" = second branch of anal vein fused to hind margin; dc = discoidal cell or quadrangle.

Results

Order Odonata Fabricius, 1793

Suborder Zygoptera Selys, 1854

Superfamily Lestoidea Calvert, 1901

Family Eolestidae n. fam.
(Figures 1, 2, 3, 4, 5, 6, 7)

Type genus. *Eolestes* Cockerell, 1940.

Diagnosis. 1) Pterostigma length ≥ 3 x width; 2) Oblique "O" crossvein present; 3) Postnodal crossveins mostly aligned; 4) MA slightly zigzagged distal of the nodus; 5) Ax2 at or just distal of the arculus; 6) Discoidal cell closed and its posterior internal angle acute; 7) IR2 and RP3/4 origin closer to the arculus than the nodus; 8) IR1-RP2, RP2-IR2 and RP3/4-MA fields with ≥ two supplementary longitudinal sectors; 9) MA-CuA (cubital) field with ≥ two supplementary longitudinal sectors; 10) IR2-RP3/4 field not expanded distally.

Genus *Eolestes* Cockerell, 1940
(Figures 1, 2, 3, 4, 5, 6, 7)

Type species. *Eolestes syntheticus* Cockerell, 1940.

Diagnosis. Same as for monotypic family.

Comment. This genus should not be confused with the invalid junior homonym *Eolestes* Bown & Schankler, 1982 for an Eocene insectivorous mammal, which was replaced by the valid name *Auroralestes* Holroyd, Bown & Schankler, 2004.

Eolestes syntheticus Cockerell, 1940
(Figures 1, 2, 3, 4, 5A, 5B, 6A, 6B)

Synonomy.
v. 1940 *Eolestes synthetica* Cockerell 1940; p. 105, figs. 1, 2.
v. 1974 *Eolestes syntheticus* Fisher 1974; p. 218.

Range. Eocene of Northwestern United States (Green River Formation near DeBeque, Colorado, and Kishenehn Formation, Pinnacle, Montana).

Holotype (UCM 19170) (Figures 1, 2, 3, 4, 5A, 6A)

Type locality and stratum. 39.5° N, 108.4, Roan Creek near de Begue, Garfield County, Colorado, USA. Green River Formation, Early Eocene, 53.5–48.5 mya (Smith *et al.* 2003).

Re-description. Part and counterpart of a fossil damselfly with all or most of four wings, five legs, the dorsal aspect of the thorax and a poorly preserved head (Fig. 1); pterothorax square, about as long as high (lateral aspect), approximately 4.8 mm long at the mid-dorsal stripe of the mesanepisternum and 3.0 mm wide (between the humeral stripes) (Fig. 2); pro-, meso- and metafemora 3.10, 4.15 and 5.47 mm in length; pro- and mesotibiae 3.36 and 4.17 mm in length; tarsi 3-segmented with pro- and mesotarsi 1.37 and 1.98 mm in length respectively; pro- and mesofemora and pro- and mesotibiae with spines, mesotibial spines gradually tapering distally with a maximum length of 0.6 mm; pro- and mesotibial apical spurs 0.32 and 0.35 mm respectively; protarsal claw 0.36 mm in length.

Forewing: Intact, hyaline, 30.62 mm long and 5.34 mm and 7.01 mm wide at nodus and widest point respectively; pterostigma four and a half cells and 2.52 mm long, 0.70 mm wide; pterostigmal brace oblique; distance between wing apex and pterostigma, pterostigma and nodus, nodus and arculus and arculus and base 3.03, 14.17, 5.74 and 5.23 mm respectively; the post-pterostigmal cell area does not appear to contain a supplementary sector; two antenodal and two antesubnodal crossveins with Ax1 basal of the separation of AA' & AA" and separated from Ax2 by 1.61 mm (Fig. 3); Ax2 distal of anterior arcular crossvein; supplementary antenodal crossveins absent; posterior arcular crossvein separating from discoidal cell 0.39 mm below RA; RP separates from RP+MA just below RA+RP so that RP+MA very short; nodal and subnodal crossveins oblique; dorsal subnodal bracket thickened (Fig. 4); 13 postnodal crossveins most of which are aligned with postsubnodal crossveins; "lestine" oblique vein "O" present 3.5 cells distal of base of RP2 between RP2 and IR2; base of IR1 four cells and 3.28 mm distal of RP2 origin; IR1 underlies a single row of cells that, proximal to pterostigma, are higher than they are wide and overlies a row of seven single cells that transition through three double cells and, distally, an area of reticulated cells. Apical fifth of left forewing torn/split, causing gross misalignment of veins/cells; base of RP2 three cells and 2.41 mm distal of subnodus and at least six cells and 6.56 mm distal of origin of IR2; IR2 and PR3/4 originate much closer to arculus than nodus. IR2 arched abruptly toward RP at base, one half cell and 0.86 mm from origin of RP3/4; IR2 underlies a row of single cells basally, after which a supplementary longitudinal sector originates proximal to level of pterostigma and branches to five supplementary sectors near wing margin; RP3/4 originates 1.33 mm from arculus and underlies a single row of single cells that extends to level of pterostigma, after which it is no longer visible; MA of right forewing slightly zigzagged only distal to subnodus; MP underlies a single row of cells that is obscured between subnodus and pterostigma; CuA a prominent vein that leaves subdiscoidal cell 0.33 mm below MP and transitions to a slightly zigzagged pattern at about level of origin of subnodus. It underlies a broad cubital field 1.81 mm in height that starts with a single cell below base of MP but transitions to contain three supplementary longitudinal veins with four rows of cells; anal field consists of a single row of cells that are either square or higher than wide; terminus of CuA at a point 2/3 of the way between nodus and pterostigma; cubito-anal field 2.64 mm in height; CuP distal of separation of AA' & AA" and halfway between Ax1 and Ax2; petiole well defined, 3.69 mm long (from base to separation of AA' and AA") and 12.05% of wing length; Petiole length relative to distance from petiole to nodus = 0.56; discoidal cell closed basally, 1.63 mm long (end of posterior arcular vein to origin of MP) and 0.81 mm wide (origin of arcular vein to origin of MAb) with an acute posterior internal angle of 25 degrees; distal side of discoidal cell (MAb) nearly perpendicular to RA (12 degrees from vertical relative to RA), and 1.01 mm in length; anterior, posterior and basal (posterior arculus) sides of discoidal cell 0.70 mm, 1.55 mm and 0.45 mm long; ratio of lengths of anterior and posterior sides of discoidal cell = 0.45; subdiscoidal cell elongate with no fusion of CuP & AA' to posterior wing margin distal of CuP; MP slightly arched as it leaves discoidal cell at an angle of 93 degrees between MP and MAb.

Hind wing: intact, hyaline, 28.84 mm long and 5.17 mm and 6.68 mm wide at nodus and widest point respectively (Fig. 5A); pterostigma three and a half cells and 2.62 mm long, 0.72 mm wide; pterostigmal brace oblique; distance between wing apex and pterostigma, pterostigma and nodus, nodus and arculus and arculus and base 2.48, 13.06, 5.36 and 5.43 mm respectively; post-pterostigmal cell area (five cells preserved only) does not appear to contain a supplementary longitudinal sector; two antenodal and two antesubnodal crossveins with Ax2 opposite arcular crossvein and separated from Ax1 by 1.65 mm; supplementary antenodal crossveins absent; subnodal crossvein oblique, nodal crossvein slightly less so; dorsal subnodal bracket slightly thickened; 11 postnodal crossveins exactly aligned with postsubnodal crossveins with exception of last two; "lestine" oblique vein "O" present four cells distal of base of RP2; base of IR1 four cells and 3.04 mm distal of RP2 origin; IR1 zigzagged to level of pterostigma and underlies a single row of cells that, proximal to the pterostigma, are higher than wide and overlies a row of seven single cells that expand distally through four double cells, four triple cells via two and then three supplementary longitudinal sectors—distal edge of wing not preserved. Base of RP2 two and a half cells and 2.23 mm distal of subnodus; IR2 and PR3/4 originate closer to arculus than nodus. IR2 underlies a row of single cells basally, followed by a gradual increase in the number of supplementary longitudinal sectors until there are three supplementary longitudinal sectors distal of pterostigma; RP3/4 underlies a row of single cells that transitions from cells longer than high to higher than long proximal to stigma; MA zigzagged from a point two cells proximal of subnodus—basal of that point, MA not preserved; MA underlies a row of cells that transitions to double cells at level of IR1 origin and then gradually to 16 small cells at wing margin; MP, not zigzagged, underlies a single row of cells that gradually transitions from square-shaped to cells higher than wide; CuA leaves subdiscoidal cell 0.29 mm below MP, becomes zigzagged as it approaches subnodus, and underlies a broad cubital field, 1.92 mm in height, that starts with a single cell below base of MP and quickly transitions through one and then two supplementary longitudinal sectors and then back to a single row of cells at wing margin (Fig. 6A); cubito-anal field (between CuA and hind margin) with a single row of cells higher than wide with the exception of the first and a terminus at a point three or four cells from terminus of MP; height of cubito-anal field 2.51 mm; CuP origin distal of separation of AA' & AA" approximately halfway between Ax1 and Ax2; petiole well defined, 3.65 mm long (from base to separation of AA' and AA") and 12.65 % of wing length; Petiole length relative to distance from petiole to nodus = 0.59; discoidal cell poorly preserved; distal side of discoidal cell (MAb) nearly perpendicular to RA and 1.2 mm in length; MP slightly arched as it leaves the discoidal cell.

Both part and counterpart also contain a small fossil tipulid dipteran.

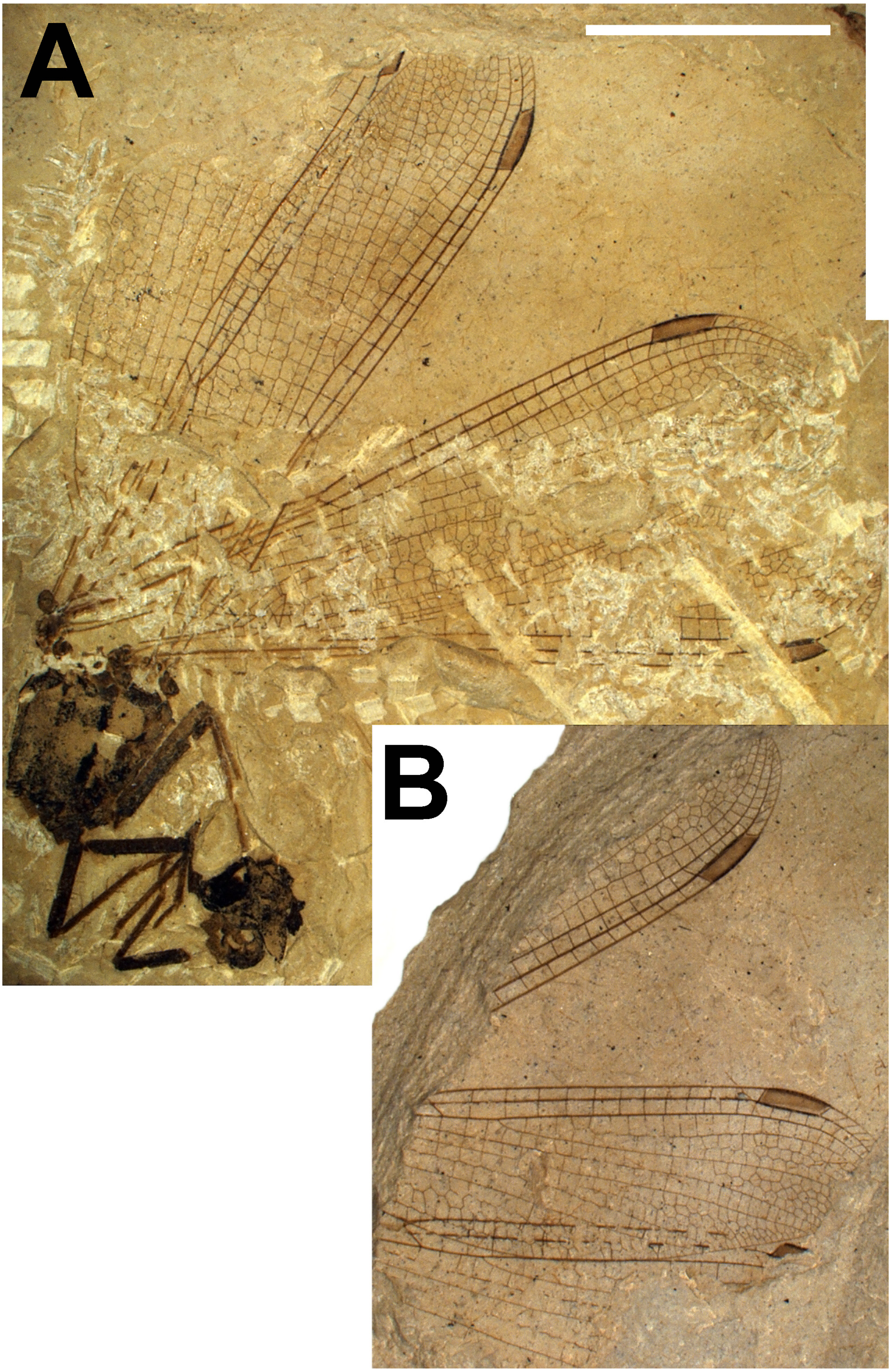

FIGURE 1. *Eolestes syntheticus* Cockerell 1940. (A) photograph of part; (B) counterpart (holotype UCM 19170). Scale bar = 10 mm.

FIGURE 2. Head and thorax of *Eolestes syntheticus* (holotype UCM 19170). Scale bar = 5 mm.

New specimen (USNM 559049) (Figures 5B, 6B)

Deposition. USNM 559049, National Museum of Natural History, Washington, D.C.

Locality and stratum. Spring site, Middle Fork of the Flathead River, Pinnacle, Montana, USA. Coal Creek Member of the Kishenehn Formation, early Middle Eocene, 46.2±0.4 or 43.5±4.9 mya (Constenius, 1996).

Description. Apical portion (≈ 70%) of a fossil damselfly wing, hyaline, 21.48 mm long and 5.13 mm and 6.35 mm wide at nodus and widest point respectively (Fig. 5B); pterostigma four cells and 2.60 mm long, 0.54 mm wide; pterostigmal brace oblique; distance between wing apex and pterostigma and pterostigma and nodus 3.22 and 13.4 mm respectively; post-pterostigmal cell area consists of three single cells proximally, four smaller cells distally and five double cells in between; nodal crossvein and subnodal crossvein oblique; anterior nodal bracket apparently thickened; 12 postnodal crossveins aligned with postsubnodal crossveins except for two most distal; "lestine" oblique vein "O" present three cells distal of base of RP2; base of IR1 four cells and 3.18 mm distal of RP2 origin, IR1 underlies a single row of cells that, proximal to the pterostigma, are higher than wide and overlies a row of nine single cells that distally expand through three double cells and, more distally, three rows of cells; base of RP2 three cells and 2.13 mm distal of subnodus; IR2 and PR3/4 appear to originate closer to arculus than nodus, although their origins are not preserved (IR2 extends basally to edge of fossil at which point it is slightly less than halfway (0.44) between RP1 and RP3/4); IR2 underlies a row of at least 18 single cells basally, followed by a gradual increase in number of secondary veins until there are eight small cells at wing margin; RP3/4relatively straight and underlies a row of single cells, although a short two-cell-long supplementary longitudinal sector appears at level of pterostigma; MA relatively straight proximal of RP2, only very slightly zigzagged thereafter, and underlies a row of cells that transitions to double cells just distal of IR1 origin and then gradually to 17 small cells at wing margin; MP relatively straight, underlies a single row of cells; CuA zigzagged throughout and terminates three cells short of end of MP. Broad cubital field 1.78 mm in height and contains two supplementary longitudinal sectors that transition to a single supplementary sector through six cells and then disappear ten cells prior to termination of MP (Fig. 6B); cubito-anal field 2.10 mm in height and with a single row of cells.

The same slab also contains a single fossil of the dipteran family Chironomidae.

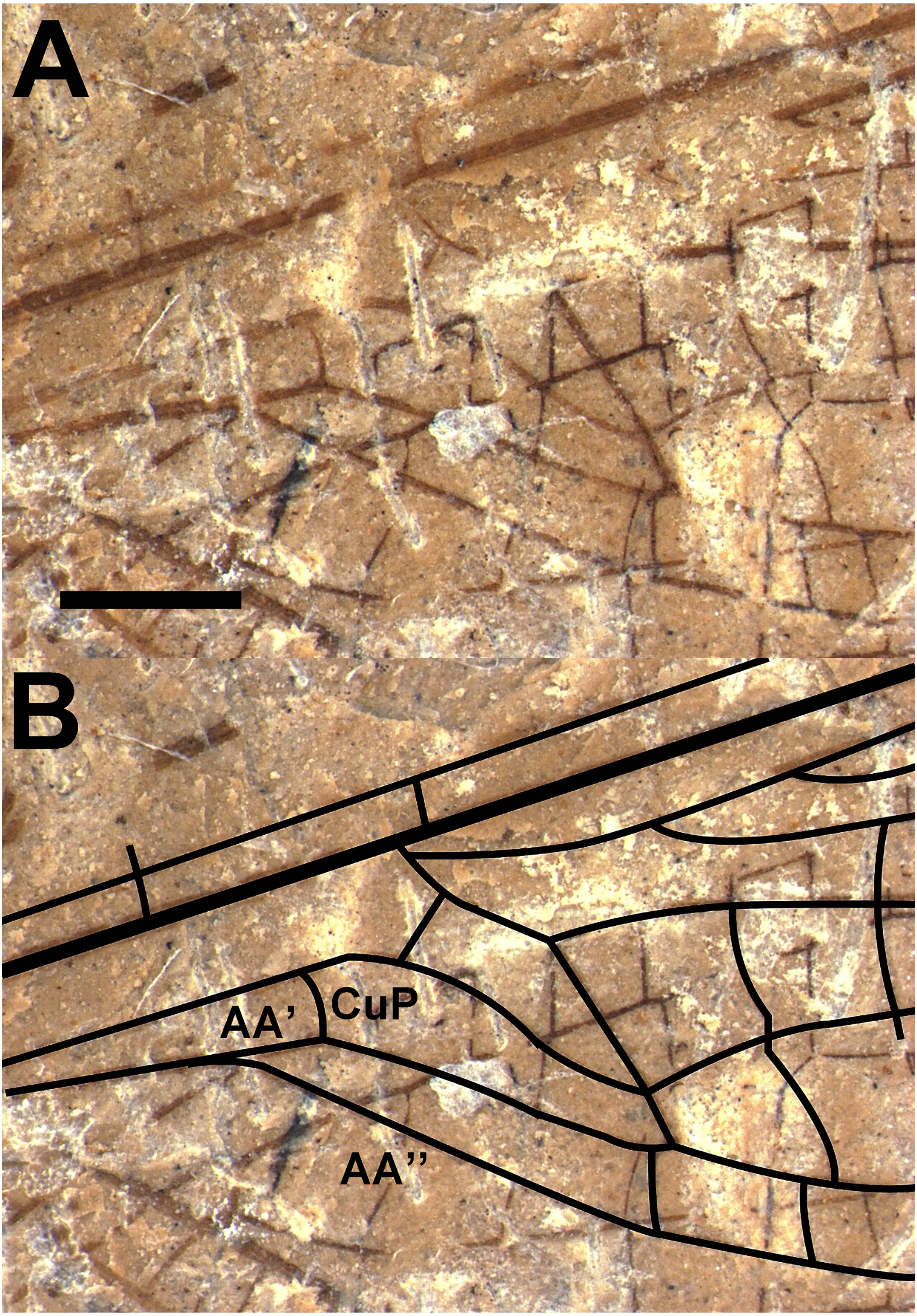

FIGURE 3. Basal portion of left forewing of *Eolestes syntheticus* (holotype UCM 19170). (A) photograph; (B) photograph overlaid with a line drawing of venation. Scale bar = 1 mm.

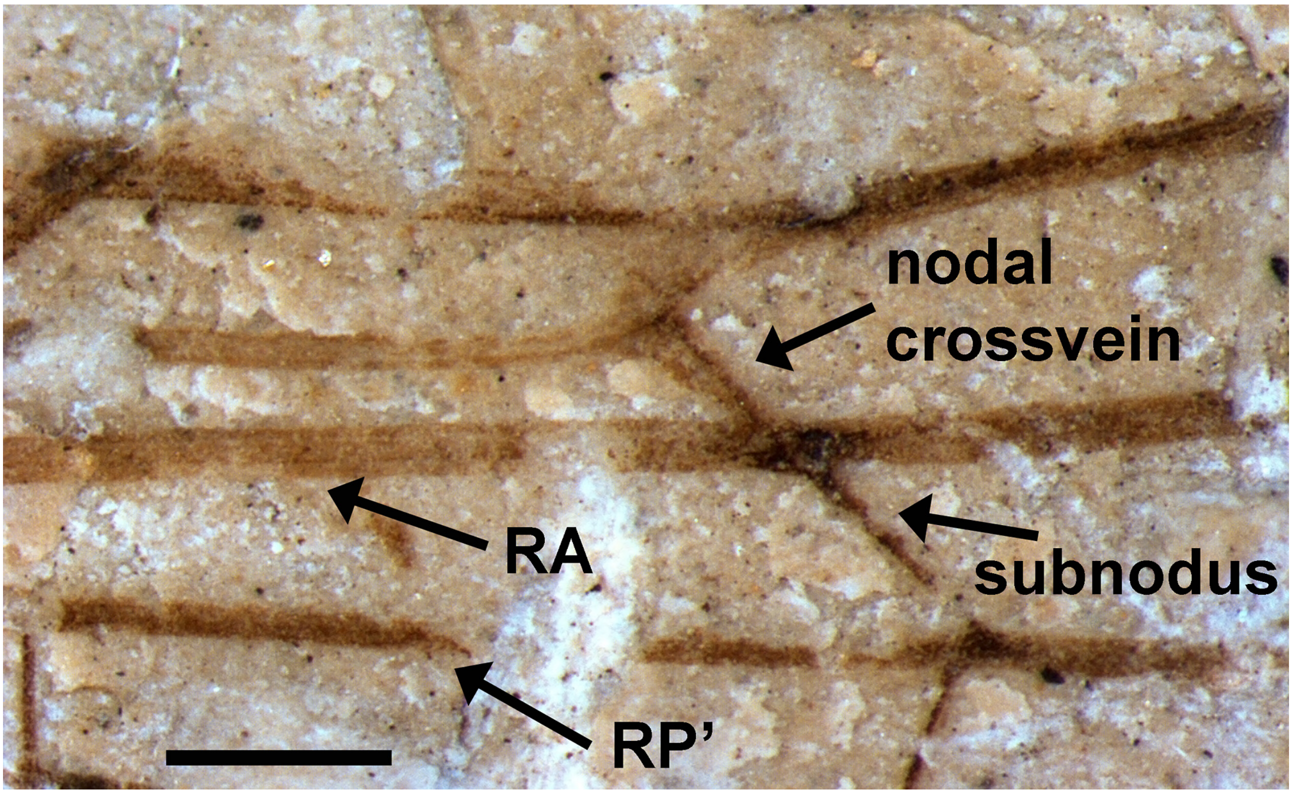

FIGURE 4. Photograph of nodus of right forewing of *Eolestes syntheticus* (holotype UCM 19170) showing the thickening of the dorsal subnodal bracket. Scale bar = 0.5 mm.

***Eolestes ramosus* n. sp.**
(Figures 5C, 6C, 7)

Holotype. USNM 559047, National Museum of Natural History, Washington, D.C.

Type locality and stratum. Disbrow Creek site, Middle Fork of the Flathead River, Pinnacle, Montana, USA. Coal Creek Member of the Kishenehn Formation, early Middle Eocene, 46.2±0.4 or 43.5±4.9 mya (Constenius, 1996).

Etymology. Species name *ramosus* from the Latin word ramosus (branching), an indication of the branching of the supplementary longitudinal sectors in the MP-CuA field.

Diagnosis. Differs from *E. syntheticus* by the following characters: 1) CuP origin at instead of distal of the separation of AA' and AA"; 2) three supplementary longitudinal sectors in the cubital field vs. two; 3) 2–4 rows of cells between distal parts of IR2 and RP3/4 vs. 1–2.

Description. An intact fossil damselfly wing, hyaline, 27.1 mm long and 6.06 mm and 7.13 mm wide at nodus and widest point respectively (Fig. 5C); pterostigma four cells and 3.05 mm long, 0.61 mm wide; pterostigmal brace oblique; distance between wing apex and pterostigma , pterostigma and nodus, nodus and arculus and arculus and base 2.43, 12.13, 5.8 and 3.66 mm respectively; petiole length relative to distance from petiole to nodus = 0.44; post-pterostigmal cell area consists of two single cells proximally, three smaller cells distally and five double cells in between; two antenodal and two antesubnodal crossveins. Ax1 opposite separation of AA' & AA" and separated from Ax2 by 1.30 mm; Ax2 opposite arcular crossvein just distal to RP origin and anterior arcular crossvein; RP separates from RP+MA just below RA+RP so that RP+MA very short; supplementary antenodal crossveins absent; posterior arcular crossvein separating from discoidal cell 0.33 mm below RA; nodus and subnodal bracket not preserved, subnodal crossvein apparently oblique; 14 postnodal crossveins exactly aligned with postsubnodal crossveins with exception of last four; "lestine" oblique vein "O" present four cells distal of base of RP2; base of IR1 four cells and 2.7 mm distal of RP2 origin, IR1 zigzagged through first three cells, underlies a single row of cells that, proximal to pterostigma, are higher than they are wide and overlies a row of seven single cells that

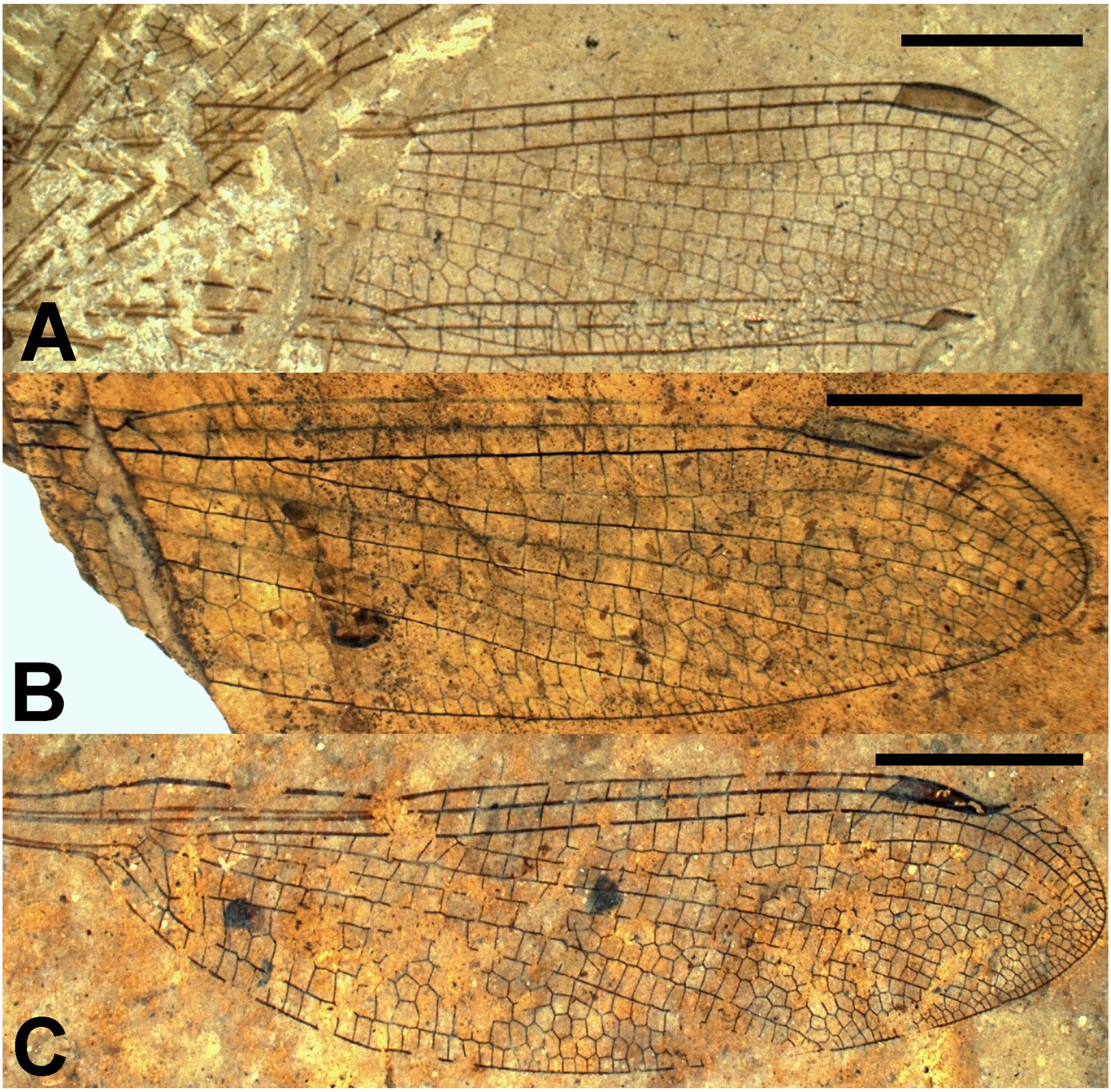

FIGURE 5. Wings of *Eolestes* spp.: (A) left hindwing of *E. syntheticus* (holotype UCM 19170); (B) *E. syntheticus* (USNM 559049); (C) *E. ramosus* (holotype USNM 559047). Scale bars = 5 mm.

distally expand through six double cells and subsequently, an area of reticulated cells with two and three secondary longitudinal veins; base of RP2 two cells and 1.46 mm distal of subnodus and six cells and 5.41 mm distal of origin of IR2; IR2 and PR3/4 originate much closer to arculus than nodus. IR2 arched abruptly toward RP at base with crossvein opposite, one cell and 0.86 mm from origin of RP3/4; IR2 underlies a row of 18 single cells basally, followed by a gradual increase in number of secondary veins until there are 11 small cells at wing margin; RP3/4 originates one cell and 1.30 mm from arculus and underlies a row of single cells that transitions from cells longer than high to higher than long before double cells appear just proximal to beginning of pterostigma; MA slightly zigzagged after a point about midway between arculus and nodus, and underlies a row of cells that transitions to double cells at level of IR1 origin and then gradually to 17 small cells at wing margin; MP underlies a single row of cells that gradually transitions from square-shaped to cells higher than wide; CuA a prominent vein that leaves subdiscoidal cell 0.29 mm below MP and transitions to a zigzagged pattern at about level of origin of RP2; it underlies a broad cubital field 2.20 mm in height that starts with a single cell below base of MP and quickly transitions through one, two and then three secondary longitudinal veins and then back to two secondary veins at wing margin (Fig. 6C); cubito-anal field consists of a single row of cells (12 distal of subnodus) that, except for the first, are higher than wide, and terminates at a point halfway between nodus and pterostigma; cubito-anal field 2.85 mm in height; CuP origin at separation of AA' & AA" (Fig. 6), directly below Ax1; petiole well defined, 2.51 mm long (from base to separation of AA' and AA") and 9.3% of wing length; discoidal cell closed basally, 1.50 mm long (end of posterior arcular vein to origin of MP) and 0.73 mm wide (origin of arcular vein to origin of MAb) with an acute posterior internal angle of 27 degrees (Note: given the curved nature of the posterior portions of MAb and MP & CuA, the angle is that between lines that align with the majority of these two veins.); distal side of discoidal cell (MAb) nearly perpendicular to RA (7 degrees from vertical relative to RA), and 1.11 mm in length; anterior, posterior and basal (posterior arculus) sides 0.52 mm, 1.45 mm and 0.39 mm long; Ratio of lengths of anterior and posterior sides of discoidal cell = 0.36; subdiscoidal cell elongate with no fusion of CuP & AA' to posterior wing margin distal of CuP; MP only partially preserved but with apparently no or very little arch as it leaves discoidal cell at angles of 93 and 76 degrees from MAb and vertical respectively.

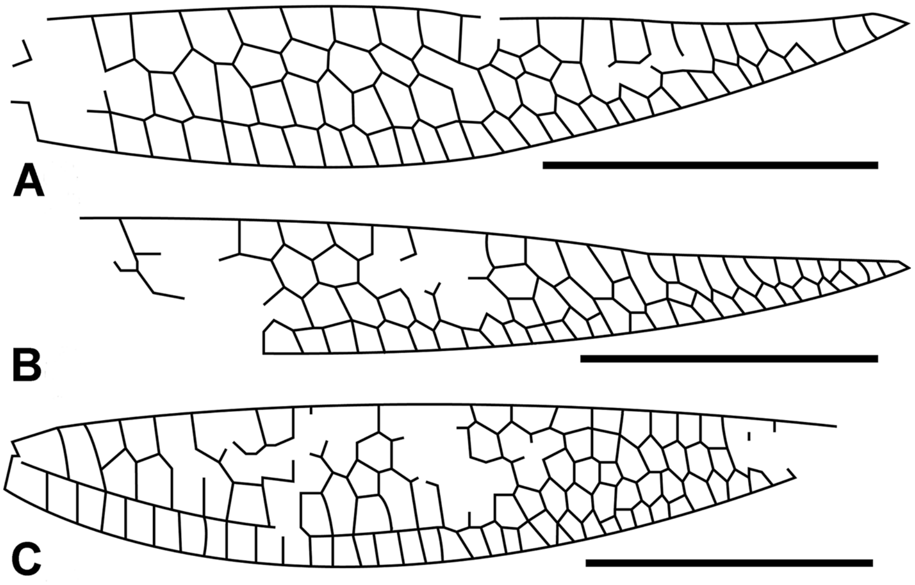

FIGURE 6. Line drawings of the cubital and cubito-anal fields of: (A) left hindwing of *E. syntheticus* (holotype UCM 19170); (B) *E. syntheticus* (USNM 559049); (C) *E. ramosus* (holotype USNM 559047). Scale bars = 5 mm.

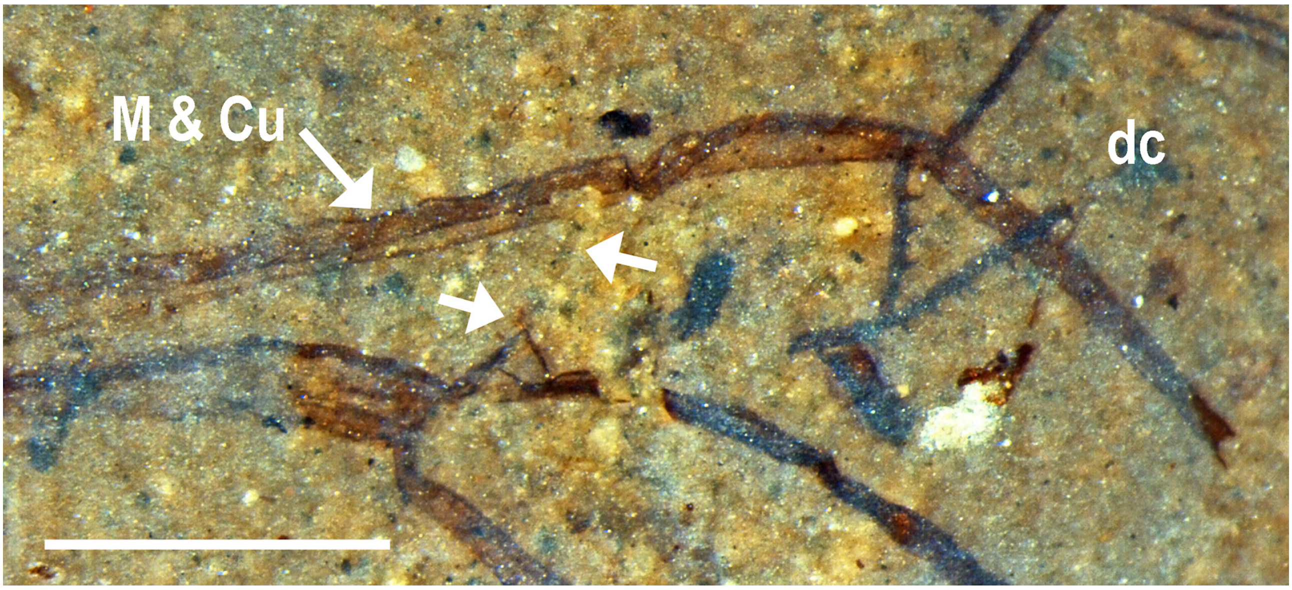

FIGURE 7. CuP vein of *Eolestes ramosus* (holotype USNM 559047). The faint course of CuP is indicated by (between) the two arrows. Scale bar = 0.5 mm.

Family undetermined

Lutetialestes n. gen.

(Figures 8, 9A, 10)

Type species. *Lutetialestes uniformis* **n. sp.**

Etymology. Genus name from the name of the geological stage (Lutetian) of the fossiliferous exposures of the Coal Creek Member of the Kishenehn Formation.

Diagnosis. As for type species, since monotypic.

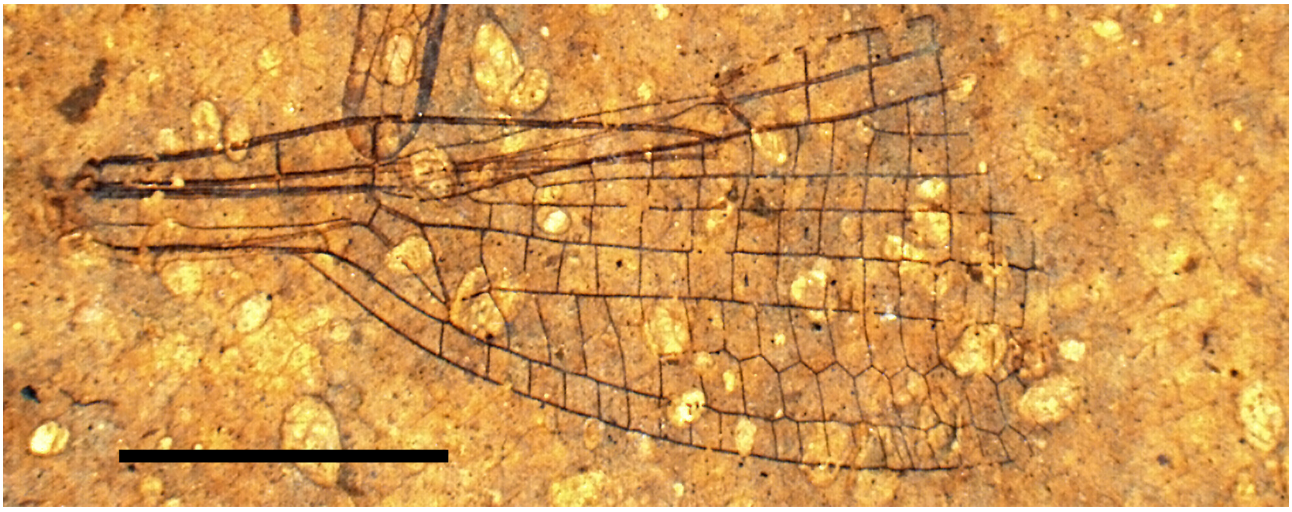

FIGURE 8. Photograph of the partial wing of *Lutetialestes uniformis* (holotype USNM 559048). Scale bar = 5 mm.

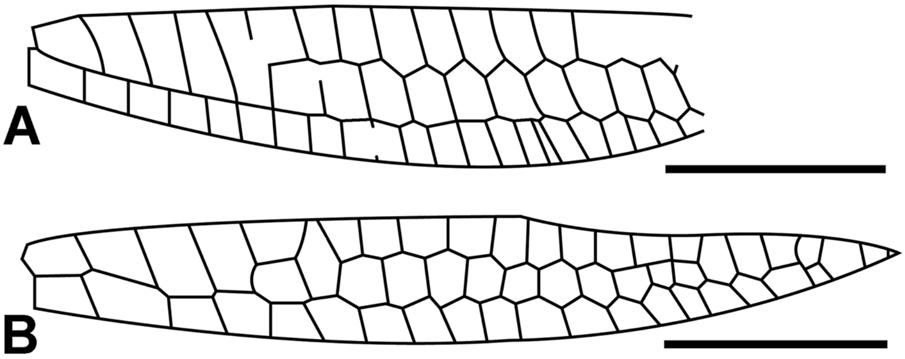

FIGURE 9. Line drawings of the cubital and cubito-anal fields of: (A) *Lutetialestes uniformis* (holotype USNM 559048); (B) *Lestes ceresti* (MNHN-LP-R.07448), redrawn from Nel & Paicheler (1994). Scale bars = 3 mm.

Lutetialestes uniformis n. sp.

(Figures 8, 9A, 10)

Holotype. USNM 559048, National Museum of Natural History, Washington, D.C.

Type locality and stratum. Disbrow Creek site, Middle Fork of the Flathead River, Pinnacle, Montana, USA. Coal Creek Member of the Kishenehn Formation, early Middle Eocene, 46.2±0.4 or 43.5±4.9 mya (Constenius, 1996).

Etymology. Species name *uniformis* from the Latin word uniformis (uniform, consistent), an indication of the very uniform shape of the cells in the cubital field.

Diagnosis. 1) MA slightly zigzagged only distal of RP2 origin; 2) Ax2 opposite anterior arcular crossvein; 3) Discoidal cell closed; 4) RP separates from RA+RP distal of anterior arcular crossvein so that there is no RP+MA vein; 5) IR2 and RP3/4 origin closer to arculus than nodus; 6) A relatively short petiole; 7) Postnodal crossveins aligned; 8) A broad cubital field consisting of five basal cells longer than wide followed by a single supplementary longitudinal sector that defines two rows of cells with the shape of isosceles right pentagons.

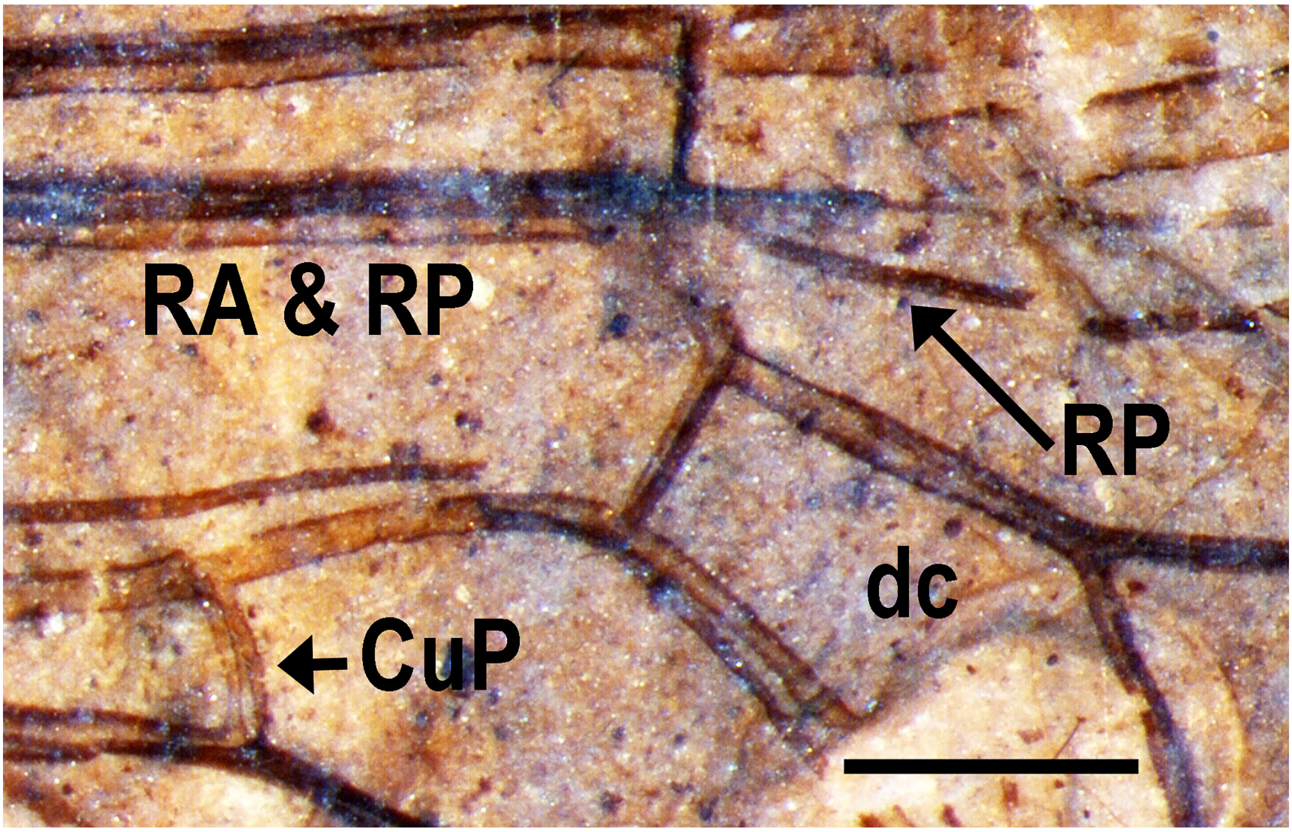

FIGURE 10. Photograph of the anterior arculus of *Lutetialestes uniformis* (holotype USNM 559048). Note RP separating from RA & RP distal of the arculus. The apparent double nature of vein CuP and the posterior side of dc is an artefact of preservation that resulted from a splitting of the two wing membranes of the single preserved wing. Scale bar = 0.5 mm.

Description. Basal half of a fossil damselfly wing (anterior veins CA & CP & ScA and ScP have broken apart from nodus, moved posteriorly approximately 1 mm and, in so doing, have caused a buckling of RP1 just distal of arculus.) (Fig. 8); wing hyaline, 14.7 mm long (from base to a point four cells distal of RP2 origin) and 5.59 mm and 6.80 mm wide at nodus and widest point respectively; distance between nodus and arculus and arculus and base 5.41 and 4.62 mm respectively; Petiole length relative to distance from petiole to nodus = 0.50; two antenodal and two antesubnodal crossveins. Ax1 0.2 mm basal of separation of AA' & AA" and separated from Ax2 by 1.45 mm; Ax2 opposite arcular crossvein and basal of RP origin; supplementary antenodal crossveins absent; posterior arcular crossvein separating from discoidal cell 0.19 mm below RA; nodal and subnodal crossveins oblique; subnodal bracket apparently not thickened; all three (first three) postnodal crossveins present exactly aligned with postsubnodal crossveins; base of RP2 three cells and 1.64 mm distal of subnodus and seven cells and 5.04 mm distal of origin of IR2; IR2 and PR3/4 originate much closer to arculus than nodus. IR2 arched abruptly toward RP at base with crossvein opposite, one cell and 0.93 mm from origin of RP3/4; RP3/4 originates one cell and 1.45 mm from arculus; MA straight proximal of origin of RP2 and slightly zigzagged distal to RP2 origin; MP with no or very little arch as it leaves discoidal cell at angles of 92 and 74 degrees from MAb and vertical respectively; CuA a prominent vein that leaves subdiscoidal cell 0.29 mm below MP and transitions to a zigzagged pattern between levels of subnodus and origin of RP2; CuA underlies a broad cubital field 1.73 mm in height that starts with a single cell below base of MP and continues through four cells 1.8 to 2.8 times as high as wide, at which point a supplementary longitudinal vein forms and delineates two rows of cells, ten cells in length (Fig. 9A). Supplementary longitudinal sector highly and very uniformly zigzagged and a defining characteristic of this specimen. Except for the very first cell, cubito-anal field cells are square in shape transitioning to higher than wide at level of subnodus; cubito-anal field 2.41 mm in height; CuP origin 0.49 mm distal of separation of AA' & AA" , approximately halfway between Ax1 and Ax2; petiole well defined, 3.44 mm long (from base to separation of AA' and AA''); discoidal cell closed basally, 1.80 mm long (end of posterior arcular vein to origin of MP) and 0.79 mm wide (origin of arcular vein to origin of MAb) with an acute posterior internal angle of 26 degrees; distal side of discoidal cell (MAb) 18 degrees from vertical relative to RA and 1.24 mm in length; anterior, posterior and basal (posterior arculus) sides 0.70 mm, 1.67 mm and 0.35 mm long; ratio of lengths of anterior and posterior sides of discoidal cell = 0.42; RP separates from RA+RP distal of anterior arcular crossvein so that vein RP+MA does not exist (Fig. 10); subdiscoidal cell elongate with no fusion of CuP & AA' to posterior wing margin distal of CuP. The same slab also contains fossil ostracods and the wing of a hemipteran.

Discussion

The damselfly superfamily Lestoidea contains 21 extant genera within four families: the monotypic Hemiphlebiidae, which is a sister-group to all other Lestoidea (Rehn 2003; Dumont et al 2010; Davies *et al.*, 2011; Dijkstra *et al.*, 2014), Perilestidae with 2 genera and 18 species, Synlestidae with 9 genera and 36 species, including the monotypic genera *Nubiolestes* and *Chorismagrion* and the 16 species of Megalestinae, and the more speciose Lestidae with 9 genera and 152 species (Schorr & Paulson, 2014). There is significant support for the monophyly of both Perilestidae (Bechly 1996, 2003; Rehn 2003; Dijkstra *et al.*, 2014) and Lestidae (Rehn 2003; Bybee *et al.* 2008; Dumont *et al.* 2010; Dijkstra *et al.*, 2014). However, there is accumulating evidence that Synlestidae is paraphyletic (ibid.). Tillyard & Fraser (1938) included the subfamilies Chorismagrioninae, Synlestinae, Perlestinae, and Megalestinae in the family Synlestidae, partly based on several shared characteristics of the primitive labial masks of their respective larvae. These several characteristics, while not unique to this clade, clearly separate Synlestidae from Lestidae (Rehn 2003). In recent molecular phylogenetic studies, Dijkstra *et al.* (2014) identified the genus *Megalestes* as a sister group to the clade (Synlestidae + Perilestidae) and Dumont *et al.* (2010) supported Megalestidae as a distinct family. However, Bechly (1996) suggested that, based on wing venation, Megalestidae is the sister group of Lestidae. In morphology-based phylogenetic studies, Rehn (2003) also placed *Megalestes* as a sister group to the Lestidae. Both *Nubiolestes* (Nubiolestinae Bechly 1996) and the monotypic family Chorismagrionidae may belong in a redefined Synlestidae (Bybee *et al.* 2008; Dumont *et al.* 2010; Dijkstra *et al.* 2014).

Herein we describe another family-level clade within the superfamily Lestoidea, Eolestidae. The rationale for this family-level assignment, as well as the placement of *Lutetialestes*, is as follows. The family Eolestidae and *Lutetialestes uniformis* are included in Zygoptera Selys, 1854, as wings are distinctly stalked with a petiole significantly longer than wide and in Euzygoptera *sensu* Bechly (1996) as a result of the several following autapomorphies: 1) branches of RP distally convergent, 2) only a single row of cells between vein CuA and the hind wing margin and 3) only two primary antenodal crossveins retained. They can be excluded from the Calopterygoidea (Caloptera *sensu* Bechly, 1996) because of the retained presence of a pterostigmal brace. Although there are no vein-based autapomorphies for Lestoidea (Lestomorpha *sensu* Bechly, 1996), Eolestidae can be excluded from Coenagrionoidea and Megapodagrionidae (paraphyletic Coenagrionomorpha Bechly, 1996) because of the presence of an oblique vein "O", a relatively long pterostigma and the absence of an arcular bracket. *L. uniformis* can be excluded from Coenagrionoidea and Megapodagrionidae due to the last of these three autapomorphies. Within Lestoidea (Lestomorpha *sensu* Bechly, 1996), Eolestidae and *Lutetialestes uniformis* are assigned to Lestiformia *sensu* Bechly (1996) due to the postnodal and postsubnodal crossveins aligned and excluded from Hemiphlebiidae Tillyard, 1926, based on the absence of all important autapomorphies of that family: 1) only 5–8 postnodal crossveins, 2) oblique vein "O" absent and 3) all intercalary veins except IR1 and IR2 suppressed, although in *L. uniformis*, the latter character is unknown.

Eolestidae differs from the extinct family Cretacoenagrionidae and *L. uniformis* is excluded from Cretacoenagrionidae based on the latter having an open discoidal cell and only 9 postnodal crossveins (Jarzembowski, 1990); both are included within Eulestiformia *sensu* Bechly (1996) due to vein MP distinctly curved after its origin at the distal angle of the discoidal cell. This latter character varies significantly in the degree of the curve of the MP vein. Tillyard and Fraser (1938) described this character as "the marked upward arching of (MP)" in Synlestidae while stating that the genus *Archilestes* "still (retained) some indication of the arching of (MP)" and counted as a principal venational character of the family Lestidae "the absence of the . . . arching upwards of (MP)". Within extant Lestidae, the first sector of MP can be arched as in, for example, *Lestes spumarius*, straight as in, for example, *L. simulans, Sympecma paedisca, Orolestes octomaculatus, Austrolestes aleison, A. analis and A. cingulatus* or, as in *L. bipupillatus*, straight in the hind wing and with an imperceptible but distinct arch in the forewing. In some species, such as *Lestes paulistus* and *Austrolestes colensonis*, what arch does exist occupies only the initial 10–20% of the sector. The MP of *Eolestes syntheticus* has a distinct but slight arch, while *E. ramosus* and *Lutetialestes uniformis* appear to have no arch; however, the proximal portion of the first sector of MP in these latter two specimens is incompletely preserved, and a definitive determination of the extent of their MP arch is not possible. Within Eulestiformia, Eolestidae differs from the family Chorismagrionidae Tillyard & Fraser, 1938, and *Lutetialestes uniformis* is excluded from Chorismagrionidae based on the latter's autapomorphy of origin of IR2 shifted several cells distal of the midfork. Both are included in Lestida *sensu* Bechly (1996), which has as an autapomorphy the basal closure of the discoidal cell.

Within Lestida, Eolestidae differs from, and *Lutetialestes uniformis* is excluded from, the family Perilestidae based on several autapomorphies: 1) apex of discoidal cell close to the hind margin of the wing, 2) IR2 distinctly shortened and arising close to the origin of RP2, 3) the posterior margin of the subdiscoidal cell (vein CuP & AA') mostly fused to the hind margin, and 4) all intercalary veins except IR1 and IR2 suppressed; this last character cannot be determined for *L. uniformis*. Both Eolestidae and *Lutetialestes uniformis* are included in Lestodea *sensu* Bechly (1996) because of the autapomorphy arculus shifted basally beneath the Ax2 crossvein. Within Lestodea, Eolestidae differs from the family Synlestidae Tillyard, 1917, *sensu* Bechly (1996), and *Lutetialestes uniformis* is excluded from this same family, because RP3 and IR2 start closer to the nodus in members of this family and because of the autapomorphy posterior margin of the subdiscoidal cell (vein CuP & AA') mostly fused to the hind margin, although this character state is not present in *Phylolestes ethelae* (Garrison *et al.*, 2010). If the genus *Megalestes* is included in the family Synlestidae, Eolestidae would still differ from Synlestidae and *L. uniformis* would still be excluded from Synlestidae based on the lack of supplementary longitudinal cells in the cubital field, the ratio of the length of the petiole to the distance from the distal end of the petiole to the nodus ≥ 1 (< 0.5 in *L. uniformis*) and the ratio of the distance from Ax1 to the separation of AA' and AA" to the distance from the separation of AA' and AA" to Ax2 ≥ 1 in *Megalestes*. The family Eolestidae differs from Lestidae Calvert 1917 as a result of two autapomorphies, MA more strongly zigzagged and area between IR2 and RP3/4 distally strongly widened with three rows of cells between these veins. The new family Eolestidae therefore differs significantly from all known extant families of Zygoptera.

Lutetialestes uniformis is included in Lestinoidea Calvert 1901 *sensu* Bechly (1996) because of two autapomorphies: 1) subnodus located between the bases of RP2 and IR2 that are widely separated and 2) vein MA at least distally zigzagged. Within Lestinoidea *sensu* Bechly (1996), *Megalestes* has MA strongly zigzagged in the distal half and the species within Lestidae have MA zigzagged along its entire trajectory (Wappler & Petrulevicius, 2007). The character state "zigzagged' therefore includes both the degree of zigzag (amplitude) and the extent of the zigzagged vein (proximal to distal). While the MA of *L. uniformis* appears to be zigzagged, it is neither strongly zigzagged nor zigzagged to any extent proximal of RP2. *L. uniformis* is excluded from the Megalestidae as a result of the lack of supplementary longitudinal cells in the cubital field, the ratio of the length of the petiole to the distance from the distal end of the petiole to the nodus ≥ 1 (< 0.5 in *L. uniformis*) and Ax1 significantly basal of the separation of AA' and AA". Although *L. uniformis* shares with Lestidae the autapomorphy distal discoidal vein MAb very oblique, so that the distal angle of the discoidal cell is very acute, it does not share other autapomorphies identified by Bechly (1996) for this family. These include nodal crossvein less oblique, anterior part of the subnodal bracket strongly thickened and MA more strongly zigzagged. In addition, *L. uniformis* differs from the species of Lestidae in that its pterothorax is square, as long as high or shorter than high (Garrison et al, 2010). According to the criteria of Fraser (1951), the character state separation of CuP & AA' from the posterior wing margin at the level of CuP eliminates all lestid genera except *Chalcolestes*; it would be excluded from Lestinae, which contains over 68% of lestid species, due to the autapomorphy arculus mainly formed by the basal discoidal crossvein, so that the discoidal cell is nearly touching the RA (Bechly, 1996); in *L. uniformis*, the basal component comprises 55% of the combined posterior and anterior arcular vein lengths. In addition, *Indolestes*, which comprises more than 70% of the species in the subfamily Sympecmatinae, would be eliminated based on CuP midway between Ax1 and Ax2, often nearer to Ax2 (Watson, 1991).

The above analysis of potential autapomorphies, as well as study of the key of Garrison *et al.* (2010), firmly establish that neither *Eolestes* nor *Lutetialestes* belongs to any of the extant families of Zygoptera. These two genera are easily distinguished by 1) *Eolestes* with two or more secondary longitudinal veins in the cubital field vs. a single secondary longitudinal vein in *Lutetialestes* and 2) the structure of the anterior arculus. In *Eolestes* spp., RP leaves RP+MA at or just below RA+RP while, in *Lutetialestes uniformis*, there is no RP+MA vein; instead, RP leaves RA+RP distal of the termination of MA at RA+RP. This morphological feature is unique within Euzygoptera *sensu* Bechly (1996) and it is a distinctive autapomorphy of the genus *Lutetialestes*; it is also present in the genus *Amphipteryx* (Calopterygoidea: Amphipterygidae). Both the two species of *Eolestes* and *Lutetia uniformis* appear to be most closely related to Lestida *sensu* Bechly (1996). Cockerell (1940), Fraser (1945), and Nel & Paicheler (1994) all noted the close relationship of *Eolestes syntheticus* to the extant genus *Megalestes*. However, previous analyses of *Eolestes syntheticus* were hampered by a dependence on Cockerell's relatively short original description and his use of figures of the distal wing fragments of the counterpart (Cockerell, 1940, figs 1, 2) which he identified as the anterior wings. In actuality, his figure 1 is of the left hind wing. Unfortunately, dégagement of the main fossil was very poorly done and destroyed much of the venation (Fig. 1A). The data and analyses reported herein reveal that *Eolestes* does not belong to Megalestidae because of the latter's long petiole (petiole length/distance from petiole to the nodus ≥ 1) and its ratio of the distance from Ax1 to the separation of AA' and AA" to the distance from the separation of AA' and AA" to Ax2 ≥ 1. Wappler & Petrulevicius (2007) stated that "The only two characters that seem to be synapomorphic for Lestidae are the strongly zigzagged MA and the area between IR2 and RP3/4 distally strongly widened with three rows of cells between these two veins". Neither the two specimens of *Eolestes syntheticus* nor *Eolestes ramosus* exhibit either of these character states.

Since Nel & Paicheler's 1994 review, seven new specimens of Eulestiformia *sensu* Bechly (1996), three of which are type specimens for new families, have been described. Three of these species are from the early Cretaceous: *Libanolestes fleck*i consists of the distal half of a wing and was assigned to Lestomorpha *sensu* Bechly (1996) based on a single autapomorphy, pterostigma with microcasters (Azar *et al.*, 2010). This specimen is much smaller (2.7 mm wing width at the distal edge of the pterostigma) than *Eolestes* spp. or *Lutetialestes*. It has no secondary longitudinal veins other than IR1, which is only 3 cells in length, and IR2. There is no physical overlap between this wing fragment and the *Lutetialestes* fossil and a comparison of the two is impossible. *Gaurimacia sophia* was assigned to the family Synlestidae based solely on the size and shape of the pterostigma and is thought to be "most closely related to *Megalestes*" (Vasilenko, 2005). However, IR2 and RP3/4 originate closer to the nodus, MA is not at all zigzagged, the nodal and subnodal crossveins are only barely oblique and the posterior angle of the discoidal cell is not acute as in *Megalestes*. These same character states and others (e.g. absence of supplementary longitudinal sectors in the cubital field) also distinguish this genus from both *Eolestes* and *Lutetialestes*. *Cretalestes martinae*, another Cretaceous specimen, was assigned to Lestoidea by Jarzembowski *et al.* (1998). Like *Libanolestes*, it has no secondary longitudinal veins other than IR1 and IR2. Although both IR2 and RP3/4 originate closer to the arculus, RP2 originates at the subnodus. Ma is very strongly zigzagged after the level of the subnodus, the postnodal crossveins are not aligned and the ratio of the lengths of the anterior to the proximal sides of the discoidal cell is 0.5 (vs. >1 in *Eolestes* and 2.0 in *Lutetialastes*). In addition, the anal cells of *C. martinae*—between the subdiscoidal cell and the level of the subnodus—are much larger than those in the cubital field, again the opposite of that found in *Eolestes* and *Lutetialastes.* All of these characters, in addition to the absence of cubital field supplementary longitudinal sectors, clearly differentiate this specimen from *Eolestes* and *Lutetialastes.*

A single specimen, *Promegalestes singularis*, has been described from the critical Paleocene epoch and assigned to Lestoidea (Petrulevicius & Nel, 2004). This specimen, a wing fragment, which consists of the middle half of a wing, is described as having a "close similarity to *Megalestes*". However, MA is not at all zigzagged, IR2 is closer to the nodus, and RP3/4 is about halfway between the nodus and the arculus as opposed to *Megalestes* as well as *Eolestes* and *Lutetialastes*. This specimen also differs from both *Megalestes* and *Lutetialastes* in the acuteness of the posterior angle of the discoidal cell; while the MAb vein in *L. uniformis* is less oblique than that of *Promegalestes*, the posterior angle of the discoidal cell in *L. uniformis* is actually more acute (31 degrees vs. 41 degrees) than that in *Promegalestes singularis*.

Three specimens have been described from the Eocene: *Frenguella patagonia* was assigned to the new family Frenguelliidae and is believed to be related to Sieblosiidae (Petrulevicius & Nel, 2003). This specimen differs dramatically from both *Eolestes* and *Lutetialastes* in that its discoidal field is open basally, it has several supplementary longitudinal sectors in the cubito-anal field, IR2 closer to the nodus, subnodal crossvein vertical and MAb directly aligned with the anterior portion of the arculus. Austroperilestidae is another new extinct family that is described as "related to Perilestidae" (Petrulevicius & Nel, 2005). The IR2 vein of this specimen, *Austroperilestes hunco*, originates at the subnodus, RP3/4 originates half-way between the subnodus and the arculus, most postnodal crossveins are not aligned and there is a prominent secondary longitudinal sector in the cubito-anal field. In addition, the posterior arcular crossvein reaches RP+MA well basal to its division, a unique potential synapomorpy with Perilestinae (Petrulevicius & Nel, 2005). All of these characters differentiate *Eolestes* and *Lutetialastes* from *Austroperilestes hunco*. Another specimen, *Priscalestes germanica*, was also assigned to a new family, Priscalestidae (Wappler & Petrulevicius, 2007). This specimen is described as close to *Promegalestes*. It differs from both *Eolestes* and *Lutetialastes* in bases of IR2 and RP3/4 closer to the nodus than the arculus, suppression of all secondary longitudinal veins other than IR1 and IR2, pterostigma overlying 11/2 cells and CuP proximal of the separation of AA' and AA".

Bechly & Wichard (2008) documented a larva and two adult specimens of a still unnamed species of Synlestidae from Eocene Baltic amber.

Several specimens that were either mentioned in Nel & Paicheler's 1994 review or not then known to be lestoids also differ from *Eolestes* and *Lutetialestes*. Cockerell & Andrews (1916) described *Megalestes angilicus* based on a wing fragment that extended from the origin of RP3/4 to just distal of the base of RP2. *Megalestes angilicus* has MA distally slightly zigzagged, the RP2 origin 5 cells distal of the subnodus, nodal and subnodal crossveins oblique and the bases of IR2 and RP3/4 proximal of the subnodus, but whether they are closer to the arculus or the nodus is not determinable. Its cubital field does not have secondary longitudinal sectors. Cockerell (1916) described an apical wing fragment that he assumed was from the same species. Kennedy (1925) however renamed this latter specimen *Oligoargiolestes oligocenum* and assigned it to the family Megapodagrionidae. Nel & Paicheler's analysis of *Megalestes angilicus* suggested that the more basal wing fragment could be assigned only to Lestoidea; Nel and Jarzembowski (1999) suggested that it could even belong to Eucaloptera (Calopterygoidea).

The family Cretacoenagrionidae, based on the fossil species *Cretacoenagrion alleni* (Jarzembowski 1990), has no definitive synapomorphies with either Coenagrionoidea or Lestoidea and is thought to be a basal lestoid (Jarzembowski *et al.* 1998). Its IR2 originates at the subnodus and RP3/4 is closer to the subnodus; the discoidal cell is open basally.

In the original description of *Lestes ceresti*, Nel (1985) described a secondary longitudinal sector in the cubital field of the specimen and noted that other fossil lestids, *L. regina* and *L. forsteri*, exhibited what was then thought to be this fossil-specific character (Fig. 9B). In the review of fossil Lestoidea, Nel & Paicheler (1994) created a "Group A" category of fossil lestids that included seven different species characterized by having "a row of at least four cells' in the cubital field. They noted an anecdotal report of a specimen of the extant *Lestes dryas* having an additional row of cells three cells in length in its cubital field and stated that the phylogenetic value of this trait was uncertain. Subsequent reports by Nel *et al.* (1997) and Nel & Jarzembowski (1999) added *L. brisaci* and *L.* aff. *regina* to Group A, a group restricted to the Eocene and Oligocene of France and Spain. Schmidt (1958) described *L. statzi* as having additional, in this case discontinuous, rows of three and four cells in the cubital fields of the specimen's forewings. Although Nel and colleagues included *L. statzi* in their Group A, they overlooked Schmidt's analysis of additional rows of cells in extant lestids. Intrigued by the uniqueness of these "Schaltzellen", Schmidt examined over a thousand specimens of the extant species *L. virens*, *L. barbarus*, *L. sponsa*, *L. dryas* and *L. macrostigma* and determined that 39.5% percent of all specimens had an additional row of cells in their cubital field. The number of cells/row in the additional row of cubital field cells varied from none to nine and only *L. virens* (97 specimens examined) did not contain extra cubital field cells. It would appear that the "Schaltzellen" are spurious in nature and that the numbers of cells/wing constitute a continuum; the definition of Group A that limits it to species with a row of at least four cells appears to be artificial. The cells that constitute the additional row of cells can be discontinuous, as in *L. regina* and *L. statzi*, can be positioned on top of one another (i.e. cubital field with two secondary longitudinal sectors) as in *L. aquissextana,* and can number as many as 12, as in *L. ceresti*, all as reported in Nel & Paicheler (1994).

The cubital fields of *Eolestes* spp. contain two or more secondary longitudinal sectors that define three and four longitudinal rows of cells; these cells do not appear to be "Schaltzellen" as reported by Schmidt (1958). We argue that the additional secondary longitudinal sector in *Lutetialestes uniformis* is unique and that the arrangement of cells is not spurious because of the very regular array of isosceles right pentagon-shaped cells. However, this latter position is very tentative, and the study of additional and more complete specimens would be desirable.

While the above discussion serves to differentiate *Eolestes* and *Lutetialastes* from all other extinct fossil specimens of Lestoidea, it says little about the phylogenetic relationship between them. Unfortunately, many of the autapomorphies used in the characterization of the various zygopteran clades are homoplastic or plesiomorphic; these include character states such as 1) absence of a lestine "O" vein; 2) basal closure of the discoidal cell; 3) postnodal and postsubnodal crossveins not aligned; 4) only one row of cells between CuA and the posterior wing margin; 5) reduction of dorsal arcular bracket; 6) arculus shifted beneath Ax2; 7) the number of cells underlying the pterostigma; 8) the very oblique MAb vein of the discoidal cell; 9) AA separating from AP just proximal to CuP; 10) a moderately petiolated wing (Bechly, 1995; Jarzembowski *et al.*, 1998; Petrulevicius & Nel, 2003, 2004, 2005; Wappler & Petrulevicius, 2007). Given this lack of definitive autapomorphic character states and the fragmentary nature of many of the relevant specimens discussed herein—only 6/14 are intact wings—it is currently impossible to generate an informative phylogenetic analysis of their relationships based, necessarily, on wing morphology.

The holotype specimen and new specimen of *Eolestes syntheticus, E. ramosus*, and *Lutetialestes uniformis*, currently are the only described species of Lestoidea from the Cenozoic of North America. However, *Lithagrion hyalinum*, originally described from the Florissant (34 Ma) by Scudder (1890) and placed in Megapodagrionidae by both Kennedy (1925) and Nel & Paicheler (1994), has been placed in Synlestidae (personal communication from Bechly referenced in Petrulevicius & Nel, 2005). A second species, *Lithagrion umbratum*, described by Scudder (1890) from the same locality, was later placed in the megapodagrionid genus *Melanagrion* by Nel & Paicheler (1994). A re-description of Scudder's type specimens of *Lithagrion hyalinum* (MCZ 392) and *Lithagrion umbratum* (MCZ 393 and MCZ 4115) is in preparation by the present authors and will confirm their placement in Lestoidea close to Synlestidae, demonstrated by the presence of a basally arched MP, a distinct lestine oblique vein, and other venational features. Another undescribed synlestid has been reported from the Middle Paleocene of Alberta, Canada (Wighton, 1982). Of the approximately 60 species of Lestoidea *sensu* Nel & Paicheler (1994), all, with two exceptions, were found in the Cenozoic of Europe. Fujiyama (1985) described two wings fragments from the Miocene of Japan, one of which may belong to Lestidae, and Nel & Paicheler (1994) described a wing fragment and larval specimens from the Oligocene-Miocene boundary of Turkey, all of which were attributed to Lestidae. Subsequent to their review, new species of Lestoidea have been described from the Late Paleocene and Early Eocene of Argentina (Petrulevicius & Nel, 2004, 2005) and the Early Cretaceous of the UK, Lebanon and Transbaikalia (Jarzembowski *et al.*, 1998; Vasilenko, 2005; Azar *et al.*, 2010). In addition, Sarzetti *et al.* (2009) described the oviposition scars of a lestid from the Eocene of Patagonia as the ichnofossil *Paleoovoidus bifurcatus*. Obviously, the collection of additional specimens of Eolestidae, *Lutetialestes* and related Zygoptera from the Green River Formation and the Coal Creek Member of the Kishenehn Formation will shed additional light on the status and relationships of these groups.

Conclusions

Damselflies make up about half of all Odonata but are more poorly represented in the fossil record than dragonflies. The most basal group of damselflies, the superfamily Lestoidea, are particularly rare in the fossil record of the New World. We herein report the discovery of several specimens of fossil lestoid damselflies from the Eocene Kishenehn Formation (approximately 46 Ma) of Montana that are very similar to the enigmatic species *Eolestes syntheticus* first described nearly 75 years ago from the Eocene Green River Formation of Colorado. Our re-examination of the Colorado specimen indicates that it, as well as another new species *E. ramosus*, belongs to a new family of fossil lestoid damselflies, Eolestidae.

Acknowledgements

We thank C. Labandeira and F. Marsh (NMNH) for administrative support, R. Johnson and P. Weil (NMNH) for translation of Schmidt (1958) and T. Karim and D. Smith (UCM) for assistance with the loan of the *Eolestes syntheticus* specimen. We also wish to thank R. Harbach (NHM) for assistance with etymology, B. Price (NMH) for photography of the *Megalestes irma* paratype, O. Flint (NMNH) for access to the NMNH type specimens and anonymous reviewers for their efforts in the evaluation of the manuscript. This is contribution number 285 of the Evolution of Terrestrial Ecosystems Consortium of the USNM.

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