



<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

References

- Azar, D., Prokop, J. & Nel, A. (2010) The first damselfly from the Early Cretaceous Lebanese amber (Odonata, Zygoptera, Lestomorpha). *Alavesia*, 3, 73–79.
- Bechly, G. (1995) Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura*, 1, 1–341.
- Bechly, G. (1996) Morphologische untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura*, 2, 1–402.
- Bechly, G. (1998) New Fossil Dragonflies from the Lower Cretaceous Crato Formation of North-East Brazil (Insecta: Odonata). *Stuttgarter Beiträge zur Naturkunde, Serie B*, 264, 1–66.
- Bechly, G. (2003) Phylogenetic systematics of Odonata. In: Schorr, M. & Lindeboom, M. (Eds.), *Dragonfly Research. Vol. 1. Zerf-Tübingen*. [CD-ROM]
- Bechly, G. & Wichard, W. (2008) Damselfly and dragonfly nymphs in Eocene Baltic amber (Insecta: Odonata), with aspects of their palaeobiology. *Palaeodiversity*, 1, 37–73.
- Bybee, S.M., Ogden, T.H., Branham, M.A. & Whiting, M.F. (2008) Molecules, morphology and fossils: a comprehensive approach to odonate phylogeny and the evolution of the odonate wing. *Cladistics*, 24, 477–514.
<http://dx.doi.org/10.1111/j.1096-0031.2007.00191.x>
- Carle, F.L., Kjer, K.M. & May, M.L. (2008) Evolution of Odonata, with special reference to Coenagrionoidea (Zygoptera). *Arthropod Systematics & Phylogeny*, 66, 37–44.
- Cockerell, T.D.A. (1916) British fossil insects. *Proceedings of the United States National Museum*, 49, 469–500.
<http://dx.doi.org/10.5479/si.00963801.49-2119.469>
- Cockerell, T.D.A. (1940) A dragon-fly from the Eocene of Colorado (Odonata: Agrionidae). *Entomological News*, 51, 103–105.
- Cockerell, T.D.A. & Andrews, H. (1916) Dragon-flies from the English Oligocene. *Proceedings of the Biological Society of Washington*, 29, 89–92.
- Constenius, K.N. (1996) Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. *Geological Society of America Bulletin*, 108, 20–39.
[http://dx.doi.org/10.1130/0016-7606\(1996\)108<0020:lpecot>2.3.co;2](http://dx.doi.org/10.1130/0016-7606(1996)108<0020:lpecot>2.3.co;2)
- Davis, R.B., Nicholson, D.B., Saunders, E.L.R. & Mayhew, P.J. (2011) Fossil gaps inferred from phylogenies alter the apparent nature of diversification in dragonflies and their relatives. *Biomedcentral Evolutionary Biology*, 11, 252–261.
<http://dx.doi.org/10.1186/1471-2148-11-252>
- Dijkstra, K.-D., Bechly, G., Bybee, S.M., Dow, R.A., Dumont, H.J., Fleck, G., Garrison, R.W., Hämäläinen, M., Kalkman, V.J., Karube, H., May, M.L., Orr, A.G., Paulson, D.R., Rehn, A.C., Theischinger, G., Trueman, J.W.H., van Tol, J., von Ellenrieder, N. & Ware, J. (2013) The classification and diversity of dragonflies and damselflies (Odonata). *Zootaxa*, 3703 (1), 36–45.
<http://dx.doi.org/10.11646/zootaxa.3703.1.9>
- Dijkstra, K.-D.B., Kalkman, V.J., Dow, R.A., Stokvis, F.R. & van Tol, J. (2014) Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). *Systematic Entomology*, 39, 68–96.
<http://dx.doi.org/10.1111/syen.12035>
- Dumont, H.J., Vierstraete, A. & Vanfleteren, J.R. (2010) A molecular phylogeny of the Odonata (Insecta). *Systematic Entomology*, 35, 6–18.
<http://dx.doi.org/10.1111/j.1365-3113.2009.00489.x>
- Fisher, C. (1974) Systematische Stellung der Gattung *Sieblusia* Handlirsch, 1906 (Zygoptera, Lestinoidea, Sieblusiidae). *Odonatologica*, 3 (4), 211–220.
- Fraser, F.C. (1945) A note on the importance of *Eolestes synthetica* Cockerell in the phylogeny of Odonata. *Proceedings of the Royal Entomological Society of London (A)*, 20, 54–56.
<http://dx.doi.org/10.1111/j.1365-3032.1945.tb01062.x>
- Fraser, F.C. (1951) Outline of a new classification for the legion Lestes Selys (Order Odonata). *Entomological News*, 62, 61–69.
- Garrison, R.W., von Ellenrieder, N. & Louton, J.A. (2010) *Damselfly genera of the New World, an illustrated and annotated key to Zygoptera*. The Johns Hopkins Press, Baltimore, 528 pp.
<http://dx.doi.org/10.1163/22119434-900000301>
- Fujiyama, I. (1985) Early Miocene insect fauna of Seki, Sado Island, Japan, with notes on the occurrence of Cenozoic fossil insects from Sado a San-In district. *Memoirs of the National Science Museum of Tokyo*, 18, 35–56.
- Jarzembowski, E.A. (1990) Early Cretaceous zygopteroids of southern England, with the description of *Cretacoenagrion alleni* gen. nov., spec. nov. (Zygoptera: Coenagrionidae; “Anisozygoptera”: Tarsophlebiidae, Euthemistidae). *Odonatologica*, 19, 27–37.
- Jarzembowski, E.A., Martínez-Delclós, X., Bechly, G., Nel, A., Coram, R. & Escuillié, F. (1998) The Mesozoic Non-Calopterygoid Zygoptera: Descriptions of New Genera and Species from the Lower Cretaceous of England and Brazil and Their Phylogenetic Significance (Odonata, Zygoptera, Coenagrionoidea, Hemiphlebioidea, Lestoidea). *Cretaceous*

- Research*, 19, 403–444.
<http://dx.doi.org/10.1006/cres.1997.0113>
- Kennedy, C.H. (1925) New genera of Megapodagrionidae with notes on the subfamily. *Bulletin of the Museum of Comparative Zoology*, 67, 291–311.
- Lak, M., Fleck, G., Azar, D., Engel M.S., Kaddumi, H.F., Neraudeau, D., Tafforeau, P. & Nel, A. (2009) Phase contrast X-ray synchrotron microtomography and the oldest damselflies in amber (Odonata: Zygoptera: Hemiphlebiidae). *Zoological Journal of the Linnean Society*, 156, 913–923.
<http://dx.doi.org/10.1111/j.1096-3642.2008.00497.x>
- Nel, A. (1985) Description d'une nouvelle espèce fossile de *Lestes* Leach, 1815, du stampien de Céreste (Alpes-de-Haute-Provence) (Odon. Lestidae). *Entomologica Gallica*, 1, 275–279.
- Nel, A. & Paicheler, J.-C. (1994) Les Lestoidea (Odonata, Zygoptera) fossils: Un inventaire critique. *Annales de Paléontologie*, 80, 1–59.
- Nel, A. & Jarzembowski, E.A. (1999) Fossil damselflies and dragonflies (Insects: Odonata) from the late Upper Eocene of Southern England. *Proceedings of the Geologists' Association*, 110, 193–201.
[http://dx.doi.org/10.1016/s0016-7878\(99\)80069-8](http://dx.doi.org/10.1016/s0016-7878(99)80069-8)
- Nel, A., Martinez-Delclos, X., Paicheler, J.-C. & Henrotay, M. (1993) Les "Anisozygoptera" fossiles - Phylogénie et classification (Odonata). *Martinia*, Numéro hors-série, 3, 1–311.
- Nel, A., Martinez-Delclos, X., Papier, F. & Oudard, J. (1997) New Tertiary Odonata from France (Sieblosiidae, Lestidae, Coenagrionidae, Megapodagrionidae, Libellulidae). *Deutsche Entomologische Zeitschrift*, 44, 231–258.
<http://dx.doi.org/10.1002/mmnd.4800440210>
- Penalver, E., Nel, A. & Martinez-Delclos, X. (1996) Insectos del Mioceno inferior de Ribesalbes (Castellón, España). Paleoptera y Neoptera poly paraneoptera. *Treballs del Museu de Geologia de Barcelona*, 5, 15–95.
- Petrulevičius, J.F. & Nel, A. (2003) Frenguelliidae, a new family of dragonflies from the earliest Eocene of Argentina (Insecta: Odonata): phylogenetic relationships within Odonata. *Journal of Natural History*, 37, 2909–2917.
<http://dx.doi.org/10.1080/0022293021000007543>
- Petrulevičius, J.F. & Nel, A. (2004) Recognition of the first fossil lestoid damselfly in South America (Insecta: Zygoptera): Biogeographic and phylogenetic remarks. *Journal of Paleontology*, 78, 798–801.
[http://dx.doi.org/10.1666/0022-3360\(2004\)078<0798:rotffl>2.0.co;2](http://dx.doi.org/10.1666/0022-3360(2004)078<0798:rotffl>2.0.co;2)
- Petrulevičius, J.F. & Nel, A. (2005) Austroperilestidae, a new family of damselflies from Early Eocene of Argentina (Insecta: Odonata). Phylogenetic relationships within Odonata. *Journal of Paleontology*, 79, 658–662.
[http://dx.doi.org/10.1666/0022-3360\(2005\)079\[0658:aanfod\]2.0.co;2](http://dx.doi.org/10.1666/0022-3360(2005)079[0658:aanfod]2.0.co;2)
- Rehn, A.C. (2003) Phylogenetic analysis of higher-level relationships of Odonata. *Systematic Entomology*, 28, 181–239.
<http://dx.doi.org/10.1046/j.1365-3113.2003.00210.x>
- Riek, E.F. & Kukalová-Peck J. (1984) A new interpretation of dragonfly wing venation based upon Early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. *Canadian Journal of Zoology*, 62, 1150–1166.
<http://dx.doi.org/10.1139/z84-166>
- Riou, B. & Nel, A. (1995) Nouveaux Odonates fossils du Miocene superieur de l'Ardeche. (Odonata: sieblosiidae, Lestidae, Libellulidae, Corduliidae, Aeshnidae). *Travaux de l'Ecole Pratique des Hautes Etudes*, 7/8, 125–144.
- Sarzetti, L.C., Labandeira, C.C., Muzón, J., Wilf, P., Rubén Cúneo, N., Johnson, K.R. & Genise, J.F. (2009) Odonatan endophytic oviposition from the Eocene of Patagonia: the ichnogenus *Paleoovoidus* and implications for behavioral stasis. *Journal of Paleontology*, 83, 431–447.
<http://dx.doi.org/10.1666/08-121.1>
- Schmidt, E. (1958) Bemerkungen über Lestiden III (Odonata). Über *Oligolestes grandis* (Statz 1935) und eine neue *Lestes*-Art aus dem Mittel-Oligozän von Rott im Siebengebirge. *Decheniana*, 111, 1–7.
- Schorr, M. & Paulson, D. (2014) World Odonata List. Available from: <http://www.pugetsound.edu/academics/academic-resources/slater-museum/biodiversity-resources/dragonflies/world-odonata-list2/> (accessed 11 March 2014)
- Scudder, S.H. (1890) The Tertiary insects of North America. United States Survey of the Territories, Washington, D.C., 734 pp.
<http://dx.doi.org/10.5962/bhl.title.2507>
- Smith, M.E., Singer, B. & Carroll, A. (2003) 40Ar/39Ar geochronology of the Eocene Green River Formation, Wyoming. *Geological Society of America Bulletin*, 115 (5), 549–565.
[http://dx.doi.org/10.1130/0016-7606\(2003\)115<0549:agoteg>2.0.co;2](http://dx.doi.org/10.1130/0016-7606(2003)115<0549:agoteg>2.0.co;2)
- Tillyard, R.J. & Fraser, F.C. (1938) A reclassification of the order Odonata. Based on some new interpretations of the venation of the dragonfly wing. With notes, preface and completion thereof. *Australian Zoologist*, 9 (2), 125–169.
- Trueman, J.W.H. (1996) A preliminary cladistic analysis of Odonate wing venation. *Odonatologica*, 25, 59–72.
- Trueman, J.W.H. (2007) A brief history of the classification and nomenclature of Odonata. *Zootaxa*, 1668, 381–394.
- Vasilenko, D.V. (2005) New damselflies (Odonata: Synlestidae, Hemiphlebiidae) from the Mesozoic Transbaikalian locality of Chernovskie Kopi. *Paleontological Journal*, 39, 280–283.
- Wappler, T. & Petrulevičius, J.F. (2007) Priscalestidae, a new damselfly family (Odonata: Lestinoidea) from the Middle Eocene Eckfeld maar of Germany. *Alavesia*, 1, 69–73.
- Watson, J.A.L. (1991) *The Australian dragonflies*. CSIRO Publishing, Collingwood, Victoria, Australia, 278 pp.
- Wighton, D.C. (1982) Middle Paleocene insect fossils from southcentral Alberta. *Proceedings of the 3rd North American Paleontological Convention*, 2, 577–578.