

A new transitional “libelluloid” family of odonates with Mesozoic affinities in the Eocene Green River Formation of Utah, USA

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The new “libelluloid” family Cordulibellulidae is described to accommodate a new genus and species *Cordulibellula inopinata* from the Eocene Green River Formation, Utah, USA. Even if its affinities remain somewhat uncertain because of the lack of information on structures others than those of the hind wing, its putative closest relatives are known from the Late Jurassic and Early Cretaceous. Therefore, this new fossil is interpreted as a “relict” taxon surviving until the Paleogene. This new addition to the odonatan paleontofauna of the Green River Formation confirms the high diversity of this clade during the Paleogene and in this formation.

Key words: Insecta, Odonoptera, Anisoptera, K/Pg boundary crisis, paleodiversity, Eocene, USA.

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Introduction

The oldest records of the anisopteran “libelluloid” group Eurypalpidomorpha Bechly, 2003, go to the Cretaceous (Fleck et al. 1999; Kohli et al. 2016), an age in accordance with its putative closest relatives the Juracorduliidae described from the Jurassic (Bechly 1998a).

The Cretaceous fossil record of the Eurypalpidomorpha is mainly composed of species originating from Lower Cretaceous deposits (e.g., Bechly 1998b; Nel and Pouillon 2020), with the sole exception of *Palaeolibellula zherikhini* Fleck, Nel, and Martínez-Delclòs, 1999, described from the Turonian (Upper Cretaceous) of Kazakhstan (Fleck et al. 1999). Therefore, the diversity of this clade is difficult to estimate during the Late Cretaceous and around the Cretaceous/Paleogene (K/Pg) boundary. This observation is further exemplified by the few Eurypalpidomorpha known from the Paleocene (e.g., Petrulėvičius et al. 1999; Petrulėvičius and Nel 2002) and question the impact of the K/Pg boundary event on this clade.

In the lowermost to middle Eocene, the Eurypalpidomorpha

families are represented by Libellulidae (Zessin 2019), Corduliidae (Scudder 1892; Bechly 2005), Urothemistidae (Nel and Fleck 2014), and the extinct Bolcacorduliidae (Gentilini 2002) and Urolibellulidae (Zeiri et al. 2015; Nel 2020). Although the Eurypalpidomorpha diversity slightly increases during the Eocene, their true burst of diversification likely took place later during the Miocene, with numerous species described through the entire epoch (<https://paleobiodb.org/>). The crown representatives of the extant Eurypalpidomorpha families occur more and more frequently and in higher diversity in the Oligocene (Nel and Paicheler 1993, 1994).

Surprisingly, the “transition” within the Eubrachystigmata (the clade encompassing the Eurypalpidomorpha) are often evidenced by only one or two fossils. As a result, the “transition” between the Paneurypalpidomorpha and the clade Eurypalpidomorpha is only documented by one fossil i.e., *Juracordulia schiemenzi* Bechly, 1998 (see Bechly 1998a). This dearth of fossil evidence complicates the interpretation of wing venation changes, but also phylogenetic reconstructions.

Here we describe a complete hind wing from the Eocene

Green River Formation in Utah, representing a new transitional family likely belonging to another intermediate between the extinct Paneurypalpidomorpha and the Eurypalpidomorpha. This formation is a hot spot of diversity for the Odonata during the middle Eocene (e.g., Zeiri et al. 2015; Bechly et al. 2020; Nel 2020, 2022).

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:4AE88F5F-6384-467B-BCC0-419C339F2C36

Institutional abbreviations.—FHPR, Utah Field House of Natural History State Park Museum, Vernal, Utah, USA.

Other abbreviations.—Bqs, crossveins between RP1/2 and IR2 basad base of RP2; CuA, cubitus anterior; CuP, cubitus posterior; IRxx, supplementary longitudinal veins between branches of RP; MAa, anterior branch of media anterior; Mab, posterior branch of media anterior; MP, media posterior; Mspl, supplementary vein in postdiscoidal area; N, nodus; PsA anterior branch of AA; postdiscoidal area, area between MAa and MP; Pt, pterostigma; RA, radius anterior; RP, radius posterior, Rspl, supplementary vein in area between IR2 and RP3/4; ScP, subcostal posterior; t, discoidal triangle.

Material and methods

The fossil was collected by the senior author (SDS) in 2010 from part of a thick sequence of strata in the upper Parachute Creek Member of Green River Formation near Bonanza, Uintah County, Utah, USA. The fossil was found in a gray, slightly dolomitic shale. The strata lie above the Mahogany layer of the oil shale (of estimated latest Ypresian age between 49.3 and 48.7 Ma; Smith et al. 2010; Lejay et al. 2015), near the upper contact with the Uinta Formation and are considered lacustrine. The shale is widespread throughout the region and is highly fossiliferous.

The specimen needed no preparation after splitting the shale. Raw photographs were taken using a Canon EOS R5 using the Canon 100mm f/2.8 L Macro IS USM lens at f/8, 0.8 sec, and ISO 100. Specimens were under 70% ethyl alcohol and photographed with polarized light and a circular polarizer on the camera. The photographs were color corrected and sharpened using Topaz Labs Sharpen AI in auto mode.

The higher classification of fossil and extant Odonoptera, as well as familial and generic characters, follow the phylogenetic system proposed by Bechly (1996, 2003). Wing venation terminology follows Riek and Kukalová-Peck (1984), as amended by Nel et al. (1993) and Bechly (1996).

Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Odonata Fabricius, 1793

Suborder Anisoptera Selys-Longchamps
in Selys-Longchamps and Hagen, 1854

Clade Cavilabiata Bechly, 1996

Family Cordulibellulidae nov.

Zoobank LSID: urn:lsid:zoobank.org:act:B5B18605-122F-4B32-A6AE-9141901B92DB

Type genus: *Cordulibellula* gen. nov.; see below.

Diagnosis.—As for the monotypic type species.

Genus *Cordulibellula* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:7A1F110A-4CF3-41E8-8C69-FECBD9BB8182

Type species: *Cordulibellula inopinata* sp. nov., by monotypy; see below.

Etymology: Named after a combination of the family names Cordulidae and Libellulidae. Gender feminine.

Diagnosis.—As for the monotypic type species.

Cordulibellula inopinata sp. nov.

Figs. 1, 2.

Zoobank LSID: urn:lsid:zoobank.org:act:B664998B-1919-451F-8BF3-80AF942020B5

Etymology: From Latin *inopinata*, unexpected; referring to the unexpected find of a “relict” “libelluloid” related to Mesozoic taxa in the middle Eocene.

Type material: Holotype FHPR 11611, part and counterpart of an isolated hind wing, partly folded and deformed.

Type locality: Lake Uinta, near Bonanza, Utah, USA.

Type horizon: Upper Parachute Creek Member, Green River Formation; middle Eocene.

Diagnosis.—Hind wing characters only. Straight gaff (= basal CuA before its branching); CuAa with at least three posterior branches; an obliquely elongate anal loop subdivided into one large and two smaller cells; MP and MAa clearly undulating; a well-defined Rspl; a zigzagged Mspl.

Description.—Preserved part of wing 29.2 mm long, ca. 6.0 mm wide, estimated length of wing 32.0 mm; distance between nodus (N) and pterostigma (Pt) 13.6 mm between pterostigma and wing apex 2.8 mm; pterostigma 3.3 mm long, 0.8 mm wide, parallel sided (distal side not more oblique than basal side), covering two long cells; pterostigmal brace aligned with basal side and weakly oblique; 11 postnodal crossveins, not aligned with the eight postsubnodal crossveins; an important “libellulid” gap in basal part of postsubnodal space; “cordulegastrid” gap present; five visible antenodal crossveins of first and second rows nearly aligned, probably nine originally, primary antenodals not preserved; arculus only partly preserved (posterior part); discoidal triangle free, isosceles, with base located close to arculus, separated by less than 1/2 length of arculus,

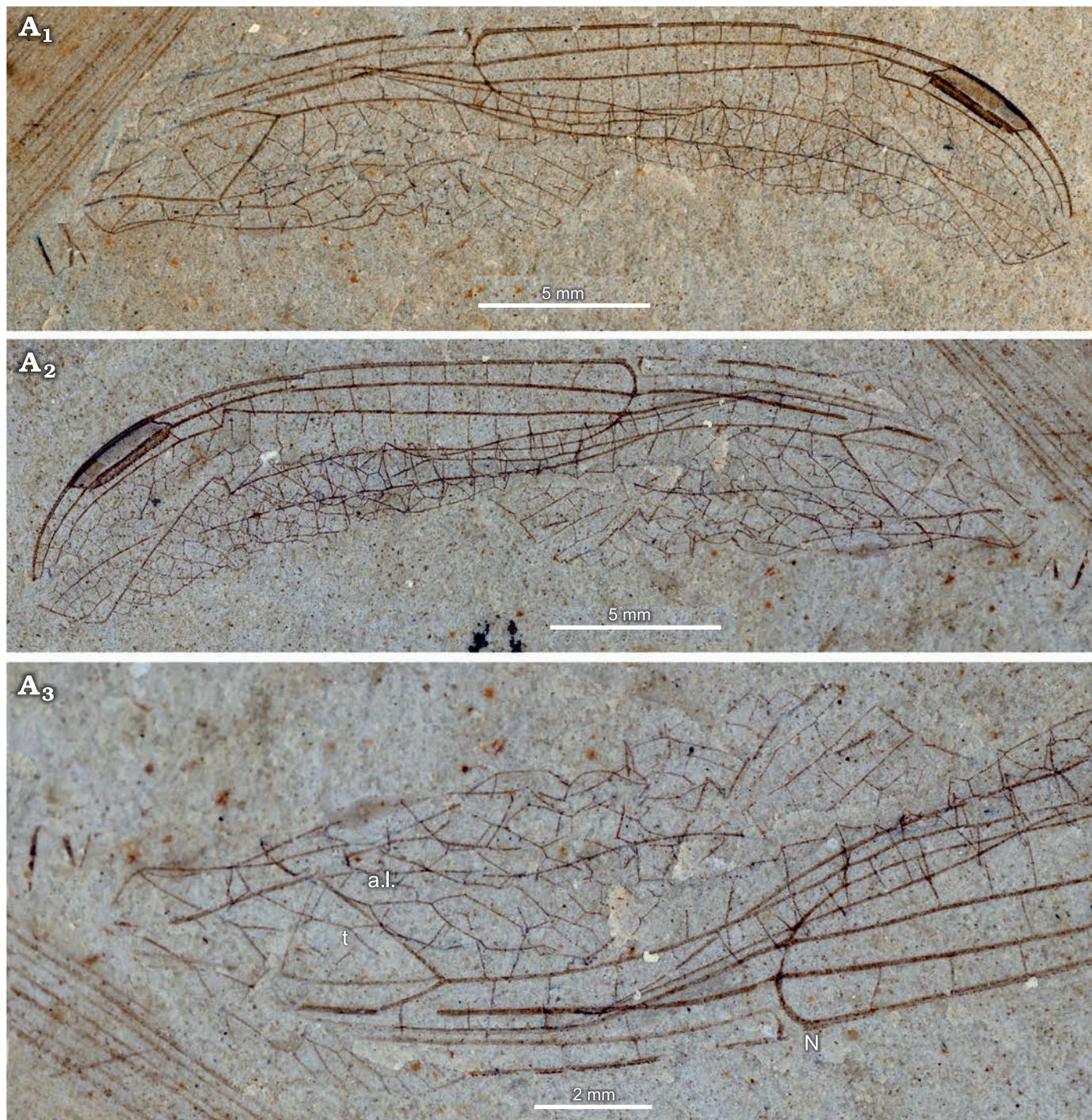


Fig. 1. Anisopteran dragonfly *Cordulibellula inopinata* gen. et sp. nov. from Lake Uinta, Utah, USA, Eocene, holotype FHPR 11611, part (A₁), counterpart (A₂), detail of wing base (A₃). Abbreviations: a.l., anal loop; N, nodus; t, discoidal triangle.

basal side of discoidal triangle (t) 1.7 mm long, anterior side 2.8 mm long, distal side (Mab) 2.8 mm long; hypertriangle likely with two crossveins, with MA distinctly curved; subdiscoidal space free, distinctly closed by an oblique PsA incompletely preserved; only CuP in submedian space; median space free; anal loop (al) transversely elongate, 4.8 mm long, max. 1.0 mm wide, narrow obliquely elongate, with a midrib and divided into one large and two smaller cells; basal CuA before its branching long but straight; CuAa with

at least three posterior branches, probably more; MP basally weakly zigzagged and distally undulated; MAa distally undulated too; postdiscoidal area rather broad, with two rows of cells basally near the discoidal triangle and a zigzagged Mspl, one row of cells between MAa and Mspl; RP3/4 poorly preserved; IR2 weakly zigzagged, parallel with RP2 in its main part, but diverging distally; two Bqs crossveins; base of RP2 aligned with subnodus; lestid oblique crossvein one cell distad subnodus; one row of cells between RP1 and

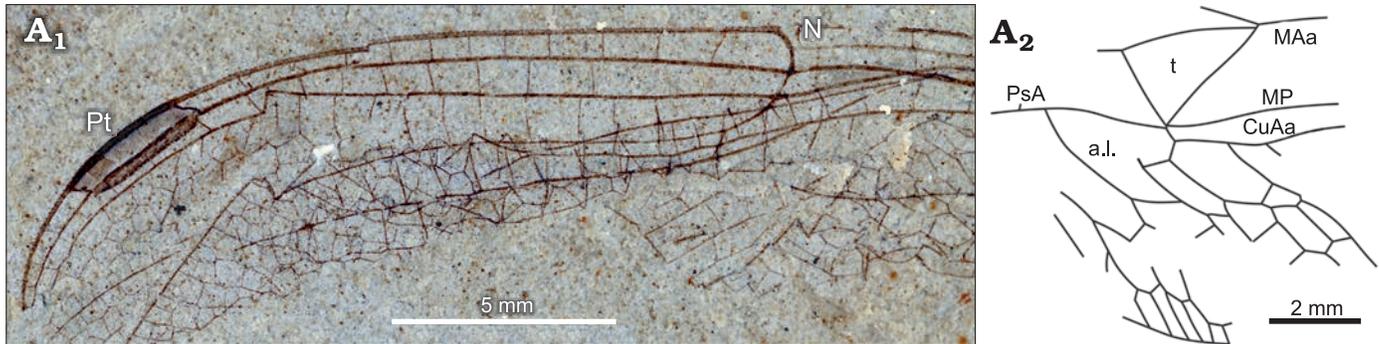


Fig. 2. Anisopteran dragonfly *Cordulibellula inopinata* gen. et sp. nov. from Lake Uinta, Utah, USA, Eocene, holotype FHPR 11611, reconstruction of wing base (A₁), detail of wing apex (A₂). Abbreviations: a.l., anal loop; N, nodus; Pt, pterostigma; t, discoidal triangle.

RP2 up to 3.5 mm basad pterostigma; a strongly zigzagged IR1; a well-defined Rspl weakly curved anteriorly, with one row of cells between it and IR2.

Stratigraphic and geographic range.—Upper Parachute Creek Member, Green River Formation, middle Eocene; Lake Uinta.

Discussion

Following the phylogenetic hypothesis of Bechly (2003), this fossil hind wing can be attributed to the “libelluloid” clade Eubranchystigmata Bechly, 2003 (extinct Hemeroscopidae Pritykina, 1977 + Neobranchystigmata Bechly, 2003) because of the following characters: distal part of antesubnodal area free of crossveins (“cordulegastrid gap”); no basal furcation of IR2 basal of the lestine oblique vein; anal loop at least elongated and enlarged, with four cells; short pterostigmata covering two complete cells; area between RP2 and IR2 distally distinctly widened, with more than one cell row in distal half; hind wing CuAa distinctly curved towards hind margin, and further shortened with four posterior branches.

It cannot be attributed to the family extinct Hemeroscopidae because its anal loop is clearly smaller than in this family (Pritykina 1977). The new fossil lacks one of the characters of the Neobranchystigmata Bechly, 2003, viz. “hind wing MP distinctly curved towards hind margin and thus somewhat shortened, ending basad level of nodus”. Nevertheless, it shows several putative synapomorphies of the Paneurypalpidomorpha Bechly, 2003, a subclade of the Neobranchystigmata: hind wing anterior margin of hypertriangle distinctly convex, because of a basally arched MA; lestine oblique vein only one cell distad subnodus; discoidal triangle unicellular; basal part of postsubnodal area free of crossveins (“libellulid gap”).

Within this group, it cannot be attributed to the Eurypalpidomorpha Bechly, 2003 (a clade encompassing the families extinct Valdicorduliidae Bechly, 1996, extinct Arariphebiidae Bechly, 1998, extinct Eocorduliidae Bechly, 1996, extinct Araripelibellulidae Bechly, 1996, Synthemi-

stidae Tillyard, 1911, Gomphomacromiidae Tillyard and Fraser, 1940, Pseudocorduliidae Lohmann, 1996, Macromiidae Needham, 1903, Austrocorduliidae Bechly, 1996, Idionychidae Tillyard and Fraser, 1940, Idomacromiidae Tillyard and Fraser, 1940, Cordulephyidae Tillyard, 1917, Oxygas-tridae Bechly, 1996, Corduliidae Selys-Longchamps in Selys-Longchamps and Hagen, 1850, Hemicorduliidae Bechly, 1996, Urothemistidae Lieftinck, 1954, extinct Urolibellulidae Zeiri, Nel, and Garrouste, 2015, and Libellulidae Leach, 1815, because it lacks the synapomorphies of the clade, viz. hind wing elongated gaff (= basal CuA before its branching) sigmoidally curved; CuAb shifted very far distally, and CuAa with only one or two posterior branches.

The transversely elongate anal loop of the new fossil reminds that of the extinct Juracorduliidae Bechly, 2003 (*Juracordulia* Bechly, 1998), except in its subdivision into three cells (free of crossveins in *Juracordulia*). It also differs from *Juracordulia* in the veins MP and MAa clearly undulating instead of being simply curved posteriorly; a well-defined Rspl (vs. none); a Mspl (even if zigzagged, vs. none) (Bechly 1998a).

The monotypic family extinct Eocorduliidae (extinct *Eocordulia* Pritykina, 1986; Cretaceous) shares with the new fossil a similar transversely elongate anal loop subdivided into smaller cells and an undulating MAa, but its Mspl is better defined, not zigzagged and its branches of CuAa are less well defined than in the new fossil (Pritykina 1986). The speciose family extinct Araripelibellulidae (extinct *Araripelibellula* Nel and Paicheler, 1994; Cretaceous) also shares with the new fossil a similar transversely elongate anal loop subdivided into smaller cells, but it has no Rspl and no Mspl, and its branches of CuAa are less well defined than in the new fossil (Nel and Paicheler 1994).

The Cretaceous extinct Valdicorduliidae, extinct Arariphebiidae, and the extinct Urolibellulidae (also described from the Green River Formation with two genera extinct *Urolibellula* Zeiri, Nel, and Garrouste, 2015, and extinct *Kohlslibellula* Nel, 2020), strongly differ from the new fossil in their elongate anal loop with a midrib and CuAa without branches (Jarzembowski and Nel 1996; Zeiri et al. 2015; Nel 2020). Lastly, the Eocene family Bolcacorduliidae being based on an isolated forewing, is hardly comparable

to the new fossil. Nevertheless, *Bolcacordulia paradoxa* Gentilini, 2002, has no Msp1 at all, while the new fossil has one, and its pterostigma is shorter, covering only one cell, vs. two in the new fossil, and its MAa and MP are weakly curved vs. clearly undulating in the new fossil (Gentilini 2002).

Conclusions

This fossil cannot be attributed to any of the known “libelluloid” families. Therefore, we consider that it belongs to a new family Cordulibellulidae fam. nov. The strong wing venation similarities of the new fossil with the extinct Juracorduliidae can support either a sister group position to this clade or a sister group position to the Eurypalpidomorpha. However, because of the poor preservation of *Cordulibellula inopinata* gen. et sp. nov. it is impossible to confidently choose between these two options.

A surprising observation is that the extinct Juracorduliidae are Late Jurassic and the oldest known Eurypalpidomorpha are Early Cretaceous. In light of the proposed hypotheses, the new fossil is a representative of a clade that should be at least from the Early Cretaceous, and in the most extreme case from the Late Jurassic. These particular affinities suggest that it can be considered a “relict” taxon in the middle Eocene. This discovery is to be linked to the presence of the other “relict” family Pseudostenolestidae Garrouste and Nel, 2015, in the Eocene of Messel (Germany) (Lenz et al. 2015), while belonging to the Mesozoic damselfly-dragonfly clade Isophlebioptera Bechly, 1996 (Garrouste and Nel 2015). Both show that some ancient, supposedly Mesozoic clades of Odonata could survive the Cretaceous/Cenozoic extinction, while others, like the Aeschniidae, probably went extinct at the K/Pg boundary (Nel 2021).

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