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**New odonatans (Odonata: Gomphaeschnidae; Synlestidae) from the Paleocene Paskapoo Formation: Systematic and biogeographical implications**

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**Abstract**

The Paleocene Paskapoo Formation in Alberta, Canada offers a unique opportunity to gain insight into insect diversity at that time. This fossil insect-rich formation has yielded a variety of fossil arthropod specimens, including several Odonata wings related to the genus *Alloaeschna* Wighton & Wilson, 1986. Herein, we demonstrate that morphological characters previously used to separate three different species are instead the result of intraspecific variability. We reinforce this demonstration using two examples of high variability and plasticity in modern species of the family Aeshnidae. Accordingly, we reinterpreted the taxonomic position of *Alloaeschna marklae* Wighton & Wilson, 1986 syn. nov. and

*Alloaeschna quadrata* Wighton & Wilson, 1986 syn. nov. as junior synonyms of *Alloaeschna paskapooensis* Wighton & Wilson, 1986. In addition, we describe the first occurrence of a Zygoptera in the Paskapoo Formation, namely *Albertalestes paskapooensis* gen. et sp. nov. (Synlestidae). Importantly, this new taxon is the first representative of the family found in North America. We also reconstructed the relationships within the Synlestidae under Bayesian inferences with a newly assembled matrix. Finally, we discuss the biogeography of the clade considering its fossil record using parsimony ancestral state reconstruction.

**Keywords:** Insecta; Odonatoptera; Zygoptera; Lestiformia; Paleodiversity

## Introduction

The Paleocene Epoch (66-56 Ma) is a key time in the evolutionary history of insect lineages because it encompasses a period of gradual warming (lasting ca. 6 Ma) and ends with a thermal optimum (Paleocene-Eocene Thermal Maximum, or PETM) (e.g. Zachos et al., 2008). These global climate changes (variations in warming and cooling periods) are presumably drivers of the diversity dynamics of insect populations (e.g. Condamine et al., 2016; Halsch et al., 2021). In fact, these climate changes may have directly affected the insect's food sources – notably the Gymnosperms (e.g. Condamine et al., 2020) – or their environment by reshaping the distribution of biomes (e.g. Korasidis et al., 2022). For instance, it has been recently demonstrated that the global warming of the Paleocene led to a worldwide modification of biome repartition and to the extension of temperate climates to high latitudes (e.g. Jouault et al., 2021; Korasidis et al., 2022). As a result, insects may have colonized new habitats, declined in former, or persisted and dispersed.

To understand how these changes shaped the repartition of insects it is important to study their biogeographical history. This can be done by studying their fossil record and

documenting new lineages and/or by reconstructing the phylogenetic relationships between species (e.g. Crisp et al., 2010). The fossil record allows us to document worldwide distributions in the past even though their current distribution is relict and restrained to a small area (Barden & Ware, 2017; Coiro et al., 2023). Similarly, the study of the relationships between extant species often provides clues on the ‘ancestral’ distribution of the clade and their evolutionary history. However, a patchy fossil record as well as a reduced sampling of the extant diversity – when relict from a flourishing diversity in the fossil record – can hamper these approaches.

Fortunately, some insect orders such as the Odonata (i.e. dragonflies and damselflies) often fossilized in lacustrine paleoenvironments thereby making it possible to accurately track their evolution (Fleck et al., 1999; Bechly et al., 2001; Nel et al., 2010; Vassilenko, 2014; Nel, 2021; Zheng, 2022). It has been demonstrated that numerous extant odonatan lineages arose during the Cretaceous and Paleocene (Kohli et al., 2021; Suvorov et al., 2022), which correlates well with their diversity during this time interval (about 20 Odonata species are known during the Paleocene: Fig. 1). Interestingly, some Paleocene deposits are still poorly studied, even though several odonatans have been described and new materials have been collected. This is the case for the Paskapoo Formation, which has yielded well-preserved odonatan specimens. We use these specimens to reinterpret the limits of three *Alloaeschna* Wighton & Wilson, 1986 species. Amongst the new material, we found a well-preserved wing of the family Synlestidae, which informs on the distribution of the family during the Paleocene and reduced the gaps in the synlestid fossil record.

The oldest records of Synlestidae are dated back to the Cretaceous (Vasilenko, 2005; Huang et al., 2022). Recently, the phylogenetic relationships between extant representatives of the family were explored using molecular data and a maximum likelihood approach (Simaika et al., 2020). This study also discussed the biogeography of the clade and suggested

a single African origin in the Synlestidae (Simaika et al., 2020). We propose new phylogenetic analyses of the extant Synlestidae using Bayesian inferences and molecular data. To reconstruct these new phylogenies, we applied additional genetic loci (five *versus* two) and reduced the number of terminal taxa. The reduction of the taxonomic sampling maximizes the completeness of our dataset. Based on the resulting consensus trees we discuss the biogeography of the family Synlestidae considering its fossil record.

## **Material and methods**

### **Taxonomic sampling and alignment**

All DNA sequences were retrieved from data available on GenBank (<https://www.ncbi.nlm.nih.gov/genbank>). Genes were selected to include coding and non-coding fragments and were extracted for five loci for 10 Synlestidae species and six outgroup taxa belonging to the families Lestidae, Perilestidae, and Hemiphlebiidae. The five genetic loci are identified as follows: 16S ribosomal RNA (16S), 18S ribosomal RNA (18S), 28S ribosomal RNA (28S), Cytochrome Oxidase I (COI), and Cytochrome Oxidase II (COII). Wherever possible, sequences with the same voucher code were privileged to limit the use of chimeric taxa and get rid of potential misidentification. To detect erroneous data, we BLAST all the sequences and checked manually all the posterior alignments. The GenBank accession numbers are available in Supplementary Data 1.

We aligned each locus individually using MAFFT v7.511 (Katoh & Standley, 2013) with the default settings and manually examined the resulting alignments to ensure that a fully codon-based alignment was generated and examined coding frames and stop codons to detect potential pseudogenes or errors using Aliview v1.28 (Larsson, 2014). The final alignments for all five loci were concatenated into a single matrix using SequenceMatrix 1.7.7 (Vaidya et al., 2011) with the external gaps recoded as question marks. The concatenated molecular matrix

contains 16 taxa and 5832 sites (419 parsimony-informative, 370 singleton sites, and 5043 constant sites) with 13.4% missing data. The alignment files are available in Supplementary Data 2. We refrain from integrating fossil taxa into a total-evidence analysis (i.e. combining molecular and morphological data) because some fossil representatives of the family Synlestidae are only known from isolated wings. This partial preservation does not allow for coding numerous key morphological characters often used to delineate extant synlestid species.

### **Partitioning Schemes and Model Selection**

We used PartitionFinder v2.1.1 software (Lanfear et al., 2016) to determine suitable partitioning schemes and corresponding models of molecular evolution for the concatenated multiple sequence alignment generated in the previous step. We designated nine data blocks representing the three codon positions for each genes. Models were searched for MrBayes ( *mrbayes*), the branch lengths set to *linked*, a Bayesian Information Criterion option (*BIC*) used for model selection and comparison, and a greedy algorithm used for schemes search (*greedy*). PartitionFinder determined six subsets from the nine data blocks (Supplementary Table 1).

### **Phylogenetic analyses**

Bayesian analyses were run in MrBayes v.3.2.7 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Ronquist et al., 2012) under the models specified by PartitionFinder for molecular data. We also run on analysis without substitution models selected *a priori* using reversible jump MCMC (rjMCMC) in MrBayes. This approach samples the posterior probability of all models in the GTR substitution family (Huelsenbeck et al., 2004). For the other parameters, we used the by default parametrization. *Hemiphlebia mirabilis* was used as

outgroup and the monophyly of the Synlestidae constrained. All analyses comprised two runs and four chains, and were launched for 20 million generations. Chains were sampled every 5000 generations and a burn-in fraction of 0.25 was used. Convergence diagnostics were checked for each analysis [i.e. average standard deviation of split frequencies <0.01, PRSF close to 1.0, and ESS > 200 in Tracer (Rambaut et al., 2018)]. All consensus trees were visualized and drawn using Figtree v.1.4.4 (Rambaut, 2009) and modified with adobe illustrator CC2019.

### **Biogeographical analyses**

We investigated the biogeography of the family Synlestidae using the parsimony ancestral state reconstruction function implemented in Mesquite (Maddison & Maddison, 2023). We created a new character matrix containing the geographic repartition of species according to five different subregions: Australia, Americas and Caribbean, Asia, Central Africa, Southern Africa (Supplementary Data 3). We then coded the distribution of species according to the data available in GBIF (<https://www.gbif.org>). Ultimately, we ran these analyses on our consensus bayesian trees, without constraining the dispersal ability of taxa.

### **Specimen origins, imaging and examination**

The Paskapoo Formation (Red Deer, Alberta) is a Paleocene unit from the western side of the Western Canada Sedimentary Basin (Glass, 1997). This Formation was deposited in a fluvio-lacustrine environment by rivers flowing in an easterly direction (Hoffman & Stockey, 2000). The Paskapoo Formation is renowned for its abundant and well-preserved paleofauna and paleoflora, and it is mostly composed of interbedded hard to soft mudstone and sandstone, with subordinate pebble-conglomerate (Glass, 1997; Hoffman & Stockey, 2000). This formation was deposited by low-energy fluvial systems under humid conditions, with

associated overbank environments including ponds and oxbow lakes (Hoffman & Stockey, 2000). The Paskapoo Formation is widespread in western Alberta, outcropping from the south in Calgary to the Hinton area.

The Tiffanian Joffre locality, near Red Deer (Hoffman & Stockey, 2000: fig. 1), and the Blackfalds Insect and Plant Site, near Blackfalds, have yielded extremely well-preserved fossil material such as plants, mammals, fishes, and insects (Wighton, 1980, 1982; Kevan et al., 1981; Baker & Wighton, 1984; Fox, 1990; Wilson, 1996a, b; Wighton & Wilson, 1986; LaPolla & Barden, 2018). The strata were dated by biostratigraphy to the middle Paleocene (Tiffanian) age using faunal remains (Fox, 1990, 1991), palynological data (Demchuk & Hills, 1991), and magnetostratigraphy (Lerbekmo et al., 1992). It is currently accepted that the age of the localities is ca. 58-60 Ma (Ti<sub>3</sub> zone: Fox, 1990; 26r reverse polarity zone: Lerbekmo et al., 1992; P4 palynostratigraphic zonation: Demchuk, 1987, 1990).

The material described herein is currently housed in the Fossil Insect Collection (E. H. Strickland Entomological Museum) at the University of Alberta (Edmonton, UAPC or UAFIC). The specimens were studied using a stereomicroscope Olympus SZX16. Photographs were taken with a Nikon D90 with an attached 60 mm lens or with a Tagarno Digital Microscope. All the photos were treated with graphic software. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software.

### **Wing venation abbreviations**

The nomenclature of the odonatan wing venation used in this paper is based on the interpretations of Riek & Kukalová-Peck (1984), as modified by Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera, as well as family and generic characters followed in the present work, is based on the phylogenetic system proposed by Bechly (1996) and Dijkstra et al. (2014) for the phylogeny of extant Zygoptera. Wing

abbreviations are summarized in Nel & Piney (2022: fig. 20.1): AA/AP, anal vein (anterior/posterior); Ax0/Ax1/Ax2, primary antenodal cross veins; arc arculus; C, costal vein; Cr nodal cross vein; CuA/CuP, cubital vein (anterior/posterior); CuAa and CuAb, first distal posterior branches of CuA; IR1 and IR2, supplementary convex longitudinal veins in radial area, emerging from the stem of RP; MA/MP, median vein (anterior/posterior); MAa, anterior branch of MA; MAb, posterior branch of MA, forming the distal side of the discoidal cell; N nodus; 'o' oblique crossvein between RP2 and IR2; Pt, pterostigma; RA/RP, radial vein (anterior/posterior) (RP is divided into three main branches RP1, RP2, and RP3/4); Sn subnodal crossvein; ScP, posterior subcostal vein; Sn, subnodus.

All taxonomic acts established in the present work have been registered in ZooBank LSID (see below), together with the electronic publication under urn:lsid:zoobank.org:pub:D5282228-2D59-46E9-B712-3DC5A71C42FD

## **Results**

### **Phylogeny and biogeography**

Our analyses result in two different topologies (Fig. 2). The support values for the extra group relationships are good, except for a variation for the clade *Perilestes* + *Perissolestes*. The clade *Archilestes* + *Austrolestes* is well supported with posterior probabilities (PP) equal to 100 (Fig. 2A). Similarly, the monophyly of *Austrolestes* is well-supported (PP = 96 or 98). The support for the clade *Perilestes* + *Perissolestes* depends on the analysis (PP equal respectively 71 and 49), but is corroborated by the geographic distribution of these genera (Fig. 2).

The topology found under the rjMCMC analysis indicates that the genera *Ecchlorolestes* + *Nubiolestes* + *Chlorolestes* form a monophyletic clade (PP = 49), with a unique African origin (Fig. 2B). This clade is not found in the other analyses as

*Ecchlorolestes* is grouped with the Australian genus *Synlestes* (PP = 43). Similarly, the position of the genus *Megalestes* greatly differs in our two analyses (Fig. 2). In the first, it is found close to the clade *Episynlestes* + *Chorismagrion* + *Phylolestes* (PP = 76) while in the second it is found close to the genus *Synlestes* (PP = 50). The ancestral state reconstruction is better resolved in the rjMCMC analysis with a unique origin of the African Synlestidae (Fig. 2B).

## Systematic palaeontology

Order **Odonata** Fabricius, 1793

Suborder **Anisoptera** Selys-Longchamps & Hagen, 1854

Family **Gomphaeschnidae** Tillyard & Fraser, 1940

Subfamily **Gomphaeschninae** Tillyard & Fraser, 1940

Genus *Alloaeschna* Wighton & Wilson 1986

**Type species.** *Alloaeschna paskapooensis* Wighton & Wilson, 1986.

*Alloaeschna paskapooensis* Wighton & Wilson, 1986

1986 *Alloaeschna marklae* Wighton & Wilson: 511, figs 9–10 syn. nov.

1986 *Alloaeschna quadrata* Wighton & Wilson: 513, figs 11–12 syn. nov.

(Figs 3–7)

**Holotype.** UAPC 6189 (= UAFIC 6189) (Fig. 3), part and counterpart collected by Betty A. Speirs the 3rd November 1982, adult ♀ with right forewing and left hindwing joined to the thorax, four abdominal segments, and fragments of right leg(s); housed in the E. H. Strickland Entomological Museum at the University of Alberta (Edmonton, Canada).

**Horizon and type locality.** Paskapoo Formation, Paleocene (Tiffanian), Blackfalds Insect and Plant Site (Dennis Wighton's site 1), Downstream from confluence with Blindman River, on left bank of Red Deer River, near Blackfalds, Alberta, Canada.

**Additional material.** *Alloaeschna marklae* Wighton & Wilson, 1986 syn. nov. (Fig. 4) UAPC 5553 (= UAFIC 5553), part and partial counterpart collected by Patricia Mitchell and Dennis C. Wighton in 1977, adult ♀ hindwing; housed in the E. H. Strickland Entomological Museum at the University of Alberta (Edmonton, Canada). Paskapoo Formation, Paleocene (Tiffanian), Blackfalds Insect and Plant Site (Dennis Wighton's site 1), Downstream from confluence with Blindman River, on left bank of Red Deer River, near Blackfalds, Alberta, Canada.

*Alloaeschna quadrata* Wighton & Wilson, 1986 syn. nov. (Fig. 5), UAPC 6181/6268 (= UAFIC 6181/6268), part and counterpart collected by Betty A. Speirs the 9 June 1980, adult forewing; housed in the E. H. Strickland Entomological Museum at the University of Alberta (Edmonton, Canada). Paskapoo Formation, Paleocene (Tiffanian), Joffre Bridge SW Insect layer (horizon C), Insect & Plant Layer, Road cut on South side of highway 11, West of 'missing infos', near Red Deer, Alberta, Canada.

**New material.** UAPC 6272/6266 (= UAFIC 6272/6266) part and counterpart collected by Betty A. Speirs in 1987 (Fig. 6), Joffre bridge SW Chert Layer, horizon B, road cut on south side of highway 11; UAPC 6261/6265 (= UAFIC 6261/6265) part and counterpart collected by Betty A. Speirs in 1987 (Fig. 7), same locality as holotype.

**Remark.** We provide a new photograph of the part illustrated in Wighton & Wilson (1986: figs. 1-2), and photographs of the counterpart not illustrated in Wighton & Wilson (1986: figs. 3-4). Similarly, we illustrate the part and counterpart of the specimen UAPC 6268/6185 (= UAFIC 6268/6185) while only the UAPC 6185 was illustrated in Wighton & Wilson (1986).

**Description.** UAPC 6272/6266 (Fig. 6): a nearly complete forewing, without coloration pattern in preserved part; pterostigma dark brown; wing 10.6 mm wide; distance between arculus and nodus 15.3 mm; distance from nodus to pterostigma 15.0 mm; Ax2 well-preserved; 13 antenodal crossveins of first row, 12 antenodal crossveins of second row; arculus angular; pterostigma elongate and narrow, ca. 1.05 mm wide, covering at least three cells, not basally recessed; pterostigmal brace strong, well aligned with basal side of pterostigma, strongly oblique; 10 postnodal crossveins not aligned with 10 postsubnodal crossveins; median space free; submedian space only traversed by CuP-crossing; hypertriangle free; discoidal triangle elongate, three-celled; MAb nearly straight, 4.8 mm long; a well-defined free subdiscoidal triangle; base of IR2 4.12 mm basal of nodus; base of RP3/4 5.3 mm basal of nodus; two crossveins between RP and IR2 basal of first oblique vein 'O'; first oblique vein 'O' 0.65 mm distad subnodus; area between RP1 and RP2 rather narrow with two-three rows of cells at level of pterostigma; base of RP2 well aligned with subnodus, RP2 smoothly undulated in its mid part; IR2 only slightly undulated, area between it and RP2 slightly widened in their undulated parts, with two-three rows of cells in its broadest part; IR2 and RP2 basally parallel, with only one row of cells; a well-developed and slightly undulated Rspl with one-two rows of cells between it and IR2; RP3/4 and MAa parallel and smoothly undulated, with one row of cells between them, except close to wing margin with two rows of cells; MAa and MP more or less parallel, postdiscoidal area weakly widened with three rows of cells at level of nodus; no Mspl; MP and CuA basally parallel with one row of rectangular cells between them; CuA with six posterior branches, cubito-anal area with four-five rows of cells between CuA and posterior wing margin; two rows of cells in anal area.

UAPC 6261/6265 (Fig. 7): a complete forewing, with basal part of membrane infuscated; pterostigma dark brown; wing length 38.11 mm, 9.55 mm wide; distance between base and

arculus 5.93 mm, between arculus and nodus 13.16 mm; distance from nodus to pterostigma 12.23 mm, from pterostigma to wing apex 5.08 mm; Ax1 and Ax2 well-preserved, with one antenodal crossvein between them; distance between Ax1 and wing base 4.07 mm; 14 antenodal crossveins of first row, 11 antenodal crossveins of second row; arculus angular; pterostigma elongate and narrow, 2.66 mm long and 1.10 mm wide, covering three cells, not basally recessed; pterostigmal brace strong, well aligned with basal side of pterostigma, moderately oblique; 9 postnodal crossveins not aligned with 8 postsubnodal crossveins; median space free; submedian space only traversed by CuP-crossing; hypertriangle free; discoidal triangle elongate, three-celled; MAb slightly angled in its basal third, 3.93 mm long; a well-defined free subdiscoidal triangle; base of IR2 ca. 3.55 mm basal of nodus; base of RP3/4 ca. 4.45 mm basal of nodus; two crossveins between RP and IR2 basal of first oblique vein 'O'; first oblique vein 'O' ca. 1 mm distad subnodus; pseudo-IR1 short, originating from RP1 below distal side of pterostigma; area between RP1 and RP2 rather narrow with three-four rows of cells between them; base of RP2 well aligned with subnodus, RP2 smoothly undulated in its mid part; IR2 only slightly undulated, area between it and RP2 slightly widened at their undulated parts, with two rows of cell at level of undulation, three rows of cells between them distally; IR2 and RP2 basally parallel, with only one row of cells; RP3/4 and MAa parallel and smoothly undulated, with one row of cells between them, except just after undulation and distally with two rows of cells; MAa and MP more or less parallel, postdiscoidal area weakly widened with three rows of cells at level of nodus; no Mspl; MP and CuA basally parallel with one row of rectangular cells between them; CuA with six posterior branches, cubito-anal area with four rows of cells between CuA and posterior wing margin; two rows of cells in anal area.

***Alloaeschna(?) nymph***

(Fig 8)

**Material.** UAPC 8502 (= UAFIC 8502) part collected by Betty A. Speirs in 1985; UAPC 8508 (= UAFIC 8508), part collected by Betty A. Speirs in 1983; housed in the E. H. Strickland Entomological Museum at the University of Alberta (Edmonton, Canada).

**Horizon and locality.** Paskapoo Formation, Paleocene (Tiffanian), Burbank, outcrops at the confluence of Red Deer River and Blindman River, about 1.2km from the Blindman River localities, Alberta, Canada.

**Description.** UAPC 8502: A nearly complete nymph (with apex of the abdomen missing), possibly an exuvia because the head seems to be dorsally opened.

Body brown without coloration pattern except on abdomen (see below), length ca. 29.0 mm; head ca. 5 mm long; mask partly preserved below head, apparently flat, of aeshnid-type; eyes large, reniform.

Thorax ca. 6.0 mm long, with right hind leg preserved, femur ca. 8.25 mm long; left wing pads putatively preserved.

Abdomen quite long, at least 16.6 mm long, 8.1 mm wide, with a distinct coloration pattern: dorsally with a median uncolored stripe bordered by another wider, brown line (on each side), these brown lines laterally bordered by an uncolored stripe followed by another brown line (apparently separated from another brown line by an uncolored stripe); seven segments preserved, of similar length but widening from base to apex, seventh the widest.

UAPC 8508: Body brown without coloration pattern except on abdomen (see below), length ca. 29.5 mm. Head and thorax poorly preserved.

Abdomen elongate, with a distinct coloration pattern: with a median uncolored stripe bordered by another wider, brown line (on each side).

**Remark.** We interpret these two specimens as *Alloaeschna* nymphs because they have proportions similar to that of the adults found in the same Formation, apparently flat masks

and elongated abdomens typical of Aeshnoptera, and also because of their patterns of coloration on the abdomen similar to those of the extant *Gomphaeschna* spp. (Kennedy, 1936), and because to date *Alloaeschna* is the sole anisopteran genus found in the Paskapoo Formation (despite the abundant material collected over more than 30 years).

### **Genus and species indeterminate 1**

(Fig 9)

**Material.** UAPC 6170/6171 (= UAFIC 6170/6171) part and counterpart collected by Betty A. Speirs in 1984 adult forewing; housed in the E. H. Strickland Entomological Museum at the University of Alberta (Edmonton, Canada).

**Horizon and locality.** Paskapoo Formation, Paleocene (Tiffanian), Joffre Bridge SW Insect layer (horizon C), Insect & Plant Layer, Road cut on South side of highway 11, West of 'missing infos', near Red Deer, Alberta, Canada.

**Description.** Distal half of a wing, preserved part ca. 31.5 mm long and ca. 11.8 mm wide; nine postnodals not aligned with eight postsubnodals; pterostigma dark brown, short, ca. 2.8 mm long and ca. 1.3 mm wide (two and an half cells long); pterostigmal brace not stronger than postsubnodals but distinctly oblique, well aligned with basal part of pterostigma; RP1 slightly undulating under and distad pterostigma; IR1 originating slightly distad pterostigma midlength; RP2 base aligned with subnodus, smoothly undulated in its mid part, separated from RP1 by one row of cells until pterostigmal brace, then separated by at least two and at most four rows of cells; first oblique vein 'O' deformed, close to subnodus; IR2 only slightly undulated, basally parallel to RP2 (with only one row of cells between them), area between it and RP2 slightly widened at their undulated parts, with two rows of cell at level of undulation, at least three rows of cells between them distally; a distinct  $R_{spl}$ , straight and with one row of cells between it and IR2.

**Remark.** The absence of ‘libelluloid’ gap in the postsubnodal area, the pterostigmal brace aligned with basal side of pterostigma, the rather short pterostigma, and overall, the area between RP1 and RP2 with only one row of cells up to one cell basad pterostigma level support an attribution to the Aeshnoptera rather than to the Petalurida, Gomphida, or the ‘libelluloid’ clade. The presence of a well-defined Rspl but with only one row of cells between it and IR2 supports an attribution to the Gomphaeschnidae. In fact, this wing is strongly similar to those of the *Alloaeschna* spp., but it is not possible to attribute it to a precise species or even genus.

Suborder **Zygoptera** Selys-Longchamps, 1854

Family **Synlestidae** Tillyard, 1917

Genus *Albertalestes* Jouault, & Nel gen. nov.

urn:lsid:zoobank.org:act:32F6C520-6485-4D2B-BFDB-22417B0B51C5

**Type species.** *Albertalestes paskapooensis* sp. nov.

**Etymology.** The genus name is a combination of the name of the Canadian state of Alberta and the genus name *Lestes*. Gender neutral.

**Diagnosis.** Forewing with long main longitudinal veins; subdiscoidal cell posteriorly closed; elongate pterostigma (i.e., covering five and a half cells); pterostigmal brace aligned with base of pterostigma; ‘lestine’ oblique crossvein strong, three and a half cells distad RP fork (into RP1 and RP2); RP fork in first third of distance between nodus and pterostigma; base of RP3/4 basad subnodus, closer to nodus than to arculus; base of IR2 below nodus and slightly anterior subnodus; area between MAa and RP3/4 wide along posterior margin of wing.

*Albertalestes paskapooensis* Jouault, & Nel sp. nov.

(Figs 10–11)

urn:lsid:zoobank.org:act:B90CD75A-E7A3-4187-8C5B-844B6F18DF26

**Type material.** Holotype UAPC 6185 (= UAFIC 6185) (part and counterpart of a nearly complete wing) collected by David Maddison the 19 September 1981 (Fig. 10); paratype UAPC 6269 (= UAFIC 6269) (part of the distal two-third of a wing), collected by Betty A. Speirs in 1980 (Fig. 11A-B). All the type specimen are housed in the E. H. Strickland Entomological Museum at the University of Alberta (Edmonton, Canada)

**Additional material.** UAPC 8152 (= UAFIC 8152) (part and counterpart of the distal two-third of a wing), collected by Betty A. Speirs in 1993 (Fig. 11C-F); housed in the E. H. Strickland Entomological Museum at the University of Alberta (Edmonton, Canada).

**Etymology.** Named after the origin of the type material i.e., Paskapoo Formation.

**Horizon and locality.** Holotype (UAPC 6185): Paskapoo Formation, Paleocene (Tiffanian), Joffre Bridge (Site 5), near Red Deer, Alberta, Canada. Paratype (UAPC 6269): Paskapoo Formation, Paleocene (Tiffanian), Joffre Bridge SW Insect layer (horizon C), Insect & Plant Layer, Road cut on South side of highway 11, West of ‘missing infos’, near Red Deer, Alberta, Canada. Additional specimen (UAPC 8152): Paskapoo Formation, Paleocene (Tiffanian), Joffre Bridge SW Insect layer.

**Diagnosis.** As for the genus, by monotypy (*vide supra*).

**Descriptions.** The three wings are very similar (see discussion).

Holotype UAPC 6185 (Fig 10): wing 32.7 mm long, 6.7 mm wide; petiole 5.5 mm long; distance from base to arculus 5.8 mm, from arculus to nodus 4.8 mm, from nodus to pterostigma 18.23 mm; from base to Ax1 4.02 mm, between Ax1 and Ax2 1.79 mm; arculus opposite Ax2; no secondary antenodal crossvein; antesubnodal space free; basal part of area between RP and MAa up to base of RP<sub>3/4</sub> free; terminal kink of costal margin reduced at nodus; nodal furrow reduced; nodal crossing Cr moderately oblique; subnodus perpendicular

to RP and RA; base of RP very close to base of arculus; stem of MA distinctly curved; MAa straight; stem of MA shorter than MAb; MAb 1.16 mm long, making an acute angle with MP+CuA; MP distinctly curved at its base (close to distal angle of discoidal cell), and distally straight; CuA nearly straight, with one-two rows of cells between it and MP; one row of cells in cubital area; discoidal cell basally closed (crossvein between MA and MP+CuA incompletely preserved); subdiscoidal cell narrow elongate, posteriorly closed; base of AA and CuP midway between Ax1 and Ax2; base of RP3/4 situated at 2/3 of distance between arculus and nodus, closer to nodus; base of IR2 situated below nodus, slightly anterior to subnodus; 20 postnodal crossveins, many of them not aligned with corresponding postsubnodals; pterostigma elongate, 3.12 mm long, 0.85 mm wide, covering five cells and a half; pterostigmal brace not stronger than postsubnodals but distinctly oblique; space between C and RA distad pterostigma with ca. 11 crossveins, two rows of cell in distal part; base of IR1 10.2 mm basad pterostigma (15 cells) and 2.2 mm distad base of RP2 (three cells); IR1 elongate, basally zigzagged and distally curved, with one row of cells between it and RP1, except close to wing margin with two rows of cells; base of RP2 five cells and a half distad subnodus, RP2 straight up to wing margin with a supplementary zigzagged longitudinal vein between it and IR1; a supplementary zigzagged longitudinal vein between RP2 and IR2; an oblique crossvein 'O' between RP2 and IR2 three cells and a half distad base of RP2; IR2 and RP3/4 weakly curved, tapering slightly and gradually towards the wing margin, with one row of cells in-between; one row of cells in postdiscoidal area up to wing margin.

Paratype UAPC 6269 (Fig 11A-B): preserved part 26.9 mm long, wing 6.5 mm wide; distance from nodus to pterostigma 15.96 mm; 16 postnodal crossveins, many of them not aligned with corresponding postsubnodals; pterostigma elongate, covering at least four cells; oblique crossvein situated one cell distad base of RP2; base of RP2 four cells and a half distad subnodus.

Additional specimen UAPC 8152 (Fig 11C-F): preserved part 17.9 mm long, wing 6.02 mm wide; distance from nodus to pterostigma 12.97 mm; at least 12 postnodal crossveins, many of them not aligned with corresponding postsubnodals; pterostigma elongate, 2.3 mm long, 0.75 mm wide, covering ca. six cells and a half.

**Remark.** These three wings likely belong to the same taxon. We support this assertion as follows; (1) they only differ in the position of the ‘lestine’ oblique crossvein, (2) four cells distad the base of RP2 in UAPC 6185 versus two in UAPC 6269, (3) the presence of 20 postnodal crossveins in UAPC 6185 versus 16 in UAPC 6269, and (4) base of RP2 five cells and a half distad subnodus in UAPC 6185 versus four cells and a half in UAPC 6269. These differences could be either due to differences between the fore- and the hind wings of the same taxon, or they could simply represent intraspecific variability.

Following the analysis of Bechly (2016), the affinities with the Caloptera Belyshev & Haritonov, 1983 are excluded because of the presence of a distinctly oblique pterostigmal brace (less oblique in paratype and additional specimen due to deformation). By contrast, it has the putative synapomorphies of the Euzygoptera Bechly, 1996 (*Lestomorpha* Bechly, 1996, and *Coenagrionomorpha* Bechly, 1996). These include; (1) longitudinal veins rather straight and long, (2) only one row of cells between CuA and the hind margin of wings, (3) only the two primary antenodal brackets Ax1 and Ax2 are retained in the antenodal space, (4) antesubnodal space without any crossveins, and (5) no antefurcal crossveins present in the space between RP and MA from arculus to midfork. Affinities with the *Coenagrionomorpha* are excluded because the pterostigma is not shortened, the postnodal and postsubnodal crossveins are not well aligned, and the ‘lestine’ oblique vein is present (Bechly, 2016).

The *Lestomorpha* have no clear wing venation synapomorphies. Within this clade, affinities with the Hemiphlebiidae Tillyard, 1926 are excluded because the new fossils have a great number of postnodals, an oblique crossvein, RP1 not kinked at the insertion of the

pterostigmal brace vein, and the presence of several secondary longitudinal veins. The new fossils share with the Cretaceous family Cretacoenagrionidae Bechly, 1996 (monotypic: *Cretacoenagrion alleni* Jarzembowski, 1990) the base of RP3/4 being closer to subnodus than to arculus, and the base of IR2 below the nodus and close to the subnodus (Jarzembowski, 1990). To date, there is no apomorphy to support the Cretacoenagrionidae, but the new fossils can be separated from this clade owing to their discoidal cell basally closed (*versus* open in *Cretacoenagrion alleni*), the highest number of postnodals (more than 12 *versus* nine), and the more developed venation between RP1 and RP2 (Jarzembowski, 1990: fig. 1).

The new fossils differ from the enigmatic Cretaceous genus *Cretalestes* Jarzembowski et al. 1998, in part because of the presence of the ‘lestine’ oblique crossvein (*versus* absent in *Cretalestes*), bases of RP3/4 and IR2 closer to nodus than to arculus (*versus* closer to arculus than to nodus), and the more developed venation between RP1 and RP2 (with at least four rows of cell *versus* two) (Jarzembowski et al., 1998: fig. 8).

The presence of a MP distinctly curved after its origin (at the distal angle of the discoidal cell) is a putative synapomorphy with the Eulestiformia Bechly, 1996 (Chorismagrionidae Tillyard & Fraser, 1938 + Lestida Bechly, 1996). The Chorismagrionidae only comprise the extant genus *Chorismagrion* Morton, 1914. The new fossils strongly differ from this genus because of their elongate pterostigma (*versus* short in *Chorismagrion*), the presence of ‘lestine’ oblique crossvein, the base of IR2 close to subnodus (*versus* four cells more distally), and the base of RP3/4 basal subnodus (*versus* being below it) (Münz, 1919: fig. 69).

The Lestida (Perilestidae Tillyard & Fraser, 1938, Synlestidae Tillyard, 1917, Megalestidae Tillyard & Fraser, 1938, and Lestidae Calvert, 1901) have a basal closure of the discoidal cell, as in the new fossils (only visible in the holotype). The crossvein closing this cell is strongly oblique in the holotype as in the lestid genus *Archilestes* Selys, 1862

(Donnelly, 1981). The new fossils differ from the Perilestidae (*Perilestes* Hagen, 1862, *Perissolestes* Kennedy, 1941, *Palaeoperilestes* Zheng et al., 2016) because of their elongate pterostigma, the presence of the ‘lestine’ oblique crossvein (not preserved in the additional specimen but likely present), the base of IR2 below subnodus instead of being four cells more distally, base of RP3/4 basal subnodus instead of being distad it (Münz, 1919: fig. 70; Kennedy, 1941; Zheng et al., 2016). The Megalestidae and Lestidae generally share with the new fossils the presence of the ‘lestine’ oblique crossvein (absent in *Archilestes*), but differ from them because they have the bases of RP3/4 and IR2 closer to arculus than to nodus (Münz, 1919: figs 39-43). The Eocene family Eolestidae (*Eolestes* Cockerell, 1940) and the Paleocene family Menatlestidae Nel & Jouault, 2022 lack the ‘lestine’ oblique crossvein and have the bases of RP3/4 and IR2 closer to arculus than to nodus (Cockerell, 1940; Greenwalt & Bechly, 2014; Nel & Jouault, 2022). The Eocene genus *Lutetialestes* Greenwalt & Bechly, 2014 (uncertain family) has a different configuration of the bases of RP3/4 and IR2 (i.e., closer to arculus than to nodus: Greenwalt & Bechly, 2014).

The new fossil shares similarities with the Synlestidae due to the positions of the bases of RP3/4 and IR2, the shape of the pterostigma, the presence of main longitudinal veins and their intercalaries, and the strongly oblique MAb. Collectively, we use these features to argue that the new fossils are considered to be a member of this family. The new fossil differs from *Synlestes* Selys, 1868, *Episynlestes* Kennedy, 1920, *Nubiolestes* Fraser, 1945, and *Chlorolestes* Selys, 1862, in the subdiscoidal cell posteriorly closed versus opened, and the presence of the ‘lestine’ oblique crossvein (Münz, 1919: figs 63, 66; Kennedy, 1920; Schmidt, 1943). *Ecchlorolestes* Barnard, 1937 and the Eocene genera *Madres* Petrulevičius, 2018 and *Inacayalestes* Petrulevičius, 2015 have a ‘lestine’ oblique crossvein, but their subdiscoidal cell is often posteriorly opened (Barnard, 1937; Petrulevičius, 2015, 2018). The genus *Ecchlorolestes* also has a comparatively shorter pterostigma (i.e. covering less cells)

(Riss, 1921). The genera *Phylolestes* Christiansen, 1948 and *Sinolestes* Needham, 1930 have a subdiscoidal cell posteriorly closed, often no ‘lestine’ oblique crossvein, and a narrower area between MAa and RP3/4 near posterior margin of wing (Needham, 1930; Schmidt, 1943; Christiansen, 1948). The new fossils also differ from *Sinolestes* because they have the base of IR2 below the nodus and subnodus (*versus* far distad nodus in *Sinolestes*) (Needham, 1930; To & Quang, 2018). Note that *Sinolestes* may have a crossvein interpreted as the ‘lestine’ oblique crossvein, but this crossvein is weak and always far distad origin of RP2. The new fossils differ from the genus *Megalestes* Selys-Longchamps, 1862, at least, because of their elongate pterostigma, their IR2 originating below nodus and subnodus (*versus* well before in *Megalestes*) (Selys-Longchamps, 1862; Gyeltshen et al., 2017; Yu & Xue, 2020).

The Cretaceous genus *Gaurimacia* Vasilenko, 2005 shares with the new fossils a subdiscoidal cell posteriorly closed and a ‘lestine’ oblique crossvein, but differs from the latter in the much shorter main longitudinal veins (i.e. the entire wing is shorter in *Gaurimacia*), the base of RP2 in a distinctly more distal position (i.e. at mi-distance between nodus and pterostigma vs. distinctly closer to nodus than to pterostigma in the new fossils), area between RP3/4 and IR2 not strongly narrowed near wing margin (*versus* widening close to wing margin), and the pterostigmal brace not aligned with base of pterostigma (Vasilenko, 2005: fig. 1). The Cretaceous genus *Cretaphylolestes* Huang et al., 2022 differs from the new fossil, at least, because of the absence of the oblique vein and a distinctly shorter pterostigma (Huang et al., 2022). Therefore, we consider that the new fossils belong to a new genus and species that can be attributed to the Synlestidae. Recently, a new genus of the family Synlestidae has been described from the Paleocene of the Menat Formation as *Palaeophylolestes* Doriath-Döhler et al., 2023 (Doriath-Döhler et al., 2023). The new specimen clearly differs from this genus, *inter alia*, because of its MAa, MP, and CuA that

reach the posterior wing margin well before the pterostigma (*versus* reaching posterior wing margin very close or below the pterostigma in *Palaeophylolestes*: apomorphic to this genus).

The specimen UAPC 8152 is not placed in the type series because numerous characters in the basal part of the wing are not preserved. The configuration of the nodus and the configuration of the IR2 base, or the conformation of the discoidal and anal area are unknown while they are used in the diagnosis of the new genus.

## Discussion

### Phylogenetic reconstructions and their biogeographical implications

Our phylogenetic analyses in Bayesian inferences, when compared with the results of Simaika et al. (2020), support similar relationships for a few genera but also conflict with the placement of some others (Fig. 2).

In our first analysis, we found the genera *Nubiolestes* and *Cholorolestes* grouped together and formed the first African radiation of the Synlestidae (Fig. 2A). The genera *Synlestes* grouped with *Ecchlorolestes* would be the second African branch of the Synlestidae (Fig. 2A). In our second analysis, we found a monophyletic clade (*Ecchlorolestes* + *Nubiolestes* + *Chlorolestes*). This topology would indicate that the African Synlestidae have a single common origin (Fig. 2B). From a parsimony perspective, this second scenario is the most likely. To date, no fossil of the family Synlestidae is known from African deposits. Note, that the posterior probabilities of these two conflictual topologies do not allow for choosing which one is the best (Fig. 2). We suggest that including the genus *Sinolestes* Needham, 1930 may help to clarify this conflict, but no molecular data are available for this taxon.

Interestingly, the monophyletic clade (*Ecchlorolestes* + *Nubiolestes* + *Chlorolestes*), found in our second analysis, resembles the topology of Simaika et al. (2020), except that the

genus *Phylolestes* is not nested within this clade (Fig. 2B). The position of *Megalestes* differs in all our analyses and from the results of previous analyses (Fig. 2; Simaika et al., 2020). In our dataset, *Megalestes* is the only Asian species. We suggest that including the genus *Sinolestes*, another Asian genus, to the analysis may help to clarify its position. The genus *Phylolestes* is found close to *Chorismagrion* in both analyses. This suggests that *Phylolestes* has independently dispersed into the Caribbean while originating from the New World. This independent dispersion was also found in previous analyses (Simaika et al., 2020).

The biogeographical history of the family Synlestidae results from millions of years of speciation and extinction processes. The latter are difficult to disentangle using the extant diversity of the clade (i.e., reduced number of species), and the scarce fossil record of the family. Nevertheless, the Cretaceous and Paleocene species of Synlestidae were distributed in relatively cold and temperate biomes in the northern hemisphere (North America and Asia; Fig. 12). This indicates that the distribution of the family has greatly changed throughout time and has likely been shaped by numerous geological and environmental events (Himalaya uplift, PETM biome changes, glaciations). In fact, the pre-PETM distribution is hardly comparable with the current distribution of the family because no Synlestidae are known from North America or southern South America today (Fig. 12). Extant species of the family are found in central Asia, eastern Australia, and southern Africa, and in Central America and the Caribbean (Fig. 12).

There are several hypotheses explaining the decline of the family in North America. The most likely one is that the temperate biome extension toward high latitude, occurring during the PETM, may have affected the habitats of *Albertalestes* leading to its disappearance and to that of other putative synlestids inhabiting North America (Fig. 12). For instance, it has been suggested that changes in plant groups in terrestrial environments often trigger faunal changes in past freshwater insect fauna (Sinitschenkova, 2003). The second hypothesis would

be that other Odonata lineages out-competed the Synlestidae leading this group to decline. This double-wedge pattern, in which one clade declines while the other thrives, is well-documented in the fossil record (Sepkoski, 1996). A similar hypothesis has been proposed to explain the decline of the Palaeodictyoptera during the Permian Period, out-competed by the Hemiptera (Labandeira, 1997).

Similarly, the extinction of the Synlestidae in the southern part of South America can be explained by 'similar' hypotheses (Fig. 12). First, the environmental modifications in the region (e.g., uplift of the Andes, aridification) are known to have greatly shaped the diversity dynamics of many plant, vertebrate and invertebrate lineages (e.g. Pérez-Escobar et al., 2022). It would not be surprising if they also affected the Synlestidae. During the Eocene Epoch, much of South America and Africa became arid (Herold et al., 2014). This aridification has constrained the distribution (migration) of some clades and caused others to decline due to local extinctions (Jouault et al., 2021; Aria et al., 2023). The extant Synlestidae are mainly found in areas where tropical or warm-temperate forests were present during the Eocene Epoch (northern South America, southern east of Africa, eastern part of Australia and central region of Asia). It would not be surprising if the Synlestidae had 'taken refuge' in certain areas with biomes favorable to their survival (Fig. 12).

Therefore, we suggest that the Synlestidae experienced several extinction events throughout their evolutionary history. We suggest that a holistic phylogenetic analysis encompassing all the fossil and extant diversity of the Zygoptera would provide further insight into the evolution of the clade and allow us to resolve unanswered questions such as their local extinction.

### **Refining the limits of the *Alloaeschna* species**

The genus *Alloaeschna* was initially divided into three species (Wighton & Wilson, 1986) largely based on the configuration of the discoidal triangle (divided into two or three cells) and the conformation of the ribs (i.e. horizontal in *A. quadrata*, while vertical in the other species). However, the plasticity of this part of the wing is extremely high in the family Aeshnidae (closely related to the Gomphaeschnidae) and the utilization of these characters to separate species has been suggested to be unreliable (Nel et al., 1994). The perfect illustration of this variability is found in the extant genus *Aeshna* for which a specimen can have a different number of crossveins in the discoidal triangle or the submedian space between its left and right wings (see. *Aeshna cf. juncea*: Fig. 13A). Such variability and the poor diagnostic value of this character were already pointed out over a hundred years ago by Cockerell (1908). We further illustrate the plasticity in wing venation of Aeshnidae by providing an illustration of a specimen of *Heliaeschna fuliginosa* Karsch, 1893 in which there is a different conformation of the discoidal triangle between the left and right forewings but also between the left and right hind wings (Fig. 13B).

All the lengths of the *Alloaeschna* forewings presented in this study fall in the intraspecific range of variability known for extant species of Aeshnoidea (38-45 mm) (Aguesse, 1968). They also have similar widths (ca. 9-10 mm) and similar discoidal triangle length-to-width ratios (0.4 to 0.45). The new specimens of *A. paskapooensis* also fill the gap originally recorded for the number of antenodals between *A. quadrata* and *A. paskapooensis*, with a first row composed of thirteen or fourteen crossveins and a second row of nine to twelve crossveins (Wighton & Wilson, 1986). Similarly, the new specimens indicate that the number of postnodals can vary between nine to eleven and the number of postsubnodals from seven to ten. Previously the species *A. quadrata* was thought to be different from *A. paskapooensis* because its pterostigma was covering more cells (3.3 versus 2.6) but the new

specimen UAPC 6261/6265 has a pterostigma covering three cells, which fills the gap used to separate the two species (Wighton & Wilson, 1986).

Another argument used previously to justify the separation of *A. quadrata* from *A. paskapooensis* was the coloration patterns present at the base of the wings of *A. quadrata* and assumed to be absent in *A. paskapooensis* (Wighton & Wilson, 1986). If the wing coloration patterns are indeed useful to separate species and often diagnostic (e.g. Jouault et al., 2022), it is important to consider the intraspecific variability of these patterns but also their possible 'maturation' between a young individual (teneral) and an older individual. Indeed, during the maturation period, dragonflies often lack their adult coloration, a phenomenon well documented in many present-day genera (e.g. *Calopteryx*, *Crocothemis*). In the present specimens, we notice the presence of darkened areas at the base of the hind wing of *A. paskapooensis* (Fig. 3B), which completely limits the diagnostic value of this character to separate *Alloaeschna* species. Therefore, in our opinion, it is impossible to reliably separate *A. quadrata* from *A. paskapooensis*.

The type specimen of *A. marklae* is poorly preserved and deformed. The deformation questions the diagnostic value of the angle (i.e. outer margin of triangle sharply angled anteriorly) used to separate *A. marklae* from *A. paskapooensis* (Wighton & Wilson, 1986). Those authors also proposed that the presence of a discoidal triangle with two cells, and a supratriangle (= submedian space) with one crossvein, are diagnostic features, but as discussed above these are extremely plastic and cannot be used to separate species (Wighton & Wilson, 1986). All the differences between *A. marklae* and *A. paskapooensis* fall in the range of intraspecific variability. Based on these comparisons, we consider the species *A. quadrata* and *A. marklae* as junior synonyms of *A. paskapooensis*, and consequently synonymized these two species under *A. paskapooensis*.

### **Paleoecological implications of the presence of nymphs or exuviae**

Fossil nymphs or exuviae of Odonata are rather rare, and in most cases, adults are found without associated nymphs or exuviae (e.g. Nel et al., 2022; Nel & Jouault, 2022). This differential fossilization is partially explained by the development of hemimetabolous insects in which the larvae and the adults often live in different environments (i.e., aquatic larval stage). If this type of development provides advantages (e.g., occupation of distinct ecological niches) it ‘biases’ the fossil record. In fact, the fossilization sites of adults can be distinct and far from the place where the nymphs lived and developed (i.e., rivers and lakes *versus* forests or more opened habitats) with different chemical proprieties. Consequently, this complicates the assignation of a given nymph to a species described based solely on images. This issue may result in two scenarios; the description, and placement of the nymphs in a distinct genus – which artificially increases the diversity of the clade – or the assignation of nymphs to the wrong genus.

In the present case, the two nymphs or exuviae are interpreted as belonging to the genus *Alloaeschna*, even if it is impossible to certify that this is a fact (Fig. 8). The discoveries of nymphs or exuviae in the same formation (and relatively close to each other in terms of distance) lead us to hypothesize that the fossilization area encompasses the place where both the larvae developed and the adults lived. Following this hypothesis and considering the fluvial origin of the Paskapoo Formation – previously interpreted to be deposited principally from fluvial to floodplain environments (e.g. Hoffman & Stockey, 2000) – and the fossil record (Glass, 1997; Hoffman & Stockey, 2000), the Paskapoo Formation was dominated by a freshwater environment with aquatic vegetation and water of relatively good quality (allowing the development of the larvae). In fact, Hoffman & Stockey (2000) described diverse stratigraphic units interpreted to represent five freshwater environments of deposition (e.g. flood plain, fluvial channel, abandoned channel, swamp, and crevasse splay).

The sandstones exhibit cross-bedding structures, ranging from medium to coarse-grained, characteristic of river channel deposits (Hoffman & Stockey, 2000). Significantly, the sandstones contain conglomeratic material. The siltstones and mudstones rich in plant fossils, as well as the presence of paleosols, have been interpreted as the presence of crevasse splays, overbank areas, and shallow swamps (see Hoffman & Stockey, 2000 for more detail). By comparison, the larvae of the extant spp. of *Gomphaeschna* (one of the closest extant relatives) live in *Sphagnum* bogs, 'cedar' swamp on aquatic herbaceous plants and/or in small pools (Kennedy, 1936; Dunkle, 1977). The larvae of Odonata are fierce predators feeding on other aquatic invertebrates or small vertebrates from their immediate environment, and we suggest that *Alloaeschna* nymphs were likely able to predate on other large invertebrates because of their large size. In the Paskapoo Formation, numerous larvae of Tipulidae (and other unidentified Diptera), some Ephemeroptera, and aquatic Coleoptera have been documented providing a sufficient diversity of prey for Anisoptera larvae (Mitchell & Wighton, 1979; Wighton, 1980).

An alternative scenario would be that the dried exuviae, which are quite robust and enduring objects, have been transported by winds (allochthonous deposit). This phenomenon is thought to occur for exuviae trapped in amber (Bechly & Wichard, 2008). In fact, the encounter of exuviae and amber is quite unlikely to occur naturally because amber is produced, most of the time, above the ground while larvae of Odonata developed in water. Therefore, it is assumed that the dried exuviae or nymphs found in amber were transported by winds that trapped them in resin flows, or that the larvae got stuck in resin flow when climbing on the trunks or grasses surrounding the water for their imaginal molt. Another unlikely scenario is that resin falls directly into the water on a nymph and engulfs it in situ. Nevertheless, if the 'allochthonous hypothesis' is retained, it is possible that the two

specimens belong either to the genus *Alloaeschna* or to another undescribed Anisoptera genus that lived in Alberta during the Paleocene.

## **Conclusion**

Our phylogenetic analyses, based on molecular data, suggest that conflictual topologies can be found when reconstructing synlestid evolution. In our present state of knowledge, it is difficult to choose which biogeographical scenario occurred. The description of the first Zygoptera from the Paskapoo Formation, namely *Albertalestes paskapooensis* gen. et sp. nov., increases the fossil diversity of the family Synlestidae. This new taxon and the two early Eocene synlestid genera in Argentina indicate that this family was much more widespread in the past, and likely experienced several local extinction events. Several divers may be responsible for these extinctions, but we suggest that the biome modifications during the Paleogene are likely involved. The study of new specimens of the genus *Alloaeschna* suggests that the previous diversity of the genus was artefactual and that only one species populated the Paskapoo Formation. In fact, the new specimens fill gaps in character variability used previously to separate the three constitutive species of the genus. This revision led to the synonymization of *A. marklae* syn. nov. and *A. quadrata* syn. nov. under *A. paskapooensis*.

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Figure captions:

**Figure 1.** Distribution of Paleocene odonatans plotted on a map of the Earth in its present configuration (modified after Jouault et al., 2020).

**Figure 2.** Bayesian trees resulting from our two analyses with results of the parsimony ancestral state reconstruction for the biogeography indicated at the node and along branches. Values at nodes represent the posterior probabilities. **A**, Using the models specified by PartitionFinder; **B**, Using the rjMCMC model. H: Hemiphlebiidae; Per: Perilestidae; Les: Lestidae.

**Figure 3.** *Alloaeschna paskapooensis* Wighton & Wilson, 1986, holotype UAPC 6189 (= UAFIC 6189), Tiffanian of Paskapoo Formation, Alberta, Canada. **A**, Forewing; **B**, Hind wing; **C**, Forewing. Scale bars represent 5 mm.

**Figure 4.** *Alloaeschna marklae* Wighton & Wilson, 1986 syn. nov. UAPC 5553 (= UAFIC 5553), Tiffanian of Paskapoo Formation, Alberta, Canada, hind wing. Scale bar represent 5 mm.

**Figure 5.** *Alloaeschna quadrata* Wighton & Wilson, 1986 syn. nov. UAPC 6181/6268 (= UAFIC 6181/6268), Tiffanian of Paskapoo Formation, Alberta, Canada. **A**, Part of forewing. **B**, Counterpart of forewing. Scale bars represent 5 mm.

**Figure 6.** *Alloaeschna paskapooensis* Wighton & Wilson, 1986, additional specimen UAPC 6272/6266 (= UAFIC 6272/6266), Tiffanian of Paskapoo Formation, Alberta, Canada. **A**, Part

of forewing; **B**, Counterpart of forewing; **C**, Interpretative drawing of forewing venation with main veins and structures labeled. Scale bars represent 5 mm.

**Figure 7.** *Alloaeschna paskapooensis* Wighton & Wilson, 1986, additional specimen UAPC 6261/6265 (= UAFIC 6261/6265), Tiffanian of Paskapoo Formation, Alberta, Canada. **A**, Part of forewing; **B**, Counterpart of forewing; **C**, Interpretative drawing of wing venation. Scale bars represent 5 mm.

**Figure 8.** Putative nymphs of the genus *Alloaeschna*, Tiffanian of Paskapoo Formation, Alberta, Canada. **A**, Specimen UAPC 8502 (= UAFIC 8502); **B**, Specimen UAPC 8508 (= UAFIC 8508). Scale bars represent 5 mm.

**Figure 9.** Indeterminate specimen of Gomphaeschnidae, UAPC 6170/6171 (= UAFIC 6170/6171), Tiffanian of Paskapoo Formation, Alberta, Canada. Scale bars represent 5 mm.

**Figure 10.** *Albertalestes paskapooensis* gen. et sp. nov., holotype UAPC 6185 (= UAFIC 6185), Tiffanian of Paskapoo Formation, Alberta, Canada. **A**, Part of forewing; **B**, Counterpart of forewing; **C**, Interpretative drawing of forewing venation with main veins and structures labeled. Scale bars represent 5 mm.

**Figure 11.** *Albertalestes paskapooensis* gen. et sp. nov., Tiffanian of Paskapoo Formation, Alberta, Canada. **A**, Paratype specimen UAPC 6269 (= UAFIC 6269); **B**, Interpretative drawing of paratype wing venation; **C**, Part of referred specimen UAPC 8152 (= UAFIC 8152); **D**, Counterpart of referred specimen UAPC 8152 (= UAFIC 8152); **E**, Interpretative drawing of wing venation of part of UAPC 8152 (= UAFIC 8152); **F**, Interpretative drawing of wing venation of counterpart of UAPC 8152 (= UAFIC 8152). Scale bars represent 5 mm.

**Figure 12.** Changes in the late Paleocene biomes with the distribution of fossil and extant Synlestidae indicated (modified from Korasidis et al., 2022).

**Figure 13.** Illustration of variability and plasticity in Aeshnidae species. **A**, Line drawing of wing bases of an extant specimen of *Aeshna* cf. *juncea* with main veins labelled; **B**, Photograph of *Heliaeschna fuliginosa* Karsch, 1893, specimen housed in MNHN. Scale bar represents 2 mm.