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The early Eocene *Swauka ypresiana* n. gen. n. sp., the oldest gossamerwing damselfly (Odonata, Epallagidae, Epallaginae) and first fossil insect described from the Swauk Formation of central Washington, U.S.A.

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Abstract

We describe *Swauka ypresiana* n. gen. n. sp., the second fossil gossamerwing damselfly (Odonata, Zygoptera, Epallagidae, Epallaginae) and its oldest occurrence. It is the first fossil insect reported from the Swauk Formation of central Washington State, U.S.A. It was recovered from the "Sandstone facies of Swauk Pass," a fluvial unit, immediately below the Silver Pass Volcanic Member of the Swauk Formation, which has a U–Pb zircon CA-ID-TIMS age of 51.364 ± 0.029 Ma. The host deposits probably represent mud-dominated floodplain lake or oxbow lake environments.

UUID: http://zoobank.org/20167852-bcbc-4f8b-b372-dffa591abd6a

Non-technical Summary

We describe *Swauka ypresiana*, a new genus and species of early Eocene (about 51 million years ago) gossamerwing damselfly. This is the second known fossil gossamerwing and the oldest occurrence. It is the first fossil insect reported from the Swauk Formation of central Washington State, U.S.A.

Introduction

Gossamerwing damselflies (Zygoptera, Epallagidae, Epallaginae) comprise 79 extant species in 9 genera (Paulson et al., 2024) that predominantly inhabit subtropical and tropical regions of eastern Asia; a single species ranges westward through the Middle East to the Balkans (Dijkstra et al., 2020). The damselflies develop in running waters, usually in forest streams, but sometimes in irrigation channels (Silsby, 2001). Epallagidae are divided into two subfamilies: the extant Epallaginae and the extinct Eodichromatinae. The Eodichromatinae have an increasingly well-known fossil record, with occurrences in North America from the Ypresian to the Priabonian or Rupelian, and in Europe from the Ypresian to the Chattian (e.g., Bechly, 1998; Petrulevičius et al., 2007; Nel et al., 2013; Bechly et al., 2020; Ferwer and Nel, 2020; Archibald and Cannings, 2021, table 1). The eodichromatine *Republica weatbrooki* Archibald and Cannings, 2021, was described from the Ypresian Tom Thumb Tuff Member of the Klondike Mountain Formation at Republic, Washington, U.S.A. (Archibald and Cannings, 2021).

Fossil Epallaginae, however, are only known from *Elektroeuphaea flecki* Nel et al., 2013, which is represented by a single specimen in late Eocene Baltic amber (Nel et al., 2013). Cockerell (1924) described *Epallagites avus* Cockerell, 1924 (Ypresian, Green River Formation, Colorado, U.S.A.) as a member of what would today be considered the Epallaginae, however, we agree with Carpenter (1992), Nel and Paicheler (1992), and Petrulevičius et al. (2007) that its only fossil is too fragmentary and poorly preserved to be considered a member of even the family. Other fossils originally associated with Epallaginae are now assigned to other taxa or are also now considered too fragmentary to be placed in any family (Nel et al., 2013).

Here, we describe a new genus and species of Epallaginae, the second fossil that can confidently be attributed to the subfamily and its oldest member. It is the second epallagid from Washington and the first fossil insect described from the Swauk Formation of central Washington, U.S.A.

Geological setting

The Swauk Formation is a fluvial, lacustrine, and volcanic unit approximately 4800 m thick in central Washington State. It is formally subdivided into one member (the Silver Pass Volcanic Member of Tabor et al., 1984) and seven informal sedimentary units (Taylor et al., 1988). Recent U–Pb zircon CA-ID-TIMS ages place the age of the base of the Swauk Formation at 59.919 ± 0.098 Ma, the age of the Silver Pass Volcanic Member at 51.364 ± 0.029 Ma, and the age of the unconformably overlying Teanaway Basalt at 49.341 ± 0.033 Ma (Eddy et al., 2016). Taylor et al. (1988, fig. 3) provide a map of the eastern Swauk basin with the fossil locality labelled "Swauk Pass."

Plant fossils similar to those of the Chuckanut Formation have been reported from the Swauk Formation, but they have not been formally analyzed taxonomically or paleoclimatically. Inferences about past vegetation and climate for the Swauk thus rely on similarities to better-studied Eocene locations such as the Chuckanut Formation (Mustoe and Gannaway, 1997; Breedlovestrout et al., 2013).

Our report identifies the first fossil insect recorded from the Swauk Formation. The fossil wing was preserved in fine mudstone recovered at an outcrop on the old Swauk Pass Road (also called Blewett Pass) in the "Sandstone Facies of Swauk Pass" (Taylor et al., 1988). This outcrop consists of sheetlike to lenticular bodies of trough cross-bedded sandstone interpreted as fluvial channel deposits, interbedded with thin sheets of ripple-laminated sandstone and mudstone interpreted as fluvial overbank deposits, including floodplain lakes or oxbow lakes. The floodplain deposits typically contain plant fossils and organic debris such as branches and disaggregated leaves. Four interbedded tuffs at the top of this exposure are interpreted as distal portions of the Silver Pass Volcanic Member (Taylor et al., 1988; Evans and Johnson, 1989). Accordingly, the fossil is interpreted as approximately the same age as or slightly older than the Silver Pass Volcanic Member at approximately 51.4 Ma.

The Swauk Formation is the fill of a fault-bounded basin between the Straight Creek fault zone and Leavenworth fault zone. As such, it is part of a complex of early Paleogene sedimentary basins within a series of strike-slip faults in central to northwest Washington and southwest British Columbia including the Chumstick, Chuckanut, Huntingdon, and other basins (see Johnson, 1984, fig. 10, for a map of these formations). The Swauk and Chuckanut formations may have been deposited in a single basin, with the Swauk subsequently transported by faulting 100–150 km southeast (Mustoe and Gannaway, 1997; Eddy et al., 2016). The Swauk and Chumstick basins might also have been joined episodically (Evans and Johnson, 1989; Evans, 1991, 1994, 2022). Alternatively, deposition in the Swauk basin may have been completed before the initial deposition in the Chumstick basin (Donaghy et al., 2021, 2022).

Materials and methods

We examined UWBM PB 56327A and B (part and counterpart) (Fig. 1), a fairly complete wing with color patterning preserved. It was found by Donald Hopkins in 1986 in the Swauk Formation of central Washington, U.S.A. at Blewett Pass, BMNHC locality B2815. We compared this with specimens and photographs of the wings of all genera of the family. Although the name Euphaeidae is more commonly used for the family (Dijkstra et al., 2014) we followed Bechly (1998, 1999) in using Epallagidae, which has priority, the subfamily name Epallaginae rather than Euphaeinae, and Eodichromatinae rather than Eodichrominae for that subfamily.

Contrary character states of compared taxa are provided in brackets. Terminology of wing morphology follows Bechly (1998): a = arculus; Ax1 and Ax2 = primary antenodal crossveins 1 and 2; C = costal vein; CuA and CuP = cubitus anterior and posterior veins; db = discoidal bracket; IR1 and IR2 = interradius veins 1 and 2; MAb = the part of MA forming the distal side of the quadrangle; MA and MP = media anterior and posterior veins; n = nodus; O = oblique vein; pt = pterostigma; RA = radius anterior vein; RP1–2 = the radius posterior distad the origin of R3–4 and basad its branching to RP1 and RP2; RP1, RP2, and RP3–4 = branches of the radius posterior; s = subnodus; ScP = subcostal posterior vein.

We used the mean annual temperature (MAT) categories of Wolfe (1975): microthermal, ≤ 13°C; mesothermal, > 13°C to < 20°C; megathermal, ≥ 20°C in our analyses.

Repository and institutional abbreviation. The fossil is housed in the collections of the Burke Museum of Natural History and Culture (BMNHC), University of Washington, Seattle, Washington, U.S.A. (UWBM PB number).

Systematic paleontology

Order **Odonata** Fabricius, 1793
Suborder **Zygoptera** Sélys, 1854
Family **Epallagidae** Needham, 1903
Subfamily **Epallaginae** Needham, 1903
Genus ***Swauka*** new genus
Figure 1

Type species. *Swauka ypresiana* n. gen. n. sp., by monotypy.

Diagnosis. As for the type species by monotypy.

Occurrence. As for its only species, below.

Etymology. The genus is named for the Swauk Formation. Gender, feminine.

Remarks. We assign *Swauka* n. gen. to the Epallagidae by the combination of (Bechly, 1998; Petrulevičius et al., 2007; Nel et al., 2013) its discoidal bracket formed by the thickened distal sides of the discoidal (MAb) and subdiscoidal (basal CuA) cells; quadrangle elongate and narrow, longer than wide; both antenodal rows with numerous accessory crossveins; and densely reticulate venation. Although some character states in part diagnostic of the Epallaginae, such as the aligned and bracket-like antenodal crossveins, cannot be established in this incomplete wing, RP1-2 appears strongly curved at its base (extreme basal portion not preserved), coming very close to, or touching, RA. This, in combination with the discoidal bracket and quadrangle shape is only found in the wings of Epallaginae, never in those of Eodichromatinae or Zacallitidae, which are otherwise similar in many ways.

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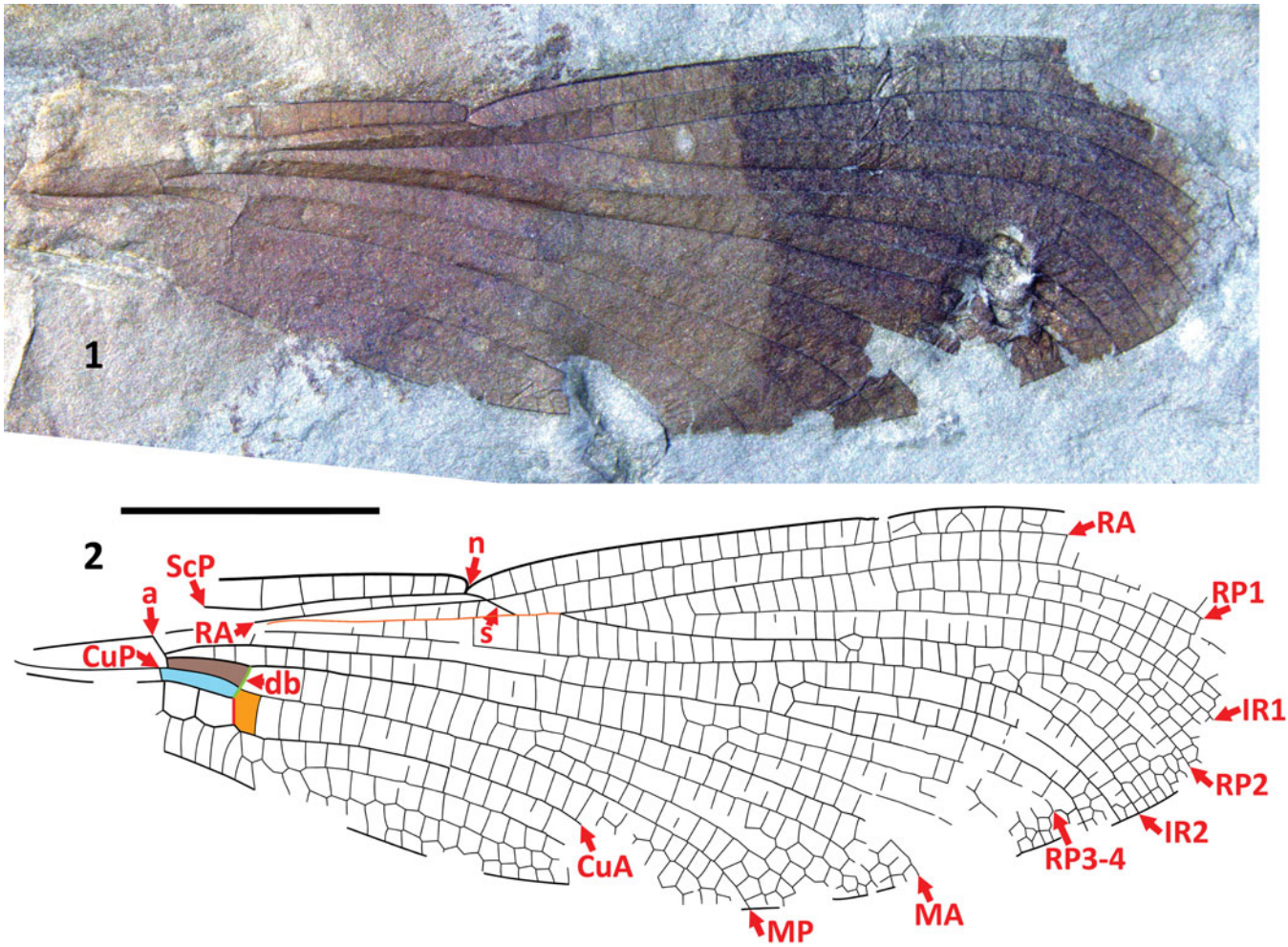

Figure 1. The holotype wing of *Swauka ypresiana* n. gen. n. sp. UWBM PB 56327A, B: (**1**) photograph of the part (A side); (**2**), drawing from both the part and counterpart (A and B sides). The discoidal bracket (thickened distal side of the quadrangle and subquadrangle) is green and CuA immediately distad the discoidal bracket is red; the quadrangle is colored light brown, the subquadrangle is light blue, and the MP–CuA space cell immediately distad the subquadrangle is orange; RP1-2 is orange; a = arculus; Ax1, Ax2 = primary antenodal crossveins 1, 2; CuA = cubitus anterior vein; CuP = cubitus posterior vein; db = discoidal bracket; IR1 and IR2 = interradius veins 1 and 2; MA = media anterior vein; MP = media posterior vein; n = nodus; pt = pterostigma; RA = radius anterior vein; RP1–2 = the radius posterior distad the origin of RP3–4 and basad its branching to RP1 and RP2; RP1, RP2, RP3–4 = branches of the radius posterior; s = subnodus; ScP = subcostal posterior vein. Scale bar = 5 mm.

Swauka ypresiana new genus new species
Figure 1

Holotype. UWBM PB 56327A and B (part and counterpart) (Fig. 1), housed in the collections of the Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, U.S.A.

Diagnosis. Distinct from other Epallaginae and all Eodichromatinae by: CuA (Fig. 1, red) continuing from discoidal bracket (Fig. 1, db green) at shallow angle to db, closer to right angle to posterior margin [closer to or subparallel with angle of posterior margin], MP–CuA space immediately distad subquadrangle (Fig. 1, orange) much wider than subquadrangle, about as wide as discoidal bracket length; and by postsubnodal and postnodal crossveins not strictly aligned (see Nel et al., 2013).

Occurrence. Mid-Ypresian of the lower Swauk Formation on the old Swauk Pass Road (also called Blewett Pass), Washington, U.S.A.

Description. Holotype wing (fore- or hind). As in the diagnosis and the following. Length ~23.5 mm preserved, presumed 24 mm complete; width 7.5 mm, widest distad nodus. Membrane infuscate throughout, lightly so basally, darker in about the distal third; poorly preserved basally, but apparently with reduced petiole. With dense crossvenation, linear supplementary veins (i.e., not zigzagged) between most main veins. Pterostigma not preserved. Nodus at ~37% wing length; nodus, subnodus with normal obliquity. Area of Ax0, Ax1, Ax2 not preserved, eight accessory antenodal crossveins preserved. Three secondary antenodal crossveins preserved in ScP–RA space. Preserved postnodal crossveins in C–RA space (30), RA–RP space (26) not aligned. Quadrangle, subquadrangle long, narrow, slightly curved posteriad, without crossveins. Discoidal bracket present, strong, with reverse obliquity. Origin of IR1 six cells distad that of RP2; RP2 origin two cells distad subnodus; no oblique vein O. Origins of RP3-4, IR2 not known, only preserved distad at about the level of discoidal bracket, about one-third distance arculus to nodus. MP with a single curve, not sigmoidal. Two large

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cells subtending subquadrangle, each subtending two crossveins to margin. CuA distinctively angled basally as in diagnosis; distad evenly curved, not sigmoidal. CuA ends on margin at, or closely basad, mid-wing (termination not preserved), accessory intercalary vein in CuA–A space.

Etymology. The specific epithet is derived from the Ypresian age of the species, recognizing it as the oldest known species of the subfamily.

Remarks. As above, the exposure where the wing of *Swauka ypresiana* n. gen. n. sp. was found can be correlated with the Silver Pass Volcanic Member of the Swauk Formation, which has a U–Pb zircon CA-ID-TIMS age of 51.364 ± 0.029 Ma. This closely matches the U–Pb zircon age of 51.18 ± 0.09 Ma of location B4131 of the Tom Thumb Tuff Member of the Klondike Mountain Formation at Republic, Washington (Rubino et al., 2021), some 200 kilometers to the northeast, where the eodichromatine *Republica weatbrooki* was found.

Paleoclimatic reconstructions of the Ypresian highlands of the Tom Thumb Tuff Member indicate an upper microthermal climate (Greenwood et al., 2005). Paleoclimatic reconstructions of Ypresian coastal lowland localities in northwest Washington/southwest British Columbia propose much warmer climates, with Chuckanut Formation localities (MRCH [Chuckanut Formation landslide of the Racehorse Creek locality of Breedlovestrout et al., 2013] Slide Member, Black Mountain Slide Member, and Racehorse Creek units) given high mesothermal and megathermal values, and the Manastash Formation ("main body") assigned megathermal values (Breedlovestrout et al., 2013).

The Ypresian(?)–Lutetian Chumstick Formation paleoflora has been interpreted as evergreen montane rainforest in its uplands and deciduous riparian forest in its lowlands (Evans, 1991). Carbonate features in paleosols are interpreted as possible evidence for seasonal/monsoonal rainfall (Evans, 1991). Carbonate clumped isotope (Δ_{47}) and oxygen isotope ($\partial^{18}O$) analysis agrees well with Pacific-derived moisture, the absence of any rain-shadow effects, and moderate paleo-elevations during deposition of the Chumstick (Methner et al., 2016).

The larvae of modern Epallaginae inhabit active stream channels. This fossil was found in probable oxbow lake or floodplain lake deposits. In fluvial environments, flooding in the active channel overbanks and sediment-laden flood waters enter adjacent oxbow lakes and floodplain lakes. As flood stage wanes, these environments become disconnected from the active channel, waters are infiltrated or evaporated, and muddy sediment is deposited. The stratigraphic record of oxbow or floodplain lakes typically shows a leaf-litter deposit at the top of the flood-event layer. These leaves floated into the oxbow or floodplain lakes during flood stage, then settled out. The damselfly in this deposit probably behaved identically. If *Swauka ypresiana* n. gen. n. sp. inhabited streams in an upper mesothermal or megathermal forest, this would be consistent with the habitats and temperature regimes of most modern gossamerwing damselflies. For example, in Vietnam, a number of epallagid genera live in forests (Phan et al., 2018) with mesothermal to megathermal climates.

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Competing interests. The authors declare none.

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