

Article

Handling Editor: Torsten Wappler

Cite this article: Archibald SB, Evans JE, Mathewes RW, Cannings RA (2024). 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. *Journal of Paleontology* **98**, 1048–1052. <https://doi.org/10.1017/jpa.2024.60>

Received: 28 June 2024

Revised: 1 September 2024

Accepted: 11 September 2024

Corresponding author:

S. Bruce Archibald;

Email: sba48@sfu.ca

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.

S. Bruce Archibald^{1–5}, , James E. Evans⁶, Rolf W. Mathewes⁵ and Robert A. Cannings⁴

¹Beaty Biodiversity Museum, University of British Columbia, 2212 Main Mall, Vancouver, Vancouver, BC, Canada, BC, V6T 1Z4

²Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia, 2020–2207 Main Mall, Vancouver, BC, Canada, V6T 1Z4

³Museum of Comparative Zoology, 26 Oxford Street, Cambridge, MA, U.S.A., 02138

⁴Royal British Columbia Museum, 675 Belleville Street, Victoria, BC, Canada, V8W 9W2

⁵Simon Fraser University, Department of Biological Sciences, 8888 University Drive, Burnaby, BC, Canada, V5A 1S6

⁶Room 255, Overman Hall, School of Earth, Environment, and Society, Bowling Green State University, Bowling Green, Ohio 43403

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 weatbrookii* 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 *Elektro euphaea 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).

© The Author(s), 2025. Published by Cambridge University Press on behalf of Paleontological Society. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

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 north-west 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 = arcus; 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, $\leq 13^\circ\text{C}$; mesothermal, $> 13^\circ\text{C}$ to $< 20^\circ\text{C}$; megathermal, $\geq 20^\circ\text{C}$ 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; Petrulėvičius 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.

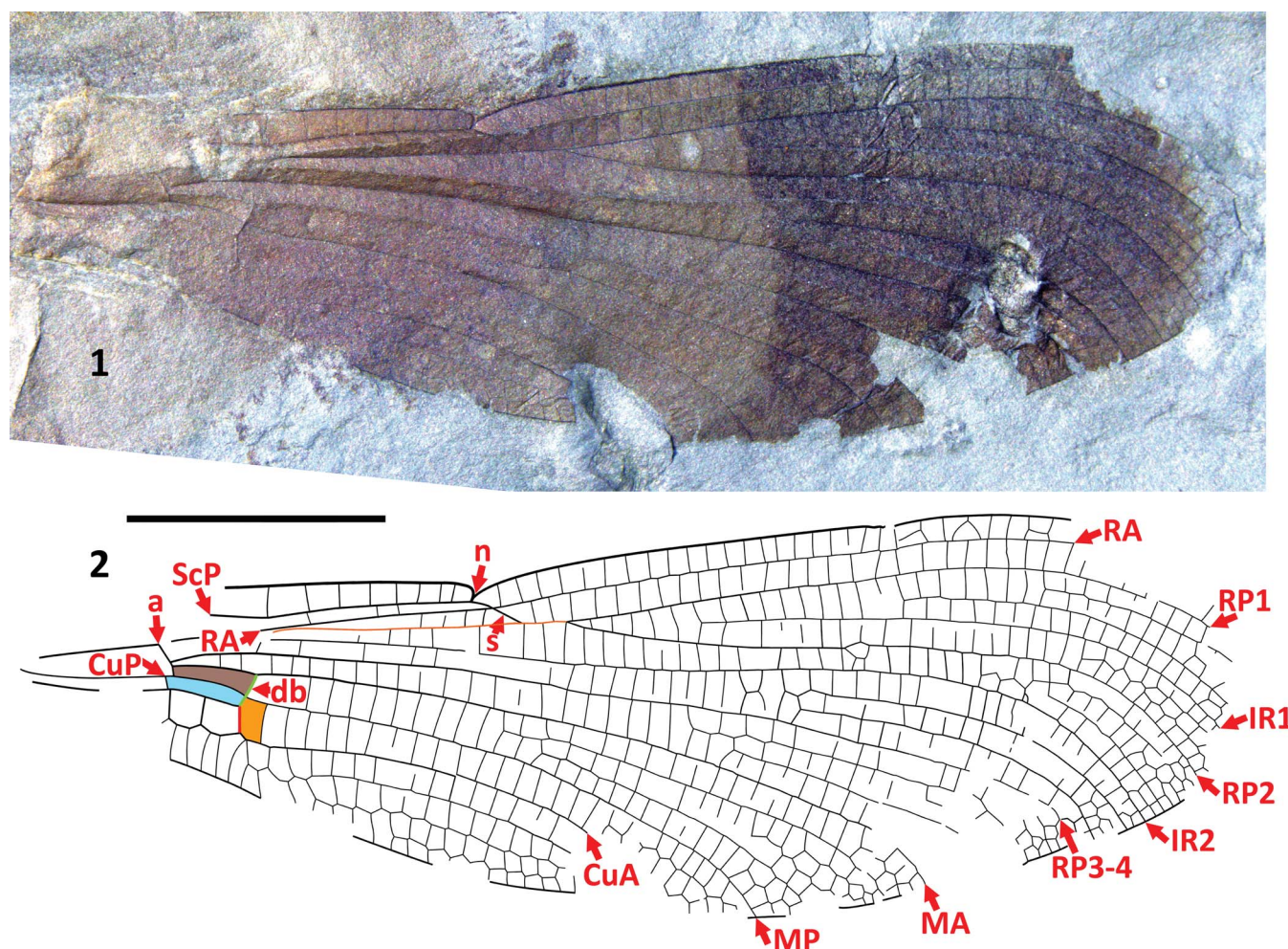


Figure 1. The holotype wing of *Swauka ypresiana* n. gen. n. sp. UWBM PB 56327A, B: (1) photograph of the part (A side); (2), drawing from both the part and counterpart (A and B sides). The discoidal bracket (thickened distal side of the quadrangle and subquadrangle) is green and CuA immediately distad 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 infusate 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

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 weatbrookii* 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 ($\delta^{18}\text{O}$) 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 epalligid genera live in forests (Phan et al., 2018) with mesothermal to megathermal climates.

Acknowledgments. We thank D. Hopkins, collector of the fossil, for donating it to the Burke Museum (Seattle, WA, U.S.A.) and for discussion of the locality; C. Strömberg, Curator of Paleobotany, and P. Wilson Deibel, Paleobotany Collections and Lab Manager at the Burke Museum for loan of

the specimen; M. Pellatt of Parks Canada (Vancouver, BC) for access to his microscope/photography equipment; and V. Makarkin of the Russian Academy of Sciences (Vladivostok) for discussion of Latin. We thank two anonymous reviewers for helpful comments that improved the manuscript. This work was partly funded by Natural Sciences and Engineering Grant 2020-05026 to RWM.

Competing interests. The authors declare none.

References

- Archibald, S.B., and Cannings, R.A., 2021, A new genus and species of Euphaeidae (Odonata, Zygoptera) from the early Eocene Okanagan Highlands locality at Republic, Washington, U.S.A.: *Zootaxa*, v. 4966, p. 392–400, <https://doi.org/10.11646/zootaxa.4966.3.11>.
- Bechly, G., 1998, New fossil damselflies from Baltic amber, with description of a new species, a redescription of *Litheuphaea carpenteri* Fraser, and a discussion on the phylogeny of Epallagidae (Zygoptera: Caloptera): *International Journal of Odonatology*, v. 1, p. 33–63, <https://doi.org/10.1080/13887890.1998.9748092>.
- Bechly, G., 1999, Epallagidae versus Euphaeidae revisited: *International Journal of Odonatology*, v. 2, p. 137–139, <https://doi.org/10.1080/13887890.1999.9748124>.
- Bechly, G., Garrouste, R., Aase, A., Karr, J.A., Grande, L., and Nel, A., 2020, The damselfly palaeofauna from the Eocene of Wyoming and Colorado, USA (Insecta, Odonata, Zygoptera): *Papers in Palaeontology*, v. 7, p. 1373–1402, <https://doi.org/10.1002/spp2.1346>.
- Breedlovestrout, R.L., Evraets, B.J., and Parrish J.T., 2013, New Paleogene paleoclimate analysis of western Washington using physiognomic characteristics from fossil leaves: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 392, p. 22–40, <https://doi.org/10.1016/j.palaeo.2013.08.013>.
- Carpenter, F.M., 1992, Superclass Hexapoda. in Kaesler, R.L., ed., *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Volume 3*: Boulder, Colorado, Geological Society of America and University of Kansas Press, 277 p.
- Cockerell, T.D., 1924, Fossil insects in the United States National Museum: *Proceedings of the United States National Museum*, v. 64, p. 1–15.
- Dijkstra, K.-D., Schröter, A., and Lewington, R. 2020, *Field Guide to the Dragonflies of Britain and Europe: Bloomsbury Wildlife Guides*: London, Bloomsbury Publishing, 336 p.
- Donaghy, E.E., Umhoefer, P.J., Eddy, M.P., Miller, R.B., and LaCasse, T. 2021, Stratigraphy, age, and provenance of the Eocene Chumstick basin, Washington Cascades; implications for paleogeography, regional tectonics, and development of strike-slip basins: *Geological Society of America Bulletin*, v. 133, p. 2418–2438, <https://doi.org/10.1130/B35738.1>.
- Donaghy, E.E., Umhoefer, P.J., Eddy, M.P., Miller, R.B., and LaCasse, T. 2022, Stratigraphy, age, and provenance of the Eocene Chumstick basin, Washington Cascades; implications for paleogeography, regional tectonics, and development of strike-slip basins: Reply: *GSA Bulletin*, v. 134, p. 2172–2176, <https://doi.org/10.1130/B36426.1>.
- Eddy, M.P., Bowring, S.A., Umhoefer P.J., Miller, R.B., McLean, N.M., and Donaghy, E.E., 2016, High-resolution temporal and stratigraphic record of Siletzia's accretion and triple junction migration from nonmarine sedimentary basins in central and western Washington: *GSA Bulletin*, v. 128, p. 425–441, <https://doi.org/10.1130/B31335.1>.
- Evans, J.E., 1991, Paleoclimatology and paleobotany of the Eocene Chumstick Formation, Cascade Range, Washington (USA): a rapidly subsiding alluvial basin: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 88, p. 239–264, [https://doi.org/10.1016/0031-0182\(91\)90068-3](https://doi.org/10.1016/0031-0182(91)90068-3).
- Evans, J.E., 1994, Depositional history of the Eocene Chumstick Formation: implications of tectonic partitioning for the history of the Leavenworth and Entiat-Eagle Creek fault systems, Washington: *Tectonics*, v. 13, p. 1425–1444, <https://doi.org/10.1029/94TC01321>.
- Evans, J.E., 2022, Stratigraphy, age, and provenance of the Eocene Chumstick basin, Washington Cascades; implications for paleogeography, regional tectonics, and development of strike-slip basins: Comment: *Geological Society of America Bulletin*, v. 134, p. 2167–2171, <https://doi.org/10.1130/B36157.1>.

- Evans, J.E., and Johnson, S.Y., 1989, Paleogene strike-slip basins of central Washington: Swauk Formation and Chumstick Formation: *Washington Division of Geology and Earth Resources, Information Circular*, v. **86**, p. 215–237.
- Fabricius, J.C., 1793, *Entomologia Systematica Emendata et Aucta. Secundum classes, Ordines, Genera, Species, Adjunctis Synonymis, Locis Observationibus, Descriptionibus. Tome 2: Hafniae [= Copenhagen]*, C.G. Proft, 519 p.
- Ferwer, W., and Nel A., 2020, A new damselfly genus and species from Baltic amber (Odonata: Zygoptera: Euphaeidae): *BSGF - Earth Sciences Bulletin*, v. **191**, 12 <https://doi.org/10.1051/bsgf/2020015>.
- Greenwood, D.R., Archibald, S.B., Mathewes, R.W., and Moss, P.T. 2005. Fossil biotas from the Okanagan Highlands, southern British Columbia and northern Washington State: climates and ecosystems across an Eocene landscape: *Canadian Journal of Earth Sciences*, v. **42**, p. 167–185, <https://doi.org/10.1139/e04-100>.
- Johnson S.Y., 1984, Stratigraphy, age, and paleogeography of the Eocene Chuckanut Formation, northwest Washington: *Canadian Journal of Earth Sciences*, v. **21**, p. 92–106, <https://doi.org/10.1139/e84-010>.
- Methner, K., Fiebig, J., Wacker, U., Umhoefer, P., Chamberlain, C.P., and Mulch, A., 2016, Eocene–Oligocene proto-Cascades topography revealed by clumped (Δ_{47}) and oxygen isotope ($\delta^{18}\text{O}$) geochemistry (Chumstick Basin, WA, USA): *Tectonics*, v. **35**, p. 546–564, <https://doi.org/10.1002/2015TC003984>.
- Mustoe, G.E., and Gannaway, W., 1997, Paleogeography and paleontology of the early Tertiary Chuckanut Formation, northwest Washington: *Washington Geology*, v. **25**, p. 3–18.
- Needham, J.G., 1903, A genealogic study of dragonfly wing venation: *Proceedings of the United States National Museum*, v. **26**, p. 703–764, <https://doi.org/10.5479/si.00963801.26-1331.703>.
- Nel, A., and Paicheler J.-C., 1992, Les Odonata fossiles: état actuel des connaissances. Huitième partie: les Caloptérygoidea fossiles (Odonata, Zygoptera): *Bulletin de la Société Entomologique de France*, v. **97**, p. 381–396.
- Nel, A., Krzeminski, W., and Szewdo, J., 2013, *Elektroeuphaea* gen. n., the oldest representative of the modern Epallaginae from Eocene Baltic amber (Odonata: Zygoptera: Epallagidae): *Insect Systematics & Evolution*, v. **44**, p. 129–140, <https://doi.org/10.1163/1876312X-44032097>.
- Paulson, D., Schorr, M., Abbott, J., Bota-Sierra, C., Deliry, C., Dijkstra, K.-D., and Lozano, F. (Coordinators), 2024, *World Odonata List: Odonata Central*, University of Alabama, <https://www.odonatacentral.org/app/#/wol/> (accessed June 2024).
- Petrulevičius, J.F., Nel, A., Rust, J., Bechly, G., and Kohls, D. 2007, New Paleogene Epallagidae (Insecta: Odonata) recorded in North America and Europe. Biogeographic implications: *Alavesia*, v. **1**, p. 15–25.
- Phan, Q.T., Kompier, T., Karube, H., and Hayashi, F., 2018, A synopsis of the Euphaeidae (Odonata: Zygoptera) of Vietnam, with descriptions of two new species of *Euphaea*: *Zootaxa*, v. **4375**, p. 151–190, <https://doi.org/10.11646/zootaxa.4375.2.1>.
- Rubino, E., Leier, A., Cassel, E.J., Archibald S.B., Foster-Baril, Z., and Barbeau Jr., D.L. 2021. Detrital zircon U–Pb ages and Hf-isotopes from Eocene intermontane basin deposits of the southern Canadian Cordillera: *Sedimentary Geology*, v. **422**, 105969, <https://doi.org/10.1016/j.sedgeo.2021.105969>.
- Selys-Longchamps, E. de, 1854, Monographie des Caloptérygines: *Mémoires de la Société Royale des Sciences de Liège*, v. **9**, 291 p.
- Silsby, J., 2001, *Dragonflies of the World*: Washington, DC, Smithsonian Institution Press, USA., 216 p.
- Tabor, R.W., Frizzell, V.A., Jr., Vance, J.A., and Naeser, C.W., 1984, Ages and stratigraphy of lower and middle Tertiary sedimentary and volcanic rocks of the central Cascades, Washington—application to the tectonic history of the Straight Creek fault: *Geological Society of America Bulletin*, v. **95**, p. 26–44.
- Taylor, S.B., Johnson, S.Y., Fraser, G.T., and Roberts, J.W., 1988, Sedimentation and tectonics of the lower and middle Eocene Swauk Formation in eastern Swauk Basin, central Cascades, central Washington: *Canadian Journal of Earth Sciences*, v. **25**, p. 1020–1036, <https://doi.org/10.1139/e88-100>.
- Wolfe, J.A., 1975, Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary: *Annals of the Missouri Botanical Garden*, v. **62**, p. 264–279, <https://doi.org/10.2307/2395198>.