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New Late Cretaceous (Cenomanian) fossil mayfly nymphs (Oligoneuriidae, Heptageniidae, Hexagenitidae) from the Redmond Formation, Labrador, Canada

André S. Mueller and **Alexandre V. Demers-Potvin**

Redpath Museum, Department of Biology, McGill University, Montréal, Québec, Canada

Corresponding author: **André S. Mueller** (email: andre.mueller@mail.mcgill.ca)

Abstract

Three new fossil mayfly (Ephemeroptera) larvae from the Redmond Formation (Cenomanian) of Newfoundland and Labrador, Canada, are described: *Alatuscapillus icarus* gen. et sp. nov. (family Oligoneuriidae), *Cruscolli sheppardae* gen. et sp. nov. (family Heptageniidae), and *Protoligoneuria borealis* sp. nov. (family Hexagenitidae). This discovery marks the first juvenile insect nymphs to be described from this formation and helps fill gaps in our understanding of the global and temporal distribution of mayflies during the Cretaceous period. Of these, *C. sheppardae* marks the oldest occurrence of the family Heptageniidae in the fossil record, while *A. icarus* and *P. borealis* mark the first fossil occurrences of the families Oligoneuriidae and Hexagenitidae in North America. The anatomy, preservation, and behaviour of these new mayfly species inferred from modern taxa consolidate the hypothesis that the Redmond Formation's palaeoenvironment was lacustrine in nature.

Key words: Ephemeroptera, Cretaceous, Oligoneuriidae, Heptageniidae, Hexagenitidae, Redmond Formation

Introduction

Ephemeropterans form a globally widespread order of aquatic insects consisting of more than 3000 extant species in 400 genera and 42 families as of 2008 (Barber-James et al. 2008). They play an essential role in aquatic ecosystems, commonly being prey items for larger organisms such as stoneflies, dragonflies, and crayfish (Brittain 1982). In the fossil record, their known diversity is much lower, with at least 255 recorded species in 140 genera and 48 families described worldwide as of 2023 (Sroka et al. 2023). Of these families, Oligoneuriidae (brush-legged mayflies), Heptageniidae (flatheaded mayflies), and Hexagenitidae (extinct minnow-like mayflies) have a very poor or non-existent fossil record in North America during the Cretaceous (Sinitshenkova and Grimaldi 2000; Bell et al. 2013; Sroka et al. 2023). In this paper, we report the discoveries of three new mayfly species described from their nymphal stages:*Alatuscapillus icarus* gen. et sp. nov., *Cruscolli sheppardae* gen. et sp. nov., and *Protoligoneuria borealis* sp. nov. These taxa are the first mayflies described from an isolated exposure of the Redmond Formation (Newfoundland and Labrador, Canada) and the first juvenile insect material to be described from that locality's palaeocommunity. These discoveries help bridge temporal gaps in North America's ephemeropteran fossil record and expand the diversity of the Redmond Formation's entomofauna.

Nomenclature acts—This work and its nomenclature acts have been registered in Zoobank: urn:lsid:zoobank.org:pub:B5EDEAB0-CA77-4C65-B9A8-074FD0FBA6DF.

Geological setting

The Redmond No. 1 iron ore mine is located in the Knob Lake District of Newfoundland and Labrador, Canada, South southeast of the town of Schefferville, Québec, Canada. It contains the only known exposure of the Redmond Formation, a 1.5 m thick claystone bed of umber colour with submillimetre-thick parallel laminations (Blais 1959). The lithology, along with an abundance of well-preserved fossil leaf impressions and articulated insect remains, is highly indicative of a lacustrine depositional environment (Demers-Potvin and Larsson 2019). After its initial discovery during iron ore prospecting in the surrounding Palaeoproterozoic Sokoman Formation, the Redmond Formation's thin deposit was destroyed during the expansion of the (now abandoned) Redmond No. 1 mine. Despite the loss of its stratigraphical context, the Redmond Formation contains a diverse angiosperm palaeoflora, whose composition indicates a Late Cretaceous (Cenomanian: 100.5–93.9 Mya) age, (Blais 1959; Dorf 1959; 1967), as well as a warm temperate climate (mean annual temperature ca. 15 °C) at a palaeolatitude of ca. 49°N (Demers-Potvin and Larsson 2019). Among the Redmond Formation's known entomofauna, seven species have been described so far: the snakefly *Alloraphidia dorfi* (Carpenter 1967), the hodotermitid *Cretatermes carpenteri* (Emerson 1967), the coleopteran *Labradorocoleus carpenteri* (Ponomarenko 1969), the antlion *Palaeoleon ferrogeneticus* (Rice 1969), the stem-phasmatodean *Palaeopteron complexum* (Rice 1969), the tettigarctid cicada *Maculaferrum blaisi*

(Demers-Potvin et al. 2020), and the baissomantid *Labradormantis guilbaulti* (Demers-Potvin et al. 2021). Brief mentions were also made of isolated blattodean wings (Dorf 1967) as well as coleopteran elytra assigned to Schizophoridae, Cupedidae, and the haliplid *Peltodytes* sp. (Ponomarenko 1969). These newly described mayflies therefore mark the first discovery of juvenile insect material from the formation.

Materials and methods

All specimens described in this study were collected from the remaining float of the Redmond Formation among tailings of the Redmond No. 1 mine during fieldwork co-directed by the Redpath Museum (RM) and the Musée de paléontologie et de l'évolution (MPE) in August 2018. In total, six mayfly specimens were recovered (MPEP1152.2, MPEP1156.5, RMIP2018.18.14, RMIP2018.18.33, RMIP2018.18.36, and RMIP2018.18.43), of which MPEP1152.2, RMIP2018.18.14, and RMIP2018.18.43 were incomplete or too poorly preserved to be described. The three best-preserved specimens (MPEP1156.5, RMIP2018.18.33, and RMIP2018.18.36) were photographed by Reflectance Transformation Imaging (Béthoux et al. 2016; Reflectance Transformation Imaging (RTI) 2019). For each, photographs were taken using a Canon EOS 5 D Mark III digital camera with a Canon MPE-65 macro lens (Canon, Tokyo, Japan) inserted inside a portable light dome. All original photographs were then optimised and processed using Adobe Camera Raw and Adobe Photoshop CC 2019 (Adobe Systems, San Jose, U.S.A.), then assembled to form an RTI file using RTI Builder software version 2.0.2 (freely available under GNU licence, using the HSH fitter). RTI files are provided along with viewer software and instructions (see Supplementary Materials (Cretaceous Labrador mayflies RTI instructions)). Additional higher resolution imaging was conducted on all six specimens (see Supplementary Materials (Figs. S1 1–7, S2 1–5, S3 1–6, RMIP2018.18.14 Fig. S4, RMIP2018.18.43 Fig. S5, and MPEP1152.2 Fig. S6)) with an Axio Zoom.V.16 microscope equipped with a 0.5× lens by Zeiss using ZEN 3.6 (ZEN PRO) software (Zeiss, Oberkochen, Germany). Z-stacks were generated for each specimen (with their area of interest set by the lens' motorised zoom), stitched using the extended depth of focus method at default parameters, and exported as PNG files. Composite photographs of the three best-preserved mayfly nymph specimens in the following figures were then extracted from their respective RTI files and Z-Stack files at different average light incidence angles and exported into paint.net (Windows, Richmond, U.S.A.), in which their respective line drawings were made. Colours were assigned according to the best interpretation of visible anatomy.

Systematic palaeontology

Order Ephemeroptera (Hyatt and Arms 1890)
Superfamily Heptagenioidea (McCafferty 1991*a*)
Family Oligoneuriidae (Ulmer 1914)
Subfamily Oligoneuriinae (Ulmer 1914)

Genus *Alatuscapillus* nov.

TYPE SPECIES: *Alatuscapillus icarus* sp. nov. by monotypy.

DIAGNOSIS: Nymphs separated from other Oligoneuriinae by presence of hair-like filaments lining the outer margins of forewing pads.

DESCRIPTION: As for its only species, below.

RANGE AND AGE: As for its only species, below.

ETYMOLOGY: The genus name *Alatuscapillus* (masc.) is formed from the Latin *alatus* (masc.), meaning winged, and the Latin *capillus* (masc.), meaning hair, referring to the "hair-like" structures found on the forewings.

REMARKS: The presence of brush-like setae on forelegs and gill tufts on maxillae are both synapomorphies of the superfamily Heptagenioidea. Of the four families within this superfamily, three possess these characteristics (Isonychiidae, Colorburiscidae, and Oligoneuriidae), while Heptageniidae is considered to have largely lost these traits. Furthermore, the gill tufts found ventrally on the maxilla are considered an autapomorphy of the families Oligoneuriidae, Isonychiidae, and Colorburiscidae (McCafferty 1991*b*). Of these, both Colorburiscidae and Isonychiidae are basal families (McCafferty 1991*a*) whose nymphs can be characterised by their hypognathous mouthparts (McCafferty 1991*b*). In contrast, *A. icarus* sp. nov. displays a prognathous mouthpart morphology. For this reason, it is deemed most parsimonious to assign *A. icarus* sp. nov. to Oligoneuriidae, as its traits are characteristic of the family. Lastly, gill 1 is located ventrally, suggesting its placement in the subfamily Oligoneuriinae (Massariol et al. 2019). Because of the significant gap this discovery creates in the oligoneuriid fossil record, the new genus *Alatuscapillus* is erected in order not to erroneously attribute *A. icarus* to an already known genus. Until further material is studied, it remains unclear whether *Alatuscapillus* is an extinct genus within Oligoneuriinae or ancestral to existing genera.

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Alatuscapillus icarus sp. nov.

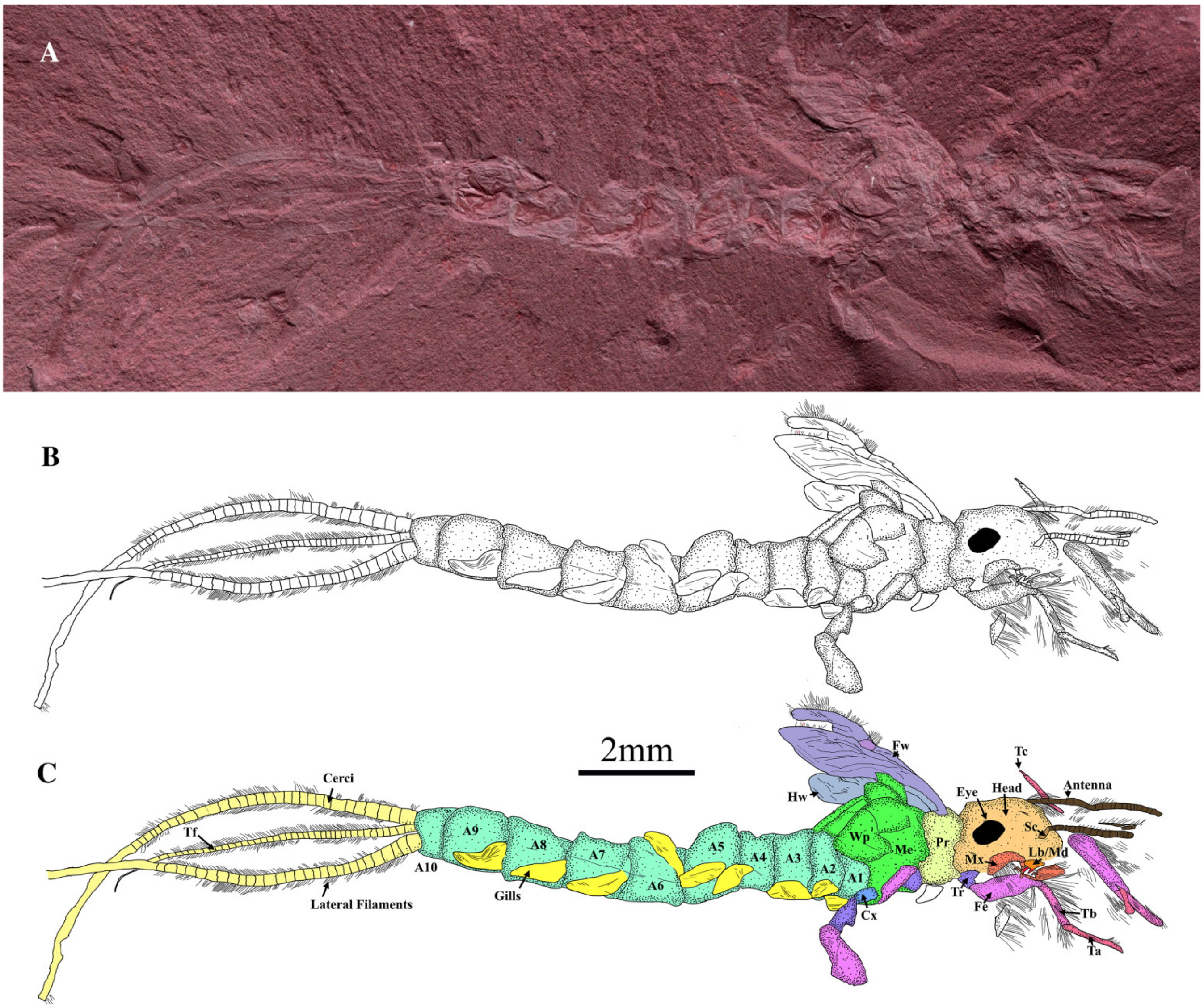
Fig. 1

TYPE MATERIAL: Holotype: RMIP 2018.18.33, impression of a mostly complete nymph preserved in right-lateral view with incomplete or detached limbs, four of which are partially visible, while the other two are either missing or hidden from view. Nymphal wing pads attached and dorsally extended.

DIAGNOSIS: As for genus, see above.

DESCRIPTION: (Figs. 1A–1C, Supplementary Materials (Figs. S1 1–7)) Nymph large, total length ~11 mm (excluding cerci), body height of 1 mm at abdomen and 1.4 mm at thorax. Antenna filiform, attached on anterior half of head, below eye. Head large, comparable in size to thorax, roughly 1.7 mm in length, and prognathous in form in relation to mouthparts. Maxilla large, with gill tufts present on ventral surfaces.

Fig. 1. Brush-legged mayfly nymph *Alatuscapillus icarus* gen. et sp. nov. (holotype RMIP2018.18.33) from the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada. (A) Photograph extracted from RTI file RMIP2018.18.33 (see online repository). (B) Interpretive line drawing. (C) Same as (B), with colour code and anatomical labels. White represents unidentifiable segments. Abbreviations: A(1–10), abdominal segments; Cx, coxa; Fe, femur; Fw, forewing; Hw, hindwing; Lb, labrum; Md, mandible; Me, mesothorax; Mx, maxilla; Pr, prothorax; Ta, tarsus; Tb, tibia; Tc, tarsal claw; Tf, terminal filament; Tr, trochanter; Wp, wingpad.



Maxillary palp divided in three visible segments. Labrum small, with no major midline notch present. Mandibles significantly less developed than maxillae. Eye large, diameter roughly a third of head length, located dorsally, slightly above ventral-dorsal midline towards posterior third of head. Prothorax roughly half of head length, (~0.7 mm). Mesonotum large, ~1.4 mm in length, covered by well developed crescent-shaped forewing pads. Forewing pads large and elongated, attached roughly at mesonotum-pronotum border. Forewing pad longitudinal venation visible with radius, media, and cubitus regions identifiable. Filament-like structures located distally on costal margin of forewing pads. Hindwing pads small and ovoid. Forelimbs attached to posterior prothorax. Tibia and tarsus roughly equal (~1 mm) in length with slightly longer femur. Forelegs covered in thick combs of setae, especially femora and tibiae, while tarsi remain largely free of setae. Single tarsal claw present. Middle leg attaches at prothorax–mesothorax barrier, while hind leg attaches at posterior end of mesothorax. Larger tibiae on hind leg compared to middle leg and foreleg. Hind leg trochanter elongated. Both middle- and hind-leg lack combs of setae like those found on forelegs. Ten abdominal segments present, of which segments 5–9 more elongate compared to segments 1–4. Abdominal segments 1–8 possess rounded gills, with gills 1 and 2 significantly reduced in size. Cerci more developed than terminal filament at ~7 and ~5 mm, respectively. Lateral filaments well developed on caudal and terminal filaments.

RANGE AND AGE: Redmond Formation, Labrador, Canada, Cenomanian.

TYPE LOCALITY: Redmond No. 1 mine, in Labrador, near Schefferville, Québec, Canada (Demers-Potvin and Larsson 2019).

ETYMOLOGY: "*icarus*" (masc.), with reference to the Greek myth of Icarus who, like this specimen, died in water in its youth with open wings. Filament-like structures on forewing pads are also reminiscent of the feathered wings of the Greek myth.

REMARKS: Some limb segments were detached during the specimen's fossilisation, likely before burial. For this reason, some features such as the mid and hind tarsi could not be described. Filament structures observed on wing pads could be attributed to venation of folded forewings, but similar filamentous structures preserved on other specimens from the Redmond Formation support these filaments being anatomical features (Demers-Potvin et al. 2020). Furthermore, due to the rugged nature of the matrix, some distinctive features of the head, wings, mouthparts, and gills were either unidentifiable or too poorly preserved.

ZOOBANK LSID: urn:lsid:zoobank.org:act:7B3412AF-0C5D-407 D-B4E3-8BD46CA6E2AF.

Superfamily Heptagenioidea (McCafferty 1991*a*)
Family Heptageniidae (Needham and Betten 1901)
Genus *Cruscolli* gen. nov.

TYPE SPECIES: *Cruscolli sheppardae* sp. nov. by monotypy.

DIAGNOSIS: Nymphs distinct from other Heptageniidae by the presence of prominent ridges on front and hind femora, small size.

DESCRIPTION: As for its only species, below.

RANGE AND AGE: As for its only species, below.

ETYMOLOGY: The genus name *Cruscolli* (neut.) is formed from the Latin *crus* (neut.), meaning leg, and the Latin *colli* (neut.), meaning hill. This is in reference to the prominent ridge-like structures found on the femora of the holotype.

REMARKS: The head and femora found on *C. sheppardae* gen. et sp. nov. are large and flattened, which are highly reminiscent of the family Heptageniidae. However, as defined by Wang and McCafferty (2004), this trait is not apomorphic to Heptageniidae since it is also found in some members of Leptophlebiidae and pannote mayflies. Nonetheless, the small plate-like gills on *C. sheppardae* sp. nov. suggest its placement in the latter groups unlikely. Further characteristics suggesting its assignment to Heptageniidae include its prognathous head and the lack of significant comb-like setae on its forelegs (McCafferty 1991*b*). With regards to more precise placement within Heptageniidae, diagnostic traits, such as the presence of a terminal filament, absence of most gills, small size, and lack of lateral filaments on cerci are insufficient for an accurate referral to an extant genus. For this reason, the creation of a new genus is proposed to include the late Cretaceous heptageniids found in what would have been northern Appalachia.

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Cruscolli sheppardae sp. nov.

Fig. 2

TYPE MATERIAL: Holotype: RMIP 2018.18.36, impression of a mostly complete, dorsally preserved nymph with detached right mid-leg, missing tarsi for three legs and most gills.

DIAGNOSIS: As for genus, see above.

DESCRIPTION: (Figs. 2A–2C, Supplementary Material (Fig. S2 1–5)) Nymph small, dorsoventrally compressed, with body length excluding cerci ~4.5 mm. Antennae filiform, with large basal pedicels, attached anterior to eyes, ~1.2 times length of the head. Head large, flattened, and rounded, ~0.7 mm in length, with large trapezoidal plates surrounding each eye. Eyes large, ~0.17 mm apart. Anterior margin present around eyes. Head prognathous in form in relation to mouthparts. Mandibles and maxillae small and roughly equal in length, with few identifiable characteristics. Thorax well defined into pronotum and mesonotum, separated into two distinct plates along medial line. Pronotum anteriorly convex and posteriorly concave. Mesonotum large and roughly equal in length to femora. Wing pads undeveloped, close at the base, and fused with metanotum. Minor wing venation visible but undefinable, otherwise mesonotum and wing pads lack identifiable characteristics. Foreleg femora enlarged and flattened, roughly ~0.7 mm in length. Tibia roughly equal in length to femur. Tarsus shorter than tibia, lacking visible segmentation. Single well developed tarsal claw present. Mid- and hind-legs similar in structure to forelegs with enlarged flattened femora, middle leg femora comparatively smaller in length. All legs appear to lack setae, fore femora, and hind femora possess ridge-like structures oriented perpendicular to their long axis. Foreleg ridges found on posterior and dorsal surfaces of femora. Hind leg ridges found on anterodorsal surfaces of femora. Abdomen elongated and narrow, divided into 10 segments, with segments 3–4 possessing small, rounded gills, with suspected presence on segments 1–8. Cerci developed and incomplete, but likely ~1.5–1.7 mm long. Terminal filament complete and as equally developed as cerci, 1.7 mm in length. Caudal filaments lack lateral filaments.

RANGE AND AGE: Redmond Formation, Labrador, Canada, Cenomanian.

TYPE LOCALITY: Redmond No. 1 mine, in Labrador, near Schefferville, Québec, Canada (Demers-Potvin and Larsson 2019).

ETYMOLOGY: "*sheppardae*" (genitive, fem), with reference to Noemie Sheppard (Monash University, Melbourne, Australia), who originally discovered the specimen.

REMARKS: Considering the nymph's small size and the rough nature of the matrix, it was difficult to determine fine details, especially with regard to identifying setae, mouthparts, and gill structures. In addition, due to the dorsoventral compression of the head, it was difficult to identify more specific

Fig. 2. Flat-headed mayfly nymph *Cruscolli sheppardae* gen. et sp. nov. (holotype RMIP2018.18.36) from the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada. Photograph (A) extracted from RTI file RMIP2018.18.36 (see online repository) (B) Interpretive line drawing. (C) Same as (B), with colour code and anatomical labels. Abbreviations: A (1–10), abdominal segments; Cx, coxa; Fe, femur; Md, mandible; Me, mesonotum; Mx, maxilla; Pr, prothorax; Ta, tarsus; Tb, tibia; Tc, tarsal claw; Tr, trochanter; Wp, wingpad.

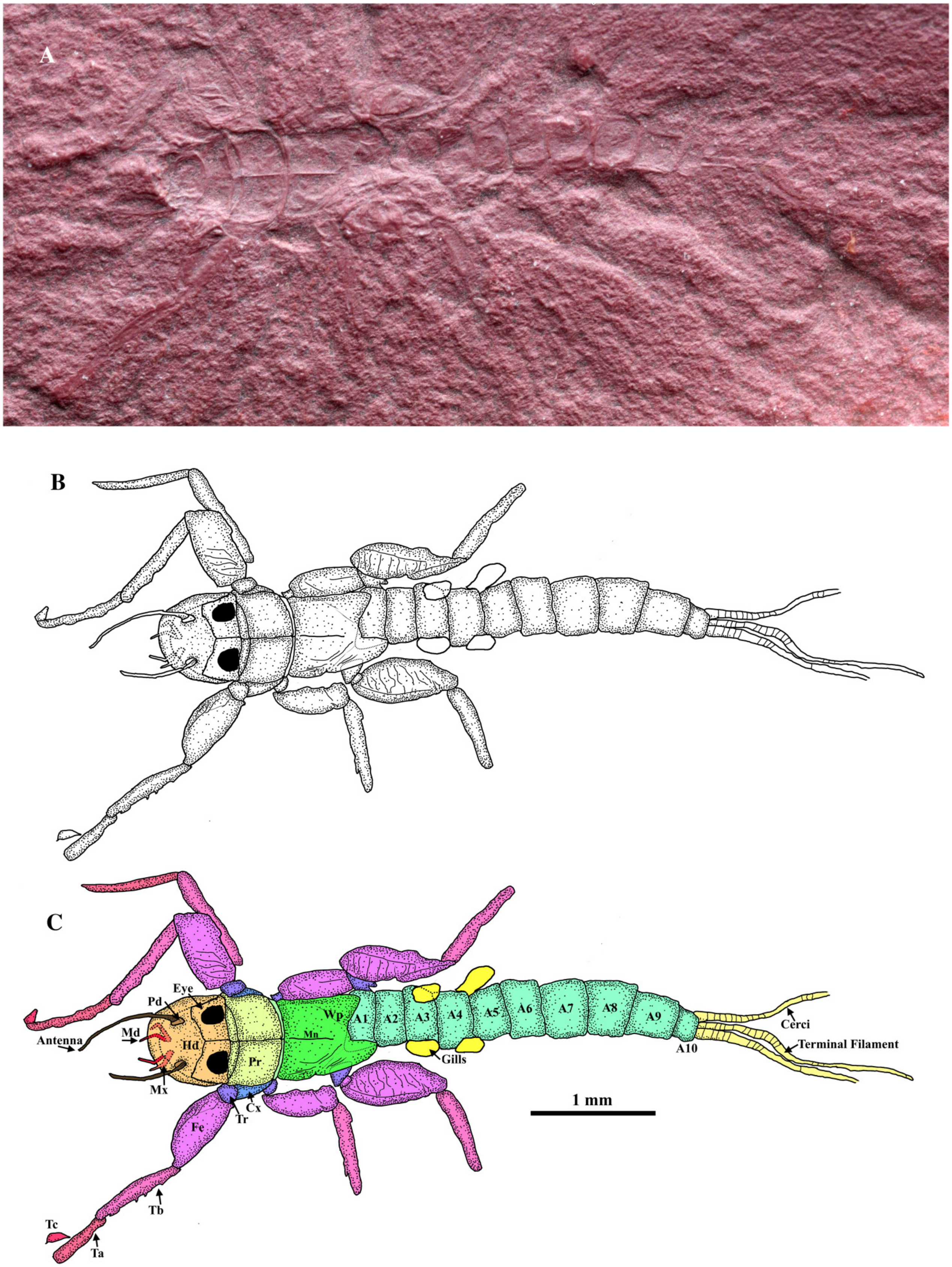
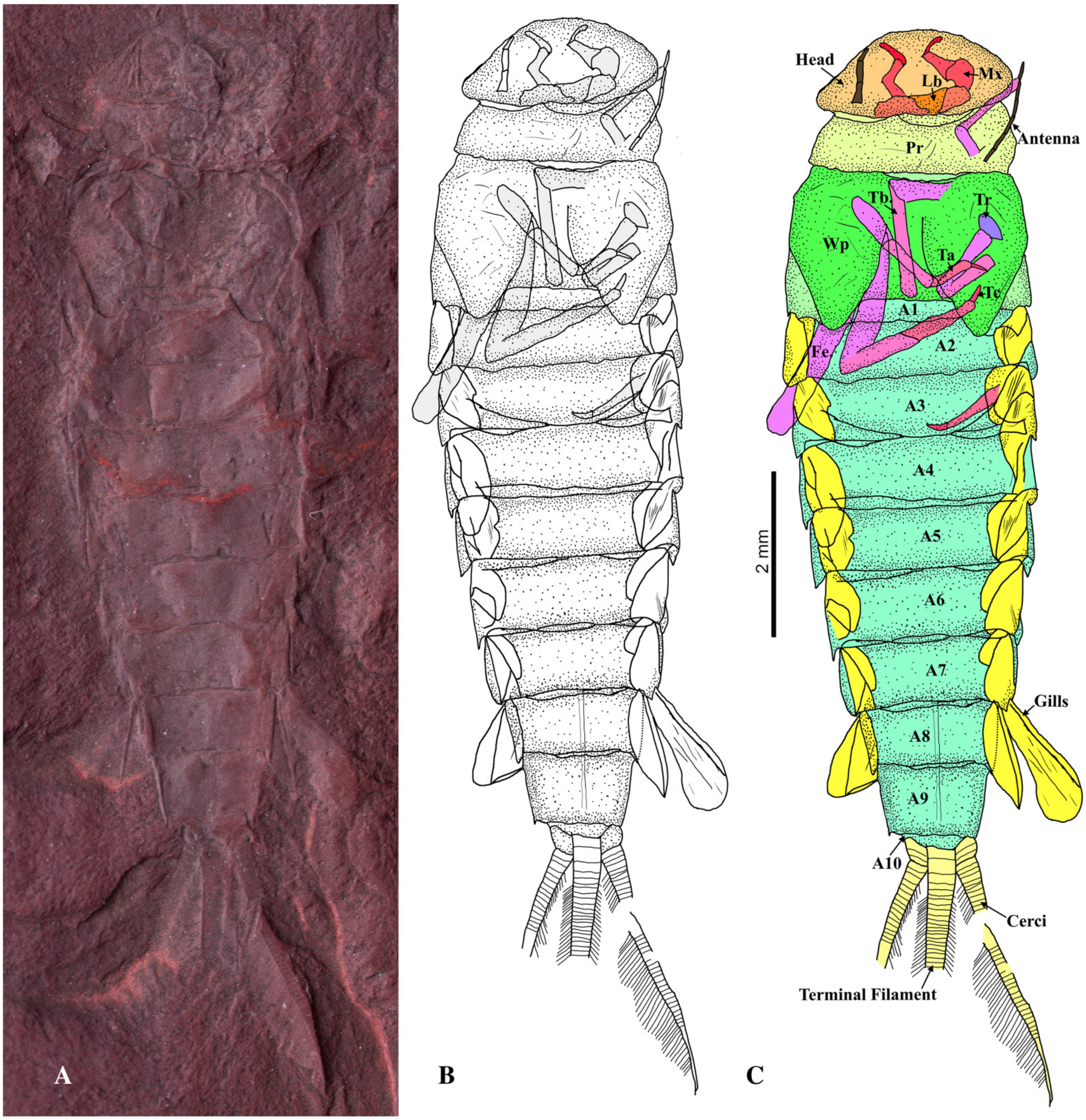


Fig. 3. Hexagenitid mayfly nymph *Protoligoneuria borealis* sp. nov. (holotype MPEP1156.5) from the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada. Photograph (A) extracted from RTI file MPEP1156.5 (see online repository). (B) Interpretive line drawing, greyed out features located below plane of head and axial exoskeleton. (C) Same as (B), with colour code and anatomical labels. Abbreviations: A (110), abdominal segments; Fe, femur; Lb, labrum; Md, mandible; Mx, maxilla; Pr, prothorax; Ta, tarsus; Tb, tibia; Tc, tarsal claw; Tr, trochanter; Wp, wingpad.



mouthpart details. Gills on abdominal segments 1–2 and 5–8 are not preserved, but their presence is very likely.

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Family Hexagenitidae (Lamere 1917)

Genus *Protoligoneuria* (Demoulin 1955)

Protoligoneuria borealis sp. nov.

Fig. 3

TYPE MATERIAL: **Holotype:** MPEP 1156.5, impression of a large, mostly complete, dorsally preserved nymph with legs folded under thorax and abdomen with fractured caudal filaments.

DIAGNOSIS: Nymphs distinct from other members of *Protoligoneuria* by enlarged 7th gill that extends medially from medial rib, body-to-7th gill length ratio of ~5.3.

DESCRIPTION: (Figs. 3A–3C, Supplementary Materials (Fig. S3 1–6)) Nymph large, minnow-like, body elongated, teardrop in form, 10 mm in length excluding cerci. Head large and transversely oval, twice as wide as it is long. Antennae longer than head, point of attachment unclear. Mouthparts well developed, with very large maxillae present, measuring more than half the length of head. No visible notching present on labrum. Pronotum wider than long and of equal width to both head and mesonotum. Mesonotum, wing pads reduced and fused. Forewing pads extending beyond ventral margin of first abdominal segment. Femora variable in size with hind leg femora largest. Single, well developed tarsal claw present. No setae visible on legs. Abdomen forms most of the body, measuring twice the length of head and thorax combined. Ten short and broad abdominal segments present, narrowing posteriorly. Abdominal segment 10 significantly reduced. Segments 1–7 possess large rounded teardrop-like gills, 7th gill enlarged at 1.9 mm long. Gills 1–6 smaller, ~0.85–1.0 mm in length. Two well developed ribs on gills, which curve medially on their distal ends. 7th gill extends medially past the medial rib. Body-to-7th gill length ratio 5.26. Cerci and terminal filament well developed, ~3.6 mm each. Cerci and terminal filaments possess dense lateral filaments.

RANGE AND AGE: Redmond Formation, Labrador, Canada, Cenomanian.

TYPE LOCALITY: Redmond No. 1 mine, in Labrador, near Schefferville, Québec, Canada (Demers-Potvin and Larsson 2019).

ETYMOLOGY: *"borealis"* (neut.), with reference to the northern Canadian locality of the discovered specimen.

REMARKS: An enlarged gill 7, a minnow-like body plan, fused wing pads and the presence of dense primary swimming setae on caudal filaments together allow for confident placement of *P. borealis* sp. nov. within Hexagenitidae (Storari et al. 2022). Previously described genera of Hexagenitidae that possess an elongated gill 7 are *Cratohexagenites*, *Protoligoneuria*, *Baikalogenites*, *Hexameropsis*, *Ephemeropsis*, *Caenoephemera*, and *Mongologenites* (Eichwald 1864; Tshernova and Sinitshenkova 1974; Sinitshenkova 1986; Lin and Huang 2001; Sinitshenkova 2017; Storari et al. 2022). The genus *Libanoephemera* (Azar et al. 2019) is not currently attributed to a family but represents a likely member of Hexagenitidae. *Protoligoneuria borealis* is significantly smaller than species of *Baikalogenites*, *Mongologenites*, *Cratohexagenites*, *Libanoephemera*, *Caenoephemera*, and *Ephemeropsis.* Furthermore, there is also a significant temporal gap and geographical separation of these taxa from *P. borealis* sp. nov. Size similar to that of *Hexameropsis selini* from Ukraine; however, gill ribs are less developed in *P. borealis* sp. nov. than in *Hexameropsis.*The significantly enlarged 7th gill (compared to preceding gills) also separates *P. borealis* sp. nov. from the previously mentioned hexagenitid genera. Its cerci are much shorter, 7th gill rounded and its body more elongate than in *Cratohexagenites*. *Protoligoneuria borealis* is remarkably similar to *Protoligoneuria limai* from the Crato Formation of Brazil (Storari et al. 2022). Both taxa possess significantly elongated 7th gills, lived during the Cretaceous, and are roughly equal in size. *Protoligoneuria* is also defined by a rounded 7th gill, a trait also present in *P. borealis.* The body-to-7th gill ratio of *P. borealis* is 5.26, which falls on the lower end of the range seen in *P. limai.* All this suggests the placement of *P. borealis* within the genus *Protoligoneuria.*

Legs and mouthparts are preserved below the body of the specimen but are highlighted for clarity in Fig. 3. The specimen's dorsolateral compression makes identification of its ventral anatomy (including legs and mouthparts) difficult because of obstructions and reduced detail. Due to the broken nature of the antennae and the caudal filaments, accurate measurements cannot be made without studying more specimens.

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Discussion

Taxonomic discussions

It remains difficult to make direct comparisons between *C. sheppardae* sp. nov. and other heptageniids from the Late Cretaceous. Those found in the Wapiti Formation of Alberta are too poorly preserved and too large for comparative identification (Bell et al. 2013), while *Amerogenia macrops* from New Jersey amber (Sinitshenkova and Grimaldi 2000) exists only in its imago stages. The large size of the Wapiti Formation specimens and their location in Laramidia together suggest that they are a distinct taxon from *C. sheppardae* sp. nov. Contrastingly, the small size of *A. macrops* is relatively consistent with that of *C. sheppardae*, suggesting possible phylogenetic proximity. However, confirming any similarity between these taxa remains difficult until further material is collected.

As for *P. borealis*, of the two species previously described within *Protoligoneuria*, nymphal material has not been described from *Protoligoneuria heloisae*, thus making comparisons difficult. In contrast, significant nymphal material exists for *P. limai* (Storari et al. 2022). Compared to *P. limai*, *P. borealis* has a more elongated body, a larger head and larger femora. Furthermore, the considerable temporal gap and geographical separation between the two species also supports the classification of *P. borealis* as its own species within *Protoligoneuria*.

Biogeographical implications

The discovery of mayflies in the Redmond Formation raises many biogeographical implications for our understanding of mayfly distribution during the Cretaceous period. First, the report of Oligoneuriidae in North America marks the first occurrence of this family in the continent's fossil record and extends the Cretaceous range of Oligoneuriidae into the Nearctic. This family has a significant pan-tropical distribution today (Massariol et al. 2019), with genetic analyses suggesting that it moved into North America from South

America around 77–46 Mya through the proto-Caribbean archipelago (which existed from 100–49 Mya) (Massariol et al. 2019). The presence of *A. icarus* in North America prior to these dates now suggests that this oligoneuriid was already present on the continent before this inferred dispersal and belongs to a now-extinct lineage. As such, the predicted dates may not completely represent oligoneuriid biogeographical patterns.

With regards to Heptageniidae, the family has already been recorded in eastern North America during the Cenomanian, as represented by *Amerogenia* from New Jersey amber (Sinitshenkova and Grimaldi 2000). The discovery of *C. sheppardae* in the Redmond Formation extends the known range of Appalachian heptageniids North into eastern Canada.

Most interestingly, the discovery of *P. borealis* marks the first occurrence of this extinct family in North America, extending its range into the Nearctic. This confirms that Hexagenitidae was a globally distributed family, as it was already known from Aptian South America (McCafferty 1990; Storari et al. 2022), Lower Cretaceous West Africa and Europe (Tshernova and Sinitshenkova 1974), Late Jurassic to Early Cretaceous East Asia (Sinitshenkova 1986; Huang et al. 2007; Sinitshenkova 2017), and Early Cretaceous Lebanon (Azar et al. 2019). The high density and Holarctic distribution of early hexagenitid fossils suggest that the family may have originated from Laurasia during the Jurassic, and eventually moved South into Africa and South America. Under this hypothesis, the similarities between the North and South American hexagenitids suggest a closer relationship, which may suggest dispersal or vicariance of hexagenitids between North and South America as opposed to dispersal or vicariance into South America from Africa or Europe.

Temporal implications

The discovery of these specimens fill large temporal gaps in the fossil record of families Oligoneuriidae, Heptageniidae, and Hexagenitidae. The discovery of *A. icarus* in the Cenomanian (100.5–93.9 Mya) (Cohen et al. 2013) marks the first oligoneuriid fossil to fill an ~120 Myr gap between the first appearance of the family represented by the extinct genus *Colocrus* from Aptian Brazil (McCafferty 1990) to modern extant taxa. The identification of *A. icarus* as an oligoneuriine also supports molecular phylogenetic predictions according to which Oligoneuriinae would have begun to emerge and radiate during the middle of the Cretaceous (Massariol et al. 2019). The discovery of *C. sheppardae* marks the oldest occurrence of the family Heptageniidae in the fossil record with the next occurrences being the Wapiti Formation's heptageniids (Bell et al. 2013) from the Campanian and the New Jersey amber *Amerogenia* imagos (Sinitshenkova and Grimaldi 2000) from the Cenomanian–Turonian boundary. This discovery pushes back the first known occurrence of the family to around 100 Ma, which has implications for our understanding of the diversification and evolution of Heptagenioidea. Contrastingly, the description of *P. borealis* marks one of the latest-ever occurrences of the now-extinct family Hexagenitidae in the entire fossil record, which is roughly coeval with *Hexameropsis elongatus* from Kachin amber (dated at ca. 98.8 Ma) (Lin et al. 2018). Cretaceous mayfly fossils are unfortunately rare, so understanding when hexagenitids may have gone extinct remains an open question until more material can be described over a larger time frame. As it stands, the first occurrence of the family Hexagenitidae consists of the genus *Shantous* from Callovian/Oxfordian China (168–160 Ma) (Zhang and Kluge 2007; Gao and Shubin 2012).

Behavioural inferences

Using modern mayfly nymphs as analogues, some behavioural and ecological inferences can be made about the lifestyles of the three described species. Like most brush-legged mayflies including Oligoneuriidae, Isonychiidae, and Colorburiscidae, it is likely that *A. icarus* used the combs of setae on its forelegs and mouthparts for filter-feeding in a flowing water environment, although some inhabit stationary water (Sartori and Brittain 2015). *Alatuscapillus icarus* also had well-developed legs, likely used for grasping a surface, which would support a filter-feeding hypothesis. Modern oligoneuriids inhabit a wide variety of different environments, including rocky streams, brooks, or sandy streams with submerged wood, which tend to have a strong water current. Similarly, modern heptageniids are best known for bottom-feeding in streams, generally living under stones and pebbles (Sartori and Brittain 2015). Their flattened body, developed tarsal claws, and strong legs allow for an easy attachment to a surface and minimise the destabilising effects of currents (Ditsche-Kuru et al. 2012). This clinger lifestyle is often found near vegetation in shallow lakes or streams, with detritus being a large part of their diet. The modern lifestyles of these families, combined with the incomplete preservation of the *A. icarus* and *C. sheppardae* holotypes, suggest that they lived in a high-energy stream environment before being transported to the lakebed post-mortem (Zhang et al. 2022).

As for the potential behaviour of *Protoligoneuria*, McCafferty (1990) suggests that hexagenitid nymphs were strong swimmers. Their robust caudal filaments were likely able to interlock thanks to their dense lateral filaments on their inner margins, allowing them to swim by vertically undulating their abdomen in a swimming pattern akin to that seen in *Ameletus* or *Isonychia* (Dodds and Hisaw 1924; Sartori and Brittain 2015). McCafferty (1990) also suggests that the large gill lamellae were also useful for swimming. When compared to *Ameletus* or *Isonychia, Protoligoneuria* has a rounder and much less torpedo-like body plan, with blunter heads and relatively shorter cerci. This could suggest greater drag on the body and thus lesser swimming efficiency compared to some of its extant counterparts. All this suggests that *Protoligoneuria* would likely have been best adapted to low-energy lake environments. This is consistent with the sediment lamination of the Redmond Formation and the large number of hexagenitids found in other lacustrine or lagoon fossil deposits (Zhang and Kluge 2007; Sinitshenkova 2017; Zhang et al. 2022). The low abundance of hexagenitid fossils in the Redmond Formation is likely due to the near complete destruction of the latter's thin local exposure by past mining activities.

It must be stated that all these hypotheses predicting the potential behaviours of the Redmond Formation's mayfly nymphs are strongly generalized based on modern or similar taxa. Considering how different Late Cretaceous freshwater ecosystems may have been from the present, and the behavioural variability of modern taxa, it remains difficult to infer the behaviours of these extinct species with any great certainty.

Further notes

The three holotypes described represent the only existing Redmond Formation material for their respective taxa as of 2024. Three other specimens have been collected, but they were so poorly preserved that no anatomical traits were identifiable aside from their generally distorted outline (Fig. S4 (RMIP2018.18.14) and Fig. S5 (RMIP2018.18.43)) or a partially preserved abdomen (Fig. S6 (MPEP1152.2)). Images of these additional specimens can be found in the Supplementary Materials. Considering this, the collection of further material will be greatly beneficial for a more comprehensive description and classification of these taxa. Unfortunately, because of the limited material, matrix, and orientation of the specimens themselves, small details such as the genitalia, mouthparts, and wing venation, which could have been used for further identification, could not be fully described. Additionally, no adult-stage remains have yet been reported from the Redmond Formation, but their discovery potential is high considering the preservation state of other described insect wing material (e.g., Demers-Potvin et al. 2020, 2021). This material would help better classify the described species in the wider context of both fossil taxa (which are best preserved in amber deposits) and modern taxa (which can be more easily examined from every angle). As such, further fieldwork is encouraged to gather this potentially significant material.

Conclusions

The discovery and description of the first Cenomanian ephemeropterans known from the Redmond Formation (*A. icarus*, *C. sheppardae*, and *P. borealis*) have significant implications for understanding the evolutionary history of mayflies. *A. icarus* marks the first occurrence of the modern family Oligoneuriidae in North America's fossil record. The discovery of *C. sheppardae* marks the earliest-ever occurrence of Heptageniidae and reinforces the widespread presence of the family across Cretaceous North America. Finally, the presence of *P. borealis* marks the first described occurrence of the extinct family Hexagenitidae in North America, reinforcing the hypothesis that the family had a significant global distribution. The description of these mayfly nymphs contributes to expanding the region's fossil insect diversity in an otherwise fossil-poor region of the world. Considering the remarkable preservation of the Redmond Formation's fossils and lack of large-scale prospecting, there remains great potential for further material to be discovered, which can be used to further refine and differentiate the newly described species.

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Author information

Author ORCIDs

André S. Mueller https://orcid.org/0009-0004-5263-7123
Alexandre V. Demers-Potvin https://orcid.org/0000-0002-9149-8427

Author contributions

Conceptualization: ASM, AVD
Formal analysis: ASM, AVD
Funding acquisition: AVD
Investigation: ASM
Methodology: ASM, AVD

Resources: AVD
Visualization: ASM
Writing – original draft: ASM
Writing – review & editing: ASM, AVD

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Supplementary material

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