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ARTICLE

A new genus and species of split-footed lacewings (Neuroptera) from the early Eocene of western Canada and revision of the subfamily affinities of Mesozoic Nymphidae

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Abstract

A new genus and new species of Nymphidae (Neuroptera) is described from the Ypresian Okanagan Highlands locality of Falkland, British Columbia, Canada: *Epinesydrion falklandensis* **new genus, new species**. This is only the fourth known Cenozoic adult specimen, and all others are less complete. It is the second specimen from the Okanagan Highlands. Currently Nymphidae has two recognised subfamilies. All Cenozoic fossils are confident members of the Nymphinae, but the subfamily assignments of almost all Mesozoic genera are problematic. The Late Cretaceous *Dactylomyius* is the only genus that might belong to Myiodactylinae. The rest may belong to the undefined stem groups of the family or to the Nymphinae, with varying levels of probability. *Mesonymphes sibirica* is transferred to *Nymphites* Haase: *N. sibiricus* (Ponomarenko), **new combination**; *Sialium minor* to *Spilonymphes* Shi, Winterton, and Ren: *Spilonymphes minor* (Shi, Winterton, and Ren), **new combination**; "*Mesonymphes*" *apicalis* does not belong to *Mesonymphes* Carpenter and may not even belong to the Nymphidae. The fossil record of the family occurs across much of the globe, but today they are restricted to Australia, New Guinea, and possibly the Philippines. Modern Nymphinae is only found in Australia. This may result from a requirement of frost-free climates, which were more widespread in the past.

Introduction

The Nymphidae (split-footed lacewings) is a small family of medium-sized to large-sized Neuroptera with eight extant genera and 35 extant valid species. They are currently restricted to Australia and adjacent islands, New Guinea (New 1982a, 1985, 1986a, 1988; Oswald 1997, 1998; Global Biodiversity Information Facility 2019), and possibly the Philippines but that record is doubtful (New 1982a). The extant genera of Nymphidae are divided into two distinct subfamilies, Nymphinae and Myiodactylinae (New 1984; Shi *et al.* 2015), which were once considered as separate families (*e.g.*, Tillyard 1926). The Nymphinae comprises three extant genera (*Nymphes* Leach, *Austronymphes* Esben-Petersen, and *Nesydrion* Gerstaecker), and Myiodactylinae, the other five.

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The Nymphidae were relatively diverse in the Mesozoic (Table 1). Twenty species have been described from their earliest appearance in the Middle Jurassic through the Late Cretaceous (Turonian) (Carpenter 1929; Panfilov 1980; Makarkin 1990a, 1990b; Ponomarenko 1992; Martins-Neto 2005; Ren and Engel 2007; Engel and Grimaldi 2008; Makarkin *et al.* 2013; Shi *et al.* 2013, 2015; Myskowiak *et al.* 2016). Their fossils are, however, rare in the Cenozoic, with only three species known, each represented by single, incomplete adult specimen: *Nymphes*? *georgei* Archibald, Makarkin, and Ansorge from the Ypresian (early Eocene) Okanagan Highlands locality at Republic (Washington, United States of America), and two species of the genus *Pronymphes* Krüger from Priabonian (late Eocene) Baltic amber: *P. mengeana* (Hagen) and *P. hoffeinsorum* Archibald, Makarkin, and Ansorge (Archibald *et al.* 2009). The single known larva from Baltic amber is also considered to belong to *Pronymphes* (MacLeod 1971). Here, a fourth adult specimen is described from the Ypresian Okanagan Highlands of Falkland, British Columbia, Canada, representing a new genus and species. We further evaluate the subfamily affinities of Cenozoic and Mesozoic fossil Nymphidae and their biogeographic implications. The generic affinities of some Mesozoic species are revised.

Material and methods

This study is based on a single specimen in lacustrine shale from a locality near Falkland, British Columbia, Canada.

Locality

This site is in the middle of the southern half of the Okanagan Highlands series of Ypresian upland lacustrine shale and coal basins that are scattered over about 1000 km of south-central British Columbia, Canada, from Driftwood Canyon near the village of Smithers in west-central British Columbia to just over the international border at Republic, Washington, United States of America (Archibald *et al.* 2011a). The locality is about 220 km northwest of Republic. It is a small, difficult to access exposure of Kamloops Group lacustrine shale on Estekwalan Mountain about 5 km northwest of the village of Falkland, British Columbia.

Uranium–lead dating from zircons recovered from an ash layer intercalated within the fossil-bearing sediment indicates an age of 50.61 ± 0.16 million years ago (see Moss *et al.* 2005). Smith *et al.* (2009) estimated a paleoelevation of greater than 1.3 km, similar or slightly higher than modern levels, and provided estimates of an upper microthermal mean annual temperature, slightly varying by method of analyses (microthermal: mean annual temperature $\leq$ 13 °C).

Although Falkland fossil insects are plentiful (S.B.A., personal observation), they have received relatively little attention. They were first mentioned by Rice (1959) who named a species of Bibionidae (Diptera) from the site (*Plecia cairnesi* Rice). The fossils that he reported were collected "northwest of Falkland" by Geological Survey of Canada geologists in 1932, though it is not clear whether this was the same exposure referred to here, and there are other local exposures more readily accessible. Rice (1959) was referenced by Wilson (1977) and Douglas and Stockey (1996) in their lists of insect-bearing deposits in British Columbia, but they did not collect there or report new taxa.

The site was shown to one of us (S.B.A.) by a local resident in June 2001. The major subsequent focus on it in recent decades has been on its plants (Moss *et al.* 2005, 2016; Smith *et al.* 2009, 2010, 2012). Its few subsequently published insects include a bulldog ant (Hymenoptera: Formicidae: Myrmeciinae: *Myrmeciites* Archibald, Cover, and Moreau; Archibald *et al.* 2006), a scorpion fly (Mecoptera: Eorpidae: *Eorpa* Archibald, Mathewes, and Greenwood; Archibald *et al.* 2013), and a parasitoid wasp (Hymenoptera: Trigonalyidae; Archibald *et al.* 2018).

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Table 1. Fossil species of Nymphidae.

Species	Age	Locality
Jurassic		
Liminympha makarkini Ren and Engel[1,2]	Bathonian/early Oxfordian[3]	China, Daohugou
Daonymphes bisulca Makarkin, Yang, Shi, and Ren[2]	Bathonian/early Oxfordian[3]	China, Daohugou
Nymphites bimaculatus Shi, Makarkin, and Ren[4]	Bathonian/early Oxfordian[3]	China, Daohugou
Mesonymphes rohdendorfi Panfilov[5]	Oxfordian/Kimmeridgian[6]	Kazakhstan, Karatau
Mesonymphes hageni Carpenter[7]	Kimmerdgian/Tithonian[8]	Germany, Solnhofen
Nymphites priscus Weyenbergh[4,9]	Kimmerdgian/Tithonian[8]	Germany, Solnhofen
Cretaceous		
Sialium sipylus Westwood[10,11]	early Berriasian[11]	United Kingdom, Durlston Bay
Nymphites sibiricus (Ponomarenko)[12]	Barremian[13]	Russia, Baissa
"*Mesonymphes*" *apicalis* Ponomarenko[12]	Barremian[13]	Russia, Baissa
Cretonymphes baisensis Ponomarenko[12]	Barremian[13]	Russia, Baissa
Baissoleon cretaceus Makarkin[14]	Barremian[13]	Russia, Baissa
Sialium sinicus Shi, Winterton, and Ren[15]	Barremian/early Aptian[16]	China, Yixian Formation
Baissoleon similis Shi, Winterton, and Ren[15]	Barremian/early Aptian[16]	China, Yixian Formation
Spilonymphes major Shi, Winterton, and Ren[15]	Barremian/early Aptian[16]	China, Yixian Formation
Spilonymphes minor (Shi, Winterton, and Ren)[15]	Barremian/early Aptian[16]	China, Yixian Formation
Olindanymphes makarkini Martins-Neto[17]	late Aptian[18]	Brazil, Crato Formation
Rafaelnymphes cratoensis Myskowiak, Huang, Azar, Cai, Garrouste, and Nel[19]	late Aptian[18]	Brazil, Crato Formation
Santananymphes ponomarenkoi Martins-Neto[17]	late Aptian[18]	Brazil, Crato Formation
Elenchonymphes electrica Engel and Grimaldi[20]	earliest Cenomanian	Myanmar, Burmese amber
Dactylomyius septentrionalis Makarkin[21]	Turonian[22]	Russia, Arkagala Formation
Paleogene: Eocene		
Epinesydrion falklandensis new species	Ypresian[23]	Canada, Falkland (Okanagan Highlands)
Nymphes? georgei Archibald, Makarkin, and Ansorge[24]	Ypresian[25]	United States of America, Republic (Okanagan Highlands)
Pronymphes hoffeinsorum Archibald, Makarkin, and Ansorge[24]	Priabonian[28]	Russia, Baltic amber
Pronymphes mengeana (Hagen)[26,27]	Priabonian[28]	Poland?, Baltic amber

[1]Ren and Engel (2007); [2]Makarkin *et al.* (2013); [3]Huang *et al.* (2018); [4]Shi *et al.* (2013); [5]Panfilov (1980); [6]Rasnitsyn and Zherikhin (2002); [7]Carpenter (1929); [8]Schweigert (2007); [9]Weyenbergh (1869); [10]Westwood (1854); [11]Jepson *et al.* (2012); [12]Ponomarenko (1992), generic placement unresolved; [13]Bugdaeva and Markevich (2012); [14]Makarkin (1990a); [15]Shi *et al.* (2015); [16]Makarkin *et al.* (2012); [17]Martins-Neto (2005); [18]Martill and Heimhofer (2008); [19]Myskowiak *et al.* (2016); [20]Engel and Grimaldi (2008); [21]Makarkin (1990b); [22]Makarkin and Khramov (2015); [23]Moss *et al.* (2005); [24]Archibald *et al.* (2009), generic placement uncertain; [25]Wolfe *et al.* (2003); [26]Pictet-Baraban and Hagen (1856); [27]Krüger (1923); [28]Perkovsky *et al.* (2007).

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The only known other Neuropteran specimen from Falkland is a poorly preserved, undescribed Chrysopidae probably belonging to the Ypresian genus *Adamsochrysa* Makarkin and Archibald (current research).

Terminology

Venational terminology follows Makarkin *et al.* (2017). That of wing spaces and finer details of venation (*e.g.*, veinlets, traces) follows Oswald (1993). Contrary character states of compared taxa are provided in brackets.

Abbreviations: AA1–AA3, first to third anterior analis; CuA, anterior cubitus; CuA1, first (proximal-most) branch of CuA; CuP, posterior cubitus; MA and MP, anterior and posterior branches of the media (M); MP1, proximal-most branch of MP; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; ScP, posterior subcosta; sv, subcostal veinlets.

Institutional abbreviations: GSC, Geological Survey of Canada, Ottawa, Ontario, Canada; PIN, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Epinesydrion Archibald and Makarkin, new genus (Nymphidae: Nymphinae)

http://zoobank.org/urn:lsid:zoobank.org:act:2C1DAB84-3B3B-4F51-8848-E51B99911C4D

Diagnosis. May be distinguished from other genera of the family by a combination of the following wing characters (see detailed comparison of the new genus in Discussion): Forewing: costal space relatively narrow; RP1 originating very far from wing base (distad origin of CuA1); M forked proximad origin of CuA1; MA, MP, anterior trace of branched portion of CuA arched; no crossvein between the branches of CuA; all anal veins forked. Hind wing: RP originating near wing base; presectoral crossveins (*i.e.*, those between R and M proximad origin of RP) absent.

Etymology. From the Greek *epi* [επι], near, and *Nesydrion*, a genus-group name. Gender masculine.

Type and only species. *Epinesydrion falklandensis* **new species**, here designated.

Epinesydrion falklandensis Archibald and Makarkin, new species

http://zoobank.org/urn:lsid:zoobank.org:act:CE2A7BF9-9888-44A7-8EB6-6C4F66E23739
Figs. 1–2.

Diagnosis. See genus diagnosis.

Material. Holotype: GSC 141064A, B (part and counterpart) was collected on 5 July 2006, by S.B. Archibald and deposited in the GSC type collections. An incompletely preserved specimen with a head, thorax with three or four very poorly preserved legs, the mostly complete right forewing, the basal portion of the right hind wing, and the fragmentary basal portions of the left wings.

Etymology. The specific epithet is a toponym formed from the name of the locality of the holotype.

Type locality and age. Falkland, British Columbia, Canada, GSC locality number V-016727; late Ypresian.

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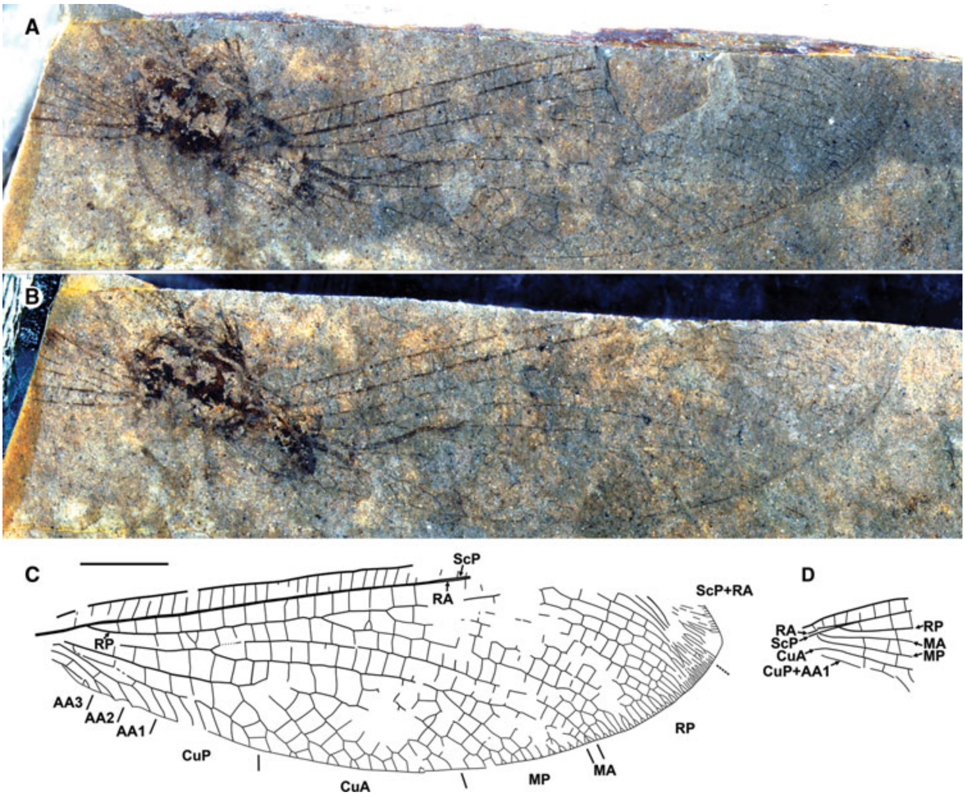

Fig. 1. *Epinesidrion falklandensis* **new genus, new species**, holotype. **A**, Part GSC 141064 A (converted to standard view, with apex to the right); **B**, counterpart GSC 141064 B; **C**, venation of the right forewing; **D**, venation of the right hind wing. Scale bar 5 mm (all to same scale).

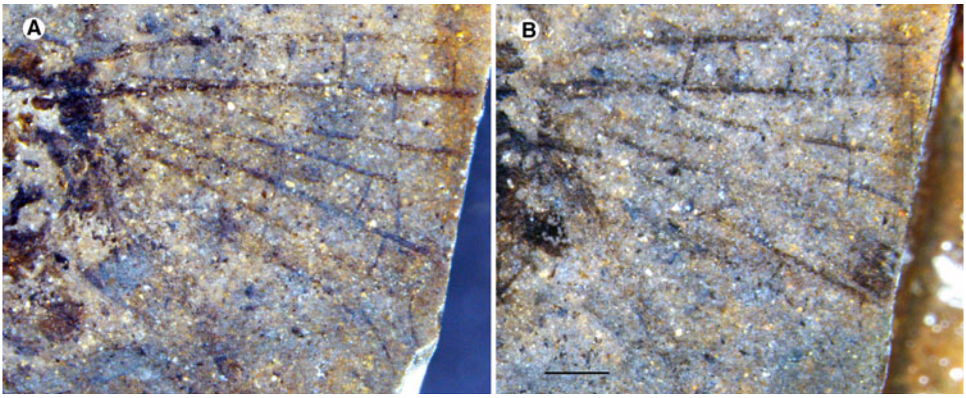

Fig. 2. *Epinesidrion falklandensis* **new genus, new species**, holotype. **A**, Right hind wing of the part GSC 141064 A (converted to standard view, with apex to the right); **B**, same of the counterpart GSC 141064 B. Scale bar 1 mm (both to same scale).

Description. Head: indistinctly preserved; diameter of eye approximately half head length. Antennae about 10 mm long, details not discernible.

Thorax: Pronotum poorly discernible. Mesonotum and metanotum dark laterally, pale medially, forming broad pale medial stripe through at least pteronotum (but possibly an artefact).

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Legs: Poorly preserved, no details discernible.

Forewing: Broadly oval with apex distinctly pointed. Length 40 mm, maximum width 12 mm at mid-wing. Trichosors poorly discernible (proximally along posterior margin not discernible, distally one trichosor between each pair of veins, poorly preserved). Macrotrichia on veins, margins almost not discernible (poorly preserved and/or short). Costal space relatively narrow, even width from near base to 2/3 wing length (apicad this, not preserved). All preserved sv are simple, rather straight, closely spaced. Posterior subcosta and R/RA are close, possibly touching, appearing as single vein without space between them (*i.e.*, subcostal space compressed) through almost all preserved portions of the wing (basal 2/3) but slightly separate basally. ScP + RA terminates at the margin beyond the apex. ScP + RA veinlets are indistinctly preserved but some deeply forked. All appear to have shallow forks near margin. Anterior radius space uniformly wide through middle half of the wing, with 11 crossveins regularly spaced between RA and RP before the origin of RP1. Presectoral crossveins are absent. Posterior radius originates close to the wing base; anterior trace of RP with nine branches, all dichotomously branched distally at different distances from the margin (RP1, RP5 most deeply branched). The proximal-most branch of RP originates at 43% of wing length. Media is deeply forked, half-way between level of origin of RP, origin of RP1, and proximad CuA1. The anterior branch of the media is arched, simple, with only shallow end-twigging. The posterior branch of the media is arched, parallel to MA, with six branches, all (except distal-most) dichotomously forked at different distance from the margin. The posterior branch of the media space is rather broad, triangular. Numerous crossveins in radial to medio-cubital spaces, not arranged in distinct gradate series. The cubitus is divided into CuA and CuP near the wing base (basad origin of RP). The CuA space is broad, triangular. Anterior trace of CuA slightly incurved before the origin of CuA1, arched after; with five branches, each forking again two to three times near margin; all connected by numerous crossveins. The CuA and CuP are connected by numerous crossveins (eight in right wing). The CuP has seven pectinate branches, none connected by crossveins. There is a single crossvein preserved between CuP, AA1 (2cu-aa), connecting CuP and the anterior trace of AA1; a basal crossvein (1cu-aa) is possible at the point where CuP and AA1 are closest. The AA1, AA2 and AA2, AA3 are each connected by a single, long crossvein. The AA1 is rather deeply forked once; AA2 and AA3 are more shallowly forked once. Wing membrane apparently hyaline throughout as preserved.

Hind wing: Basal-most fragment is preserved, likely somewhat torn; apparently the ScP is positioned posteriad RA by damage (Figs. 1–2). Costal space is relatively narrow. Subcostal veinlets are simple, straight. Basal portions of MA and MP are obscured; the fork of M is not visible, apparently very near the wing base. The RP originates near the wing base; no presectoral crossveins are detected. Basal portions of CuA, CuP + AA1 are preserved. Crossveins between RA to CuP are relatively scarce. Wing membrane apparently hyaline.

Discussion

The validity and relationship of *Epinesydrion*

Two genera of Nymphidae were previously known from the Eocene: the extant *Nymphes* from the Okanagan Highlands of North America (but see below) and the extinct *Pronymphes* from Priabonian Baltic amber (Krüger 1923; Archibald *et al.* 2009). A larva from Baltic amber was assigned to *Pronymphes* (see Weidner 1958, fig. 7; plate 14, figs 4–5; MacLeod 1971, figs. 5–7). *Pronymphes* and *Epinesydrion* confidently belong to the Nymphinae, possessing diagnostic character states of the subfamily (see below). Both are clearly similar to the nymphine genus *Nesydrion* (four extant Australian species). These three genera share two forewing character states: the deeply forked M [shallowly forked in *Nymphes* and *Austronymphes*] and a lack of crossveins between the branches of CuP [present in *Nymphes*].

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Epinesydrion differs from *Nesydrion* and *Pronymphes* by MA, MP, and a part of the anterior trace of CuA, distad CuA1 being clearly arched, and by its triangular CuA space. This triangular CuA space is also characteristic of *Nymphes*, which, however, differs from *Epinesydrion* in other ways (*e.g.*, as above). Three of four species of *Nesydrion* possess one to three presectoral crossveins in the hind wing, but no presectoral crossveins are found in *Epinesydrion*. The colour pattern of the mesonotum and metanotum of *Epinesydrion falklandensis* (*i.e.*, dark entirely or only laterally with possible pale broad medial stripe) also strongly differs from that of any species of *Nesydrion* where this is generally pale but sometimes with a dark median stripe.

It is noteworthy that, except at the base, ScP and R/RA appear fused and so the subcostal space appears missing. Such an apparent fusion of these veins also occurs in the holotype of the Late Jurassic *Nymphites priscus* (Weyenbergh) (see Shi *et al.* 2013, figs. 1–2). The subcostal space is clearly discernible (often well developed) in all other fossil species except the proximal basal part of *Nymphes? georgei* (generic classification uncertain), which is missing in its only known fossil (see Archibald *et al.* 2009, fig. 1A). We believe it to be likely that this close approach of ScP and RA in *Epinesydrion* indicates the absence of subcostal crossveins in the space or at least the presence of very short thyridiate crossveins (incomplete crossveins that allow folding or bending of the wing). In all species of *Nesydrion*, there are numerous thyridiate crossveins in the subcostal space, which often almost reach RA but do not touch it (Shi *et al.* 2015). This suggests that the apparent lack of the subcostal space may be an artefact resulting from the space collapsing postmortem due to the absence of structural support from the connecting crossveins.

The forewings of *Epinesydrion* differ from those of all Mesozoic genera by their triangular CuA space and CuA1 originating only slightly distad the fork of M. The origin of CuA1 is located far distad the fork of M in all Mesozoic genera except in *Baissoleon* Makarkin and *Olindanymphes* Martins-Neto. Further, M in these genera is strongly arched as in *Epinesydrion*. Their CuPs, however, have only one to two branches, whereas it is strongly pectinate in *Epinesydrion*, with six branches.

Epinesydrion is, therefore, clearly a distinct genus. As above, the proximal forking of M suggests that it is closely related to *Nesydrion* and *Pronymphes* but more distantly to them than they are to each other because of the triangular CuA space in the forewing, a certainly apomorphic state occurring within the family that these do not possess. However, this is shared by *Nymphes*, which alternatively suggests that *Epinesydrion* is more closely related to it.

It should be noted that the genus *Nymphes* has been reported from the nearby Okanagan Highlands locality at Republic (*N.? georgei*), which is nearly of the same age (Fig. 3) (Archibald *et al.* 2009). Unfortunately, this record is of a single hind wing that lacks the basal portion, precluding comparison of key character states with *Epinesydrion falklandensis*. Therefore, *N.? georgei* could belong to *Epinesydrion* and so we treat it here as a species of uncertain generic placement. No preserved morphology rules out this possibility. Resolving this requires the discovery of a comparable forewing of *N.? georgei* or of a more complete hind wing of *Epinesydrion*.

Diversity of Nymphidae

This family is monophyletic based on two putative synapomorphies of adults: the presence of thyridiate crossveins in the subcostal space and their possession of a bifid arolium (Shi *et al.* 2015). However, such crossveins or a bifid arolium have not been detected with confidence in fossil species. Carpenter (1929, fig. 1) figured the crossveins in this position as complete in *Mesonymphes hageni* Carpenter, and Shi *et al.* (2013) speculated that thyridiate crossveins are "probably" present in *Nymphites bimaculatus* Shi, Makarkin, and Ren as its ScP possesses few, small projections posteriorly. Nevertheless, fossil specimens may be confidently assigned to Nymphidae by the following combination of wing character states: (1) ScP and RA are distally fused; (2) ScP + RA enters

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Fig. 3. Distribution of fossil and extant Nymphidae. Jurassic localities (black dots): 1, Daohugou, China; 2, Karatau, Kazakhstan; 3, Solnhofen, Germany. Cretaceous localities (blue dots): 4, Durlston Bay, United Kingdom; 5, Baissa, Russia; 6, Yixian Formation, China; 7, Crato Formation, Brazil; 8, Burmese amber, Myanmar; 9, Arkagala Formation, Russia. Cenozoic localities (brown dots): 10, Falkland, Canada; 11, Republic, United States of America; 12, Baltic amber. The present-day distribution is shown in red.

the wing margin posteriad the apex; (3) trichosors are present; (4) M originates near the wing base (there are no presectoral crossveins), and (5) M is not fused with CuA in the forewing. Only Nymphidae and all Nymphidae share this combination except *Baissoleon*, where ScP + RA enters the wing margin before the apex (it is assigned to the family by characters 1, 3–5, and general similarity of the venation to that of Nymphidae, for example, by the nonpectinate AA1 in the forewing [pectinate in all Osmylidae possessing characters 1, 3–5]).

Extant. Extant Nymphidae form two distinct groups of genera, which constitute the subfamilies Myiodactylinae and Nymphinae. According to Shi *et al.* (2015), the species of Nymphinae are easily distinguished from those of the Myiodactylinae by: (6) the presence of tibial spurs, at least on the hind legs [absent]; (7) the narrow costal space in the forewing [broad, often with multiple forked sv]; (8) crossveins between the branches of CuA in the forewing [absent]; (9) short AA1 in the forewing [long]; and (10) at least several rows of linking crossveins between branches of MP in the hind wing [few linking crossveins]. They also differ in the morphology and behaviour of the larvae. Those of Myiodactylinae are rounded and flattened dorsoventrally (New 1983; New and Lambkin 1989) and are arboreal, living on leaves (in *Osmylops* Banks, with a green body) or dwell in the litter (those of *Norfolius* Navás are brown). The larvae of Nymphinae (known only in *Nymphes*) are elongate, dwell in the litter, and carry debris for camouflage (New 1982b, 1986b).

Cenozoic. Based on these adult character states, both *Epinesydrion* and *Pronymphes* – the Nymphidae genera known only as fossils in the Cenozoic – may be assigned to Nymphinae with certainty, as they conform to all of these, except that the presence or absence of tibial spurs (character 6) and hind wing crossvenation (character 10) cannot be assessed in *Epinesydrion* by preservation, and the hind wing MP branches (character 10) in *Pronymphes* are connected by only a single row of linking crossveins. *Pronymphes* does, however, possess tibial spurs (Pictet-Baraban

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and Hagen 1856). The Baltic amber larva tentatively assigned to *Pronymphes* clearly belongs to the Nymphinae by its elongate body, the rugose texture of the cuticle of the head, the presence of distinct dorsal and ventral rows of lateral scoli on the abdomen, and the vestiture of setae with globular tips as in *Nymphes* (MacLeod 1971). However, as *Nymphes* is the only extant nymphine genus whose larva has been described, the position of this larva within the subfamily remains unresolved.

Mesozoic. The subfamily assignments of almost all Mesozoic genera are more problematic than are those of the Cenozoic. Makarkin (1990b) suggested that *Dactylomyius* Makarkin (Fig. 3) probably belongs to the Myiodactylinae, and *Mesonymphes* Carpenter certainly to the Nymphinae. Shi *et al.* (2015) made the first attempt to resolve the phylogeny of the family, including the five Mesozoic genera. They assigned *Baissoleon*, *Sialium* Westwood, and *Nymphites* Haase to the Nymphinae; *Spilonymphes* Shi, Winterton, and Ren to the Myiodactylinae; and *Liminympha* Ren and Engel were considered sister to Nymphinae + Myiodactylinae (see Shi *et al.* 2015, fig. 5). Below, we evaluate the subfamily and genus assignments of all Mesozoic genera and conclude that some of these may be incorrect.

All Mesozoic genera are at least superficially similar in some ways to the Nymphinae except *Dactylomyius* from the Late Cretaceous of northeastern Siberia. As in the Nymphinae, their wings are relatively narrow, and tibial spurs are preserved in some species (*e.g.*, *Nymphites bimaculatus*, *Baissoleon similis* Shi, Winterton, and Ren). Shi *et al.* (2015) treated the presence of these spurs as apomorphic in the Nymphinae; however, it is plesiomorphic, as it is present in all families of Neuropterida (including extinct families wherever legs are preserved well enough to evaluate), and their absence (including in the Myiodactylinae) is an apomorphy.

The relatively narrow wing shape of Mesozoic genera is a generalised condition, which often occurs in the order and so lacks diagnostic value in resolving their subfamily affinities. Even in extant taxa, forewings of nymphine species are sometimes broader than those of myiodactyline species (*e.g.*, length/width ratio is 2.99 in *Nesydrion diaphanum* Gerstaecker, and 3.20 in *Osmylops ectoarticulatus* Oswald), though the forewings in the Myiodactylinae are usually broader than those of Nymphinae.

The venation of Mesozoic taxa varies to a large extent among genera. The monotypic genus *Dactylomyius* differs most strongly. It is known by the mostly complete, broad hind wing of *D. septentrionalis* Makarkin (Fig. 3). Its venation is most similar to that of *Myiodactylus*, especially by its dilated costal space, dense crossvenation, and wing shape but differs by its nonpectinate MP [pectinate in *Myiodactylus*], the broad space between CuA and CuP [narrow in *Myiodactylus*], and the very long CuA with its distal branches strongly curved anteriorly [moderately long with all branches only slightly curved in *Myiodactylus*]. Reexamination of the holotype shows that the interpretation of the veins by Makarkin (1990b) was partly incorrect: the anterior branch of MP in that work is actually MP; the posterior branch of MP is actually CuA; Cu is actually CuP or CuP + AA1; and A1 is probably AA2. This is supported by CuA being clearly concave, as is characteristic of the hind wings of all Neuroptera (see Makarkin *et al.* 2009). This is perhaps the single fossil genus whose assignment to the Myiodactylinae appears possible, even though it bears a number of notable dissimilarities in its venation with *Myiodactylus*.

Other Mesozoic genera are superficially similar to the Nymphinae, and most may be divided into four groups.

(1) The Middle Jurassic to Early Cretaceous *Liminympha* Ren and Engel, *Daonymphes* Makarkin, Yang, Shi, and Ren, *Nymphites*, *Mesonymphes*, *Sialium*, and *Spilonymphes*. These form a relatively homogeneous group characterised by a very deeply forked M; MA with few branches; MP and CuA are pectinate, with long branches; the origin of CuA1 is located far distad the fork of M; CuP is strongly pectinate; and AA1 is often relatively strongly branched (forked two to three times, rarely more). Their general venation pattern is clearly more similar to that of Nymphinae

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than Myiodactylinae. However, some features contradict this. For example, AA1 has more branches than in extant Nymphinae (similar to the condition seen in the myiodactyline *Osmylops*). Also, there is only one row of crossveins between branches of MP in the hind wings, not several as in extant genera of Nymphinae. It is possible that all genera of this group belong to stem Nymphidae or are sister to Myiodactylinae + Nymphinae.

Of these, only *Liminympha* was considered as sister to the remaining Nymphidae by Shi *et al.* (2015), presumably based on a recurrent humeral veinlet, no crossveins between distal branches of RP, and the antennae longer than half wing length (an apomorphy shared with the extant *Nymphes aperta* New). However, the head with antennae is missing in both the part and the counterpart (see the photograph of the part in Ren and Engel (2007, fig. 1) and of the counterpart in Makarkin *et al.* (2013, fig. 3)), so we assume that the apparent long antennae of the original description are actually artefacts of preservation. The humeral veinlet is recurrent in *Liminympha makarkini* Ren and Engel, *Daonymphes bisulca* Makarkin, Yang, Shi, and Ren and *Sialium sinicus* Shi, Winterton, and Ren, while it is crossvein like in all other Nymphidae. It is not branched or has a single, short branch (in *Daonymphes*). The presence of the recurrent humeral veinlet is probably a symplesiomorphy of the family. The absence of crossveins between distal branches of RP appears to be a good character to help separate genera but probably nothing more. By these reasons, consideration of *Liminympha* as the single sister genus to the remaining Nymphidae appears insufficiently based.

The genus *Spilonymphes* (with one species: *Spilonymphes major* Shi, Winterton, and Ren) was assigned to the Myiodactylinae by Shi *et al.* (2015). We believe that this is incorrect. Indeed, the venation of *S. major* does not significantly differ from that of *Sialium minor* Shi, Winterton, and Ren, which was considered to belong to Nymphinae by Shi *et al.* (2015). Here, we transfer *S. minor* to the genus *Spilonymphes*, in particular based on the presence of an important synapomorphy: the hind wing intramedian space is slightly but clearly expanded in the region of the origin of MP1, and distad this MP is slightly curved in both *S. minor* and *Spilonymphes major* (and see below). Shi *et al.* (2015) assigned *Spilonymphes* to the Myiodactylinae based solely on its slightly broader forewing in the costal space than is typical of Nymphinae genera; however, they mentioned that such a forewing costal space is present in some other Mesozoic genera (*e.g.*, *Daonymphes* and *Elenchonymphes* Engel and Grimaldi). Moreover, this space is not especially broad; it is nearly of the same width as in, for example, *Nymphites* and *Mesonymphes*. These two congeneric species have been assigned to two subfamilies; we believe that they belong to neither.

(2) The Early Cretaceous genus *Cretonymphes* Ponomarenko, represented by three specimens of *C. baisensis* Ponomarenko, possesses a forewing (the holotype) and two isolated hind wings (Ponomarenko 1992, fig. 1). These share a similar dense crossveins throughout. However, the holotype may not be conspecific or even congeneric with the hind wings (which belong to a single species with certainty). The forewing differs from that of the previous group by the forking of M slightly distad, its pectinate MA and its MP with few pectinate branches. By these reasons, *Cretonymphes baisensis* is most similar to *Rafaelnymphes cratoensis* Myskowiak, Huang, Azar, Cai, Garrouste, and Nel. The hind wing is unique within the family, as its CuP is strongly pectinate, with 13 branches. All other Nymphidae (including the oldest) have their hind wing CuP with a maximum of two branches, except *Sialium sinicus*, whose pectinate CuP bears five to six branches. If these three wings belong to the same species, then *Cretonymphes* should be considered as stem Nymphidae. If not, only the hind wings belong to stem Nymphidae, whereas the forewing may be tentatively assigned to crown Nymphinae by the narrow costal space and the presence of crossveins between branches of CuA in the forewing.

(3) The Early Cretaceous *Rafaelnymphes cratoensis* (Myskowiak *et al.* 2016). It is the single fossil species (and genus) whose M in the forewing is forked in its distal part (much distad the origin of RP). In this aspect, its venation is most similar to that of some species of *Nymphes*, differing mainly by the configuration of its CuA. Therefore, the nymphine assignment of the genus appears reasonable. However, although the legs are partly present in this fossil, tibial

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spurs were not detected (possibly, however, because of their small size). Also, the hind wings appear markedly longer than the forewings in the resting position (*i.e.*, they are slightly longer, or at least not shorter than the forewings), while lengths of the forewings and hind wings of all extant Nymphinae (and Nymphidae) appear equally long in the resting position (*i.e.*, the hind wings are actually shorter than the forewings) (see Myskowiak *et al.* 2016, figs. 4–5). Despite this, *Rafaelnymphes* Myskowiak, Huang, Azar, Cai, Garrouste, and Nel may be tentatively assigned to Nymphinae by the narrow costal space and the presence of crossveins between branches of CuA in the forewing.

(4) The Early Cretaceous genera *Baissoleon* and *Olindanymphes* (Makarkin 1990a; Martins-Neto 2005). These are probably closely related. They are smaller than other Mesozoic genera and differ further from them by the forewing CuP with few branches (one to two), a distinct pterostigmata in both wings, and ScP + RA entering the margin before the apex (slightly beyond the apex in *Olindanymphes*). The forewing with a pectinate CuP and ScP + RA entering the margin far beyond the wing apex is characteristic of all extant genera of both subfamilies. By these reasons, we find the assignment of *Baissoleon* to the Nymphinae Shi *et al.* (2015) to be uncertain. We believe it more likely that these two genera belong to stem Nymphidae.

The systematic positions of *Elenchonymphes* and *Santananymphes* Martins-Neto are unclear, and they might be associated with any or none of the above genera.

Elenchonymphes was described based on the distal 2/3 of the forewings and hind wings of the type species *E. electrica* Engel and Grimaldi, from earliest Late Cretaceous Burmese amber. The preserved venation of both wings appears rather atypical (*e.g.*, the RA space is narrowed at the distal crossvein in both wings, and CuA is strongly incurved in the forewing).

Four larvae from Burmese amber described as *Nymphavus progenitor* Badano, Engel, and Wang were assigned to the Nymphinae. They have the typical morphology of the subfamily, differing only in details (Badano *et al.* 2018, figs. 3c, S1h, S2a [not S2e as cited by them]). They are, however, represented by different instars, which might not belong to a single species and even genus; they might even be conspecific with *E. electrica*.

Santananymphes ponomarenkoi Martins-Neto was inadequately described, and so its systematic position cannot be evaluated without examination of the holotype.

In summary, the great majority of fossil genera may be assigned either to stem Nymphidae (most Mesozoic genera) or to Nymphinae (Late Cretaceous Burmese amber larvae, tentatively the Early Cretaceous *Rafaelnymphes*, and all Cenozoic genera). We find that both Nymphinae and Myiodactylinae (if *Dactylomyius* is a member) might have existed by the mid-Cretaceous, consistent with Shi *et al.* (2015) who believed that these groups likely diverged during "the Middle Jurassic or Early Cretaceous at the latest" (p. 478). The Early Cretaceous Nymphidae are more diverse than those of the Jurassic.

Taxonomic remarks

Sialium minor differs from the type species *Sialium sipylus* (known only from a hind wing) and *S. sinicus* by the following hind wing morphology: RP1 has few dichotomous branches distally [posterior trace of RP1 is pectinately forked in these two species]; the intramedian space is slightly dilated towards the origin of MP1 as MP distad MP1 is slightly arched [MA and MP are nearly parallel]; and CuA is gradually bent to the margin [nearly parallel to the margin from most part]. The venation of *S. minor* is most similar by these and other character states similar to that of *Spilonymphes major* from the same locality. The configuration of the hind wing intramedian space shared by these two species is especially important as it does not occur in other genera of Nymphidae. This may be considered a synapomorphy, a diagnostic trait grouping them together. Here, we transfer *Sialium minor* to this genus: *Spilonymphes minor* **new combination**. Both species occur in the Yixian Formation of China and have similar forewing colour patterns.

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Mesonymphes sibirica Ponomarenko does not belong to the genus *Mesonymphes*. Examination of the holotype shows that the drawing of the hind wing (Ponomarenko 1992, fig. 2b) is in part incorrect and that its venation is actually most similar to that of the genus *Nymphites*. There is a single row of linked crossveins between the branches of MP and CuA in both the forewings and hind wings, similar to the condition seen in *N. bimaculatus* (Shi *et al.* 2013, fig. 6). This row of crossveins is not present in *Mesonymphes* (*i.e.*, *M. hageni* and *M. rohdendorfi* Panfilov). *Mesonymphes sibirica* is transferred here to *Nymphites*: *Nymphites sibiricus* (Ponomarenko, 1992) **new combination**.

Mesonymphes apicalis Ponomarenko also does not belong to *Mesonymphes*. This species is represented by a distal fragment of a wing, which was interpreted by Ponomarenko (1992) as a hind wing. The proximal branches of RP in this wing are strongly convergent towards the outer wing margin, which is not characteristic of any known genera of Nymphidae, and so it may not belong to this family. A more complete wing is required to resolve its position.

Menon *et al.* (2005), Shi *et al.* (2015), and Myskowiak *et al.* (2016) considered *Araripenymphes* Menon, Martins-Neto, and Martill to belong to the Nymphidae (one species: *A. seldeni* Menon, Martins-Neto, and Martill from the late Aptian Crato Formation). However, this unusual genus is most similar to *Cratosmylus* Myskowiak, Escuillié, and Nel, also from the Crato Formation, for which the monotypic subfamily Cratosmylinae was erected within the Osmylidae by Myskowiak *et al.* (2015). Makarkin *et al.* (2017) suggested that these two genera form the family Cratosmylidae, closely related to Nymphidae and together with the Cretaceous Babinskaiidae form the epifamily Nymphidoidae (see Makarkin *et al.* 2018, fig. 16). *Araripenymphes* strongly differs from the genera of Nymphidae by the origin of RP being distant from the wing base, the presence of many presectoral crossveins in the forewing, and the very short CuA in the hind wing.

Biogeography

The distribution of Nymphidae in the past was much wider than today. Their fossils have been found across Asia and Europe in the Jurassic; in Asia, Europe, and South America in the Cretaceous; and in Europe and North America in the Eocene (Fig. 4).

Today, they are restricted to Australia, north through New Guinea and possibly, but doubtfully, the Philippines (see Introduction). All records outside of Australia are of species of the Myiodactylinae (Fig. 5) (New 1985, 1988). The Nymphinae is restricted to Australia, where it is widespread, mostly but not exclusively in eastern coastal regions from Queensland south to Tasmania (New 1982a, 1985, 1986a, 1988; Oswald 1997, 1998; Global Biodiversity Information Facility 2019).

The Nymphidae – more specifically the Nymphinae – is not the only insect group found in the Okanagan Highlands that is restricted to the Australian region today. These include the parasitoid Peradeniidae (Hymenoptera) found in southeastern Australia and Tasmania (Masner 1993); the ant subfamily Myrmeciinae (Hymenoptera: Formicidae) found in Australia, New Caledonia, and introduced in New Zealand (summary: Archibald *et al.* 2006); and termites of the family Mastotermitidae (Isoptera) that range in northern Australia and southern New Guinea (probably recently introduced) (Šobotník and Dahlsjö 2017).

Other Okanagan Highlands insects today range in the Australian region, are restricted in other places, and are scattered worldwide: parasitoid wasps of the family Monomachidae, rare in Australia and tropical regions of the New World (Masner 1993); an undescribed species of *Megymenum* Guérin-Menéville (Hemiptera: Dinidoridae) distributed in the Australian and Oriental regions (Kocorek and Ghate 2012), and green lacewings of the subfamily Nothochrysinae (Neuroptera: Chrysopidae), which mostly inhabit Mediterranean and semi-Mediterranean climates around the world, including portions of southern Australia (Archibald and Mathewes 2000; Archibald *et al.* 2010, 2011b, 2014a, 2014b, 2018).

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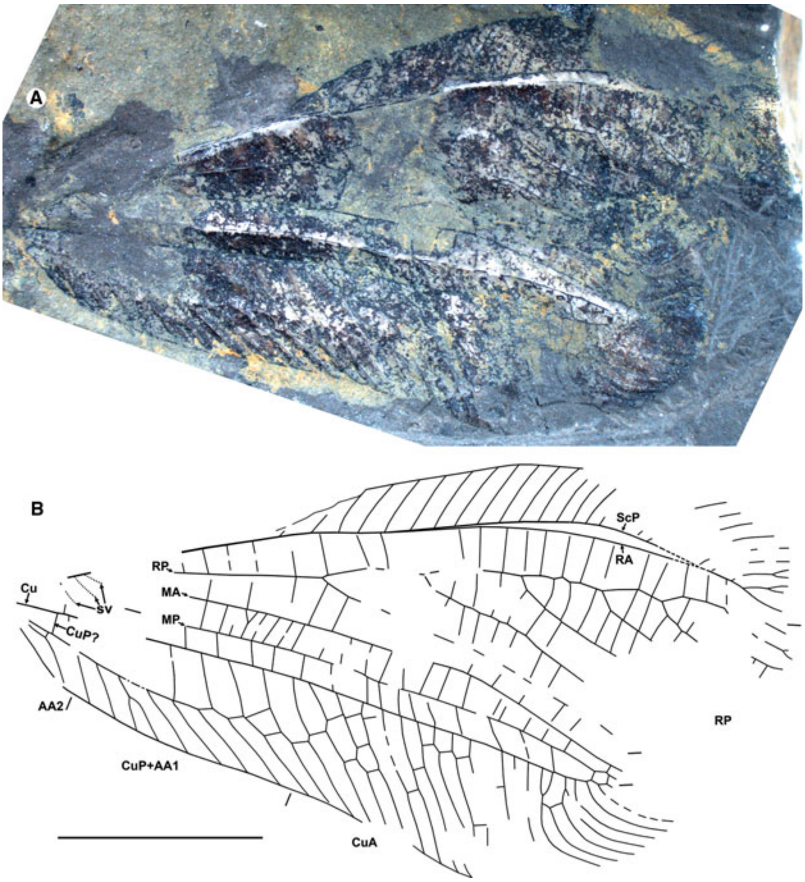

Fig. 4. *Dactylomyius septentrionalis* Makarkin, the sole fossil species possibly belonging to the Myiodactylinae, holotype PIN 1832/7. **A**, Photograph; **B**, drawing. Scale bar 5 mm (both to same scale).

Although these insects inhabit climates with a wide range of mean annual temperatures, from cooler mid-latitudes to hot low latitudes, all tend to share milder winters. This is also modelled for the Okanagan Highlands, where there appears to have been no frost days even in its coldest months, despite mostly microthermal mean annual temperatures (*e.g.*, Archibald and Farrell 2003; Archibald *et al.* 2010; 2014b). The modern range of Nymphinae, extending from the tropics of north Australia to the cool temperate climate of Tasmania, similarly shares milder winters.

Other insects found in the Okanagan Highlands that are not found in Australia today also show a similar pattern of occurrences in regions of mild winters throughout the Cenozoic to the present. For example, the single extant species of Eomeropidae (Mecoptera) inhabits the mid-latitude coastal Valdivian forest of Chile, with temperate but mild winters (Archibald *et al.* 2005), and Pachymerina (Coleoptera: Chrysomelidae: Bruchinae), which are found in frost-free regions of the New and Old World where the palms that they feed upon grow (Archibald *et al.* 2014b).

Eocene climates were globally equable, with frost-intolerant insects, vertebrates, and plants extending their ranges into high latitudes, such as palms (Arecaceae) and Crocodilia in temperate climates north to the Arctic Ocean (summaries: Archibald *et al.* 2010, 2014b). The post-Eocene shift in global climate regime may then have restricted both thermophilic and cold-intolerant organisms to low latitudes for differing reasons: thermophilic taxa because of extra-tropical decrease in the mean annual temperatures and the cold-intolerant taxa by extra-tropical decrease in the coldest month mean temperatures.

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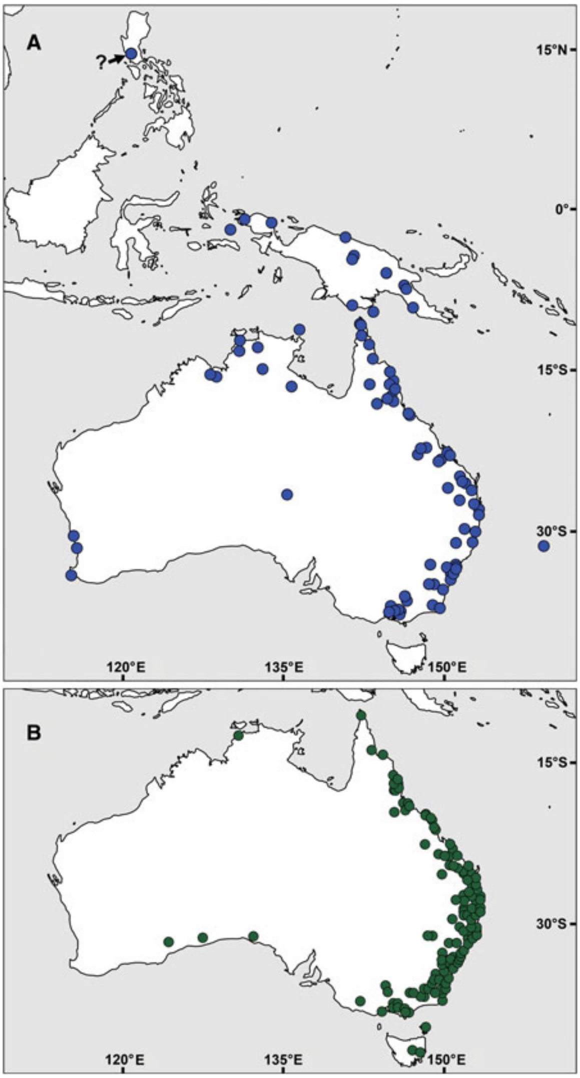

Fig. 5. Present-day distribution from data of New (1982a, 1985, 1986a, 1988), Oswald (1997, 1998), and Global Biodiversity Information Facility (2019). **A**, Myiodactylinae; **B**, Nymphinae. The reported occurrence of *Myiodactylus* at Mindanao, the Philippines, is doubtful (see New 1982a).

This would have ended the mixed tropical/temperate communities of the Okanagan Highlands, for example, forests with spruce and palms; tropical cockroaches (Blattodea: Blaberidae: Diplopterinae) and aphids (Hemiptera: Aphididae), extirpating cold-intolerant taxa (heat-requiring taxa would have never been present in these mostly upper microthermal climates) (Archibald and Farrell 2003; Archibald *et al.* 2010). Only Okanagan Highlands insects that could adapt to colder winters would have been able to persist there and in other extra-tropical regions where later Cenozoic broadened temperature seasonality lowered winter temperatures, for example, aphids, Siricidae (Hymenoptera), and Raphidioptera (Archibald and Mathewes 2000; Archibald and Rasnitsyn 2015; Makarkin *et al.* 2019); those that could not would have had their ranges moved or reduced to regions of the world without harsh winters, or would have gone extinct. Even cooler southern regions of modern Australia do not experience the extremes of winter cold common throughout the Northern Hemisphere

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in similar extra-tropical latitudes (Archibald *et al.* 2010, fig. 1). This expansion of extra-tropical temperature seasonality (particularly Northern Hemisphere) and associated change in insect community composition since the post-Eocene global climatic downturn could, for example, in part explain the overturn in dominance within green lacewings from the Nothochrysinae to the Chrysopinae since the Eocene (Makarkin and Archibald 2013; Archibald *et al.* 2014a).

If this model is correct, then the Nymphinae (and, more broadly, the Nymphidae) may persist in the Australian region by its possession of the key climatic similarity with the Ypresian Okanagan Highlands of mild winters independent of the mean annual temperature. Its absence in similar climates around the world (where, *e.g.*, Nothochrysinae inhabit today) may be due to regional extirpations resulting from historical contingencies.

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