New early Eocene Siricomorpha (Hymenoptera: Symphyta: Pamphiliidae, Siricidae, Cephidae) from the Okanagan Highlands, western North America

S. Bruce Archibald,[1] Alexandr P. Rasnitsyn

Abstract—We describe three new genera and four new species (three named) of siricomorph sawflies (Hymenoptera: Symphyta) from the Ypresian (early Eocene) Okanagan Highlands: Pamphiliidae, *Ulteramus republicensis* **new genus, new species** from Republic, Washington, United States of America; Siricidae, *Ypresiosirex orthosemos* **new genus, new species** from McAbee, British Columbia, Canada; and Cephidae, *Cuspilongus cachecreekensis* **new genus, new species** from McAbee and another cephid treated as Cephinae species A from Horsefly River, British Columbia, Canada. These are the only currently established occurrences of any siricomorph family in the Ypresian. We treat the undescribed new siricoid from the Cretaceous Crato Formation of Brazil as belonging to the Pseudosiricidae, not Siricidae, and agree with various authors that the Ypresian *Megapterites mirabilis* Cockerell is an ant (Hymenoptera: Formicidae). The Miocene species *Cephites oeningensis* Heer and *C. fragilis* Heer, assigned to the Cephidae over a century and a half ago, are also ants. Many of the host plants that sircomporphs feed upon today first appeared in the Eocene, a number of these in the Okanagan Highlands in particular. The Okanagan Highlands sites where these wasps were found also had upper microthermal mean annual temperatures as are overwhelmingly preferred by most modern siricomorphs, but were uncommon in the globally warm Ypresian, only found then in higher elevations and highest latitudes.

Introduction

The infraorder Siricomorpha (Hymenoptera: Symphyta) was proposed in the framework of a classical taxonomic approach as an explicitly paraphyletic assemblage to collectively treat the Pamphilioidea, Siricoidea, and Cephoidea, taxa that share a closed head capsule between the oral and occipital orifices and larval phytophagy (Rasnitsyn 1980). In recent analyses (Sharkey 2007; Heraty *et al.* 2011; Peters *et al.* 2011; Ronquist *et al.* 2012; Klopfstein *et al.* 2013), it has been regularly recovered as a grade sister to the Tenthredinoidea and ancestral to the Vespina (that is, Orussoidea + Apocrita, see Rasnitsyn and Zhang 2010). Here, we describe new species of Pamphiliidae, Siricidae, and Cephidae, the only currently established Ypresian (early Eocene) Siricomorpha.

Pamphiliidae

The Pamphiliidae today has over 300 species that mostly range through temperate and boreal regions of the Holarctic, but are also known into Mexico and in the Oriental Region to Myanmar and India (Taeger *et al.* 2010). It is divided into three subfamilies: the extant Pamphiliinae and Cephalciinae, and the extinct Juralydinae. Their larvae spin silk, forming webs in which they live either singly or in sometimes large groups; those of Cephalciinae feed on conifer foliage of the Pinaceae, and of Pamphiliine on angiosperm leaves, which they roll (Benson 1945; Middlekauff 1964; Smith 1988; Goulet 1993).

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All known species of the family before the Oligocene are currently assigned to the Juralydinae: *Juralyda udensis* Rasnitsyn (Uda Formation, Transbaikalia, Russia, Late Jurassic); *Scabolyda orientalis* Wang *et al.* (Jiulongshan Formation, China, late Middle Jurassic); *S. incompleta* Wang *et al.* (Yixian Formation, Liaoning, China, Early Cretaceous) (Wang *et al.* 2014a); and *Atocus defessus* Scudder (Florissant, Colorado, United States of America, latest Eocene), its youngest known occurrence.

The Cephalciinae appeared in the Oligocene with *Tapholyda caplani* Cockerell (Cockerell 1933, 1940; in *Tapholyda* Rasnitsyn: Rasnitsyn 1983) (Creede Formation, Colorado, United States of America); and then in the Miocene with the extant genus *Acantholyda* Costa: the formerly recognised French species *A. grangeoni* Riou (Riou 1999), which was synonymised with the extant *A. erythrocephala* (Linnaeus) by Nel (2004) and possibly *A. ribesalbesensis* Penãlver and Arillo in Spain (Penãlver and Arillo 2002; Nel 2004). The Pamphiliinae has no known fossil record.

Siricidae

Extant horntail wood-wasps (Siricidae) consist of about 122 species in 10 genera (Schiff *et al.* 2012) assigned to the subfamilies Siricinae and Tremicinae. They are serious forest pests, attacking stressed trees (conifers and angiosperms), drilling into wood to insert eggs, mucus, and fungal spores or bits of hyphae (review of siricid natural history: Schiff *et al.* 2012). The tree dies as the larvae bore through the wood and feed on the phytotoxic fungus that flourishes as their mucus compounds weaken the tree's immune system.

The native ranges of the majority of modern siricids are restricted to the Holarctic, from northern boreal forests through those of mid latitudes, but a few are found south into Mexico, Cuba, The Dominican Republic, rarely and at times questionably in Central America, and in Papua New Guinea, the Malay Peninsula, and lower latitudes of sub-Saharan Africa (Smith 1988; Schiff *et al.* 2012). They have been introduced in a number of southern hemisphere countries (Schiff *et al.* 2012; Malagon-Aldana *et al.* 2014).

The modest fossil record of the family (*sensu stricto*) was recently summarised by Wedmann *et al.* (2014, table 1, "crown-group Siricidae"). We emend their list by considering the specimen from the Crato Formation of Brazil (Osten 2007) to belong to the Pseudosiricidae; adding two unnamed specimens from the Early Cretaceous (Albian) of the Emanra Formation in the Russian Federation (Gromov *et al.* 1993, fig. 14); and we agree with various authors (*e.g.*, Lutz 1986; Jarzembowski 1996; Bolton 2014) that the enigmatic *Megapterites mirabilis* Cockerell from the Ypresian Bournemouth Group, United Kingdom, is an ant. We propose that the Brazilian Crato Formation specimen belongs to the Pseudosiricidae by similarity of its wing venation, best exemplified by the Early Cretaceous *Myrmicium heeri* Westwood (see Rasnitsyn *et al.* 1998), with which it shares a long, proclival 1-Rs, unlike Siricidae, wherein 1-RS is vertical or reclivous.

Cephidae

The Cephidae are distinctively slender sawflies whose larvae are known for feeding on tissues in the stems of grasses and woody plants. They can be major pests of grains. Today, they have about 170 species in 24 genera of three subfamilies – all but four species placed in the Cephinae (Taeger *et al.* 2010). Like the Pamphiliidae and Siricidae, they predominantly range in the temperate/boreal Holarctic, with few species found outside of this: in the western hemisphere, one south of the United States of America in Mexico; and in the eastern hemisphere two in Madagascar, and one each in Vietnam, Kalimantan, Sulawesi, and Australia (Goulet 1993; Smith 1997, 1999; Smith and Shinohara 2002; Smith and Schmidt 2009; Taeger *et al.* 2010).

They have a scant fossil record, with a single species each in the earlier (Barremian?) and later (Aptian) Early Cretaceous of Baissa (*Mesocephus sibiricus* Rasnitsyn), eastern Siberia, and Bon-Tsagan, Mongolia (*M. ghilarovi* Rasnitsyn), respectively; and the Late Eocene (Priabonian) Florissant (*Janus disperditus* Cockerell) and Baltic amber (*Electrocephalus stalendorffi* Konow) (summarised by Taeger *et al.* 2010), all assigned to the Cephinae. Heer (1847) described two species from the Miocene (Sarmatian) of Oeningin, Germany, *Cephites oeningensis* Heer and *C. fragilis* Heer, which he considered to be cephids, but judging from his illustrations (Heer 1847, plate XIII, fig. 17, and plate XIV, fig. 1) are unquestionably ants (possibly Myrmicinae).

Here, we describe new siricomorph genera and species from the Ypresian Okanagan Highlands localities in far-western North America: the pamphiliid *Ulteramus republicensis* **new genus, new species** from Republic, Washington, United States of America, either a member of the Pamphiliinae or Cephalciinae; the siricid *Ypresiosirex orthosemos* **new genus, new species** from McAbee, British Columbia, Canada, which we place in the Siricinae (see subfamily concept, below); and the cephid *Cuspilongus cachecreekensis*, **new genus, new species** from McAbee and the un-named Cephinae species A from Horsefly River, also in British Columbia, both of which we assign to the Cephinae.

Materials and methods

The fossils described here are preserved in lacustrine shales from Republic, Washington, United States of America, and McAbee and Horsefly River, British Columbia, Canada. These are localities of the Okanagan Highlands series of Ypresian basins that occur scattered across about a 1000 km transect from north-central Washington, United States of America, to west-central British Columbia, Canada (map and overview: Archibald *et al.* 2011). Although their climates and floras vary in detail, these localities broadly represent a mixed mesophytic montane forest in many ways similar to that of the modern North American eastern deciduous zone, but including plant genera that are now extinct or found in low latitudes (Greenwood *et al.* 2005; Moss *et al.* 2005).

The Republic site is an exposure of the Tom Thumb Tuff Member of the Klondike Mountain Formation within the town itself. Radiometric dating gives a latest Ypresian age of 49.4 ± 0.5 million years old (Wolf *et al.* 2003). The McAbee locality consists of exposures of an unnamed formation in south-central British Columbia near the town of Cache Creek. ^{40}Ar/^{39}Ar analysis gives a radiometric age of 52.90 ± 0.83 million years old (Archibald *et al.* 2010). The Horsefly River localities in the central Cariboo region of southern British Columbia are exposures of laminated shales of an unnamed formation that have received extensive attention in particular from M.V.H. Wilson (*e.g.*, Wilson and Barton 1996; Barton and Wilson 2005). Horsefly River does not have a radiometric age estimate, but the great similarity of its fauna and flora (including palynomorphs, see Moss *et al.* 2005) firmly associates it temporally with the other lacustrine basins of the Okanagan Highlands, all of which are dated within the latter half of the Ypresian (Archibald *et al.* 2011).

We follow the wing vein and cell terminology of Rasnitsyn (1969, fig. 1). The vein seen in some hymenopteran forewings (*e.g.*, the new pamphiliid: Fig. 1) between M + Cu and 1A (but truncate, not joining 1A) is not present and named in that figure. We treat this as “ap-Cu” (appendix of Cu). The identity of this vein as a branch of Cu or a crossvein is currently not clear, and so we use this provisional, neutral term that does not express an opinion. The cells resulting from its division of 1cua when it is present we call 1cua1 and 1cua2. Terminology of other morphology follows Huber and Sharkey (1993).

Institutional abbreviations: The Burke Museum of Natural History and Culture (Seattle, Washington, United States of America), BM; Brandon University (Brandon, Manitoba, Canada), BU; Thompson Rivers University (Kamloops, British Columbia, Canada), TRU; and the Royal British Columbia Museum (Victoria, British Columbia, Canada), RBCM.

Order Hymenoptera Linnaeus, 1758
Infraorder Siricomorpha Rasnitsyn, 1980
Superfamily Pamphilioidea Cameron, 1890
Family Pamphiliidae Cameron, 1890
Subfamily *incertae sedis*
Genus *Ulteramus* Archibald and Rasnitsyn, new genus

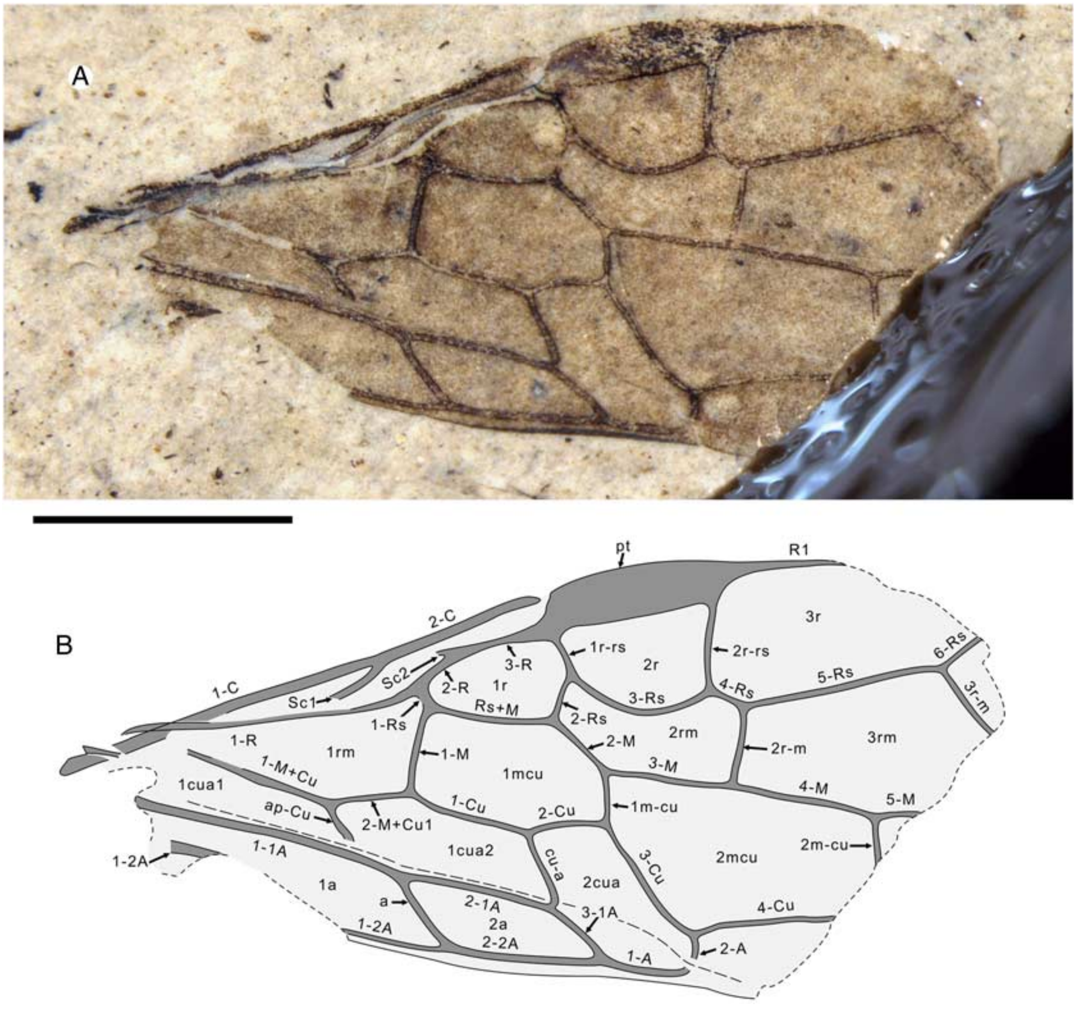
Type species. *Ulteramus republicensis* Archibald and Rasnitsyn, new species. Here designated.

Diagnosis. As for its only species: forewing easily separated from those of all other pamphiliid genera by Sc2 joining R distad 1-Rs.

Description. As for the only species (see below).

Etymology. The genus name is formed from the Latin *ulter*, meaning on the farther side, and *ramus*, meaning branch, referring to the distal position of the joining of Sc1 and R, distinctive within the Pamphiliidae. Gender masculine.

Fig. 1. *Ulteramus republicensis* new genus and species, holotype forewing UWBM 77532: A, photograph; B, drawing; both to scale, 2 mm.



Ulteramus republicensis Archibald and Rasnitsyn, new species

(Fig. 1)

Material. BM accession number UWBM 77532 (part only); A mostly complete and well-preserved forewing, only missing portions of the apical-most and basal-most portions and the region between C and R mostly folded and damaged; housed in the BM collection; collected by Wesley Wehr in 1993. Labelled: HOLOTYPE, *Ulteramus republicensis* Archibald and Rasnitsyn, 2015.

Diagnosis. Forewing easily separated from those of all other pamphiliids by Sc2 joining R distad 1-Rs.

Description. Forewing. Length as preserved (with basal-most, apical-most portions missing) about 7.3 mm, width about 3 mm; present portions of membrane evenly infuscate, apparently smooth without coreaceous or corrugated region; pterostigma sclerotised, large, about half width of cell 2r; basal portion of Sc mostly missing by damage, folding; Sc1 joins C basad level of 1-Rs, apical stub of Sc2 joins R distad 1-Rs; 1-Rs present, short, about quarter length of 1-M (but see Discussion); 3-Rs deeply curved (cell 2r wide); 4-Rs long; 2r-m inclined basad; Rs + M about 1.4 length of 1-M; 1r-rs normal (not shortened or weakened); angle of 1-M to 1-Cu just over 90°; ap-Cu stub present, sinuate, not joining A;

2-M about 0.58 Rs + M length; cell 2a length about 1.8 times width.

Etymology. The specific epithet *republicensis* refers to the known locality of this species.

Age and locality. Ypresian; Klondike Mountain Formation exposure A0307B (BM locality code), Republic, Washington, United States of America.

Discussion. The new species is excluded from the Juralydinae, as it clearly lacks its diagnostic forewing characters (*e.g.*, in Juralydinae, 1-Rs is longer and the ap-Cu stub is missing: see Wang *et al*. 2014a). It is possible that it is a member of either the Pamphiliinae or Cephalciinae, but determining which is problematic. The only reported forewing character that separates them is membrane texture in the apical region: in the Cephalciinae it is irregularly coriaceous and in the Pamphiliinae it is longitudinally corrugated, *i.e.*, with distinct folds (Benson 1945). Unfortunately, most of this region is not preserved in the single specimen of the new species, although the apicalmost portion that is present appears smooth as preserved.

The new genus and species are clearly separated from all other described pamphiliids by its distal joining of Sc2 and R, a condition seen in Xyelidae (Rasnitsyn 1969, figs 69, 77), but not previously known within the Pamphiliidae. Sc2 appears here to be a stub, but much of the vein may be damaged or obscured by folding in this area. A better fossil is needed to resolve this. Some other venational character states are of interest.

Vein segment 4-Rs is comparatively long; often in pamphiliids, this is short, such that 2r-rs and 2r-m join Rs closely. 1-Rs is confidently present and short, unlike in the cephalciine *Caenolyda* Konow or the pamphiliine genera *Pseudocephaleia* Zirngiebl and *Kelidoptera* Konow. Details of its morphology might be importantly distinctive, but, unfortunately, are not preserved clearly at this level in this specimen. It may be thicker, much thicker, or about the same width as M as they join; M may or may not bend sharply immediately before their joining. A specimen with this region better preserved is needed to clarify these issues.

If the new species belongs to the Pamphiliinae, *Neurotoma* Konow is further excluded, as Sc1 is absent in that genus; and from *Pseudocephaleia* and *Kelidoptera*, where vein 1r-rs is extremely short and distinctively very narrow. Apart from the form of Sc2, *U. republicensis* in many ways resembles species of the pamphiliine genera *Onycholyda* Takeuchi and *Pamphilius* Latreille. If it is a member of the Cephalciinae, *Caenolyda* is further excluded, as Sc1 does not extend to the pterostigma as in that genus. *Acantholyda* and *Cephalcia* Panzer also differ in the form of the stub ap-Cu, which is either absent, or short, or subvertical in these genera (Beneš 1968), in contrast to the long, oblique stub almost reaching A in the new genus. *Chinolyda* Beneš also bears such a long, oblique ap-Cu. While Beneš placed *Chinolyda* in the cephalciine tribe Cephalciini, he noted that it bears a variety of character states that appear ambiguous at the subfamily level. Given available evidence, it cannot be ruled out that *Chinolyda* is the surviving remnant of a lineage embracing *Ulteramus* as well.

A more complete fossil is needed to determine if *U. republicensis* extends the age of an extant subfamily back to the Ypresian, or if the history of the family becomes more complex with the establishment of a new, extinct subfamily.

Superfamily Siricoidea Billberg, 1820 (1802)

Family Siricidae Billberg, 1820 (1802)

Ypresiosirex Archibald and Rasnitsyn, new genus

Type species. *Ypresiosirex orthosemos* Archibald and Rasnitsyn, new species. Here designated.

Diagnosis. Separated from other genera of Siricidae as provided in the diagnosis of its only species, below.

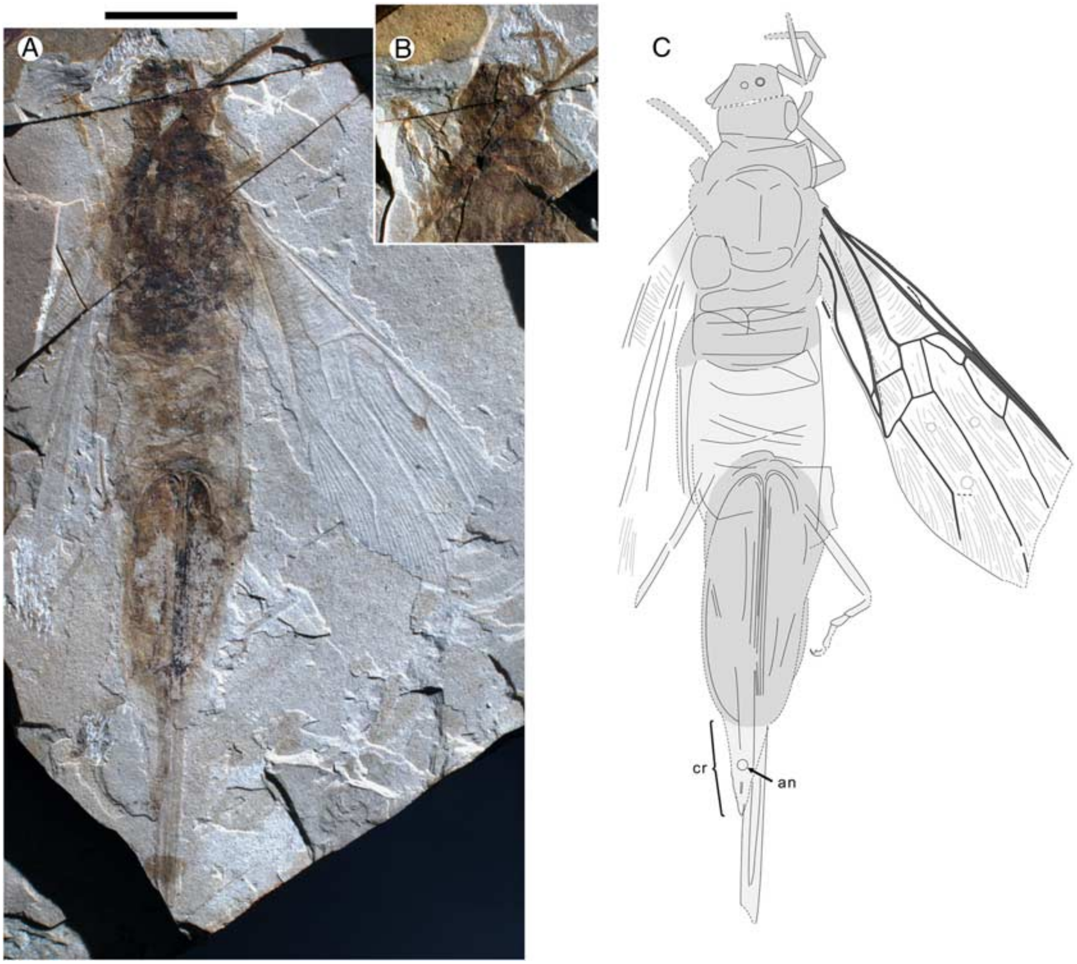
Description. Female as in description of its only species, below.

Etymology. The generic name is formed from Ypresian, referring to its age, and *Sirex* Linnaeus (horntail wood-wasp). Gender masculine.

Ypresiosirex orthosemos Archibald and Rasnitsyn, new species
(Figs. 2–5)

Type material. Holotype: RBCM.EH2015.004.0001.001A&B (part; counterpart), Figures 2–5, a mostly complete and generally well-preserved female; housed in the RBCM collection. Labelled: HOLOTYPE, *Ypresiosirex orthosemos* Archibald

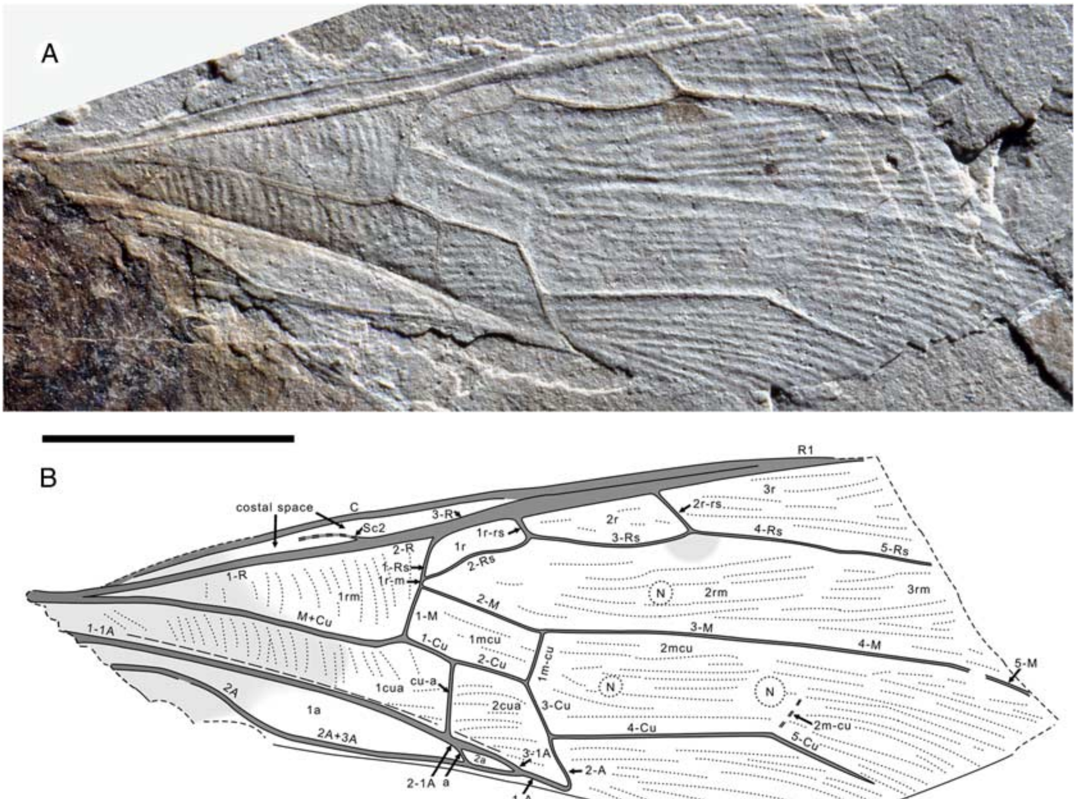
Fig. 2. *Ypresiosirex orthosemos* new genus and species, holotype (RBCM.EH2015.004.0001.001 A&B). A, photograph, part; B, head, thorax of counterpart; C, drawing. Abbreviations: cr is cornus, an is anus; all to scale, 10 mm.



and Rasnitsyn 2015. Collected by SBA at McAbee, British Columbia, in the mid-1990s.

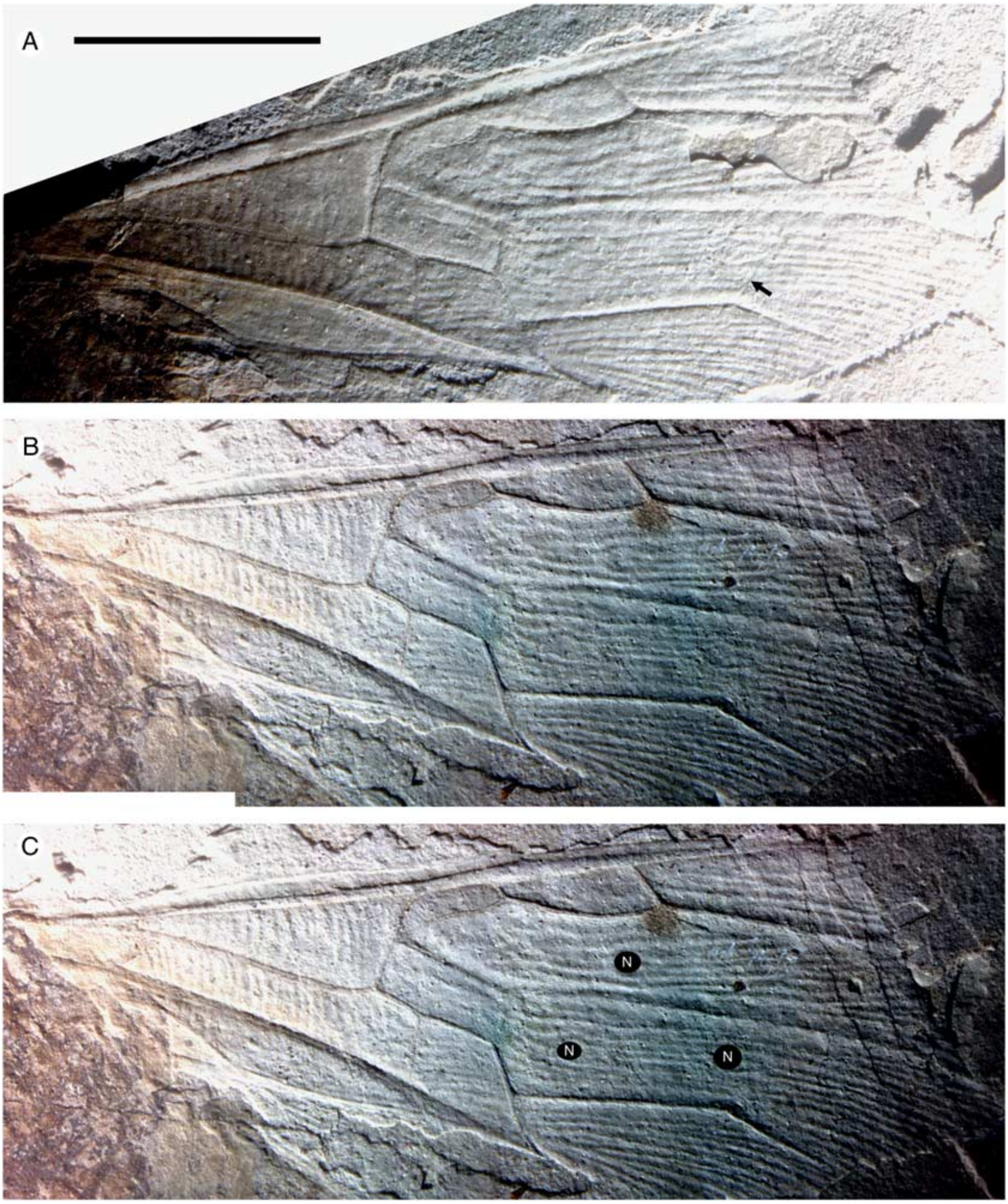
Diagnosis. May be easily separated from all Siricoidea by transverse corrugation in forewing basal cells (1rm, 1cua, 1a in part), also from all Siricoidea but Siricidae *sensu stricto* (comprised of former Siricinae + Tremecinae, *i.e*., Siricinae *sensu* Rasnitsyn 1969) by presence of female metasomal horn; or by forewing anal cell with loop (bend of 2A, creating membrane space in extant species known to enclose a rough membrane patch bearing cenchri, forming a wing locking device) in basal rather than subbasal position. May be separated from all genera of Siricidae *sensu stricto* by loss or extreme weakening of crossveins 2r-m, 3r-m, 2 m-cu (either absent or weak: not as tubular or nebulose veins, *i.e*., not darkened, so invisible in fossils); or by interanal crossvein "a" placed well distad cu-a (proximad cu-a or at most subaligned with it in other genera). Additionally it differs from *Tremex* Jurine*, Eriotremex* Benson*, Afrotremex* Pasteels, *Teredon* Norton species by the female cornus distinctly longer than wide; from *Eriotremex, Afrotremex*, *Xeris* Costa*, Siricosoma* Forsius, *Teredon* species by the absence of Rs + M; from *Tremex, Eriotremex, Afrotremex*, *Xeris, Siricosoma* species by cu-a positioned distad basal third of cell 1mcu.

Fig. 3. Forewing of *Ypresiosirex orthosemos*: A, photograph of the part (A side); B, drawing. Dotted ovals with "N" are nygmata: see Figures 4B–4C, 5. Some morphology in drawing not present in the photograph of the part in A is preserved on the B side, *e.g.*, more of the posterior margin of the wing, see Figure 4A. Both to scale, 10 mm.



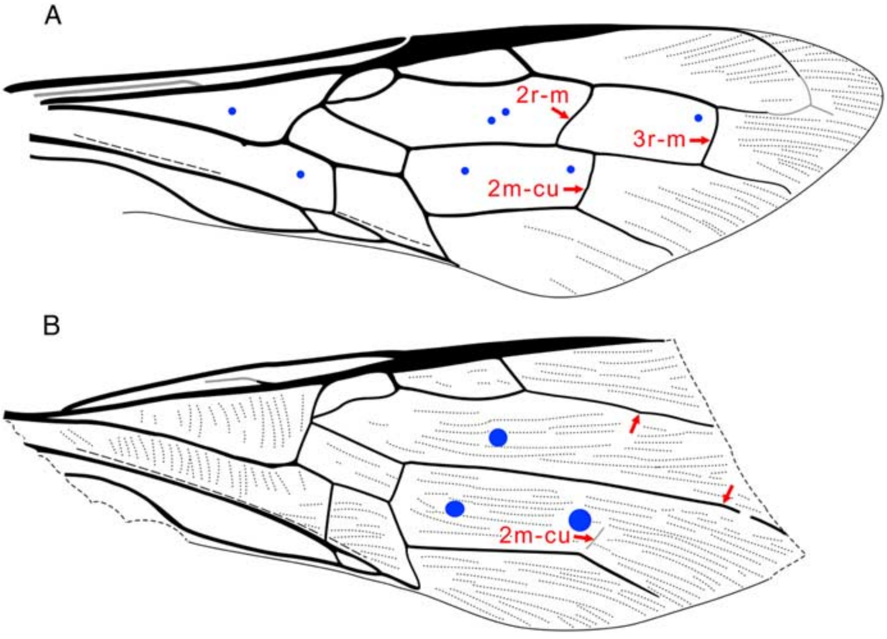
Description (female). Overall length 59.3 mm anterior of head to tip of cornus, 67.9 mm including ovipositor (incompletely preserved, tip missing). Body dorsum apparently darkly coloured except for mid-abdominal section (but preserved caudal abdomen colouration may be of ventral surface). Head, thorax integument where visible densely but not deeply pitted, pits particularly large on lateral pronotal dorsum; otherwise morphology difficult to interpret except that head appears long (at least about as long as wide); pronotal sides somewhat converged forwards; hind margin deeply excised; mesonotum longer than usual, with long medial suture, notauli widely diverging. Legs: Imperfectly preserved, ordinary as visible. Forewing: length 34.5 mm preserved, estimated complete length (based on dimensions of *Urocerus* Geoffroy wing, see Fig. 5) 37 mm; maximum width 12.4 mm; hyaline except basal quarter infuscate; Sc2 joining R basad Rs for distance equal to that between 1-Rs, 1r-rs; cells 1r, 1mcu not touching; ap-Cu, crossveins 2r-m, 3r-m absent or extremely weak (not tubular nor nebulose; no trace detected as preserved), portion of 2 m-cu detected but very weak (Fig. 4A), characteristic bends in M + Cu, Rs, M, Cu indicate lost positions; membrane strongly transversely corrugated in basal cells (1rm, 1cua, at least partly 1a), strongly longitudinal corrugated in cells 2r, 3r, 2rm, 3rm, 1mcu, 2mcu, 2cua, and all outer wing membrane preserved; crossvein a distad cu-a, forming small cell 2a below cell 2cua; vein 2A + 3A adjacent to posterior margin in about distal half of cell 1a; tracing its direction proximal (Fig. 3) indicating basal loop reaching wing base or near so; free vein 3A absent.

Fig. 4. Further features of the forewing of *Y. orthosemos* photographed under oblique lighting: A, counterpart (RBCM.EH2015.004.0001.001B) showing weak 2m-cu crossvein indicated by arrow (note some morphology preserved on B side not on A side *e.g.*, more complete posterior margin); B, part (RBCM.EH2015.004.0001.001A) showing nygmata; C, same as A with nygmata indicated "N". All to scale, 10 mm.



Three nygmata detected: two in cell 2mcu and one in cell 2rm (Fig. 4B, 4C). Hindwing: fragmentarily, indistinctly preserved if at all. Abdomen: only mid portion well visible (otherwise obscured by heavier sclerotised coxae, basal ovipositor structures), lacking rough sculpture; valvifers

Fig. 5. Comparison of forewings of A, *Ypresiosirex orthosemos* and B, *Urocerus gigas* with crossveins and nygmata (blue dots) indicated.



2 + 3 almost half as long (16.2 mm) as estimated length of forewing; cornus wedge-shaped, twice as long as wide, half as long as valvifers 2 + 3, with circular anus midlength.

Etymology. The specific epithet *orthosemos* means "with vertical stripes" in Greek, referring to the distinctive transverse corrugation in the forewing basal cells.

Age and locality. Ypresian; McAbee, British Columbia, Canada.

Discussion. The taxonomic position of *Y. orthosemos* as a member of the superfamily Siricoidea is beyond doubt by its characteristic general appearance, with a long, straight, and strong ovipositor coupled with other distinctive traits of living horntails, that is, a strongly corrugated wing membrane, moderately narrow ribbon-like costal space, reclival Rs base, basal position of the anal loop, and the presence of the metasomal cornus in the female. However, the higher-level systematics within the superfamily is not as clear today as it appeared to be a few decades ago (Rasnitsyn 1969, 1988) due to the accumulation of new described (Wedmann 1998; Rasnitsyn and Zhang 2004a, 2004b; Wedmann *et al.* 2014), re-interpreted (Nel 1988, 1991; Rasnitsyn *et al.* 1998), and undescribed fossils that complicate matters, a development that deserves at least a short discussion.

The siricoid families Anaxyelidae, Xiphydriidae, and the enigmatic Daohugoidae are confidently defined and require no further special consideration here. The remaining siricoids consist of the living and fossil Siricidae *sensu stricto* (*i.e.*, Siricinae + Tremecinae = Siricinae *sensu* Rasnitsyn 1968), and an array of fossil taxa that include recent discoveries of debatable position. These Mesozoic species are usually grouped now as the Auliscinae, Gigasiricinae, and Sinosiricinae, subfamilies of Siricidae (Rasnitsyn 1969, 1980, 1988; Carpenter 1992; Taeger *et al.* 2010; the latter two papers add also Praesiricidae, which rather belong to Pamphilioidea: Wang *et al.* 2014a and references therein), and the Protosiricidae and Pseudosiricidae (= Myrmiciidae).

All of these five are insufficiently known and not firmly defined as separated from each other, nor in cases from the Siricidae *sensu stricto*. For instance, Siricidae *sensu stricto* and Pseudosiricidae are putatively synapomorphic in the strong corrugation of their wing membrane; Siricidae is further apomorphic in having 1-Rs reclival (proclival in Pseudosiricidae), the anal loop basal (probably subbasal in Pseudosiricidae: see Rasnitsyn 1969, fig. 17 versus 18) and the metasomal cornus present in the female (never reported in Pseudosiricidae). Sinosiricinae are similar to Siricidae *sensu stricto* in many wing characters (except for clearly subbasal anal loop and the absence of corrugation – at least not as preserved), but differ in lacking the modification of the transmesonotal suture characteristic of Siricidae *sensu stricto* and unknown otherwise except in the Auliscinae. Auliscinae is supposedly synapomorphic with Siricidae *sensu stricto* in the above modification of the transmesoscutal suture (laterally curved forward) and has 1-Rs vertical and not proclival, similar to another siricid apomorphy. In turn, Gigasiricinae species generally differ from those of Auliscinae in having 1-Rs proclival and by the presence of a longitudinal Sc (not found in Auliscinae). However, in *Liasirex* Rasnitsyn 1-Rs is practically vertical, and the structure of Sc is only known in a few Auliscinae (Rasnitsyn 1968). In turn, Protosiricidae definitely differ from Gigasiricinae only by a longer and proclival 1-Rs, which is a comparatively modest distinction: when creating this family, they were differentiated from Siricidae *sensu lato* in lacking the transmesoscutal suture (Rasnitsyn and Zhang 2004a). However, evidence of this structure in Gigasiricinae has not been found (A.P.R., personal observation). As a result of these issues, the five Mesozoic families that are now known to form the bulk of Siricoidea constitute an assemblage that is difficult to confidently subdivide, and so have obscure internal relations.

Ypresiosirex is firmly established as a member of Siricidae *sensu stricto* by the presence of an apical cornus on the female abdomen, and by its forewing with a strongly corrugated membrane, reclival 1-Rs, and strictly basal anal loop. Siricidae *sensu stricto* is sufficiently distinguished from this otherwise confusing group of siricoid taxa, and so here, we limit ourselves to consider the new Okanagan Highlands horntail in the context of that taxon and set aside the problem of the structure of Siricoidea as a whole.

Within the Siricidae *sensu stricto*, the issue of subfamily composition bears some examination. Wedmann *et al*. (2014) recently revisited the significant problem of differentiating the Siricinae and the Tremicinae, its generally accepted subfamily level groups. They demonstrated convincingly the absence of serious reasons to maintain these as distinct taxa, an opinion with which we concur. Further to the morphological and molecular evidence that they discuss, host plant association has often been cited as consistent between these putative taxa, with siricine larvae characterised as feeding within conifer wood and tremicines within angiosperms. However, while those genera assigned to the Siricinae where host plants are known (*Sirex*, *Urocerus*) do feed within conifers, the host plants of the others (*Sirotremex* Smith, *Xoanon* Semenov) are not known; of those assigned to the Tremicinae, *Tremex* feeds in angiosperms, *Xeris* (+*Neoxeris*, within Tremicinae: Schiff *et al*. 2012) feeds in conifers, *Eriotremex* in both conifers and angiosperms, *Afrotremex* has a very restricted record of an angiosperm host, and the host plants of *Siricosoma* (in Tremicinae: Schiff *et al*. 2012) and *Teredon* are not known (Smith 2008; Schiff *et al*. 2012; Goulet 2014). Therefore, this is also too weak a character to separate the Tremicinae. By these reasons, we treat the Siricidae *sensu stricto* as composed of a single subfamily, the Siricinae (we consider it highly likely that at least some of the Mesozoic taxa referred to above will be considered as further subfamily-level groupings within a confidently defined Siricidae following revision).

*Ypresiosire*x is unique within the family and within Hymenoptera as a whole by the distinctive, apomorphic transverse corrugation of its basal forewing membrane, by the loss of crossveins 2r-m and 3r-m (and 2 m-cu portion present but very weak, barely detectable: see Fig. 4A), and by the distal position of the interanal crossvein. The remaining venational characters and long and narrow cornus of the new genus are, however, comparable to those of *Urocerus* (Fig. 5), providing support for that genus to be considered as a possible analogue in the modern fauna.

The forewing of *Y. orthosemos* shows three nygmata, organs of unknown function found on the wings of insects such as Hymenoptera, Mecoptera, and Neuroptera (Wang *et al*. 2014b). They are rarely detected in fossil Hymenoptera (Wang *et al*. 2014b), and have never before been reported in fossil Siricidae. Nygmata have been described numerous times in the wings of Okanagan Highlands fossil Neuroptera (Makarkin and Archibald 2003; Archibald and Makarkin 2006).

Superfamily Cephoidea Neuman, 1834
Family Cephidae Neuman, 1834
Subfamily Cephinae Kirby, 1882
Cuspilongus Archibald and Rasnitsyn, new genus

Type species. *Cuspilongus cachecreekensis*, Archibald and Rasnitsyn new species. Here designated.

Diagnosis. Separated from other genera of Cephidae as in the diagnosis of its only species, below.

Description. As in description of female of its only species, below.

Etymology. The generic name *Cuspilongus* is formed from the Latin *cuspis*, meaning a lance, and *longus*, meaning long, referring to its extremely extended ovipositor. Gender masculine.

Cuspilongus cachecreekensis Archibald and Rasnitsyn, new species
(Figs. 6–7)

Type material. Holotype: F-1545 (part), F-1546, (counterpart): a very complete female specimen but lacking legs, abdomen somewhat obscurely preserved, housed in the TRU collection, collected by John Leahy ay McAbee, British Columbia. Labelled: HOLOTYPE, *Cuspilongus cachecreekensis*, Archibald and Rasnitsyn 2015.

Diagnosis. Females most easily separated from all other extant Cephidae by ovipositor almost as long as forewing: extant cephids have ovipositor at most half as long as forewing. Separated from fossil Cephidae (which mostly lack preserved ovipositor) by: *Mesocephus sibiricus* Rasnitsyn (Early Cretaceous, Baissa) differs by 3r cell short, wide, by 1-M distinctly bent before junction with Rs; *M. ghilarovi* Rasnitsyn (Early Cretaceous, Bon-Tsagan) differs by 1-Rs longer, by 3r cell wider (1:3.8 versus 1:5); *Janus disperditus* Cockerell (Priabonian, Florissant), assigned to an extant genus, differs by 2-M very long, by 3-Cu short; *Electrocephus stralendorffi* Konow (Priabonian Baltic amber) differs by short ovipositor, smaller (length 6 mm) more robust body, 3-Cu short.

Description (female). Overall length about 14 mm anterior of head to tip of abdomen (but somewhat damaged, distorted) excluding ovipositor. Head, thorax integument where visible dark, abdomen light coloured; no portions identifiable as belonging to any leg preserved. Antennae: elements apparently of similar width (but, preserved in disarticulated sections), apparently mostly dark, lighter apically. Forewing: length about 12 mm (practically complete); width unknown by preservation; membrane hyaline or very lightly infuscate, except intercostal space dark; veins dark. 1-Rs more than half as long as 2-Rs, 1r-rs complete, joins R at pterostigma base; cell 3r five times as long as wide; 2r-rs joins pterostigma near mid-point; 2r-m gently bent; 3r-m, 2 m-cu rather straight; 2-M (between Rs + M, 1 m-cu) almost non-existent, cell 1rm shorter than 2rm, 4-M longer than half 2r-m, 1-Cu about 2/3 length of cu-a; distinct bend in 2A near base, directed posteriad, apicad this subparallel 1A. Hindwing: membrane hyaline or very lightly infuscated; 3r-m, m-cu, cu-a present. Abdomen: mostly damaged, indistinctly preserved other than ovipositor, which is long, about 11 mm, curved downward; small portion of sheath preserved (Fig. 6).

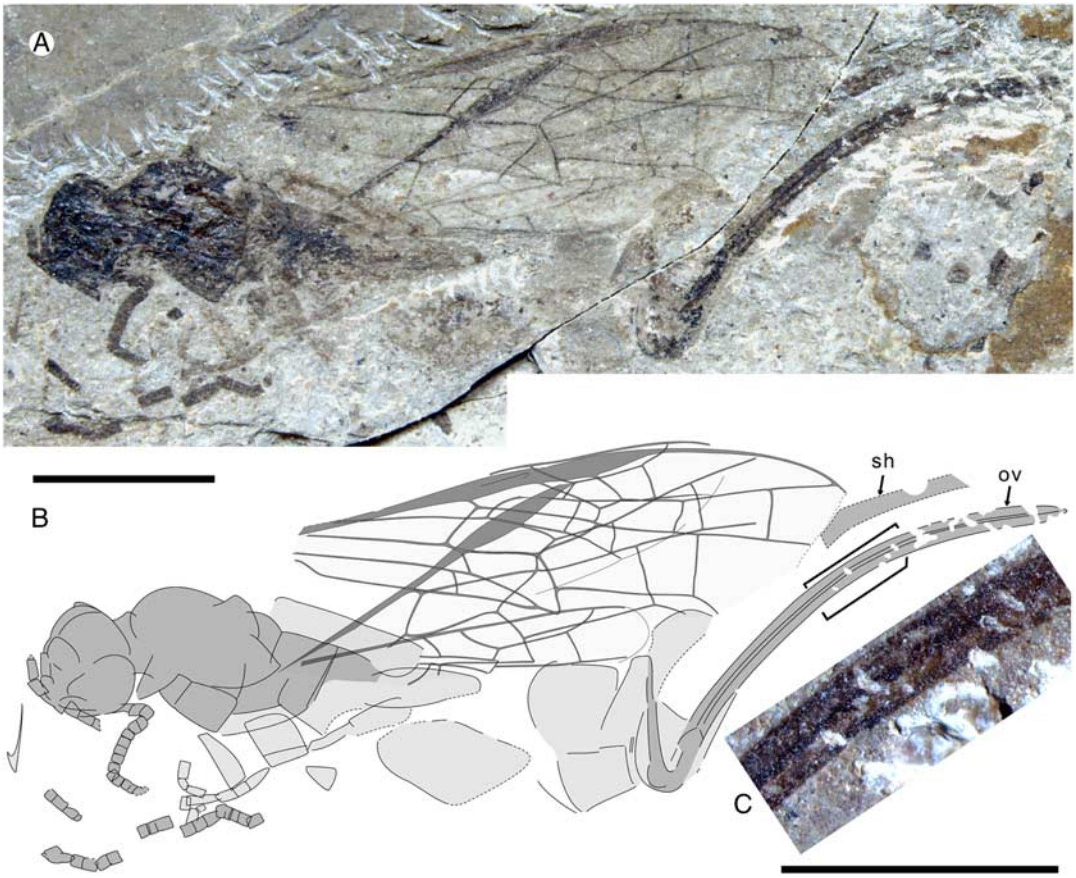
Etymology. The specific epithet is formed from the name of the nearby town of Cache Creek, some 8 km to the west of the McAbee site.

Age and locality. Mid-Ypresian; McAbee, British Columbia, Canada.

Discussion. The new species is confidently assigned to Cephinae by the darkened intercostal region and the ovipositor sheath curved downward (Benson 1946; Smith and Schmidt 2009). It is further separated from the Athetocephinae by 2r-rs joining the lower margin of the pterostigma near the mid-point, and from the Australcephinae by the forewing with 3r-m present, 1r-rs meeting pterostigma at the base, not in the middle region near 2r-rs, the pterostigma longer and narrower, and cell 2r not unusually small as in that subfamily.

Most of the described fossil cephids are in need of revision – there are new, undescribed Cretaceous specimens and more material of the currently little-known *M. ghilarovi* (A.P.R., personal observation), and the descriptions of the Eocene species are over a century old, outdated, and inadequate by modern standards (*E. stralendorffi*: Konow 1897; *J. disperditus*: Cockerell 1913). We translate Konow's (1897) Latin "feminae vagina exerta" to mean the ovipositor, or perhaps the sheath, just protruding behind the abdominal apex and not unusually long as in *Cuspilongus*.

Fig. 6. *Cuspilongus cachecreekensis* new genus and species, Cephidae from McAbee (F-1545/1546): A, photograph of the part (F-1545); B, drawing, showing combined morphology preserved on both part and counterpart: C, close-up photograph of portion of ovipositor indicated in B. Abbreviations: sheath, sh; ovipositor, ov. A, B to scale, 4 mm; C scale, 2 mm.



Cephinae species A

(Figs. 8A–D)

Material. Two isolated forewings, mostly complete but missing basal portions, RBCM.EH2015.005.0001.001 and RBCM.EH2015.005.0001.002, collected by S.B.A. 2.x.2001 at Horsefly River (Black Creek Road), housed in the RBCM collections.

Description (forewing). Forewing length 10 mm, width 3.8 mm (RBCM.EH2015.005.0001.002 as preserved, fairly complete); membrane distinctly infuscate. 1-Rs less than half 2-Rs length, cell 3r four times as long as wide, 2-M scarcely longer than 1-Rs, cell 2rm longer than 3rm, 4-M at most half as long as 2r-m, 2 m-cu distinctively bent.

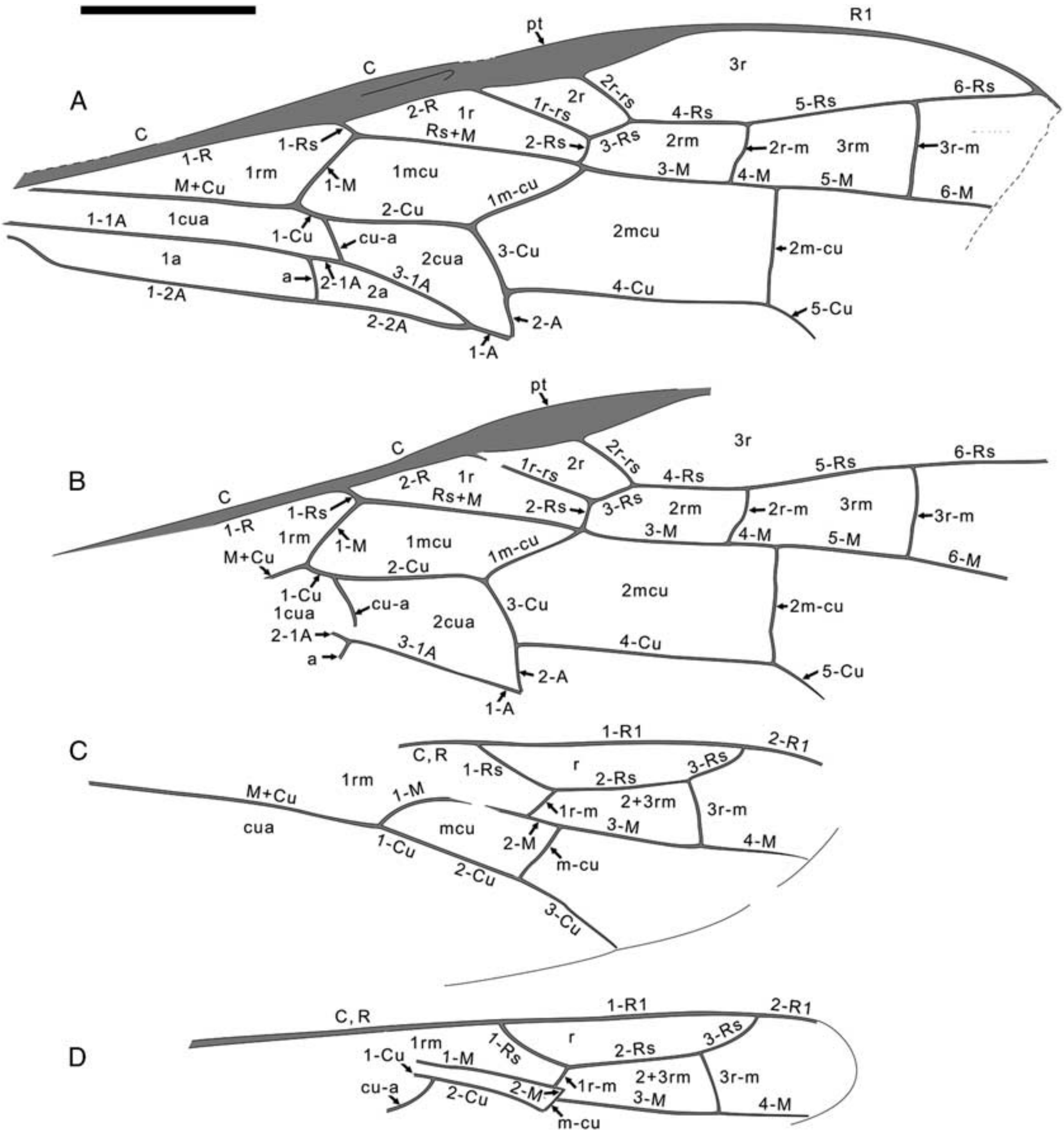
Age and locality. Ypresian; Horsefly River, British Columbia, Canada.

Discussion. We assign it to the Cephinae by characters of the forewing discussed for *C. cachecreekensis* above. Distinct from *C. cachecreekensis* by 1-Rs, 4-M and cells 3r, 3rm shorter; 2-M longer; 2 m-cu bent. We consider these Horsefly River forewings to be confidently conspecific by the close agreement of their morphologies.

Siricomorpha in the Ypresian

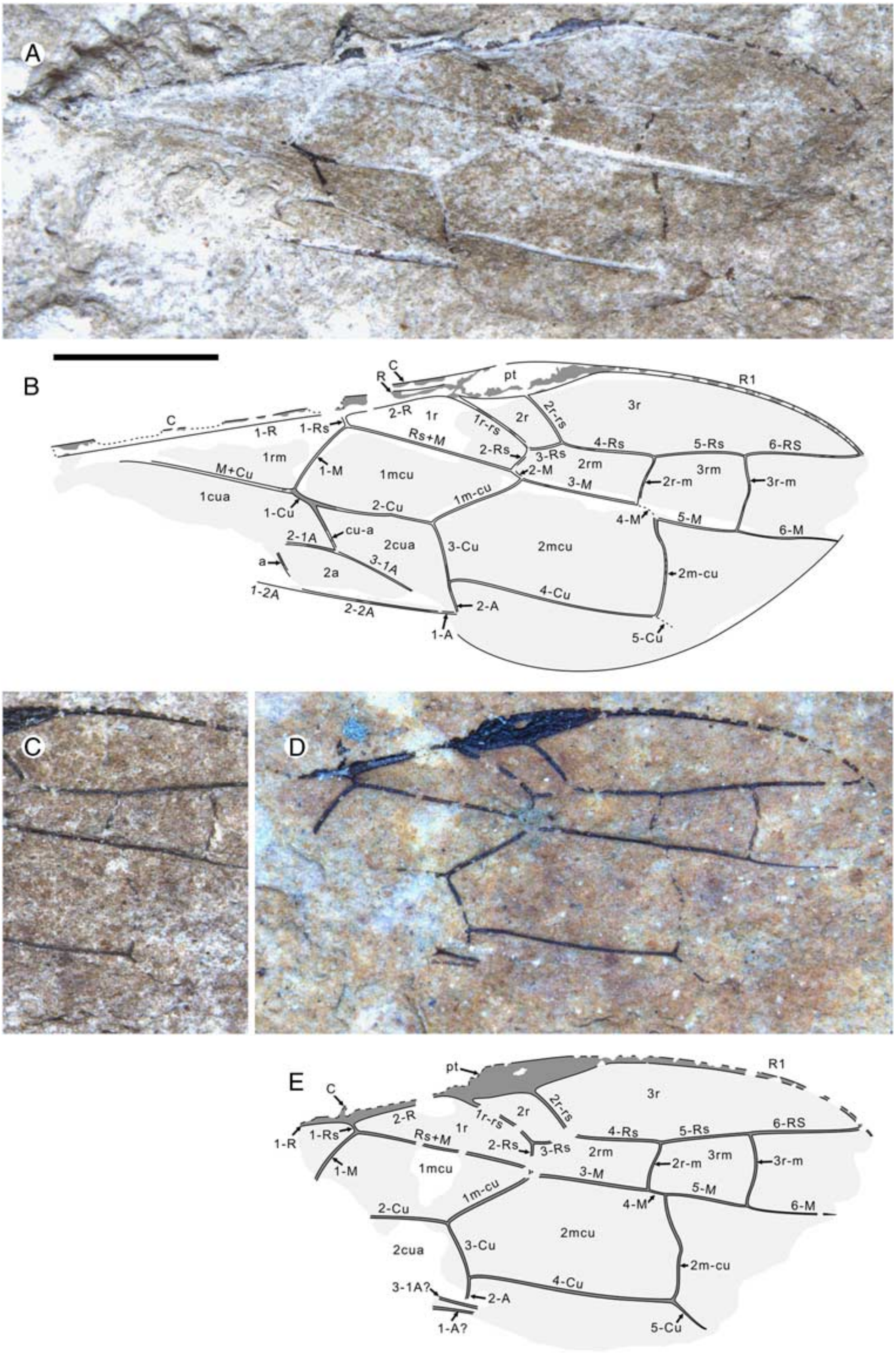
The new species described here are the only Siricomorpha currently established in the Ypresian. By this time, forest communities had recovered from low floral diversity following the

Fig. 7. Cephidae from McAbee (F-1545/1546), wings: A, B, forewings; C, D, hind wings; only cells mentioned in the text are labelled; all to scale, 2 mm.



K-Pg extinction event (particularly in North America) to reach high levels of community richness into mid-latitude localities such as those of the Okanagan Highlands (Archibald *et al.* 2010; Smith *et al.* 2012). This included the radiation and appearances of many modern genera belonging to groups characteristic of or most diverse in modern northern temperate regions (*e.g.*, Rosaceae: DeVore and Pigg 2007; Betulaceae: Pigg *et al.* 2003; Fagaceae: Bouchal *et al.* 2014). Ichnofossil evidence of plant-insect interactions shows highly disturbed food webs followed by a rebound through this interval, apparently differing in intensity across the globe, *e.g.*, perhaps affecting North America more severely than Europe and South America (Labandeira *et al.* 2002; Wilf *et al.* 2005, 2006; Currano *et al.* 2008; Wappler *et al.* 2012; Donovan *et al.* 2014; and see brief review in Archibald *et al.* 2014a).

Fig. 8. Cephidae from Horsefly River: A, photograph of RBCM.EH2015.005.0001.002; B, drawing of RBCM. EH2015.005.0001.002; C, partial photograph of RBCM.EH2015.005.0001.001, dry (shows membrane infuscation better); D, photograph of RBCM.EH2015.005.0001.001 wetted with ethanol (shows venation better); E, drawing of RBCM.EH2015.005.0001.001; all to scale, 2 mm.



Okanagan Highlands localities contain the oldest confident fossil record or oldest macrofossil record of a number of important modern genera of angiosperms, *e.g.*, *Rubus* Linnaeus, *Sorbus* Linnaeus, *Prunus* Linnaeus, *Crataegus* Linnaeus (Rosaceae); and *Betula* Linnaeus, *Corylus* Linnaeus, and *Carpinus* Linnaeus (Betulaceae) and the conifers *Abies* Linnaeus, *Picea* Dietrich (Pinaceae) and *Thuja* Linnaeus (Cupressaceae) (Crane and Stockey 1987; Wehr and Schorn 1992; Schorn and Wehr 1996; Pigg *et al.* 2003; DeVore and Pigg 2007, 2010).

The Republic forest contained many host plants that pamphiliid larvae feed on today, such as *Rubus*, *Prunus*, *Sorbus*, *Crataegus* and *Spiraea* Linnaeus (Rosaceae); *Betula*, *Corylus*, *Carpinus*, and *Alnus* Miller (Betulaceae); *Populus* Linnaeus (Salicaceae); *Quercus* Linnaeus (Fagaceae); *Cornus* Linnaeus (Cornaceae); *Acer* Linnaeus (Sapindaceae); and such conifers as *Pinus* Linnaeus, *Abies*, *Picea*, and *Tsuga* (Endlicher) Carrière (Pinaceae) (larval hosts: Benson 1945; van Achterberg and van Aartsen 1986; Smith 1988; Republic flora: Greenwood *et al.* 2005; Moss *et al.* 2005; DeVore and Pigg 2010). Schorn and Wehr (1996) estimated that the Republic flora contains the richest conifer record in the Paleogene. The McAbee forest included many plants associated with extant siricids: the conifers *Abies*, *Pinus*, and *Picea* (Pinaceae), *Juniperus* Linnaeus, *Thuja*, *Chamaecyparis* Spach, and *Sequoia* Endlicher (Cupressaceae); and the angiosperms *Acer* (Sapindaceae), *Fagus* Linnaeus and *Quercus* (Fagaceae), *Carya* Nuttall (Juglandaceae), *Fraxinus* Linnaeus (Oleaceae), *Populus* (Salicaceae), and *Ulmus* Linnaeus (Ulmaceae) (larval hosts: Schiff *et al.* 2012; McAbee flora: Greenwood *et al.* 2005; Moss *et al.* 2005 and references therein). (The references cited above refer to *Quercus*, *Juniperus* and *Fraxinus* at these Okanagan Highlands sites, but we treat the *Quercus* and *Juniperus* classifications as tentative, as they have not been confirmed there by fossil reproductive structures; we report here confirmation of *Fraxinus* at McAbee by two samaras, see Fig. 9)

Today, the major centres of cephid diversity are in grasslands of the Mediterranean and Eurasian steppes, particularly where they merge with temperate forests (Benson 1946). They are well known for feeding on grasses (Poaceae), however, they also feed on some dicots, mostly of the Rosaceae (*Rosa* Linnaeus, *Rubus*, *Agrimonia* Linnaeus, *Filipendula* Miller, *Sanguisorba* Linnaeus, *Pyrus* Linnaeus, *Malus* Miller), but also of the Salicaceae (*Populus*, *Salix* Linnaeus), Papaveraceae (*Papaver* Linnaeus), Fagaceae (*Quercus*), Grossulariaceae (*Ribes*), and Adoxaceae (*Viburnum* Linnaeus) (Benson 1945; Scheibelreiter 1978; Smith 1988; Wei and Smith 2010; Budak *et al.* 2011). The molecular phylogeny of Budak *et al.* (2011) suggests a host shift (or shifts) from grasses in more basal cephines to these other groups, although they recognised the limitations of conclusions that can be drawn from their phylogeny based on a single gene fragment.

Fig. 9. *Fraxinus* samara from McAbee confirming its presence there; specimen SBA 335, in the BU McAbee collection, collected by S.B.A. at McAbee, British Columbia, 22.vi.2000 (a second specimen: SBA 235, collection information the same, also in the BU collection). Identification by M. DeVore. Scalebar is 10 mm.

Pollen, phytolith, and proxy mammal tooth evidence show grasses as old as the Late Cretaceous (Maastrichtian), but as minor, cryptic community elements. The oldest known grass macrofossil is from the Paleocene-Eocene boundary, and their abundant fossil record does not appear until the Miocene (Strömberg 2005, 2011 and references therein). Grass fossils of any kind have not been reported in the Okanagan Highlands, but dicots that are modern hosts of Cephinae are known from McAbee (*Populus*, *Salix*, *Quercus*, and *Ribes*) and Horsefly River (*Salix*, *Quercus*, and *Ribes*) (Greenwood *et al.* 2005; Moss *et al.* 2005).

The fossil record of Cephinae, however, extends to the Early Cretaceous (see Introduction), before grasses or any of the other modern host-plant groups are known or are thought to have originated. This, combined with the richness of Eocene non-grass cephine host plants and the rarity of grass fossils until the Miocene suggests a more complex history of host plant interactions than could be indicated by a molecular phylogeny of extant representatives.

Modern siricomporphs overwhelmingly prefer temperate to cool Holarctic climates. The latter half of the Ypresian, however, was the globally warmest sustained interval of the Cenozoic, known as the Early Eocene Climatic Optimum (Zachos *et al.* 2008). Eocene climates with mean annual temperatures comparable to those of the temperate/boreal Holarctic ranges of most modern siricomorphs are only known in polar regions (*e.g.*, the Canadian High Arctic: Basinger *et al.* 1994) and high elevations, such as the Okanagan Highlands (Rouse *et al.* 1971; Wolfe *et al.* 1998; Greenwood *et al.* 2005; Smith *et al.* 2009). The three Okanagan Highlands sites considered here had mesic climates with upper microthermal mean annual temperature of about 10–13 °C, like that of Portland, Oregon or Vancouver, British Columbia today, but distinctly differing by their mild, frost-free winters (Greenwood *et al.* 2005; Moss *et al.* 2005; Archibald *et al.* 2011, 2014b).

The Okanagan Highlands localities represent a unique set of factors known nowhere else at this time combined with an extensive, well-preserved fossil insect assemblage during an early stage of formation of modern temperate terrestrial ecosystems. Here, we see the first evidence of siricomporphs taking on their modern ecological character with the appearance of many of the host plants associated with them today set in an environment with their preferred modern climate, conditions apparently restricted to this series of sites and present here for the first time.

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