Early Eocene big headed flies (Diptera: Pipunculidae) from the Okanagan Highlands, western North America

S. Bruce Archibald,[1] Christian Kehlmaier, Rolf W. Mathewes

Abstract—Three new species of Pipunculidae (Diptera) are described (one named), from the early Eocene (Ypresian) Okanagan Highlands of British Columbia, Canada and Washington State, United States of America: *Metanephrocerus belgardeae* **new species** from Republic, Washington; and Pipunculidae species A and Pipunculinae species A from Quilchena, British Columbia. We re-describe the late Eocene (Priabonian) species *Protonephrocerus florissantius* Carpenter and Hull from Florissant, Colorado, United States of America, and assign it to a new genus proposed here, *Priabona* **new genus**. Pipunculinae species A is the oldest known member of the family whose wing lacks a separated M_2 vein; previously this had been known in species only as old as Miocene Dominican amber. This is a presumably derived character state that is predominant in modern species. Molecular analysis indicates an origin of the Pipunculidae in the Maastrichtian; the morphological and taxonomic diversity seen here in the Ypresian is consistent with an early radiation of the family. This is concordant with the radiation of Auchenorrhyncha, upon which they mostly prey, which is in turn associated with the early Paleogene diversification of angiosperm-dominated forests recovering from the K-Pg extinction event.

Résumé—Nous décrivons trois nouvelles espèces de Pipunculidae (Diptera), dont une est nommée, de l'éocène inférieur (yprésien) des terres hautes de l'Okanagan en Colombie-Britannique, Canada, et de l'état de Washington, États-Unis d'Amérique: *Metanephrocerus belgardeae* **nouvelle espèce** de Republic, Washington et Pipunculidae espèce A et Pipunculinae espèce A de Quilchena, Colombie-Britannique. Nous décrivons de nouveau l'espèce *Protonephrocerus florissantius* Carpenter et Hull provenant de l'éocène supérieur (priabonien) de Florissant, Colorado, États-Unis d'Amérique, et la plaçons dans le nouveau genre *Priabona* **nouveau genre** que nous proposons ici. Pipunculinae espèce A est le membre connu le plus ancien de la famille dont l'aile ne possède pas de nervure M_2 séparée; cette caractéristique n'avait pas jusqu'à présent été signalée plus antérieurement que chez des espèces de l'ambre du miocène de la République Dominicaine. Il s'agit vraisemblablement de l'état dérivé du caractère qui prédomine chez les espèces modernes. Une analyse moléculaire situe l'origine des Pipunculidae au maastrichtien; la diversité morphologique et taxonomique observée ici dans l'yprésien s'accorde bien avec une radiation hâtive de la famille. Cela est aussi en accord avec la radiation des Auchenorrhyncha, dont la plupart des Pipunculidae se nourrissent, et qui est elle-même associée à la diversification au paléogène inférieur des forêts dominées par les angiospermes qui se remettent de l'extinction K-Pg.

Introduction

Pipunculidae (Diptera) is a family of generally small flies that are immediately striking in appearance for possession of almost spherical heads that are mostly covered by their compound eyes. They have about 1400 described and perhaps as many as 2700 total extant species distributed

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Table 1. Localities and ages of fossil Pipunculidae.

Species	Age	Locality
Undescribed[1]	Eocene (~54–56.0 Ma: Ypresian)[2]	Fur Fm, Denmark
Pipunculidae species A[3,4]	Eocene (51.5 ± 0.4 Ma: Ypresian)[5]	OKH: Quilchena
Pipunculinae species A[3,4]	Eocene (51.5 ± 0.4 Ma: Ypresian)[5]	OKH: Quilchena
Metanephrocerus belgardeae new species[4]	Eocene (49.4 ± 0.5 Ma: Ypresian)[6]	OKH: Republic
Verrallia andreei Aczél[7]	Eocene (Priabonian)[8]	Baltic amber
Verrallia exstincta Meunier[9]	Eocene (Priabonian)[8]	Baltic amber
Verrallia kerteszia Meunier[9]	Eocene (Priabonian)[8]	Baltic amber
Protoverrallia succinia (Meunier)[9]	Eocene (Priabonian)[8]	Baltic amber
Nephrocerus oligocenicus Carpenter and Hull[10]	Eocene (Priabonian)[8]	Baltic amber
Cephalosphaera baltica Carpenter and Hull[10]	Eocene (Priabonian)[8]	Baltic amber
Metanephrocerus collini (Carpenter and Hull)[10]	Eocene (Priabonian)[8]	Baltic amber
Priabona florissantius (Carpenter and Hull)[10]	Eocene (34.07 ± 0.10 Ma: Priabonian)[11]	Florissant, United States of America
Eudorylas species A[12]	Miocene (15–20 Ma: Burdigalian-Langhian)[13]	Dominican amber
Eudorylas? species B[12]	Miocene (15–20 Ma: Burdigalian-Langhian)[13]	Dominican amber

The age of Baltic amber is not precisely known, and is considered older in the Eocene by some authors; we follow Perkovsky *et al.* (2007) in considering it to be Priabonian (late Eocene) in age. OKH = Okanagan Highlands. The specific epithet "*exstincta*" (*Verrallia exstincta* Meunier) was misspelled "*extincta*" by Carpenter and Hull (1939). The question mark states that the specimens most liekly belongs to Eudorylas.

1, Bonde *et al.* (2008); 2, Chambers *et al.* (2003), and see discussion by Archibald *et al.* (2006); 3, Archibald and Mathewes (2000); 4, this paper; 5, Villeneuve and Mathewes, 2005; 6, Wolf *et al.* (2003); 7, Aczél (1948); 8, Perkovsky *et al.* (2007); 9, Meunier (1903); 10, Carpenter and Hull (1939); 11, Evanoff *et al.* (2001); 12, De Meyer (1995); 13, Iturralde-Vinent and MacPhee (1996).

worldwide (Rafael and Skevington 2010). The family is well known for their endoparasitic larvae, all of which (where known) develop within Auchenorrhyncha, with the exception of *Nephrocerus* Zetterstedt, whose larvae have been found in adult Tipulidae (Diptera) (Koenig and Young 2007; Kehlmaier and Floren 2010). Rafael and Skevington (2010) recently provided a brief summary of their natural history.

The oldest currently known fossil pipunculid is from the earliest Ypresian (early Eocene) Fur Formation of Denmark (Bonde *et al.* 2008). The remaining fossils are from later in the Eocene (Baltic amber; Florissant, Colorado, United States of America) and the early Miocene (Dominican amber) (Table 1). Here, we expand knowledge of the fossil record of the family to include the mid to late Ypresian, describing three new species (one named) from the Okanagan Highlands series of deposits of far-western North America (Archibald *et al.* 2011). Two are based on specimens from Quilchena, British Columbia, Canada, mentioned briefly by Archibald and Mathewes (2000), and a third is based on a new specimen from the Klondike Mountain Formation at Republic, Washington, United States of America. We also examined the single known specimen of the late Eocene (Priabonian) *Protonephrocerus florissantius* Carpenter and Hull from Florissant, Colorado, re-describe it, and transfer it to a new genus that we propose here.

Material and methods

Localities

The mid to late Ypresian material that we examined here consists of three specimens preserved as compression fossils in lacustrine shales recovered from two of the Okanagan Highlands series of fossiliferous depositional basins. These occur sporadically over about a 1000 km of south-central British Columbia, Canada, into north-central Washington, United States of America. The region was covered by a forest that was broadly similar to (and perhaps the antecedent of) the modern Eastern Deciduous Zone of eastern North America, but also included plant taxa that are now extinct, or range in East

Asia (*e.g.*, *Metasequoia* Hu and Cheng; Cupressaceae) or low latitudes (*e.g.*, palms) (Greenwood *et al.* 2005). This was a temperate-climate upland during the warmest sustained portion of the Cenozoic (Zachos *et al.* 2008). Archibald *et al.* (2011) recently summarised the environment and paleontology of these deposits, and Greenwood *et al.* (2005) and Moss *et al.* (2005) treated their climates and forest communities in detail.

Quilchena

The Quilchena basin contains conglomerate, sandstones, minor coal and fossilifereous lacustrine shales, and mudstones of the Coldwater Beds (Cockfield 1948). The locality where specimens in this paper were collected is on the west side of Quilchena Creek, which has been radiometrically dated as mid-Ypresian (51.5 ± 0.4 Ma) based on argon-argon dating of sanidine (Villeneuve and Mathewes 2005). A diverse fossil flora was supplemented by new collections of plants and insects (Archibald and Mathewes 2000). Leaf margin analysis and nearest living relative analysis indicate that Quilchena was the warmest of the Okanagan Highlands localities, with mean annual temperature (MAT) estimated as lower mesothermal ~15 °C (Greenwood *et al.* 2005).

Republic

The Klondike Mountain Formation bears a rich record of insect, plant, and other fossils recovered from exposures in and near the town of Republic, Ferry County, north-central Washington. It is late Ypresian, 49.4 ± 0.5 Ma old (Wolfe *et al.* 2003). The fossil described here was collected at exposure B4131, within the town of Republic. The climate was mesic, with an upper microthermal MAT of about 9–11 °C by leaf physiognomy, and a few degrees warmer by nearest living relative bioclimatic-based analysis, and mild winters with few, if any frost days (Greenwood *et al.* 2005).

The re-described species is from Florissant Formation lacustrine shale at Florissant, Colorado, United States of America.

Florissant

The Florissant Formation has a long history of paleontological work on its rich flora and insect fauna, as summarised by Meyer (2003). It is radiometrically dated as 34.07 ± 0.10 Ma, *i.e.*, late Priabonian (Evanoff *et al.* 2001). Like the Okanagan Highlands, it preserves a temperate-climate montane forest community, but about 15–18 million years younger. Climatic estimates indicate a similar to higher MAT than the Okanagan Highlands, ranging from 10.8–17.5 °C by various analyses (review by Smith 2008).

Terminology

Morphological terminology follows previous works by C.K. (*e.g.*, Kehlmaier 2005). Geochronology follows Gradstein *et al.* (2012). Abbreviations of institution names are: SR, The Stonerose Interpretive Center, Republic, Washington (WA), United States of America; SFU, Simon Fraser University, Burnaby, British Columbia (BC), Canada. Ma is Mega annum, million years. The abbreviation K-Pg (Cretaceous-Paleogene) is used rather than the outdated K-T (Cretaceous-Tertiary).

Systematics

Subfamily Nephrocerinae Carpenter and Hull
Tribe Protonephrocerini Aczél
Genus *Metanephrocerus* Aczél
Metanephrocerus belgardeae Archibald, Kehlmaier, and Mathewes, new species
(Fig. 1)

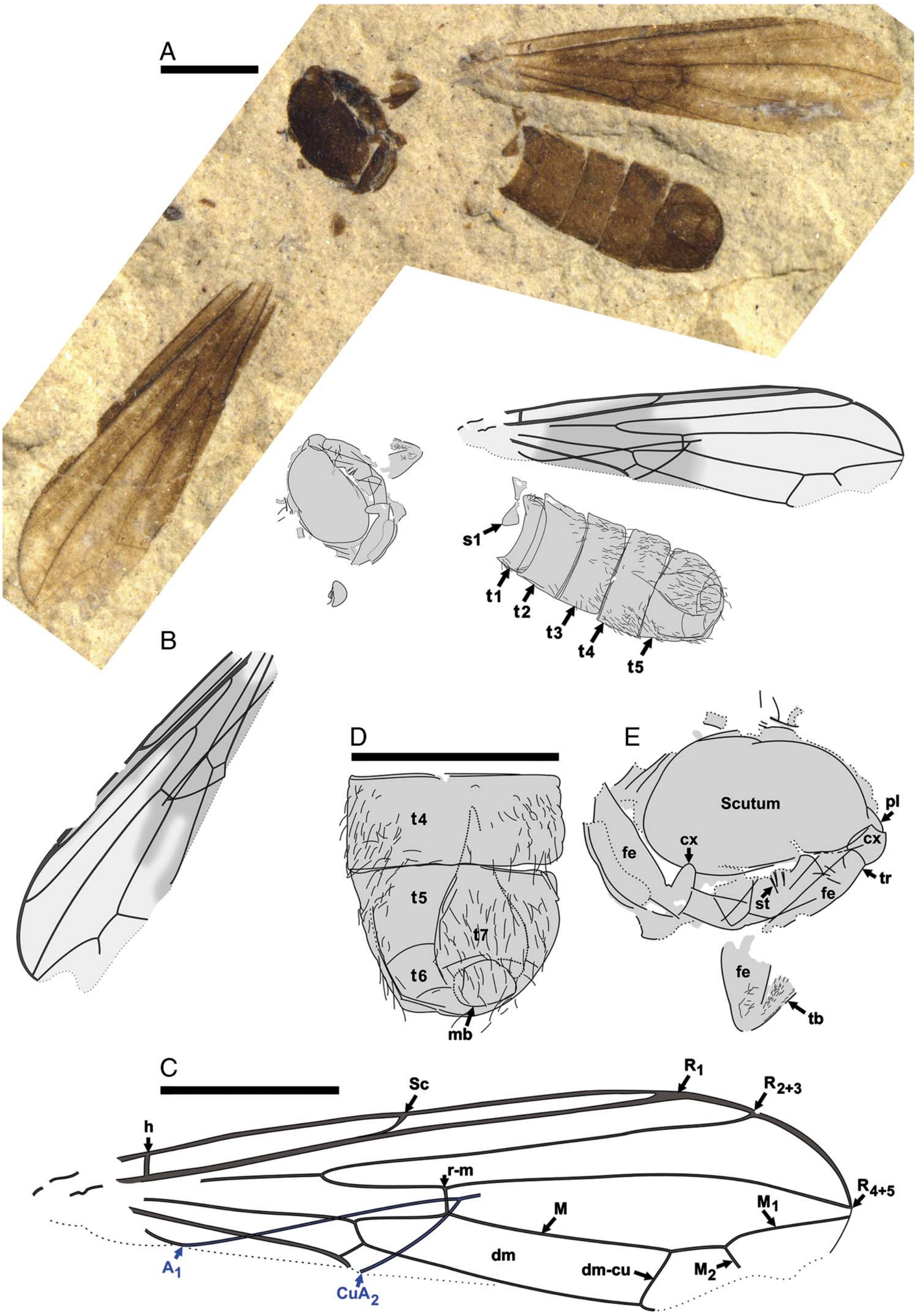
Diagnosis. Separated from other species of Protonephrocerini by large size, wing 9.2 mm long (others:<6 mm); and by wing colouration (others: hyaline apart from pterostigma).

Etymology. The specific epithet is a patronym formed from the surname of Ms. Azure Rain Belgarde, collector of the holotype, recognising her contribution in donating this specimen to the Stonerose Interpretive Center.

Material. Holotype: SR 08-06-02; part only. A female with both wings, which are clearly preserved, but with their basal posterior portions folded; clearly preserved abdomen in dorsal aspect; damaged and somewhat indistinct thorax, also in dorsal aspect; and possibly parts of the legs (see Discussion; Fig. 1), all disarticulated, in close proximity. Housed in the SR collection. Collected by Azure Rain Belgarde at Republic, Washington, exposure B4131, 9 May 2007.

Description. Female. Head absent. Thorax indistinctly preserved (see Discussion; Fig. 1).

Fig. 1. *Metanephrocerus belgardeae* Holotype, SR 08-06-02. (A), photograph; (B), drawing; (C), labelled drawing of wing (veins labelled in blue, *i.e.*, A_1, CuA_2, are folded over); (D), detail of the distal portion of the abdomen; (E), details of the preserved portions of the thorax and legs. Abbreviations: wing veins: cx, coxa; dm, discal medial cell; fe, femur; mb, membrane that enables great articulation between tergites 6 and 7, great mobility of the ovipositor; pl, postpronotal lobe; s1, sternite 1; st, setae, which we treat as pleural setae (see text); t1-t7, tergites 1–7; tb, tibia; tr, trochanter. A, B to scalebar; C to scalebar; D, E to scalebar; all = 2 mm.



Legs fragmentary, portions preserved, separated from thorax. Apex of femur with some stronger bristles possibly part of anterior row of bristles. Wing. Length 9.3 mm; width not determinable as preserved (folded). Membrane heavily infuscated in basal half except basalmost portion; weakly infuscated in apical half, most distinctly along veins. Pterostigma complete, very long. Third costal section as long as second costal section, 3X fourth costal section. R_{4+5}, M_1 terminate separately at apex. M_2 present, about half M_{1+2} stem length. Crossvein r-m joins cell dm shortly basad its basal third. Cell dm upper margin (sections 2, 3 of vein M_{1+2}) angled where r-m joins cell dm but both sections individually straight. Crossvein dm-cu straight, without appendix. M_1 gently curved distad dm-cu to margin. Anal vein (A_1) developed, joining CuA_2 before wing margin (presence of anal lobe not determinable as posterior half of wing hind margin folded in both wings). Abdomen. Length from anterior midpoint of tergite 1 to posterior tip ~4.4 mm as preserved. Sternite 1 preserved as two small triangular sclerotised plates. Tergite 1 without a distinct lateral patch of long setae. However, lateral portions of tergites 1, 2 with longer setae, roughly 0.2 mm. Tergites 1–6 sparsely, evenly covered with short setae (roughly 0.13–0.15 mm), slightly longer towards tergite posterior margin (best preserved on tergites 3, 4). Suture between tergites 5, 6 faintly visible. Abdomen broadest in posterior half tergite 4 (~2.1 mm). Ovipositor appears (see preservation, below) rather short (extending towards anterior margin of tergite 4), base clearly roughly trapezoid (tergite/sternite 7), slightly less than half width of tergite 5. Membrane between tergite 6, 7 that enables great ovipositor articulation, visible as ovate region. Morphology distad base of ovipositor (suture between tergites 7, 8; tergite 9, *i.e.*, actual piercer) indistinctly preserved.

Locality and age. Republic, WA, late Ypresian.

Discussion. The thorax is quite poorly preserved, perhaps somewhat crushed as well as indistinct, and its characters are difficult to interpret, and we describe few details of its morphology. The postpronotal lobe, the scutum, and possibly also the scutellum are visible; however, a distinct suture/fold between the scutum and scutellum cannot be discerned. The only apparent longer bristles visible are likely disarticulated from the thorax, and so their preserved positions are not informative as to whether these belong to the scutum, and are notopleural setae, or to the anepimeron, and are pleural setae (other detected thoracic setae might also have had their positions shifted post mortem). However, their lengths are consistent with that of pleural setae (notopleural setae are much longer), which, therefore, we consider these to be. The reduction of sternite 1 is the normal condition in Pipunculidae, and the two small, rather triangular portions preserved in this specimen might well have constituted a single, larger sternite 1 with translucent margins.

SR 08-06-02 is distinct from species belonging to Pipunculinae and Chalarinae by the following.

Pipunculinae: by its long third costal section (Pipunculinae: shorter); and by the third section of M (anterior margin of cell dm distad crossvein r-m) being long and straight (Pipunculinae: normally distinctly curved posteriad; in *Collinias* Aczél and some *Tomosvaryella* Aczél straight but much shorter).

Chalarinae: separated from *Verrallia* Mik, *Jassidophaga* Aczél by shorter lateral abdominal setae (in *Verrallia* and *Jassidophaga*, these are longer); the long third costal section (in *Verrallia* and *Jassidophaga*, it is shorter); and by ovipositor shape (in *Verrallia* and *Jassidophaga*, the base is more elongate). It is separated from *Chalarus* Walker by size (species of *Chalarus* are ~2–3 mm long) and wing venation, which is partly reduced in *Chalarus*.

We assign this new species to the Nephrocerinae and Protonephrocerini respectively, based on its combination of wing venation character states discussed above and below. The monophyly of this subfamily is in question (Skevington and Yeates 2000), although within this group as defined, it is most easily excluded from the Nephrocerini (one genus: *Nephrocerus*) by possession of six unmodified abdominal segments (in the *Nephrocerus* female, there are seven); by its long third costal section (in *Nephrocerus*, this is very short); and by the presence of a pterostigma (absent in *Nephrocerus*).

The other tribe of Nephrocerinae, the Protonephrocerini, has two described genera, *Protonephrocerus* Collin and *Metanephrocerus* Aczél (we treat a new, third genus as tribe *incertae sedis*, below). Monophyly of the Protonephrocerini was supported by the analysis of

Skevington and Yeates (2000), but the relationships among its three species was unresolved.

The length of the setae, discussed above as pleural setae, is consistent with *Metanephrocerus*, although longer setae might be absent as a taphonomic artefact. More significantly, R_{4+5} terminates on the wing margin not as far below the apex as in *Protonephrocerus*, but rather as in *Metanephrocerus*. Although this region is folded in both wings, an anal lobe is evident, consistent with the condition found in the Baltic amber *Metanephrocerus collini* Carpenter and Hull, but lacking in the extant *Protonephrocerus chiloensis* Collin (present in *Priabona florissantius*, see below) (Fig. 2). By these factors, we assign this species to *Metanephrocerus*, although tentatively, awaiting more complete specimens to add further clarity to this determination. We exclude this species from *Priabona* as in the diagnosis of that genus, below.

At ~9.3 mm in length, the wings of SR 08-06-02 are among the largest known in the family; only those of *Nephrocerus* are larger, reaching up to 12 mm, *e.g.*, *Nephrocerus scutellatus* (Macquart). The wings of *Claraeola nigripennis* (Hardy) reach 9 mm, and those of *Amazunculus* Rafael species are up to 8.5 mm in length; all others are smaller. Second, its pattern of wing infuscation is distinct from any other Protonephrocerini; indeed, from any other pipunculid. Such broad wing colouration is only found in a few members of Eudorylini (Pipunculinae): *Amazunculus* (in three species: all with the basal third completely coloured); *Basileunculus* Rafael (in three species: entire wing equally dark) and *C. nigripennis* (entire wing equally dark).

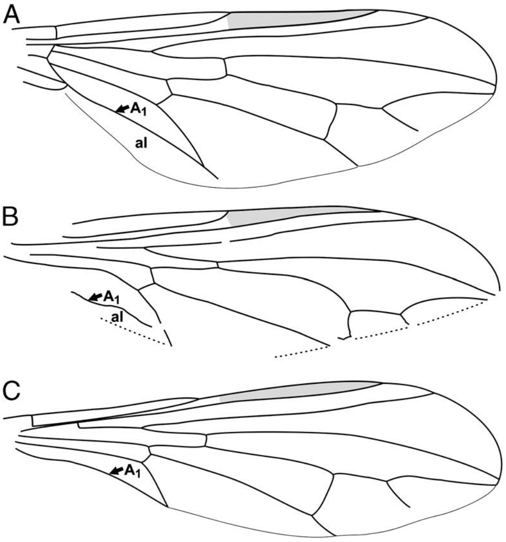
Tribe *incertae sedis*

Genus *Priabona* Archibald, Kehlmaier, and Mathewes, new genus

Etymology. The genus name is derived from "Priabonian", the age of the Florissant Formation from which the genus is known, which is in turn named for the small village Priabona in the northern Italian region of Veneto, the locality of the traditional type section of the age (Gradstein *et al.* 2012). Gender masculine.

Diagnosis. *Priabona* is defined here as a distinct evolutionary lineage of generic rank tentatively placed within the Nephrocerinae, separated from others of that subfamily by the following character states (*e.g.*, Fig. 2). Femora with at least some dark peg-like spines ventrally (others, absent); third section of vein M_{1+2} strongly bent, *i.e.*, upper margin of cell dm (as in some Pipunculinae, not other Nephrocerinae). Further distinct from *Metanephrocerus*, *Protonephrocerus* by posterior margin of head distinctly incised halfway up; further from *Protonephrocerus* by presence of anal lobe. Further distinguished from *Nephrocerus* by flagellum with pointed tip below (kidney-shaped, rounded below in *Nephrocerus*); by mid, hind femora with longer setae anteriorly/antero-dorsally towards apex (absent in *Nephrocerus*); by wing with darkened pterostigma (absent in *Nephrocerus*); by long third costal section (very short in *Nephrocerus*).

Fig. 2. Comparative wings of (A), *Metanephrocerus collini* (late Eocene, Baltic amber), redrawn from Aczél (1948); (B), *Priabona florissantius* (late Eocene, Florissant, Colorado, United States of America); (C), *Protonephrocerus chiloensis* (extant, Chile, drawn from a specimen in the collection of the Finnish Museum of Natural History). *Metanephrocerus collini* and *P. florissantius* possess an anal lobe (al) posteriad vein A_1, which *P. chiloensis* lacks. In (B), the dotted lines indicate the folded, damaged margin of the wing, which extends at least some amount further; in the basal portion, exact wing margin is indistinct, but the presence of an anal lobe is confident by detected microtrichia covering the membrane. Not to scale.



Description. As for its only species.

Type species. *Protonephrocerus florissantius* Carpenter and Hull, **here designated**.

Included species. *Priabona florissantius* (Carpenter and Hull), new combination.

Discussion. *Priabona* is excluded from the Chalarinae by morphology of the flagellum, which is similar to that of Pipunculinae; by the distinctly incised posterior margin of the head; and also by the presence of at least some dark peg-like spines ventrally on the femora, which are absent in that taxon (although also absent in other Nephrocerinae). While the morphology of the flagellum does suggest a pipunculine affinity, it is excluded from that subfamily by the distinctly incised posterior margin of the head and the presence of longer setae anteriorly/anterodorsally towards the apex of the mid and hind femora. It is further distinct from some Pipunculinae by the darkened pterostigma of the wing and the strongly bent third section of vein M_{1+2}, (*i.e.*, the upper margin of cell dm, not drawn so strongly curved by Carpenter and Hull 1939: fig. 5).

Although this genus does not conform to the tribe concepts of either Nephrocerini or Protonephrocerini as currently defined, we hesitate to erect a new tribe for it, particularly given its tentative placement in the Nephrocerinae. We, therefore, treat it here as tribe *incertae sedis*, awaiting clarification of its affinity at this level from new fossils.

Priabona florissantius (Carpenter and Hull), new combination (Fig. 3)

Protonephrocerus florissantius Carpenter and Hull, 1939: 14.

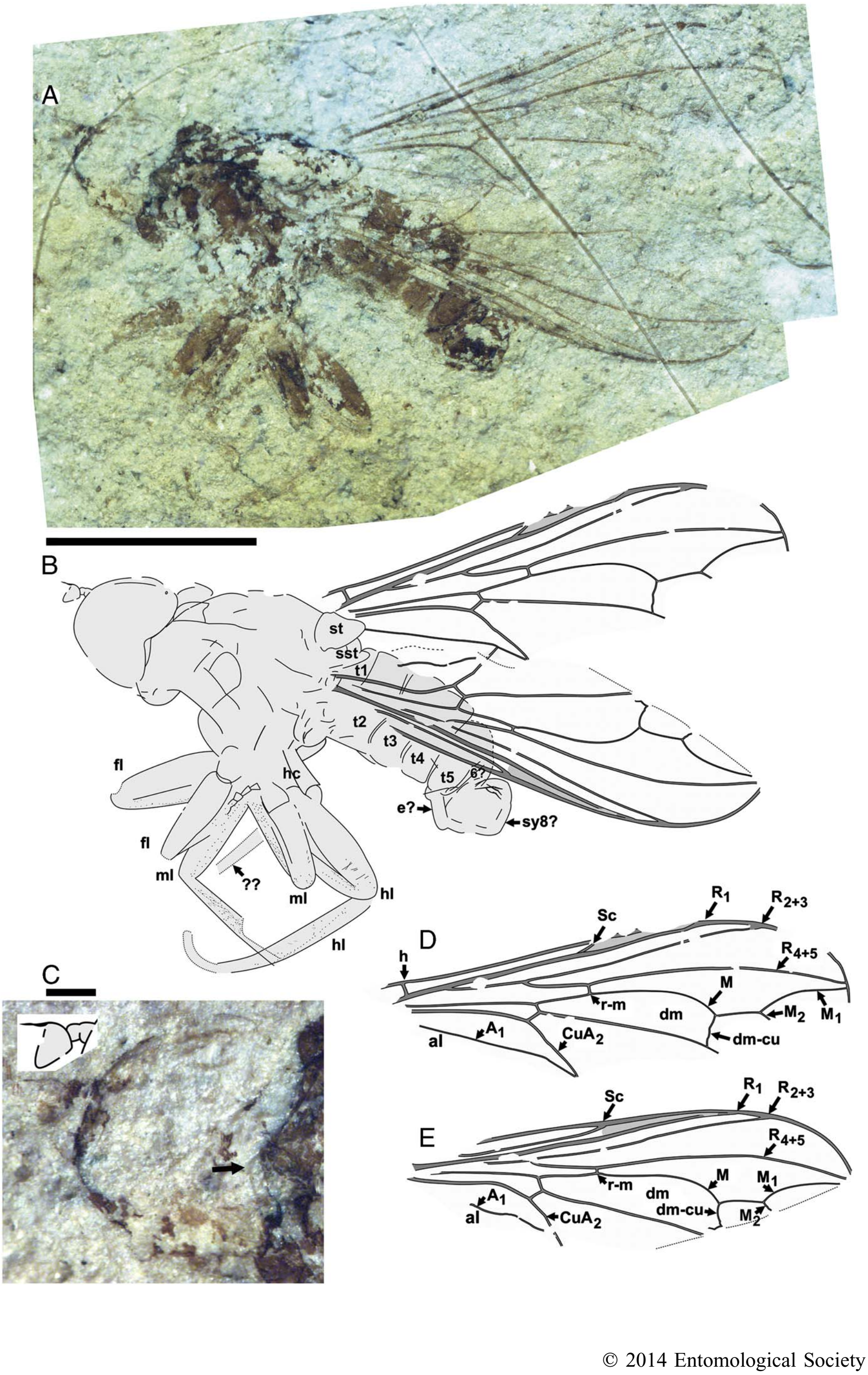
Revised diagnosis. This sole species of *Priabona*, distinguished from others of Nephrocerine as in genus diagnosis.

Revised description. Body length 4.5 mm. Head. No details (*e.g.*, frons, ocellar triangle, mouth parts) confidently discernable, except antennae with small scape, pedicellus, Pipunculinae-like flagellum with pointed tip ventrally. Arista introduced anterodorsally, of ordinary length, thickened towards its base. Posterior margin of head appears distinctly notched/incised half way up. Occiput not discernable from ommatidia of compound eye; its dimension unknown. Thorax. Scutum, scutellum, subscutellum discernible, as in Fig. 3. Arrangement of thoracic sclerites, chaetotaxy unknown by preservation. No distinct long bristles detected, probably detached from body if present. Legs. All six legs partly visible (especially femora, tibiae). Coxae, trochanters not clearly discerned. One profemur with some small, dark peg-like spines posteroventrally near apex. One mid femur with small dark peg-like spines forming an anteroventral and a posteroventral row. One hind femur with small dark peg-like spines anteroventrally towards apex. One mid femur with three long anterodorsal setae at apex, some short, dorsal setae forming two rows. One hind femur with anterodorsal row of longer setae visible in apical third. Tibiae with longitudinal rows of minute dark setae. No distinctly longer bristles or setae detected. Tarsi hardly visible, but basitarsus of one hind leg appears rather short. Wing. Length 4.6 mm; width not determinable as preserved (posterior margins folded or indistinct). Membrane hyaline except pterostigma. Pterostigma complete, touching Sc. Third costal section about half second section length, 2.5X fourth costal section. R_{4+5}, M_1 terminate separately at apex. Stem length of M_{1+2} straight, slightly longer than dm-cu, which is damaged in both wings. M_2 present, length unknown by wing damage. Distad branching of M_2, M_1 moderately curved. Crossvein r-m joins cell dm shortly before its basal third. Cell dm upper margin (sections 2, 3 of vein M_{1+2}) angled where r-m joins cell dm; section 3 strongly curved. Anal vein (A_1) developed, apparently joining CuA_2 before wing margin (with some doubt: region somewhat damaged). Presence of anal lobe discernible by presence of wing membrane posteriad anal vein. Abdomen. Tergites 1–5 confidently discerned. Longer lateral bristles on tergite 1 not detected, but few setae covering tergites (longest ~0.1 mm). Interpretation of structures posterior to tergite 5 ambiguous (see Discussion). Tergite 6 clearly present, but size not determinable.

Material examined. Holotype: MCZ 3976; part only. A complete specimen of undeterminable sex, with body preserved in lateral aspect, covered with a coating of Canada balsam.

Locality and age. Florissant, Colorado, late Priabonian.

Fig. 3. *Priabona florissantius*, holotype, MCZ 3976. (A), photograph; (B), drawing; (C), closeup photograph of head, with eye notch indicated by arrow; inset drawing of antenna; (D), labelled drawing of right wing; (E), labelled drawing of left wing (reversed left-right for comparison). Diagonal lines showing in photograph are cracks in the Canada balsam coating, not in the rock. Much of the precise wing hind margins in (B), (C), (D), are difficult to determine precisely (where dotted lines absent), and are represented as likely here; presence of anal lobes confidently established by wing membrane microtrichia. Wings are hyaline apart from pterostigma, but appear lightly infuscated by their covering of microtrichia. On legs, dashed lines indicate indistinct edges; dots indicate setal bases. al = anal lobe, ?? = unaccounted for leg portion (possibly another insect?). All to scale = 2 mm.



Discussion. Determination of the sex of this insect with any confidence is not possible. The globular structure at the apex of the abdomen might be interpreted either as the sytergosternite 8, in which case this is a male, or as part of the female terminalia including the ovipositor.

Subfamily Pipunculinae Aczél

Pipunculinae species A (Fig. 4)

Pipunculidae indet. Archibald and Mathewes, 2000: 1449, Table 1, fig. 9D.

Description. Body: little known as preserved; complete length estimated close to 5 mm judging from wing length. Head, legs absent. Thorax apparently without any distinct bristles (as preserved). Wing: length 4.7 mm preserved (more complete wing), likely ~4.8 mm complete; width ~1.4 mm; third costal section close to 1.5 length of fourth; R_{4+5} ending below wing apex; ratio between fourth, fifth costal section 1:2.3; R_{4+5} rather straight; R_{4+5} and M_{1+2} separate to margin; M_{1+2} simple, M_2 absent; M bounding cell dm distad r-m rather straight, only gently curved distally; crossvein r-m joins cell dm at basal fifth; cell dm comparatively long, narrow, with upper margin (sections 2, 3 of M_{1+2}) rather straight, only gently curved distally; M_{1+2} distad cross-vein dm-cu to margin weakly sinuate; dm-cu straight, without appendix; anal vein A_1 developed; anal lobe narrow. Abdomen. Tergite 1–4 partly preserved. Tergite 2, 3 same length (about 0.6 mm). Short setae visible on tergites 2–4 apparently evenly, sparsely distributed as preserved.

Material. Q-0397 (part only): a mostly incomplete specimen of unknown sex. Preserved: posterior part of thorax (scutum, scutellum); parts of tergites 1–4 (in dorsolateral aspect); both wings, largely intact, apparently not greatly distorted. Housed in the collection of SFU, collected by R.W.M., late 1990s.

Locality and age. Quilchena, BC; mid-Ypresian.

Discussion. The body and wing lengths of Q-0397 are within the ranges seen in other published pipunculid fossils. Despite its fragmentary state and the lack of longer bristles or setae on the posterior margin of the scutellum and tergites, the fully coloured pterostigma, the moderately long third costal section, the presence of an anal lobe, and the absence of vein M_2 makes it most likely that this specimen belongs to the Pipunculinae. The fact that R_{4+5} reaches the wing margin below the wing's apex represents a synapomorphy shared with *Protonephrocerus* and *Metanephrocerus* (although distinctively further below the apex in *Protonephrocerus*, see above), genera currently placed within the Nephrocerinae. However, there is growing evidence for a paraphyletic Nephrocerinae with Protonephrocerini (*Protonephrocerus* and *Metanephrocerus*) as sister to Pipunculinae (Skevington and Yeates 2000), in which case, this character state would be plesiomorphic. The location of crossvein r-m is very basal relative to cell dm, a state found in many *Dorylomorpha* Aczél and some *Cephalops* Fallén (both Pipunculinae). Further, the comparatively narrow and long cell dm with its upper margin, which is only gently curved distally, resembles the condition found in Microcephalopsini (Pipunculinae). There has been considerable dispute among Pipunculidae workers as to whether the presence/absence of a separated vein M_2 is a valid character for distinguishing genera (Kehlmaier 2006; Kehlmaier and Assmann 2010). Undoubtedly a plesiomorphic character state, the current knowledge of Pipunculidae systematics indicates that both character states can be present within some genera, *e.g.*, *Claraeola* Aczél, *Pipunculus* Latreille, and *Verrallia*.

Subfamily incertae sedis

Pipunculidae species A (Fig. 5)

Pipunculidae indet. Archibald and Mathewes, 2000: 1449, Table 1.

Description. Body. Head. Partly preserved but distorted; no diagnostic features can be assessed. Thorax. Scutum, scutellum clearly visible but no evidence for chaetotaxy detected. One pleural surface visible but no fine structures discernible. Legs not preserved. Wing. Length ~5.9 mm, width ~2.0 mm; "right" (see Discussion) wing seems somewhat detached from body; colouration indistinctly preserved, but pterostigma clearly visible in distal portion of Sc space; third costal section about 3X length of fourth; R_{4+5}, M_1 terminate separately at wing apex. M_2 present, its apical portion missing due to damaged rock; crossvein r-m vaguely visible on one wing, meets

Fig. 4. Pipunculinae species A, Q-0397. (A), photograph; (B), drawing; (C), labelled top wing in (A) and (B); (D), bottom wing in same orientation as (C) for comparison. Wing membrane is hyaline apart from pterostigma; appearance of light infuscation results from microtrichia. Scale = 2 mm.

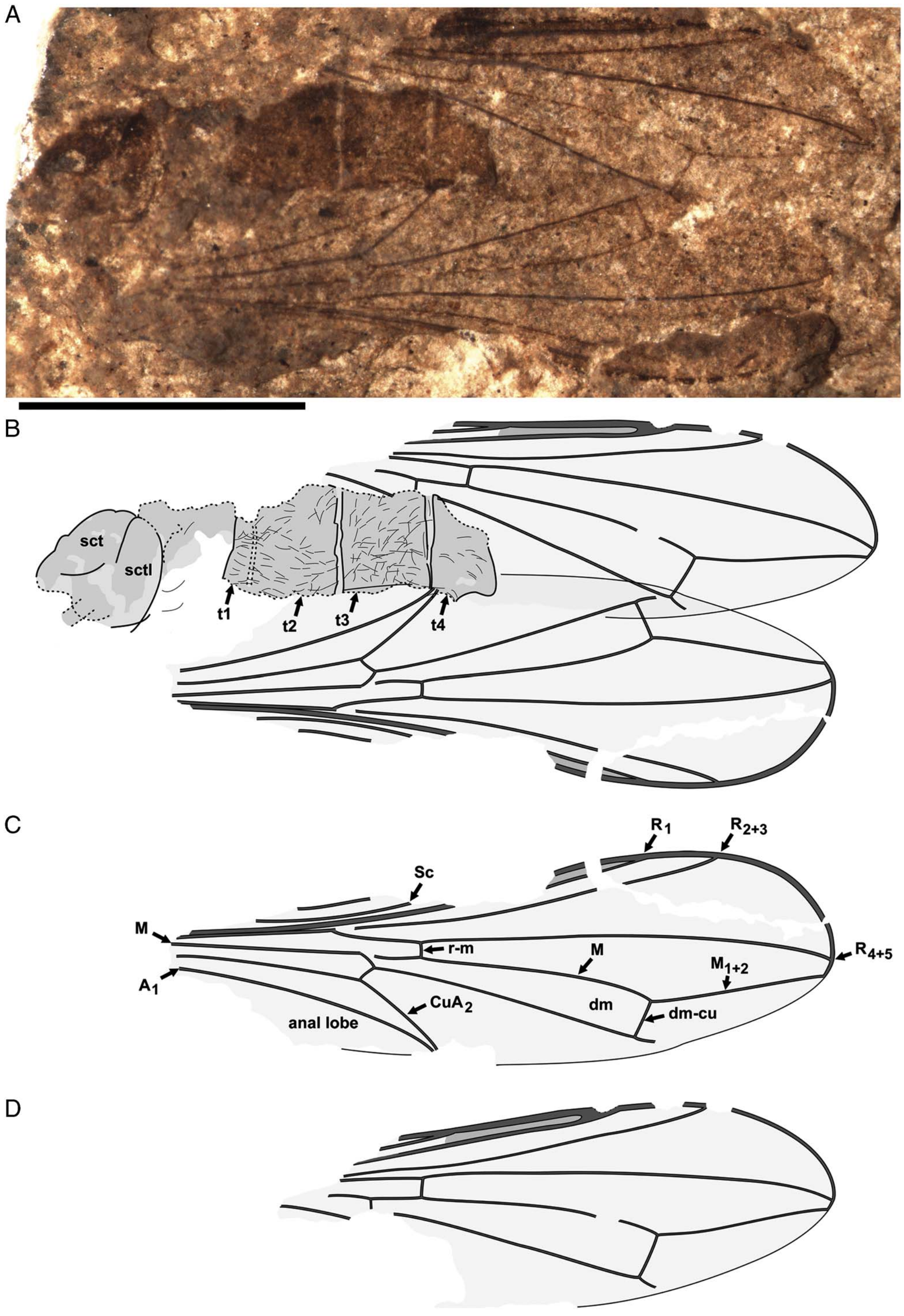
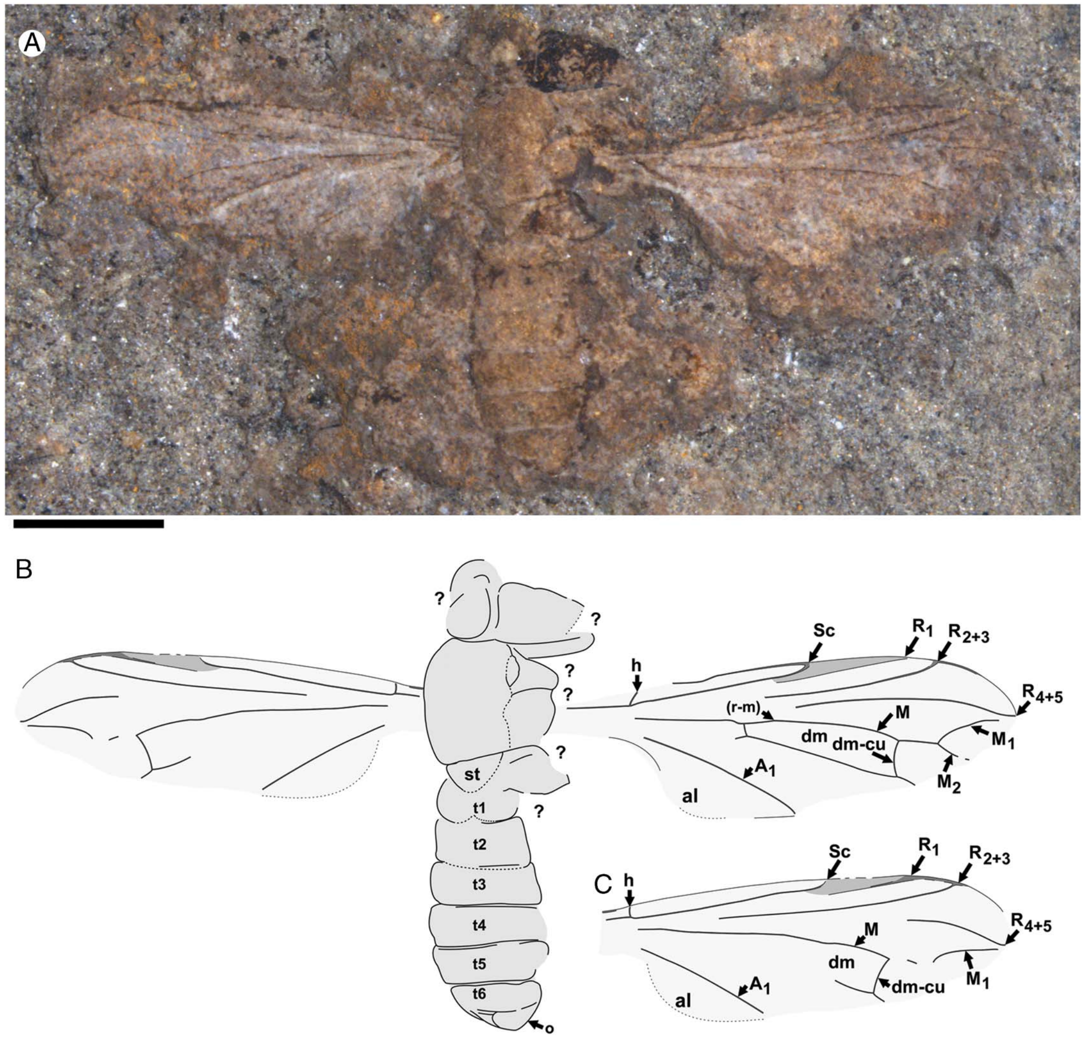


Fig. 5. Pipunculidae species A, Q-0118 (A), photograph; (B), drawing; (C), labelled left wing in (A) and (B). Abbreviations as in Fig. 1, except o = base of ovipositor. (r-m) = inferred joining point of crossvein r-m with M by characteristic bend in M. All to scale = 2 mm.



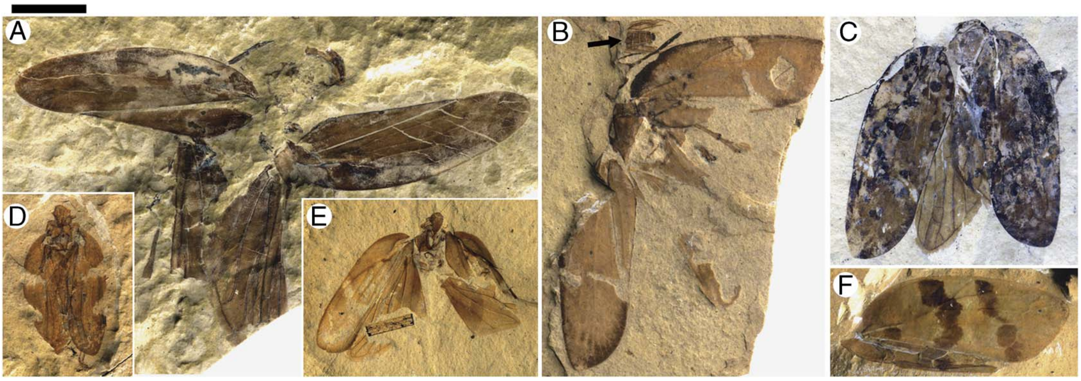
cell dm shortly before its basal third (at point where M is slightly angled); crossvein dm-cu gently curved, without appendix. M_1 gently curved distad branching of M_2 to wing margin; A_1 developed; anal lobe present, developed. Abdomen. Approximately 3.1 mm length from posterior tip of scutellum to posterior tip of abdomen. Tergites 1–6, base of ovipositor (tergite 7) visible. No comments can be made concerning chaetotaxy as preserved.

Material. Q-0118 (part only), a rather complete female, with legs and part of the head missing and indistinctly preserved wings, in dorsal aspect, except the head and thorax are in dorsolateral aspect; housed in the collection of SFU. Collected by R.W.M. at Quilchena, British Columbia, in the mid-1990s.

Locality and age. Quilchena, BC; mid-Ypresian.

Discussion. Placement of this specimen within a genus or even subfamily is not possible due to insufficient preservation of diagnostic characters. However, it can be excluded with certainty from *Nephrocerus* (six abdominal segments), *Protonephrocerus* (anal lobe present), *Chalarus* (wing venation complete), and *Tomosvaryella* and *Dorylomorpha* (pterostigma present). The curvature of crossvein dm-cu on

Fig. 6. A sample of Auchenorrhyncha from Republic, Washington, United States of America. (A), SR 95-01-19; (B), SR 87-28-11; (C), SR 96-10-04; (D), SR 06-31-08; (E), SR 06-28-01; (F), SR 09-42-01B (forewing). Where known, almost all Pipunculidae are endoparasites of mostly Auchenorrhyncha, which were plentiful and diverse in the Okanagan Highlands. The great size of *Metanephrocerus belgardeae* is not surprising, given that North American Eocene Auchenorrhyncha include numerous impressively large species like these (Scudder 1890, p. 315: "some of them are gigantic"; 1895, p. 14: "we are struck by the great size of these insects"). Note *Plecia* (Diptera: Bibionidae) in 6B (black arrow) for size comparison. All from Republic exposure B4131 (like *M. belgardeae*) except (A) and (C), which are from A0307, about 800 m south of B4131. All SR collection. All to scale = 1 cm.



both wings indicates that this is not merely an artefact. A distinctly curved dm-cu is only known in *Amazunculus* (Eudorylini) (Skevington and Yeates 2001: fig. 4A), but a weak curvature as seen in our specimen does occur in other genera as well (*e.g.*, *Eudorylas* Aczél and *Pipunculus*) (Rafael 1986; Rafael and Menezes 1999).

We refer to the "right" wing in the description, meaning as depicted in Fig. 5. There was no counterpart to this fossil found, which is preserved without relief on the rock; therefore, it is impossible to know if this side were the mirror image side of the pair, and whether this wing is the right or left wing.

Evolutionary implications of the Okanagan Highlands Pipunculidae

The new Okanagan Highlands species indicate that the general outline of modern Pipunculidae diversity was set early in its history. The molecular analysis of Wiegmann *et al.* (2011) indicates that it is sister to the Schizophora, and that these diverged in the late Cretaceous, about 70 Ma ago in the Maastrichtian. The considerably differing morphologies of these new species – representing two of the three modern subfamilies (Nephrocerinae, Pipunculinae) – show a high degree of diversification by the mid to late Ypresian, only about three million years after the oldest known pipunculid fossil from the early Ypresian Fur Formation of Denmark (Bonde *et al.* 2008). This diversity is further increased shortly after in the Priabonian, as seen in *Priabona florissantius* and the Baltic amber species (Table 1), which include the third extant subfamily (Chalarinae). The joined M_{1+2} in the Okanagan Highlands Pipunculinae species A shows the presence of this derived character state, dominant in modern species, over twice as old as was previously known from Miocene Dominican amber (De Meyer 1995).

The Eocene history of the Pipunculidae is set in the greater ecological/evolutionary context of recovery following the K-Pg extinction crisis. In western North America, Cretaceous floras and insect leaf herbivory ichnofossil data show high diversity plant communities and plant–insect interactions, which were replaced by largely depauperate plant communities and highly disturbed food webs during a prolonged Paleocene recovery (Wilf and Labandeira 1999; Johnson and Ellis 2002; Labandeira *et al.* 2002; Wilf and Johnson 2004; Wilf *et al.* 2006). Outside North America, however, extinctions may have been less severe with greater distance from the Chicxulub bolide impact site, or recovered more rapidly, or both (Iglesias *et al.* 2007; Wappler *et al.* 2009).

In the Ypresian, plant and insect diversities regained high levels at least into mid-latitudes, with modern tropical levels of species richness in insects and plants found in the Okanagan Highlands (Wilf *et al.* 2003; Archibald *et al.* 2010; Archibald *et al.* 2012; Smith *et al.* 2012). Insect leaf feeding damage also indicates a return to balanced, highly diverse food webs (Labandeira 2002; Wilf *et al.* 2005; Currano *et al.* 2008; Wappler *et al.* 2012).

Where known, Pipunculidae are almost exclusively parasitoids of Auchenorrhyncha (Hardy 1987; Skevington and Marshall 1997; Rafael and Skevington 2010; but see Koenig and Young 2007; Kehlmaier and Floren, 2010), who, like pollinators and some other phytophagous insect groups (*e.g.*, phytophagous Coleoptera and Lepidoptera), underwent large-scale Paleogene diversification (Grimaldi 1999; Grimaldi and Engel 2005). By the late Ypresian, auchenorrhynchs had become rich, prominent community elements in these diverse forests (Fig. 6); over 97 species were recently illustrated from Republic (Archibald *et al.* 2012), and 55 were recovered in a three-week collecting effort at the nearby Okanagan Highlands McAbee locality (Archibald *et al.* 2010). Although Quilchena is less sampled, their fossils are anecdotally common there as well.

The Pipunculidae is, then, an exemplar in miniature of a broad Paleogene ecological/evolutionary revolution. Its early history is concordant with expanding food web dynamics during recovery from the K-Pg extinction, the diversification and spread of complex, species-rich angiosperm-dominated forest types, and the associated radiation of phytophagous insects and their predators, the Pipunculidae among them.

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