SYSTEMATICS

Bulldog Ants of the Eocene Okanagan Highlands and History of the Subfamily (Hymenoptera: Formicidae: Myrmeciinae)

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ABSTRACT The presence of the ant subfamily Myrmeciinae is established in the Early Eocene (Ypresian) Okanagan Highlands localities of Horsefly River, Falkland, McAbee (British Columbia, Canada) and Republic (Washington state, United States) and in the Mo-clay Ølst and Fur Formations (Denmark). Nine new species in four new genera (three orthotaxa: *Ypresiomyrma* n. gen., *Avitomyrmex* n. gen., and *Macabeemyrma* n. gen.; one parataxon: *Myrmeciites* n. gen.) are described. Seven are placed in the Myrmeciinae: *Ypresiomyrma orbiculata* n. sp., *Ypresiomyrma bartletti* n. sp., *Avitomyrmex elongatus* n. sp., *Avitomyrmex mastax* n. sp., *Avitomyrmex systenus* n. sp., *Macabeemyrma ovata* n. sp., and *Myrmeciites herculeanus* n. sp.; two further species are tentatively placed in the subfamily, *Myrmeciites* (?) *tabanifluviensis* n. sp. from Horsefly River, and *Myrmeciites* (?) *goliath* n. sp. from McAbee. Two further myrmeciine ants are treated as *Myrmeciites* incertae sedis, a male from Falkland and a female (worker or queen) from Republic. *Pachycondyla rebekkae* Rust and Andersen, from the earliest Ypresian of Denmark, is reassigned to the genus *Ypresiomyrma*, within the Myrmeciinae. The fossil record indicates a northern hemisphere origin of the subfamily. The presence of *Ypresiomyrma* in Denmark and British Columbia further reflects the well-documented Paleogene cross-North Atlantic distributions of biota. The known fossil record of the Myrmeciinae is restricted to the Eocene.

KEY WORDS Myrmeciinae, Formicidae, ant evolution, Eocene, Okanagan Highlands

The ant subfamily Myrmeciinae is today represented by ≈90 species in two genera: the "bulldog" or "jack jumper" ants *Myrmecia* F. (≈89 spp.); and *Nothomyrmecia* Clark (one sp.), the "dinosaur" or "living fossil" ant (Taylor 1978, Watts et al. 1998, Bolton 2003, Ward and Brady 2003). Both are confined to the Australian region: *Myrmecia* in Australia, New Caledonia, and introduced in New Zealand; and *Nothomyrmecia,* originally reported from the coastal sage west of Esperance in Western Australia, and now well known in the southern Australian Eyre Peninsula (Taylor 1978, Bolton 1994, Watts et al. 1998, Lester 2005) (Fig. 1).

Brown (1953) placed *Nothomyrmecia* in the Myrmeciinae (taxonomic history provided by Bolton 2003), although some authors retain it in the monotypic Nothomyrmeciinae (see discussion by Dlussky and Perfilieva 2003, Dlussky and Rasnitsyn 2003). Here, we follow Bolton (2003), and other authors listed therein) in including it in the Myrmeciinae. Molecular data provide robust support for the Pseudomyrmecinae as the sister taxon to the Myrmeciinae, together comprising the myrmeciomorph group, firmly contained within the "formicoid clade," which excludes some early diverging poneromorphs (Saux et al. 2004, Ward and Brady 2004, Ward and Downie 2005). Baroni Urbani (2000) synonymized *Nothomyrmecia* under the Eocene genus *Prionomyrmex,* consequently replacing the subfamily name Nothomyrmeciinae with Prionomyrmecinae; this was later shown to be unjustified by Ward and Brady (2003) (ongoing discussion: Baroni Urbani 2005).

The subfamily has been unconfirmed in the Mesozoic. *Cariridris bipetiolata* Brandão and Martins-Neto, from the Lower Cretaceous (Albian) Santana Formation of Brazil, originally assigned to the subfamily (Brandão et al. 1989), has subsequently been treated as not a myrmeciine, and as not an ant (e.g., Grimaldi et al. 1997, Bolton 2003, Dlussky and Rasnitsyn 2003, Ward and Brady 2003). Wilson and Hölldobler (2005) suggested that a series of ants recently described from the Late Cretaceous (Turonian) of Botswana (Dlussky et al. 2004) might be myrmeciines. *Myanmyrma gracilis* Engel and Grimaldi, from latest Albian Burmese amber, also has been discussed as a possible member of the subfamily (Engel and Grimaldi 2005, Grimaldi and Engel 2005, Wilson and Hölldobler 2005).

The established fossil record of the subfamily consists of five Eocene species described in two genera: *Prionomyrmex longiceps* Mayr and *Prionomyrmex janzeni* Baroni Urbani from Lutetian to Priabonian (see discussion below) Baltic amber (Mayr 1868, Baroni Urbani 2000); *Archimyrmex rostratus* Cockerell from the Ypresian of the Green River Formation of Colo-

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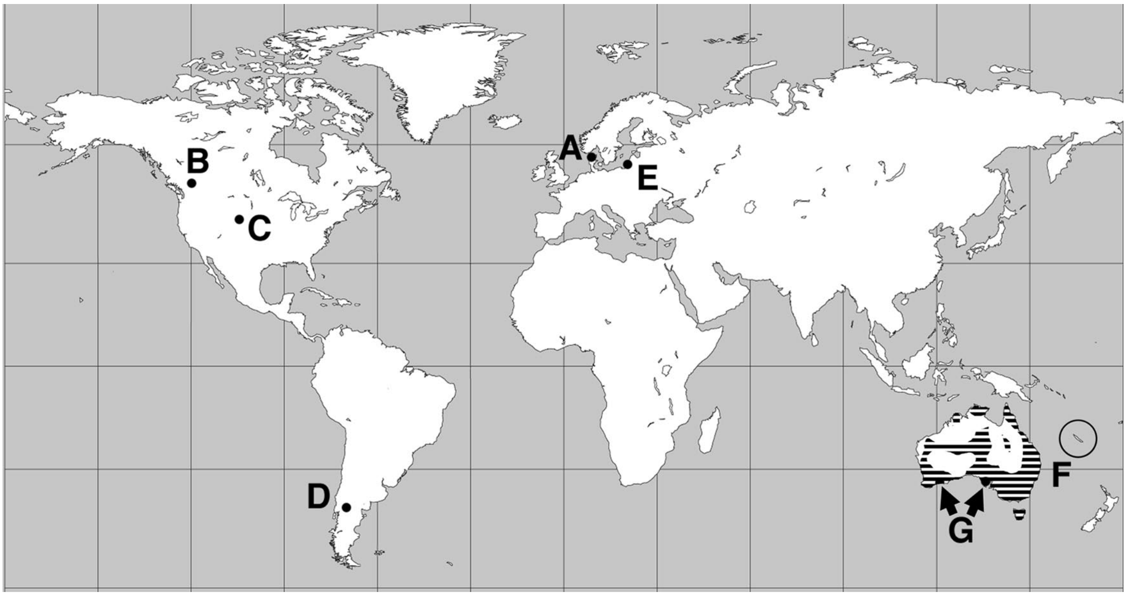

Fig. 1. Map of occurrences of Myrmeciinae. (A) Mo-clay, Denmark, earliest Ypresian (*Ypresiomyrma*). (B) McAbee, British Columbia mid-Ypresian (*Ypresiomyrma*, *Avitomyrmex*, *Macabeemyrma*, *Myrmeciites*). (C) Green River Formation, Colorado, mid-late Ypresian (*Archimyrmex*). (D) Ventana Formation, Argentina, early Lutetian (*Archimyrmex*). (E) Baltic amber, Lutetian (possibly younger, see text) (*Prionomyrmex*). (F) Australian region, modern (*Myrmecia*) (Australia, stripes; New Caledonia, circled). (G) southern Australia, Esperance (west), and the Eyre Peninsula (east), modern (*Nothomyrmecia*). Range of extant Myrmeciinae based on Shattuck (1999) and Bolton (1994).

rado (Cockerell 1923, Dlussky and Rasnitsyn 2003), and *Archimyrmex smekali* Rossi de Garcia and *Archimyrmex piatnitzkyi* Viana and Haedo Rossi from the Lutetian Ventana Formation of Argentina. Scudder (1895), p. 121, reported a species "falling near" *Prionomyrmex*, from the Oligocene beds at Oeningen, Germany, but this record needs confirmation.

Here, we describe nine new species of ants in four new genera, three orthotaxa and one parataxon (collective genus) (these terms sensu Rasnitsyn 1986, 1996) from the Ypresian McAbee, Falkland and Horsefly River localities in British Columbia. Seven species are assigned to the Myrmeciinae, and two species have a possible myrmeciine affinity; we treat a myrmeciine ant from Republic, Washington, as *Myrmeciites* incertae sedis. In addition, *Pachycondyla rebekkae* Rust and Andersen is shown to be a myrmeciine and is placed with two of the McAbee species in the new genus *Ypresiomyrma.*

Materials and Methods

Material Examined. This study is based on the examination of 14 impression fossil specimens from lacustrine shale of Okanagan Highlands localities at Horsefly River, McAbee, Falkland and Republic, and six specimens from marine shale of the Stollenklint Clay (Mo-clay: Ølst Formation), Isle of Fur, Denmark.

Okanagan Highlands fossils were collected by hand quarrying with light tools; blocks of shale at these localities usually split along fine, easily separating bedding-planes. The collectors of some McAbee specimens did light preparation on them, presumably with an air scribe. Minor preparation in a few instances was subsequently done on a few of the specimens at the Museum of Comparative Zoology (MCZ) with an insect pin held in a pin vise. Only 2003.2.9 CDM 033 (*Myrmeciites* incertae sedis: Falkland male) received extensive preparation, generously provided by A. Rasnitsyn. Specimens were examined at the MCZ with a Leica MZ7.5 microscope.

Hypotype Designation. Some specimens (e.g., those of *Myrmeciites* incertae sedis) are not types of new taxa, but they are still designated type material, hypotypes. Although the hypotype designation, a described, figured, or listed specimen (Schenk and McMasters 1956), is not recognized and regulated by the International Code of Zoological Nomenclature (International Trust for Zoological Nomenclature 1999), it is found useful, particularly in some paleontological collections, to ensure special care of often rare specimens that have appeared in the literature, and to facilitate their ready accessibility to future workers.

Illustration. Drawings were done directly from the specimens with the use of a camera lucida microscope attachment. These represent information taken from both part and counterpart (where available); therefore, morphology may be present on the drawing that is not evident from the photograph of the part. Distilled water or alcohol was added to some fossils at times, to enhance visibility. In drawings, dashed lines indicate faintly seen morphology or the edges of missing or obscured regions. Digital photography was done with a JVC 3-charge-coupled device camera adapted to interface with Auto-Montage version 4.0 (Synoptics Inc., Frederick, MD; Syncroscopy 2002) attached to a Leica MZ12.5 microscope. In photographs and drawings, specimens are figured in standard alignment, body facing left, isolated wings with the apex to the right.

Terminology. *Morphology.* Morphological terminology follows Bolton (1994), except for forewing venation, which follows Brown and Nutting (1950), as modified by B. Bolton (personal communication). Venation abbreviations used are as follow: C, costa; Sc, subcosta; R1, first branch of radius; Rs, radial sector; M, media; Cu cubitus; and A, anal vein. Abdominal segments 3 and 4 are AIII and AIV, respectively.

Measurements. Few of the standard measurements reported for ants may be reliably determined on these compression fossil specimens. Those that we find measurable, we report using the following standard abbreviations: HW, head width, width in full face view across the widest part of the head, excluding the eyes; HL, head length, in full face view, the length from the transverse level of the posteriormost part of the head to the anteriormost level of the anterior clypeal border; SL, scape length from the base of the shaft (excluding the condylar bulb) to apex; and WL, Weber's length, the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum. In addition, where possible, we report the maximum height of AIII relative to that of AIV as AIII/AIV, and the ratio of head length to Weber's length, HL/WL as a means of comparison. By the partial nature of these specimens, overall body length cannot be given with precision; we provide rough estimates of the total life length of these ants for their general comparative value.

Geochronology. We follow the age boundaries and terminology as currently set by the International Commission on Stratigraphy (2004) (http://www.stratigraphy.org/). These include (in Ma, *Mega annum,* million years)

Thanetian (late Paleocene): 58.7 ± 0.2–55.8 ± 0.2 Ma
Ypresian (Early Eocene): 55.8 ± 0.2–48.6 ± 0.2 Ma
Lutetian (early Middle Eocene): 48.6 ± 0.2–40.4 ± 0.2 Ma
Bartonian (late Middle Eocene): 40.4 ± 0.2–37.2 ± 0.1 Ma
Priabonian (Late Eocene): 37.2 ± 0.1–33.9 ± 0.1 Ma
Rupelian (early Oligocene): 33.9 ± 0.1–28.4 ± 0.1 Ma
And other, Cretaceous time units, defined below.

Climatic. We use the terminology of Wolfe (1979) for mean annual temperature (MAT) categories: microthermal, <13°C; mesothermal, >13°C, <20°C; megathermal, >20°C, avoiding terms such as "tropical," which not only refers to climatic regimes but also to geographic regions in the modern world.

Institutional abbreviations. CDM, the Courtenay and District Museum, Courtenay, British Columbia, Canada; GMUC, the Geological Museum of the University of Copenhagen, Copenhagen, Denmark; GSC, the Geological Survey of Canada, Ottawa, Ontario, Canada; MCZ, the Museum of Comparative Zoology, Cambridge, MA; and TRU, Thompson Rivers University (formerly University College of the Cariboo, hence, "UCC" numbers), Kamloops, British Columbia, Canada.

Phylogenetic Analysis. *Morphological Data Sets.* In our analyses, we used an adapted version of the MORPH1 data set of Ward and Brady (2003). MORPH1 included 15 taxa: 13 extant (12 ant + Vespidae), *A. piatnitzkyi* and *A. smekali* combined, and the Cretaceous *Sphecomyrma* Wilson and Brown. We made the following changes to MORPH1.

Like Ward and Brady (2003), we scored the character states of the Argentine species *A. piatnitzkyi* and *A. smekali* from published descriptions and figures (Viana and Haedo Rossi 1957, Rossi de Garcia 1983), differing only slightly with their findings, as listed below. To this we added the character states of *A. rostratus* from descriptions and figures of Dlussky and Perfilieva (2003) and Dlussky and Rasnitsyn (2002) for a combined *Archimyrmex* character set of all three species. We include the *Archimyrmex* data set only in our "Fossil Genera" analysis.

Character 13. Ward and Brady score the compound eyes of the Argentine species of *Archimyrmex* as large and convex. Although these (and those of the other fossil ants examined here) seem uniformly large and oval in known specimens, we cannot confirm convexity as preserved; therefore, we code them as "?".

Characters 50 and 51. They scored the diaphanous longitudinal keel on poststernite of AIII (50) and sinuous medial protrusion of AIII near the apical margin (51) as absent on the Argentine *Archimyrmex* species; we find these character states not determinable on Argentine *Archimyrmex* as preserved and figured (or on any compression fossil directly examined), and so we scored these characters as "?" for all compression fossils.

Character 53. We altered this to include not only those ants that have a postpetiole when viewed in dorsal aspect, but also those fossil ants only known in lateral aspect where the presence or absence of a postpetiole can be determined.

Characters 54 and 55. We code *Paraponera* Fr. Smith as "0/1" for dorsal mid-length of AIII ≤80% that of AIV (54) and also height of AIII ≤80% that of AIV (55), as these were both variable in specimens that we examined.

We added character 75. AIII (0) anterior dorsal surface vertical (or close to) in lateral aspect (AIII often block-shaped) or forms a distinct postpetiole; (1) bell/cone-shaped, dorsal surface smoothly rounded in lateral aspect; may have constriction between AIII and AIV but is not distinctly postpetiolate.

The Danish species *Y. rebekkae* showed all character states scored for the genus *Ypresiomyrma.* The *Ypresiomyrma* analysis, therefore, tests not only the relationship of the genus but also of *Y. rebekkae* to taxa in the adapted MORPH1 data set. In placing the Danish species in the genus *Pachycondyla*, Rust and Andersen (1999) specifically compared it with large, African species of *Pachycondyla.* Therefore, we added *Pachy-*

condyla tarsata (F.) to the amended MORPH1, which is both large and African.

Several outgroups were used to examine the relationships of fossil taxa with extant subfamilies. The wasp family Vespidae was used to root the tree, with no assumption that the ingroup taxa constitute a monophyletic lineage.

Four data sets were analyzed, each added separately to the modified MORPH1 data set: "*Ypresiomyrma*" (=*Y. rebekkae*), "*Avitomyrmex*," "*Macabeemyrma*," and "Fossil Genera," which included these three genera + *Archimyrmex.* For these taxa, the morphological characters where coded at the generic level, combining those of their species. Species of the collective genus *Myrmeciites* presented too few characters to score with confidence for meaningful analysis and were excluded from the phylogenetic analysis.

Phylogenetic analyses. To infer relationships among the taxa, phylogenetic analyses were preformed using PAUP* versrion 4.0b10 (Swofford 2002). For all analyses, the most parsimonious (MP) tree(s) was recovered using the branch-and-bound algorithm. To measure the robustness of branching patterns of the parsimony trees, bootstrap analyses (bs) (Felsenstein 1985, Hillis and Bull 1993) were executed using the branch-and-bound option for 1,000 replicates.

Taxonomic Treatment. *Subfamily Level.* Assignment of compression fossil genera and species of the collective genus to the Myrmeciinae is discussed under Systematic Placement after their descriptions under Systematics, supported by findings provided by phylogenetic analysis.

Genus Level. Those species that we identify as myrmeciines but whose specimens lack preserved characters used in generic assignment are assigned to the collective genus *Myrmeciites.* The names of collective groups are regulated by the International Code of Zoological Nomenclature (International Trust for Zoological Nomenclature 1999, articles 1.2.1, 10.3, 23.7, and others cited below). Rasnitsyn (1986, 1996) discussed the use of parataxonomy in fossil insects.

Species level. We do not treat most minor variation in wing venation as useful in separating these ants at the species level. These are listed in species discussions. Although such differences are diagnostically useful for defining species in many insect groups, ants display intraspecific venational variation within the range of many of those differences found within this assemblage.

Fossil Localities

Okanagan Highlands (Canada, United States)

The Okanagan Highlands series of coal, sandstone, and lacustrine shale formations were deposited from the mid- to late Ypresian (and possibly in some localities into the early Lutetian, pending results of new radiometric dating: J. Mortensen and S.B.A., current research), in upland basins distributed sporadically more than 1,000 km from northeastern Washington State to west-central British Columbia.

The Okanagan Highlands forest is hypothesized to have been the antecedent of the modern eastern North American deciduous zone, although with a component of floral elements not found there today: lineages now restricted to eastern Asia, e.g., *Metasequoia;* that are extinct; and are today restricted to low latitudes (Greenwood et al. 2005). A temperate, mesic, and seasonally equable climate is inferred for the region by paleobotanical analyses. The presence of frost-intolerant biota (e.g., palms at most localities, a cycad and the banana-relative *Ensete* at Republic) indicates mild winters, with the coldest month mean temperature >5°C (Greenwood and Wing 1995, Greenwood et al. 2005, Moss et al. 2005). Paleobotanical indicators support an upper microthermal MAT by leaf margin analysis and upper microthermal to, in places mid-mesothermal MAT by nearest living relative of flora analysis; Greenwood et al. (2005) and Moss et al. (2005) discussed the climate and ecology of Horsefly River, Falkland, McAbee, Republic, and other Okanagan Highlands localities in detail.

Many thousands of insect fossils have been recovered from the various sedimentary basins of the Okanagan Highlands (S.B.A., current research). Ants have previously been reported from Horsefly River, Hat Creek, Quilchena, and Republic (Douglas and Stockey 1996, Dlussky and Rasnitsyn 1999, Poinar et al. 1999; Archibald and Mathewes 2000, Dlussky and Rasnitsyn 2003), and are also currently known from One Mile Creek (current research) (map of localities, see Greenwood et al. 2005: Fig. 1).

Horsefly River. Shale beds of an unnamed formation of an unnamed group are exposed on the Horsefly River for roughly 8 km north and east of the town of Horsefly in the central Cariboo region of British Columbia. The exposure where the holotype of *M.* (?) *tabanifluviensis* was found is east of Horsefly, called "Horsefly 3" by Moss et al. (2005) and Greenwood et al. (2005). A radiometric age has not been provided for the Horsefly sediments, although they are considered coeval with the other, Ypresian Okanagan Highland sediments (≈49–52 Ma) by biostratigraphic constraint (Moss et al. 2005, and references therein).

McAbee. The McAbee locality is near the town of Cache Creek in the Thompson-Okanagan region of south-central British Columbia, Canada. These are beds of an unnamed formation of the Kamloops Group, often referred to informally as the "McAbee Formation" or as an exposure of the "Tranquille beds." It is assigned an age of ≈51 Ma by recalculation of ^{40}K-^{40}Ar data from volcanic ash layers intercalated between shale beds (Ewing 1981).

Falkland. This is a locality of Kamloops Group lacustrine shale of an unnamed formation, located northwest of the town of Falkland, British Columbia, in the Columbia-Shuswap region of south-central British Columbia. Its age is mid-Ypresian, 50.61 ± 0.16 Ma by preliminary U-Pb dating from zircons (J. Mortensen and S.B.A., unpublished data).

Republic. The fossil ant reported here was collected from the Tom Thumb Tuff Member of the Klondike Mountain Formation, in a locality ≈30 km northwest of the town of Republic in Ferry County, northeastern Washington state. Although fossils of this formation are generally referred to as "from Republic," this outcrop is a little-known exposure, not from other, well-documented outcrops in and near Republic proper (e.g., Wolfe and Wehr 1987). The Tom Thumb Tuff has been assigned a late Ypresian age of 49.42 ± 0.54 Ma by ^{40}Ar-^{39}Ar decay (Wolfe et al. 2003).

Mo-clay (Denmark)

The Mo-clay consists of the marine Fur and Ølst Formations in the northern Jutland region of Denmark. The 101 specimens of *Y. rebekkae* reported by Rust and Andersen (1999), which include those examined by us, were all found on the Island of Fur, almost all from exposures of the Stolleklint Clay. The Stolleklint Clay is an informal unit of fine-grained laminated, olive-black, silty clay, in the lowest portion of the Haslund Member at the base of the Ølst Formation (Beyer et al. 2001). A few specimens were recovered from Fur Formation sediments lying stratigraphically above the Ølst. Fur Formation insects typically are recovered from calcareous cementstones found within the diatom-rich varved sediment (Larsson 1975, Rust 1999).

Mo-clay volcanic ash layers are numbered from +140 (highest) to −39 (lowest), with the lower boundary of the Fur Formation at or close to ash layer −33; ash layers −34 to −39 occur in the Stollenklint Clay (Heilmann-Clausen et al. 1985, Knox 1997). Over 20,000 insect fossils have been collected from the Mo-clay, primarily from two main beds of the insect-rich Fur Formation: the "upper insect layer" between ash layers +25 and +30 and the "lower insect layer" between −21 and −29 (Larsson 1975, Rust 1999). The Stolleklint Clay ant specimens were found at the level of ash layer −33, immediately below the Fur Formation boundary; the few Fur Formation specimens were found in the lower insect layer between ash beds −24 and −28 (Rust and Andersen 1999). All specimens examined by us were from the Stolleklint Clay. The Stollenklint Clay is generally megafossil-poor (Beyer et al. 2001, Willumsen 2004).

An Ypresian age of 54.04 ± 0.14 Ma has been determined for layer +19 and 54.52 ± 0.05 Ma for layer −17 by the Ar^{40}-Ar^{39} method (Chambers et al. 2003). The Paleocene–Eocene boundary is now defined as coincident with the beginning of the carbon isotope (δ^{13}C) excursion at 55.8 ± 0.2 Ma, found in the basal ≈15 m of the Ølst Formation (Aubry et al. 2003; Schmitz et al. 2004). Therefore, these ants are earliest Ypresian.

The marine Mo-clay insect assemblage seems to be composed of insects imported by both active transport, i.e., migration or individual flight, and through passive transport by offshore winds (Larsson 1975; Ansorge 1993; Rust 1998, 1999, 2000). Rust (1998) discussed taphonomy of ant specimens and inferred that the ants were probably imported by active flight in mating swarms (Rust 1999). Archibald and Makarkin (2006) suggested that portions of the insect fauna could have been transported an undetermined distance from the north by diatom mats moving southward along the Scandinavian coast.

Ventana Formation (Argentina)

Petrulevicius (1999) assumed that the Patagonian Rio Pichileufú locality where Viana and Haedo Rossi (1957) found *A. piatnitzkyi* belongs to the Ventana Formation, which also bears *A. smekali* (Rossi de Garcia 1983). Wilf et al. (2005) provide an early Lutetian age for a nearby exposure at Rio Pichileufú of 47.46 ± 0.05 Ma from ^{40}Ar-^{39}Ar analysis.

Green River Formation (United States)

The lacustrine oil shales of the Green River Formation occur in large areas of southwestern Wyoming, northwestern Colorado, and northeastern Utah. *A. rostratus* fossils have been found in the Piceance Creek member of Colorado. Recent ^{40}Ar-^{39}Ar geochronology shows the Green River Formation to have been deposited over roughly 5 Ma, from ≈53.5 to 48.5 Ma, or mid-Ypresian into (barely) the earliest Lutetian (Smith et al. 2003, 2004). Within this range, the precise ages of the localities bearing these ants have not been determined (Fig. 19: gray line); as the ages of McAbee, Falkland, Republic, and apparently Horsefly River lie within Green River Formation time, we consider the Green River *A. rostratus* to be roughly contemporaneous with the Okanagan Highlands ants, pending further analysis.

Baltic Amber

The majority of Baltic amber is found in the *Blaue Erde* ("Blue Earth"), dated 44.1 ± 1.1 Ma (middle Lutetian) by K-Ar dating (Ritzkowski 1997). Some, but not as much amber comes from the "Wilde Earth," a member below the Blue Earth. A sample from the upper Wilde Earth was dated at 47.0 ± 1.5 Ma (earliest Lutetian) (Ritzkowski 1997). Although a Lutetian estimate for the age of Baltic amber insects is currently most conservative, there are difficulties with this age determination, which remains under debate.

These radiometric ages were determined from glauconites, at times problematic (Aubry et al. 1989, Obradovich 1989). Further uncertainty is added by possible redeposition of Baltic amber from older sediments, because it has a low specific gravity and floats in salt water (Weitschat and Wichard 2002). The amber-producing forest may have persisted for an extended period, perhaps as long as 10 Ma (Weitschat and Wichard 2002, Keyser and Weitschat 2005). A younger, Priabonian determination of the Blue and Wilde Earths is supported by marine microfossil biostratigraphy (Kosmowska-Ceranowicz and Müller 1985, Kosmowska-Ceranowicz 1987).

Systematics
Family Formicidae
Subfamily Myrmeciinae
Ypresiomyrma Archibald, Cover and Moreau, n. gen.

Type Species. *Ypresiomyrma orbiculata.*

Diagnosis. Queens separated from all other genera of Myrmeciinae by a combination of: single-segmented waist; mandibles triangular, shorter than head capsule length; head capsule about as long as broad; petiole, gaster normal in proportions, not notably slender as in *Avitomyrmex.*

Queen. Large (body length ≥20 mm) myrmeciine ants with the following characters.

1. Head variable in shape, but always about as long as broad
2. Mandibles triangular, elongate, with eight to 12 coarse (not spiniform) teeth, approximately two-thirds HL
3. Eyes, where known, large, well developed, placed at or anterior to cephalic mid-length
4. Mesosoma wing bearing, generalized in form
5. Forewing venation generalized within Myrmeciinae
6. Propodeal dorsum rounded in lateral aspect, without projections
7. Petiole lacking anterior peduncle; node conical, well developed; attached to AIII without notable constriction, length, height subequal
8. AIII bell-shaped in both lateral (all spp.) and dorsal (known only in *Y. rebekkae*) aspects, without constriction at junction with AIV
9. Sting well developed.

Included Species. *Y. orbiculata, Y. bartletti,* and *Y. rebekkae.*

Etymology. The generic name refers to the Ypresian age, and *-myrma,* from the Greek *myrmex,* meaning "ant." Gender: feminine.

Ypresiomyrma orbiculata Archibald, Cover and Moreau, n. sp.
(Figs. 2, 16M, 17A)

Diagnosis. Easily separated from other species of the genus by strongly rounded posterior corners of the head (*Y. bartletti* and *Y. rebekkae:* subangulate), by shape of petiole (Figs. 2, 17A).

Holotype Queen. As in diagnosis, Figs. 2, 16M, 17A, and the following. Length estimated ≈2.5 cm in life. *Head:* eyes large, oval, maximum length oriented anterodorsally, located at cephalic mid-length; antenna not determinable; mandibles with approximately seven to eight teeth. *Mesosoma: Wings:* forewing with closed cells 1 + 2r, rm, mcu, (distal portion of 3r not preserved), rm hexagonal, mcu pentagonal; Rs.f1 joins Sc+R close to right angle, about equal angles between Rs.f1, M.f1, Rs+M; Rs.f2, Rs.f3 apparently gently curved, almost straight; M.f1 gently curved; 2rs-m parallel with M.f2, Rs.f1; 1m-cu faintly preserved, apparently subparallel with M.f1, joins Cu basad joining M; cu-a joins A distad joining of M+Cu; cell cua apparently closed (Cu.f2 faintly preserved); Cu1 present. *Petiole:* convex, smoothly sloping; vertex of node at petiolar mid-length. *Measurements:* HW, 4.4 mm; HL, 4.0 mm; WL, 7.0; AIII/AIV height, 0.70; HL/WL, 0.57.

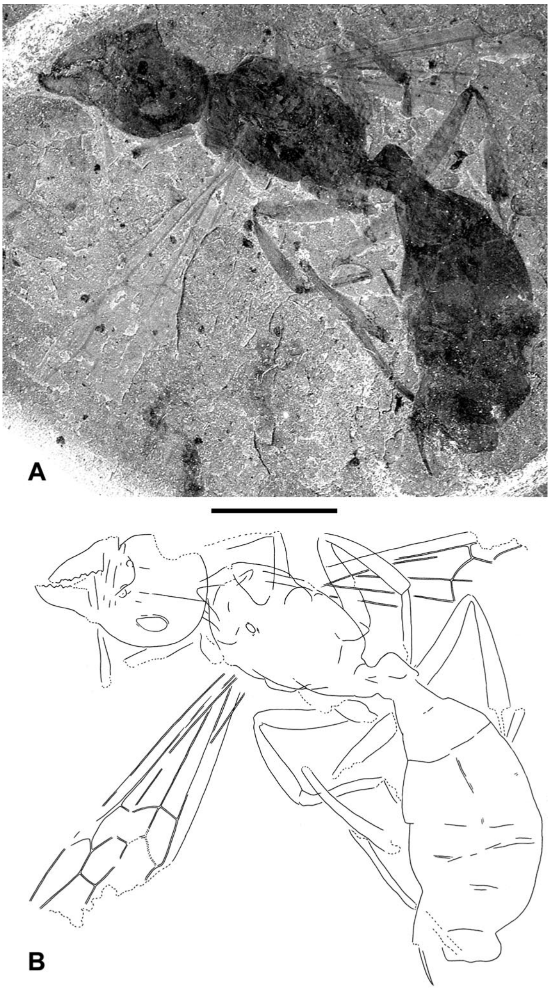

Fig. 2. *Y. orbiculata,* queen, habitus of holotype. (A) Photograph of part. (B) Drawing, from both part and counterpart. Scale bar = 5 mm, both to scale.

Type Material. HOLOTYPE: UCCIPR L-18 F-749, part; UCCIPR L-18 F-750, counterpart. Large well-preserved queen with much of the forewings present, with much of venation visibly preserved, legs indistinctly preserved. In the collection of TRU; collected by unknown person, donated by David Langevin in 2002. Labeled: HOLOTYPE, *Ypresiomyrma orbiculata* Archibald, Cover and Moreau.

Locality and Age. CANADA: British Columbia: the McAbee locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Etymology. From the Latin *orbiculatus,* "circular" or "rounded", referring to the shape of the head capsule.

Discussion. As in Materials and Methods, it is not clear which of the following details of forewing ve-

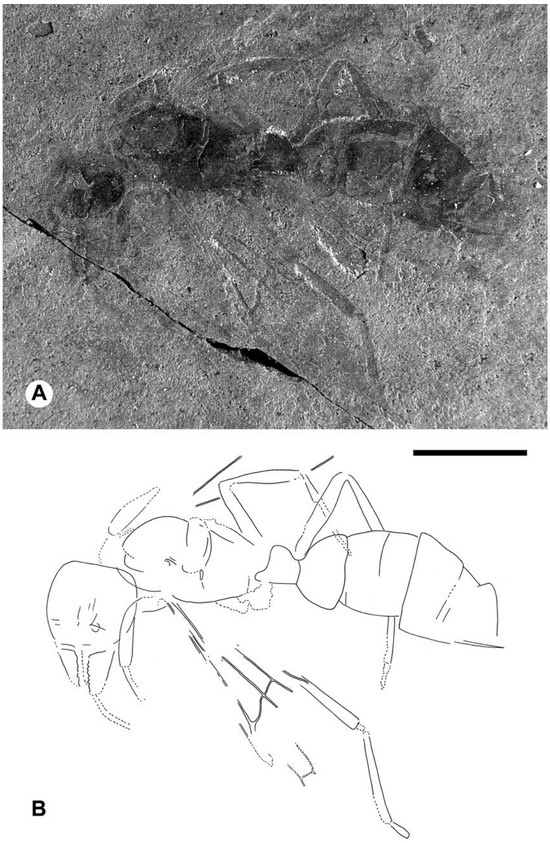

Fig. 3. *Y. bartletti*, queen, habitus of holotype. (A) photograph of part. (B) Drawing, from both part and counterpart. Scale bar = 5 mm, both to scale.

nation represent individual variation of this specimen, and which are stable within the species, i.e., are diagnostically useful. The holotype differs most from other myrmeciine forewings by: 2rs-m is parallel with M.f2 and Rs.f1; and from all but the holotype of *M.* (?) *tabanifluviensis* by cu-a joining A distad its joining M+Cu, meeting A at slight angle from perpendicular (usually perpendicular, but in the holotype of *Archimyrmex rostratus,* cu-a joins A proximad joining M+Cu).

Ypresiomyrma bartletti Archibald, Cover and Moreau, n. sp.

(Figs. 3, 16I, 17C)

Diagnosis. Separated from *Y. orbiculata* by distinctly subangulate posterior corners of head, from *Y. rebekkae* by smaller size, from both by petiole shape (Figs. 3, 17C).

Holotype Queen. As in diagnosis, Figs. 3, 16I, 17C, and the following. Length estimated ≈2.0 cm in life. *Head:* antennae not preserved; eyes not distinguishable as preserved; mandibles with ≈10, uniformly developed teeth. *Mesosoma: Wings:* forewings partially, indistinctly preserved, preserved portions generalized as in subfamily: M.f1 apparently bent near M+Cu, but possibly damage; 2rs-m present, cell rm closed; cu-a joins M+Cu at branching of M.f1, Cu.f1. *Petiole:* with nearly vertical anterior face, rounded vertex, gently sloping posterior face; with apparently greater constriction at joining to AIII than *Y. orbiculata. Measurements:* HL, 3.7 mm; HW, 3.9 mm; WL, 6.3 mm; HL/WL, 0.59.

Type Material. HOLOTYPE: GSC type number 127632a (part) 127632b (counterpart). Alate queen, preservation low-contrast with matrix, in mostly dorsolateral aspect, partly lateral aspect; mostly complete but faintly preserved portions of forewings; legs somewhat disarticulated and portions not preserved; housed in the GSC collection; collected by Rod Bartlett in September 1994. Labeled: HOLOTYPE, *Ypresiomyrma bartletti* Archibald, Cover and Moreau, GSC type number 127632a (part) 127632b (counterpart), collector number MB01045a (part), MB01045b (counterpart).

Locality and Age. CANADA: British Columbia: the McAbee locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Etymology. The specific epithet is a patronym in honor of Rod Bartlett, who collected this specimen and generously donated it to the GSC. He has contributed to paleontology in British Columbia over the last decade by his involvement with the Vancouver Paleontological Society and the British Columbia Paleontological Alliance, by his volunteer work at the Geological Survey of Canada in Vancouver, and by his donation of a number of significant specimens to institutional collections.

Ypresiomyrma rebekkae (Rust and Andersen), n. comb.

(Figs. 4-6, 16G and H, 17B)

Pachycondyla rebekkae: Rust and Andersen 1999: 331–348, Figs. 1–6 [in Ponerinae].

Diagnosis. Most easily separated from other species of *Ypresiomyrma* by petiole shape (Figs. 2–6, 17A–C); further, from *Y. orbiculata* by subangulate posterior corners of head capsule (strongly rounded in *Y. orbiculata*), from *Y. bartletti* by larger size (estimated life length of queen, ≈2.5 cm; *Y. bartletti,* ≈2.0 cm).

Queens and Males. A detailed description is provided by Rust and Andersen (1999). Further to this (queens): AIII/AIV height (Paratype Danekræ 94), ≈0.75.

Material Examined. All from Stolleklint, Fur, Denmark; in the collection of GMUC. 1) HOLOTYPE: Danekræ 94: a complete (but mostly missing legs), rather well-preserved alate queen with partially preserved wings; collected by Rebekka Madsen; labeled (part and counterpart): 16-A4218; DK 94. PARATYPES. 2) Part and counterpart: a queen on the same rock as the holotype (also Danekræ 94), lacking wings, gaster strongly bent under. 3) Danekræ 83, GM1995.9A: (part) a well-preserved queen, mostly complete but missing caudal portion of gaster and

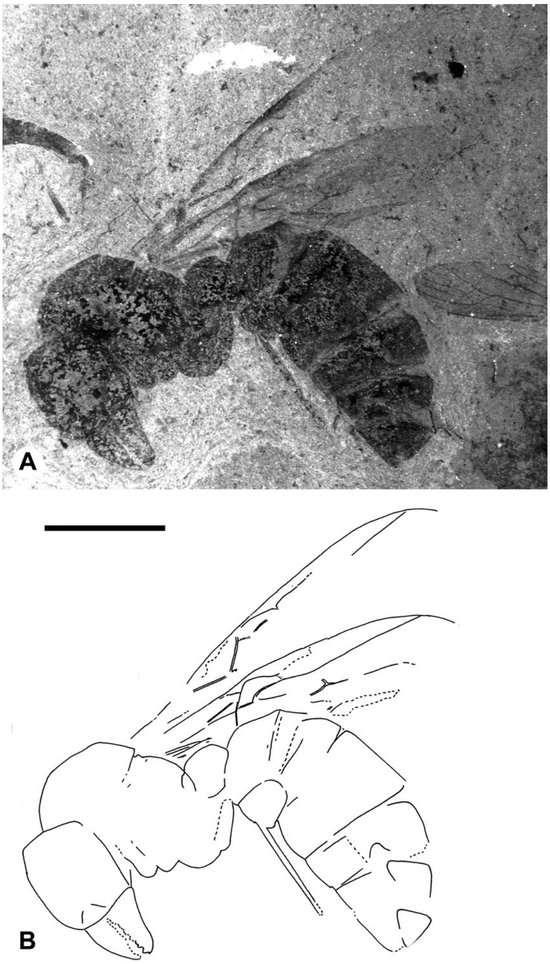

Fig. 4. *Y. rebekkae*, queen, habitus of holotype. (A) Photograph of part. (B) Drawing, from both part and counterpart. Scale bar = 5 mm, both to scale.

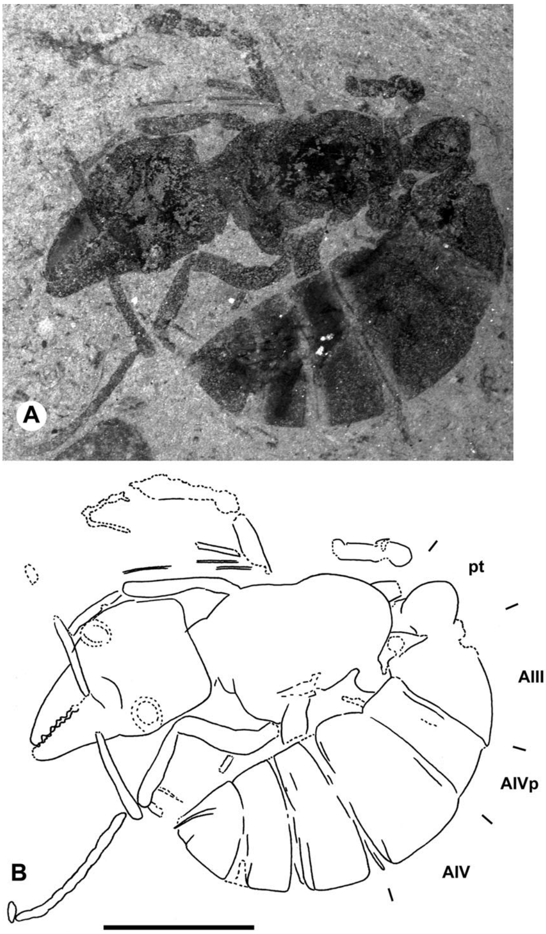

Fig. 5. *Y. rebekkae*, queen, habitus of paratype, Danekræ 93 (same rock as holotype). (A) Photograph of part. (B) Drawing, from both part and counterpart. pAIV, presclerite of AIV. Scale bar = 5 mm, both to scale.

partial wing portions only; (counterpart) fragments collectively labeled on container; part and counterpart labeled DK 83, 1995.9A, 16-3573. 4) Danekræ 61: GM 1994.9: a queen with well-preserved head, mesosoma, and ventral portions of the gaster; labeled DK 61, 1994.9, and Stolleklint 8/8 92 LEG. M.M. 5) Danekræ 60: GM 1994.8; part: a rather complete queen, but lacking wings and much of the legs, preserved in dorsal aspect; labeled DK60, 1994.8, 16-3964; counterpart: a fragment with the mesosoma and leg portions, same labeling. 6) Danekræ 302, labeled DK302 and I396, a male with suggested wing fragment.

Locality and Age. DENMARK: Isle of Fur: Stolleklint and Manhøj; Ølst and Fur Formations; Eocene: earliest Ypresian.

Discussion. Rust and Andersen (1999) listed 101 specimens housed in various museums and private collections, all collected from Stolleklint, except one specimen from Manhøj, Fur, Denmark. The six specimens that we examined are from these 101, housed in the GMUC.

The only complete forewing (Fig. 16H) assigned to the species by Rust and Andersen (1999) (see their Fig. 3A) is an isolated specimen, not examined by us (CM No. 16-A3417: Madsen private collection). They supported the association of this wing with the holotype by comparison with portions of forewings preserved attached to bodies or portions of bodies on five other specimens. We examined a specimen of a body with articulated portions of a forewing, Danekræ 83 (GM1995.9A) (Figs. 6A and B, 16G). The portions of this wing preserved basad of Rs.f5 match closely when images of these wings are superimposed; although Rs.f5, the distal part of the pterostigma, and the wing apicad of that seem bent, damaged, and are not comparable. We find the association of CM No. 16-A3417 reasonable; nonetheless, we hope for future specimens with better preserved wings articulated to bodies to strengthen this determination.

Rust and Andersen (1999) (see their Fig. 5B) assigned a specimen of an ant to this species (Danekræ 302, specimen MM No. I 396), which they considered

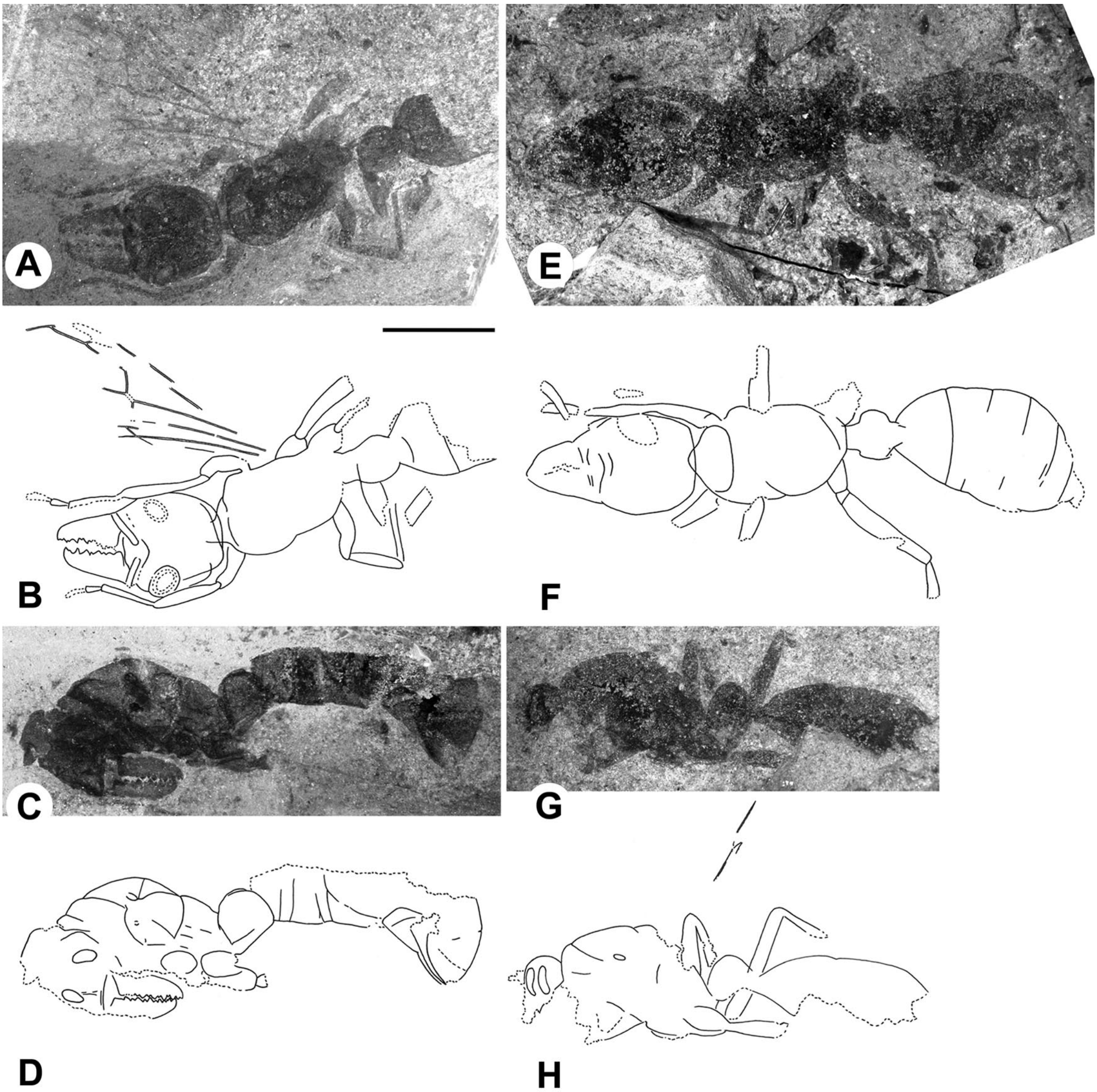

Fig. 6. *Y. rebekkae*, habitus of paratypes, Danekræ 83. (A) Photograph of queen, Danekræ 83, part. (B) Drawing of Danekræ 83. (C) Photograph of queen, Danekræ 61. (D) Drawing of Danekræ 61. (E) Photograph of queen, Danekræ 60. (F) Drawing of Danekræ 60. (G) Photograph of male, Danekræ 302. (H) Drawing of Danekræ 302. Scale bar = 5 mm, all to scale.

to be a male by its general appearance, including smaller size and comparatively slender shape. We examined the counterpart (presumed by its minor differences, cf. Figure 6H and their Fig. 5B). This specimen, however, bears only suggested fragments of wings, without meaningfully preserved venation to compare with those of queens assigned to *Y. rebekkae.* Nevertheless, its distinctly male habitus and great general morphological similarity with that of the queen of *Y. rebekkae,* together with their stratigraphic association renders this assignment reasonable in our view.

The known forewing specimens of this species are most obviously distinct from *Myrmecia* by cell mcu slightly greater in height than cua (smaller in *Myrmecia*); *Y. orbiculata, A. rostratus, M.* (?) *tabanifluviensis* by crossvein cu-a perpendicular to A (not perpendicular in those); *A. elongatus, A. mastax* by M.f2 longer than Rs+M (shorter in those); *A. piatnitzkyi* by Rs.f1 much shorter than M.f1 (*A. piatnitzkyi,* close to equal length); *A. smekali* by crossvein 1m-cu shorter than M.f2 (*A. smekali,* slightly longer).

Avitomyrmex Archibald, Cover and Moreau, n. gen.

Type Species. *Avitomyrmex mastax* n. sp.

Diagnosis. Queens and workers distinguished from other genera of Myrmeciinae by distinctly slender habitus, particularly notable in the petiole, gaster; fur-

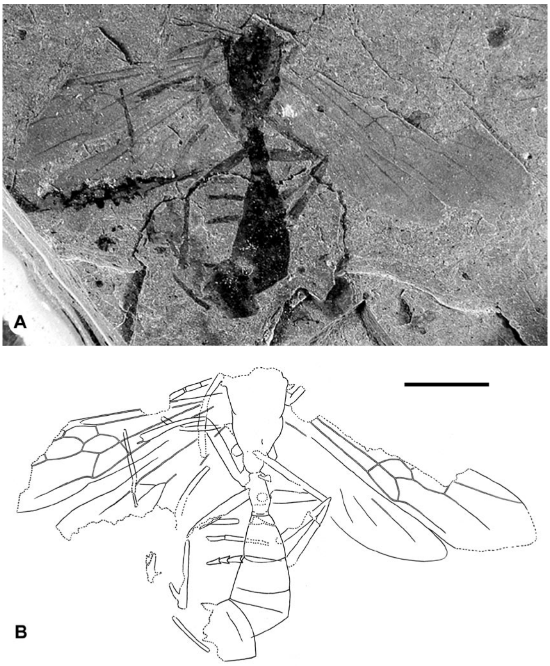

Fig. 7. *A. elongatus*, queen, habitus of holotype. (A) Photograph. (B) Drawing. Scale bar = 5 mm, both to scale.

ther from *Nothomyrmecia* by petiole with peduncle absent or indistinct.

Queens and Workers. Large-sized myrmeciine ants with notably slender habitus, having the following characters.

1. Eyes, large, well developed where known
2. Mandibles poorly preserved, but subtriangular, apparently not coarsely toothed (in single known specimen)
3. Mesosoma generalized, wing-bearing (queens)
4. Propodeal dorsum rounded in lateral aspect, without spines or teeth where known
5. Petiole where known, node rounded, peduncle absent or very short
6. Gaster notably slender, **AIII** cone/bell-shaped, joined to **AIV** without apparent constriction; **AIII** smaller than **AIV** (dorsal aspect known in *A. elongatus, A. mastax;* lateral aspect known in *A. systenus*)
7. Sting present, well developed, clearly visible in *A. systenus* type specimens.

Included Species. *Avitomyrmex elongatus* n. sp., *A. mastax* n. sp., and *A. systenus* n. sp.

Etymology. The genus name *Avitomyrmex* is from the Latin *avitus*, "grandfatherly", "old", "ancient" and *myrmex*, Greek for ant. The gender is masculine.

Avitomyrmex elongatus Archibald, Cover and Moreau, n. sp.

(Figs. 7, 16J)

Diagnosis. May be separated from other members of the genus by larger overall size: estimated life length >2 cm (*A. mastax*, ≈1.5 cm), forewing ≈18 mm (*A. mastax*, ≈13 mm); *A. systenus* too small to reasonably represent worker caste (see discussion).

Holotype Queen. As in diagnosis, Figs. 7, 16J and the following. Length estimated >2 cm in life. *Head:* not preserved. *Mesosoma:* alate, length at least twice maximum width. *Forewing:* 1 + 2r, 3r, rm, mcu, cua closed; rm hexagonal, mcu pentagonal; rm, mcu, cua about equal height; cu-a joins M+Cu at branching to M.f1, Cu.f1; Rs.f1 branches from Sc+R close to perpendicular; Cu1 present. *Hindwing:* little known. *Petiole:* preserved in dorsal aspect; length at least twice maximum width; maximum width at two-thirds length; broadly joined to **AIII**. *Gaster:* slender, caudal portion poorly known; **AIII** narrowly conical, joining **AIV** without constriction; **AIV** wider than **AIII**.

Type Material. HOLOTYPE: 2003.2.8CDM032 (part only). Preserved in dorsal aspect, lacking head, fore- and hind wings well preserved, but portions of anterior margins of forewings missing, caudal portion of gaster partially disarticulated, housed in the CDM collection. Labeled: HOLOTYPE, *Avitomyrmex elongatus* Archibald, Cover and Moreau, and with the collector number SBA2832.

Locality and Age. CANADA: British Columbia: the McAbee locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Etymology. From the Latin *elongatus*, "prolonged" referring to the slender habitus of this species.

Discussion. Because of its greater size, *A. elongatus* is unlikely to be conspecific with either the known queens of *A. mastax* or the unknown queens of *A. systenus.* In extant myrmeciines, the size differences between conspecific queens and workers are generally smaller than that between the holotype of *A. elongatus* and the types of *A. systenus.*

The forewings of the holotype are distinct from *A. mastax* by length, estimated ≈18 mm (queen) (*A. mastax*, estimated ≈13 mm, queen); *Myrmecia* by cell mcu equal or slightly larger in height than cua (smaller in *Myrmecia*); *Archimyrmex, Nothomyrmecia, Y. orbiculata, Y. bartletti* by M.f1 smoothly curved (straight or almost in *Archimyrmex, Nothomyrmecia, Y. orbiculata*, bent near M+Cu in *Y. bartletti*); *Archimyrmex* by cu-a joins M+Cu at branching to M.f1 and Cu.f1 (joins M+Cu just under half crossvein length basad in *Archimyrmex*); *Y. orbiculata* and *M.* (?) *tabanifluviensis* by cu-a perpendicular to A (at angle in those); *Y. rebekkae* by M.f2 shorter than Rs+M.

Avitomyrmex mastax Archibald, Cover and Moreau, n. sp.

(Figs. 8, 16K)

Diagnosis. May be separated from all other Myrmeciinae by small mandibles (about half head length); further from *A. systenus* by head capsule morphology, petiole dorsum smoothly rounded (not angulate); from *A. elongatus* by smaller size (queen forewing length: *A. mastax*, ≈13 mm; and *A. elongatus*, ≈18 mm).

Holotype Queen. As in diagnosis, Figs. 8, 16K, and the following. Length estimated ≈1.5 cm in life. *Head:*

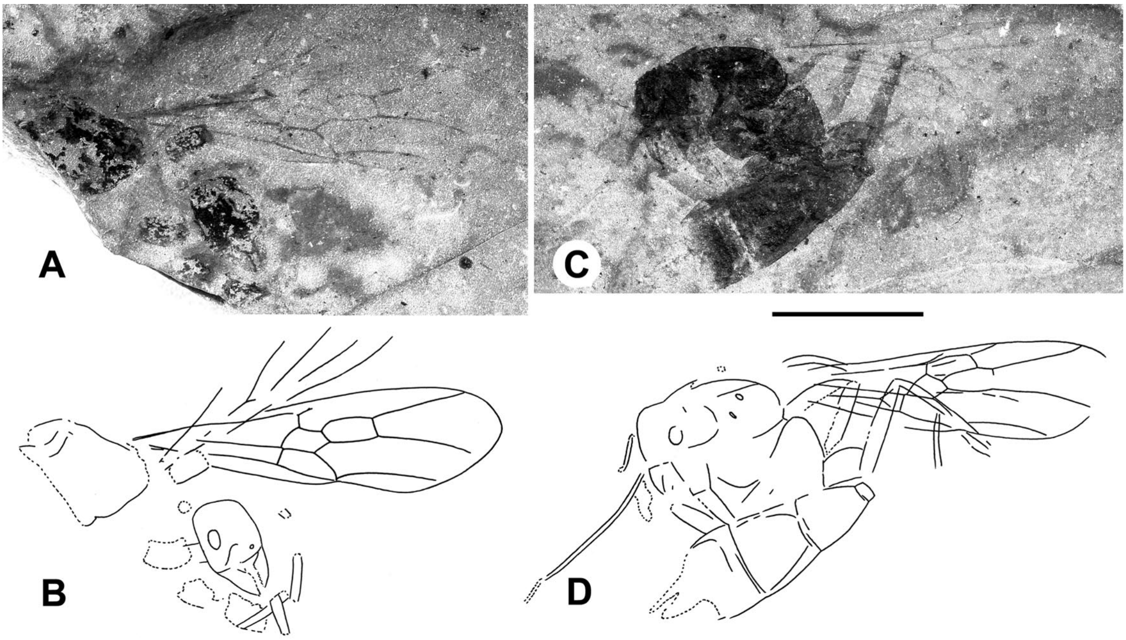

Fig. 8. *A. mastax*, queen, habitus of holotype (A and B) and paratype (C and D). (A) Photograph. (B) Drawing. Scale bar = 5 mm, both to scale. (C) Photograph. (D) Drawing. Scale bar = 5 mm, all to scale.

head capsule subquadrate; compound eye large, ovate; mandibles short (less than half head length), with more than eight (≈10) evenly sized small teeth. *Forewing:* length ≈13 mm; 1 + 2r, 3r, rm, mcu, cua, closed; rm hexagonal, mcu pentagonal; rm, mcu, cua about equal height; cu-a joins M+Cu at branching to M.f1, Cu.f1; Rs.f1 joins Sc+R close to perpendicular; Cu1 present. *Petiole (paratype queen):* preserved in lateral aspect; with low, evenly rounded dorsal surface. *Gaster (paratype queen):* AIII, AIV morphology as defined for the genus; caudal portion, sting not preserved. *Measurements:* HW, 2.0 mm; HL, 2.3 mm.

Type Material. HOLOTYPE: UCCIPRL-18 F-850. A fairly clearly preserved forewing, broken portions of other forewing; head, parts of body, mostly unclear. In the collection of TRU. Labeled: HOLOTYPE, *Avitomyrmex mastax* Archibald, Cover and Moreau.

PARATYPE: UCCIPRL-18 F-929. A mostly complete specimen, with forewing (but not as clearly preserved as that of the holotype), at least part of a poorly preserved head, the mesosoma and petiole in lateral aspect, and gaster somewhat disarticulated, in dorsal (?) aspect, portion caudad AIV missing/indistinct. In the collection of TRU. Labeled: PARATYPE, *Avitomyrmex mastax* Archibald, Cover and Moreau.

Locality and Age. CANADA: British Columbia: the McAbee locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Etymology. From the Greek *mastax*, for "jaw", or "mandible" referring to its mandible size, notably small within the subfamily, but common within the family.

Discussion. The forewings of the holotype and paratype are distinct from *Myrmecia* by cell mcu about equal in height to cua (smaller in *Myrmecia*); *Y. orbiculata* and *M.* (?) *tabanifluviensis* by cu+a perpendicular to A (joins at angle in those); and from *Y. rebekkae* by M.f2 shorter than Rs+M.

Avitomyrmex systenus Archibald, Cover and Moreau, n. sp.
(Figs. 9-10, 17E)

Diagnosis. This species can be most easily distinguished from *A. mastax* by head capsule pointed (*A. mastax*, subquadrate), petiole dorsum angulate (*A. mastax*, smoothly rounded); from *A. elongatus* by size (too small to reasonably represent *A. elongatus* worker caste; see Discussion).

Holotype Worker. As in diagnosis, Figs. 9, 10, 17E, and the following. Length estimated ≈1.5 cm in life. *Head:* mandibles three-fourths head length as preserved (possibly longer); posterior border of head capsule tapering to a point in profile; eyes large, at approximately one-third head length, apparently elliptical but poorly preserved. *Mesosoma:* pronotum nearly flat or weakly convex in profile; metanotal groove present; propodeum evenly rounded, lacking teeth or spines (paratype). *Legs:* indistinctly preserved, but relatively long in proportion to body size. *Petiole:* height, length about equal; attachment to propodeum obscured by leg; attachment to gaster broad, without constriction at juncture; node bluntly pointed; low, highest point at about half petiole length. *Gaster:* narrow as a whole, length ≈3 times maximum diameter; AIII strikingly narrow, posterior margin twice height of anterior margin; sting well developed,

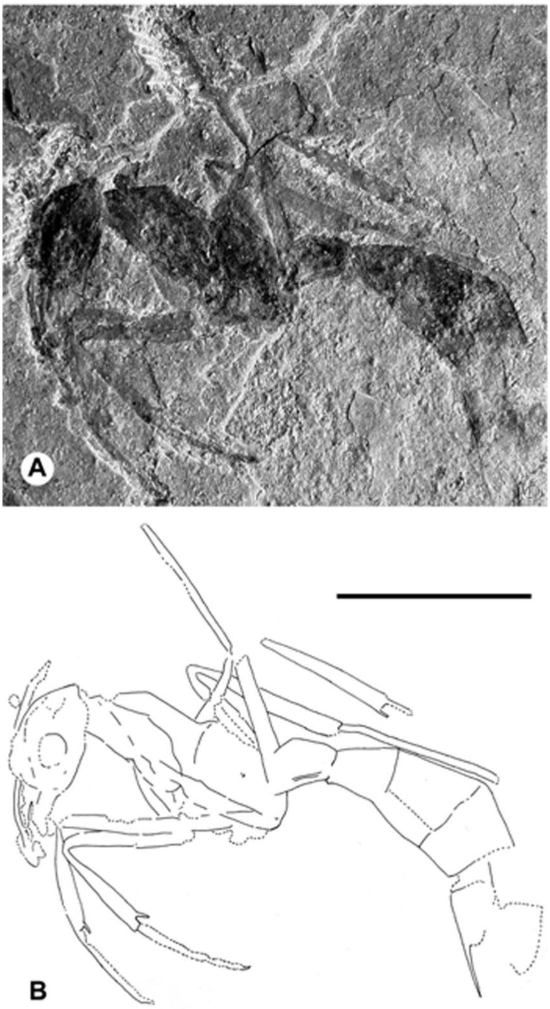

Fig. 9. *A. systenus*, worker, habitus of holotype. (A) Photograph. (B) Drawing. Scale bar = 5 mm, both to scale.

long. *Measurements: Holotype:* HL, 2.9 mm; WL, 5.5 mm; AIII/AIV height, 0.66; HL/WL, 0.53. *Paratype:* WL, 5.3 mm.

Type Material. HOLOTYPE: 2003.2.11 CDM 035 (part only); a worker, generally well preserved in lateral aspect, but with head poorly preserved and caudal portion of gaster indistinct with legs faintly preserved, mostly present; housed in the CDM collection; collected by SBA in May 2001. Labeled: HOLOTYPE, *Avitomyrmex systenus* Archibald, Cover and Moreau, and with the collector number SBA 1164.

PARATYPE: UCCIPR L-18 F-989; a worker, generally well preserved in lateral aspect, but with head poorly preserved and caudal portion of gaster indistinct with legs mostly present; deposited at TRU; collected by unknown person, donated to TRU by David Langevin in 2001. Labeled: PARATYPE, *Avitomyrmex systenus* Archibald, Cover and Moreau.

HYPOTYPE: UCCIPR L-18 F-825, tentatively assigned to this species; a worker, fairly preserved, legs indistinct, gaster enlarged, presumably swollen; deposited in the collection of TRU; collected by unknown person, donated to TRU by David Langevin in 2001. Labeled: HYPOTYPE, *Avitomyrmex systenus* (Archibald, Cover and Moreau, 2006).

Locality and Age. CANADA: British Columbia: the McAbee locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Etymology. From the Greek *systenos*, "tapering to a point," referring to the shape of the pointed apex of the head capsule.

Discussion. The differing head capsule, mandible and petiole morphologies of this species confidently rules out the possibility that it represents the worker caste of *A. mastax.* Furthermore, we believe it not be the worker caste of *A. elongatus*, as the size difference is distinctly less between these than between conspecific modern myrmeciine queens and workers. Discovery of the head of an *A. elongatus* queen will add further clarity.

UCCIPR L-18 F-825 is tentatively referred to this species by shape of the head, and, as can be determined, of the mesosoma and petiole. Weber's length is difficult to measure due to preservation, seeming shorter (≈5 mm; holotype, 5.5 mm; paratype, 5.3 mm), but this difficulty may be due to a slight dislocation of the head post mortem, obscuring the anteriodorsal point of the mesosoma. The gaster of this specimen is much wider as preserved than that of the holotype or paratype (Figs. 9 and 10); however, in this case, we cannot discount that this is a taphonomic artifact.

Macabeemyrma Archibald, Cover and Moreau, n. gen.

Type Species. *Macabeemyrma ovata.*

Diagnosis. Queens distinguished from those of other genera of Myrmeciinae by elongate-oval head in frontal aspect, ≈1.5 times as long as wide. Mandibles elongate, not subtriangular (exact shape not determined, below); elongate, subtriangular in all other Myrmeciinae except *Myrmecia* (elongate sublinear/linear) (*A. mastax* subtriangular, but not elongate, see below).

Queen. Large myrmeciine ants with the following characters.

1. Head notably longer than broad
2. Mandibles as preserved shifted, rotated from life position, apparently elongate (clearly not subtriangular as in *Ypresiomyrma*), but distal portions not clearly preserved; dentate, but teeth not well preserved
3. Eyes possibly preserved, if so, large, convex, situated anteriorly, abutting posterior clypeal margin
4. Mesosoma preserved in lateral aspect; large
5. Wings not known
6. Propodeal dorsum rounded in lateral aspect, without spines or teeth

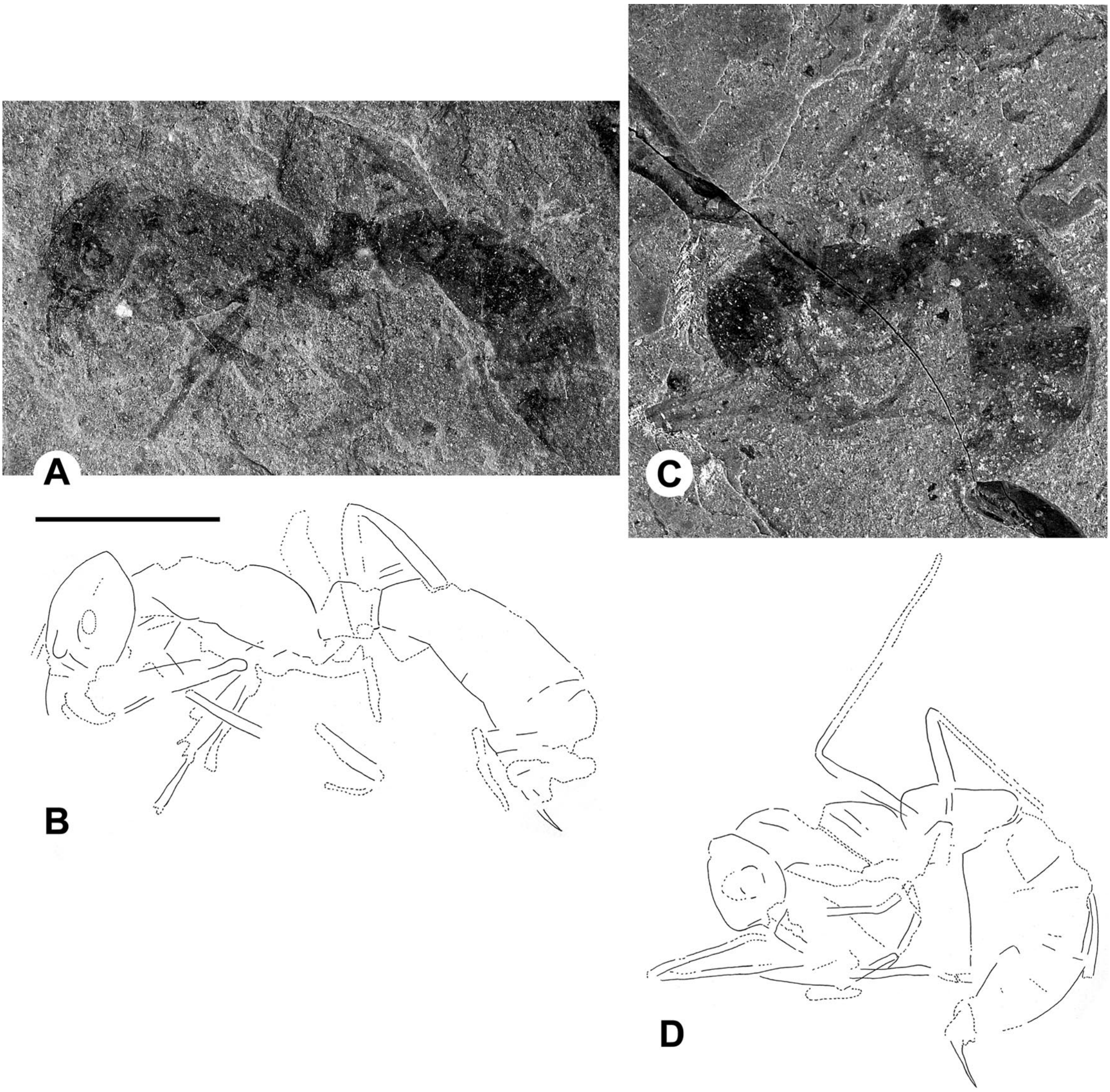

Fig. 10. *A. systenus*, worker, habitus of paratype (A and B) and of UCCIPRL-18 F-825, tentatively assigned to the species (C and D). (A) Photograph of paratype. (B) Drawing of paratype. (C) Photograph of worker, UCCIPR L-18 F-825. (D) Drawing of UCCIPR L-18 F-825. Scale bar = 5 mm, all to scale.

7. Petiole apedunculate, conical-rounded; length, height subequal; broadly attached to AIII
8. Gaster: AIII cone-shaped, joined to AIV without apparent constriction, smaller than AIV.

Included Species. *Macabeemyrma ovata.*

Etymology. The genus name is a toponym, Macabee- (from McAbee, the type locality of the species) and -myrma (from the Greek *myrmex,* "ant"). Gender: feminine. It is formed "*mac-*" not "*mc-*" in accordance with recommendations (linguistic appendices) in the third edition of the *International Code of Zoological Nomenclature* (not included in the fourth edition, but in effect) ("Appendix D: Recommendations on the formation of names. III. Names based on personal names. Article 21a" in International Trust for Zoological Nomenclature 1985).

Macabeemyrma ovata Archibald, Cover and Moreau, n. sp.

(Figs. 11, 17D)

Diagnosis. As in generic diagnosis.

Holotype queen. As in generic description, diagnosis, Figs. 11, 17D, and the following. Length estimated ≈2.5 cm in life. *Measurements:* WL: 7.0; AIII/AIV height, 0.75.

Type Material. HOLOTYPE: UCCIPR L-18 F-844 (part); UCCIPR L-18 F-856 (counterpart). Mostly

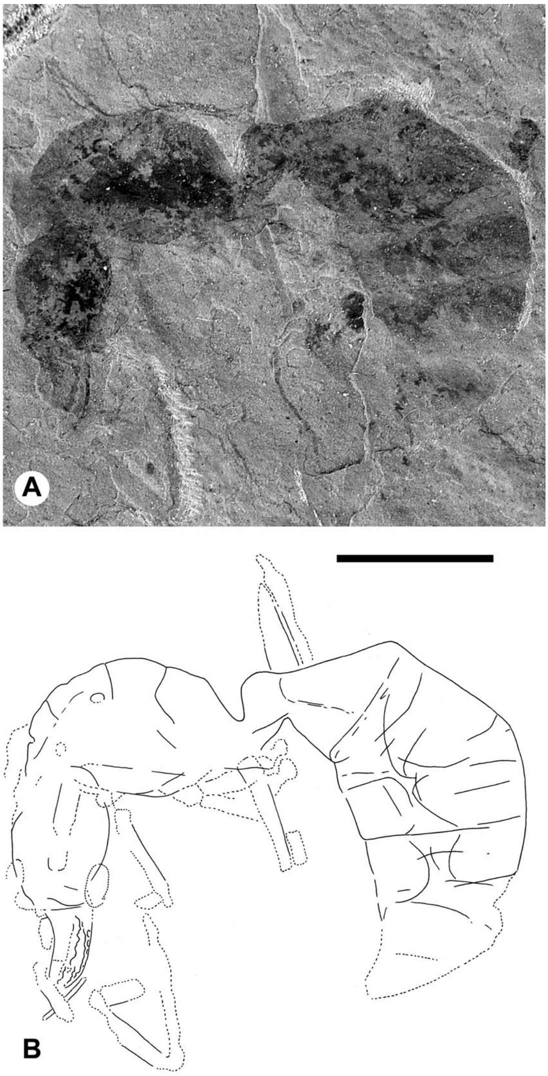

Fig. 11. *M. ovata*, queen, habitus of holotype. (A) Photograph of part. (B) Drawing, from both part and counterpart. Scale bar = 5 mm, all to scale.

complete, but rather poorly preserved queen, some parts of legs, without wings (or not preserved). Deposited at TRU; collected by unknown person, donated to TRU by David Langevin in 2002. Labeled: HOLOTYPE, *Macabeemyrma ovata* Archibald, Cover and Moreau.

Locality and Age. CANADA: British Columbia: the McAbee locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Etymology. From the Latin *ovatus,* "egg-shaped", referring the head capsule.

Discussion. This fossil is preserved in a rather soft, friable bedding layer, with poor, low-contrast preservation, and so much of it is indistinct. The eyes seem to be preserved, but faintly. If so, then they are situated at the anterior-most position of the head capsule, as in *Myrmecia,* rather than mid-head as in *Nothomyrmecia.*

Myrmeciites Archibald, Cover and Moreau, n. gen.

Etymology. From *Myrmeci*[*inae*] + the Latin suffix *-ites* "having the nature of", a traditional suffix often used in forming genus names of fossils. Gender masculine.

Discussion. As a collective group, a description or diagnosis is not provided for *Myrmeciites.* This generic name is proposed for all fossil ant species referable to the subfamily Myrmeciinae, yet whose orthotaxonomic generic position is unclear by the poor or incomplete preservation of their present specimens. Collective groups do not have type species (International Trust for Zoological Nomenclature 1999: articles 13.3.2, 42.3.1, 66, and 67.14).

Myrmeciites herculeanus Archibald, Cover and Moreau, n. sp.
(Figs. 12, 17G)

Diagnosis. May be separated from other species of the subfamily by petiole shape most similar to that of *Prionomyrmex,* but mandibles notably shorter than head-length (*Prionomyrmex,* equal to head-length) and eyes apparently smaller, placed at or near posterior corners of head (*Prionomyrmex,* much larger, at head mid-length); overall size.

Holotype Worker. As in diagnosis, Figs. 12, 17G, and the following. Length estimated >2 cm in life. *Head:* mandibles mostly poorly preserved, but clearly elongate, well developed, length indeterminable as preserved; compound eyes indistinct as preserved. *Antennae:* scape long, clearly longer than head length; funiculus long, filiform. *Mesosoma:* workerlike, not wing-bearing; mesonotum distinct, clearly separated from pronotum and propodeum by sutures; propodeal dorsum rounded, without spines or teeth. *Legs:* long relative to body size; tarsal claws detected on one pretarsus, with apparent aroleum (left hind leg). *Petiole:* apedunculate, node conical with rounded apex; several longitudinal striations apparent low on lateral surface; about as long as high; broadly attached to AIII. *Gaster:* helicium robust; AIII bell-shaped; gaster posterior of AIII incomplete/poorly preserved. *Measurements:* SL, 5.2 mm; WL, 8.8 mm.

Type Material. HOLOTYPE: UCCIPR L-18 F-974; Large worker; mostly well preserved in lateral aspect, but lacking much of posterior of gaster; no counterpart; housed in TRU; collected by unknown person, donated to TRU by David Langevin in 2002. Labeled: HOLOTYPE, *Myrmeciites herculeanus* Archibald, Cover and Moreau.

Locality and Age. CANADA: British Columbia: the McAbee locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Etymology. The specific epithet *herculeanus* is formed from the Latin name (Hercules) of the Greek hero Heracles, referring to the large, sturdy habitus of this ant.

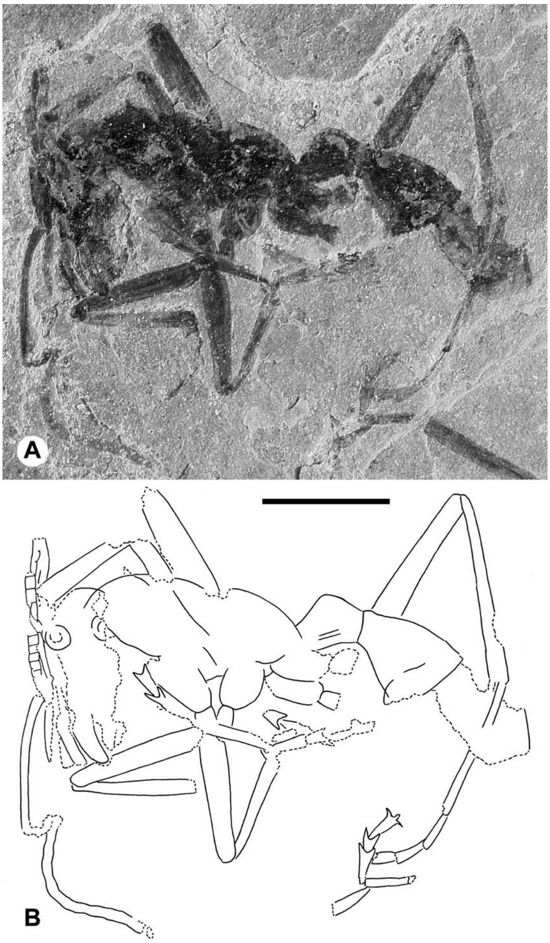

Fig. 12. *M. herculeanus*, worker, habitus of holotype. (A) Photograph. (B) Drawing. Scale bar = 5 mm, both to scale.

Discussion. It may be thought that this specimen represents the worker caste of one of the above species of McAbee Myrmeciinae; we think that this is most unlikely, as this specimen is among the largest examined, including queens. In extant myrmeciines, queens are always somewhat larger than the associated workers—never smaller.

Although we find this species most comparable with those of *Ypresiomyrma*, we place it in the collective genus *Myrmeciites*, given the partial condition of the sole specimen available.

Myrmeciites incertae sedis
Specimen 2003.2.9 CDM 033
(Figs. 13, 15N)

Male. As in Figs. 13, 15N, and the following. Length 2 cm as preserved, likely only 1–2 mm more in life. *Head:* anterior of head capsule poorly preserved; width nearly equal of maximum width of mesosoma, widest behind eyes; posterior corners apparently rounded. Eyes large, placed at approximate cephalic mid-length. Mandibles short, subtriangular, dentate. Antennae unusually long, perhaps two thirds total body length; relatively wide; no apical club; scape poorly preserved, apparently short. *Mesosoma:* robust, wing-bearing, approximately a third body length. *Forewing:* length ≈15 mm; 1 + 2r, 3r, rm, mcu, cua closed; rm hexagonal, mcu pentagonal; 1m-cu joins M+Cu basad their separation, subparallel with M.f1; cu-a joins M+Cu within half its length proximad branching of M.f1, Cu.f1; Cu1 present. *Petiole:* dorsal aspect: slightly longer than broad; lacking peduncle; node apparently present, dark band indicate likely blunt-transverse apex. *Gaster:* AIII, AIV, AIV preserved in dorsal aspect: normally robust for a myrmeciine male, not slender as in *Avitomyrmex.* Possible indication of slight constriction between AIII, AIV. *Measurements:* HL, 2.9 mm; HW, 2.7 mm.

Type Material. HYPOTYPE: 2003.2.9 CDM 033a (part) 2003.2.9 CDM 033b (counterpart). Male, almost complete, but missing much of the hind wings, caudal tip of gaster; preserved in dorsal aspect. In the CDM collection; collected by SBA, September 2002. Labeled: HYPOTYPE *Myrmeciites* incertae sedis (Archibald, Cover and Moreau, 2006); collector number SBA1188a (part) SBA1188b (counterpart).

Locality and Age. CANADA: British Columbia: the Falkland locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Discussion. This ant is excluded from *Avitomyrmex* by its normally robust habitus, however, head shape, used in distinguishing *Ypresiomyrma* from *Macabeemyrma* is equivocal, because male and female head shapes are often not tightly correlated. It may even belong to another, new genus. It is possible that there is a slight constriction between AIII and AIV, although this is tentative. Further specimens, particularly that reveal lateral petiole morphology, may clarify its generic position.

Specimen SR05-03-01
(Figs. 14A–C, 17F)

Queen or Worker? As in Figs. 14A–C, 17F, and the following. Length estimated ≈1.5 cm in life. *Head:* eye located posterior to midpoint of head capsule; mandibles ≈two-thirds head length. *Mesosoma:* relatively bulky, suggestive of alate female. *Petiole:* obscured as preserved, nodiform. *Gaster:* AIII joined to AIV without apparent constriction; AIII smaller than AIV; sting prominent. *Measurements:* HL, 2.9 mm; WL, 4.6 mm; AIII/AIV height (AIII height measured as height of posterior margin of AIV presclerite), 0.79; HL/WL, 0.63.

Type Material. HYPOTYPE: SR05-03-01, part, counterpart. A generally well-preserved queen, in lateral aspect, lacking wings, caudal portions of the mesosoma missing or obscured, portions of the petiole and gaster obscured or covered by legs. Collected by Nils Larsen, housed at SR. Labeled: HYPOTYPE, *Myrmeciites* incertae sedis (Archibald, Cover and Moreau, 2006).

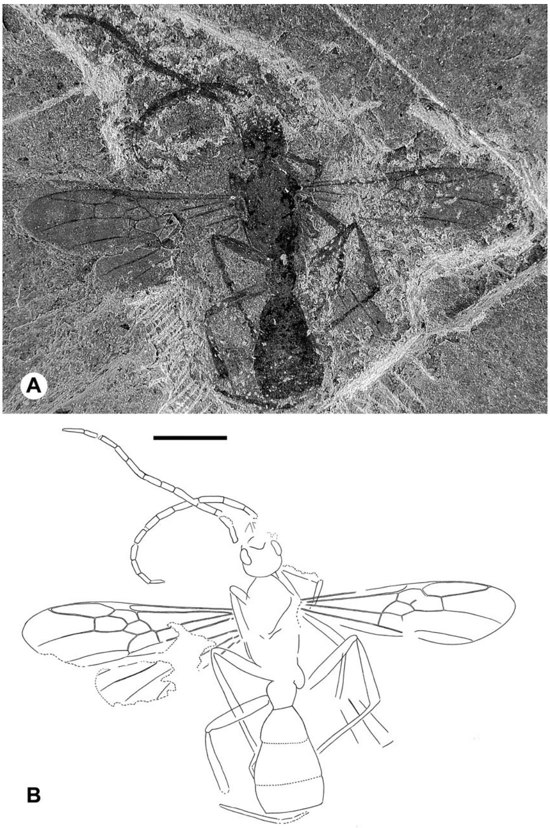

Fig. 13. *M.* incertae sedis (2003.2.9 CDM 033), male. (A) Photograph of part. (B) Drawing, from both part and counterpart. Scale bar = 5 mm; A and B to scale.

Locality and Age. USA: Washington state: Republic region; Klondike Mountain Formation; Eocene: late Ypresian.

Discussion. We interpret this specimen as a queen, although it may possibly be a worker. Because the forewing is not known, the head capsule and mandibles are only known in lateral aspect, and overlying legs obscures much of the petiole, we assign it to the collective genus *Myrmeciites* for lack of sufficient characters preserved. As a queen, it would be easily separable from other species of the subfamily by a combination of overall size; a single segmented waist; eye shape, placement and size; and its normally robust habitus. However, considered as a worker, it is possible that this belongs to *Y. bartletti,* although this is speculative, given the poor preservation of the relevant characters.

Myrmeciites (?) *goliath* Archibald, Cover and Moreau, n. sp.
(Fig. 14D and E)

Diagnosis. May be separated from other Eocene ant species by its large size, except those of the genus *Formicium,* from which it is easily separated by antennae, leg lengths (small in formiciine queens); further from all species of Myrmeciinae by size, length of worker >2.5 cm in life (WL, 10.0 mm); further from ants of this assemblage by head smaller in relation to mesosoma (HL/WL).

Holotype Worker or Queen?As in diagnosis, Fig. 14D and E, and the the following. Length >2.5 cm in life (perhaps close to 3 cm). *Head:* mandibles seem about or just less than half head length; head strongly rounded, flattened only on ventral side; compound eye suggested as preserved, apparently well developed. *Mesosoma:* massive, without indication of wings. *Legs:* large, long, consistent with general habitus. *Petiole:* present, but poorly preserved. *Gaster:* indistinct, apparently without postpetiole. *Measurements:* HL, 4.8 mm; WL, 10.0 mm; HL/WL, 0.48.

Type Material. HOLOTYPE: UCCIPR L-18 F-999, F-1000: part, counterpart. Large ant preserved in dorsolateral aspect, 25 mm as preserved (posterior portion of gaster missing); mostly well preserved, but lacking much of posterior of gaster; counterpart; housed in TRU; collected by unknown person, donated to TRU by David Langevin in 2002. Labeled: HOLOTYPE, *Myrmeciites* (?) *goliath* Archibald, Cover and Moreau.

Locality and Age. CANADA: British Columbia: the McAbee locality; Kamloops Group, unnamed formation; Eocene: Ypresian.

Etymology. The specific epithet is from the name of the biblical giant Goliath, referring to the immense size of this ant.

Discussion. *Myrmeciites* (?) *goliath* is among the largest ants; total body length of the worker is over 2.5 cm, and perhaps close to 3 cm. Workers of the extant Amazonian *Dinoponera* Roger are up to 4 cm in length (Fourcassie and Oliveira 2002), and ants of the extinct Eocene subfamily Formiciinae were truly immense: queens had forewings up to 60 mm in length (Lutz 1986, Bolton 2003).

The only known specimen is probably a worker, but it could be a queen. The size and shape of the mesosoma are inconclusive, and there is no evidence of wings.

Poor overall preservation of critical characters renders determination of caste and subfamily uncertain, however, its general habitus is consistent with the other myrmeciine ants from this locality, indicating that it is best tentatively associated with them, pending better preserved specimens.

Myrmeciites (?) *tabanifluviensis* Archibald, Cover and Moreau, n. sp.
(Figs. 15, 16O)

Diagnosis. May be separated from other species of Okanagan Highlands assemblage, from other Eocene ants bearing this generalized formicid wing venation except *A. piatnitzkyi* by size: forewing length ≈12 mm, next smallest known forewing *A. mastax* ≈13 mm; from *A. piatnitzkyi* by forewing venation: *M.* (?) *tabanifluviensis,* cu-a joins M+Cu at fork of M, Cu; *A. piatnitzkyi,* cu-a joins M+Cu ≈ half cu-a length from fork of M, Cu.

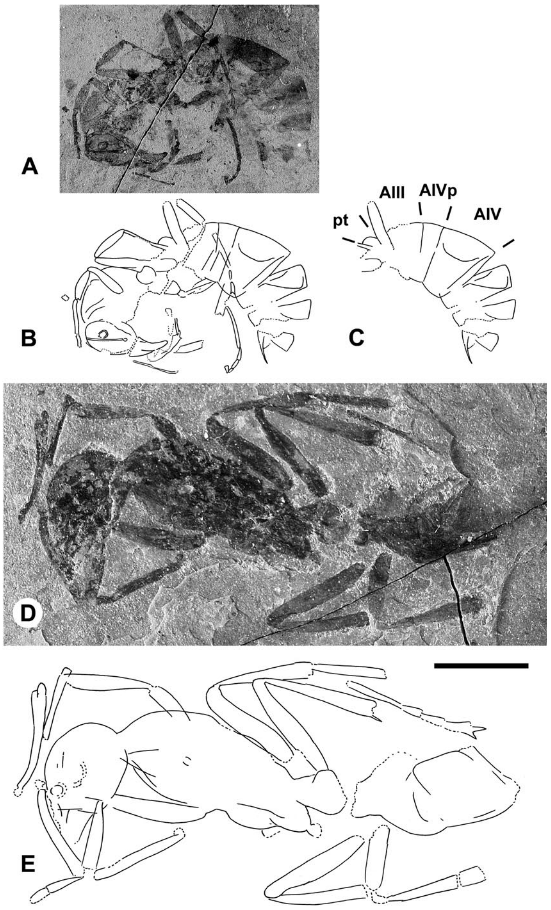

Fig. 14. habitus and detail of *M.* incertae sedis (SR05-03-01) queen (possibly worker) (A–C) and the holotype of *M.* (?) *goliath* worker (possibly queen) (D and E). (A) Photograph. (B) Drawing. (C) Drawing of gaster indicating abdominal segments (legs and rock fracture shown in 14B removed; pAIV, presclerite of AIV). (D) Photograph. (E) Drawing, from both part and counterpart. Scale bar = 5 mm, A–D to scale.

Reproductive, Sex Undetermined. As in diagnosis, Figs. 15, 16O, and the following. Length >1.5 cm in life. *Head:* not preserved. *Mesosoma:* poorly preserved, well developed, wing bearing; scutellum prominent, oval. *Forewing:* length ≈12 mm; 1 + 2r, 3r, rm, mcu, cua closed; rm hexagonal, mcu pentagonal; 1m-cu joins Cu basad joining M, subparallel with M.f1; cu-a joins M+Cu within half its length proximad branching of M.f1, Cu.f1; Cu1 present (indistinct). *Legs:* right legs well preserved: two metatibial spurs present, one spur long, one narrow, shorter; mid-, hind tarsal claw with prominent preapical tooth. *Petiole:* in dorsal aspect: with short narrowing at propodeal insertion, lacking distinct peduncle. *Gaster:* poorly, mostly not preserved; helcium slightly visible; AIV incompletely preserved, likely distorted, gaster posterior to this not preserved.

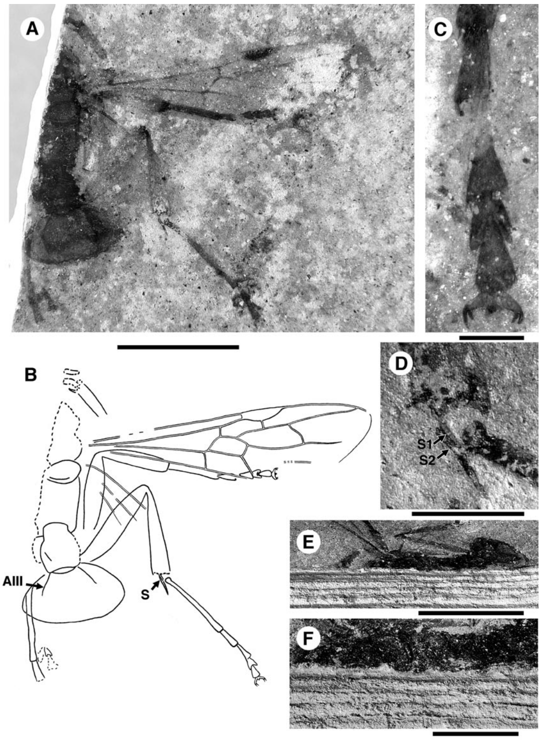

Fig. 15. *M.* (?) *tabanifluviensis*, habitus of holotype. (A) Photograph. (B) Drawing. (C) Detail of right mesotarsomeres and pretarsal claws. (D) Detail of metatibia, indicating spurs. (E) Oblique angle of fossil showing varve couplets formed of light and dark laminae. (F) Close-up of E, showing fossil on edge of light diatom lamina. S1, = spur 1; S2, spur 2. A and B to scale, scale bar = 5 mm; C, scale bar = 0.5 mm; D, scale bar = 1 mm; E, scale bar = 5 mm; F, scale bar = 2 mm.

Type Material. HOLOTYPE: 2003.2.10 CDM 034: part only. Unusually well preserved in portions, in dorsal aspect; lacking head, much of gaster, much of left side; in the CDM collection; collected by SBA, IX-2001. Labeled: HOLOTYPE, *Myrmeciites* (?) *tabanifluviensis* Archibald, Cover and Moreau, and with the collector number SBA847.

Locality and Age. CANADA: British Columbia: Horsefly River (Black Creek Road locality); unnamed group and formation; Eocene: Ypresian.

Etymology. The specific epithet alludes to the Horsefly River, the locality of the holotype. It is formed from *Tabanus* L., a horsefly genus name; the Latin *fluvius,* "river"; and the suffix *-ensis,* indicating "place" or "origin."

Discussion. Although differences in wing venation are usually not considered useful in separating ant taxa at the species level (see Materials and Methods, Taxonomic Treatment), a relatively wide separation of cu-a joining M+Cu from the fork of M and Cu, at about half of the length cu-a, seems stable within *Archimyrmex* species (and apparently in *Y. rebekkae*), separating these from *M.* (?) *tabanifluviensis.*

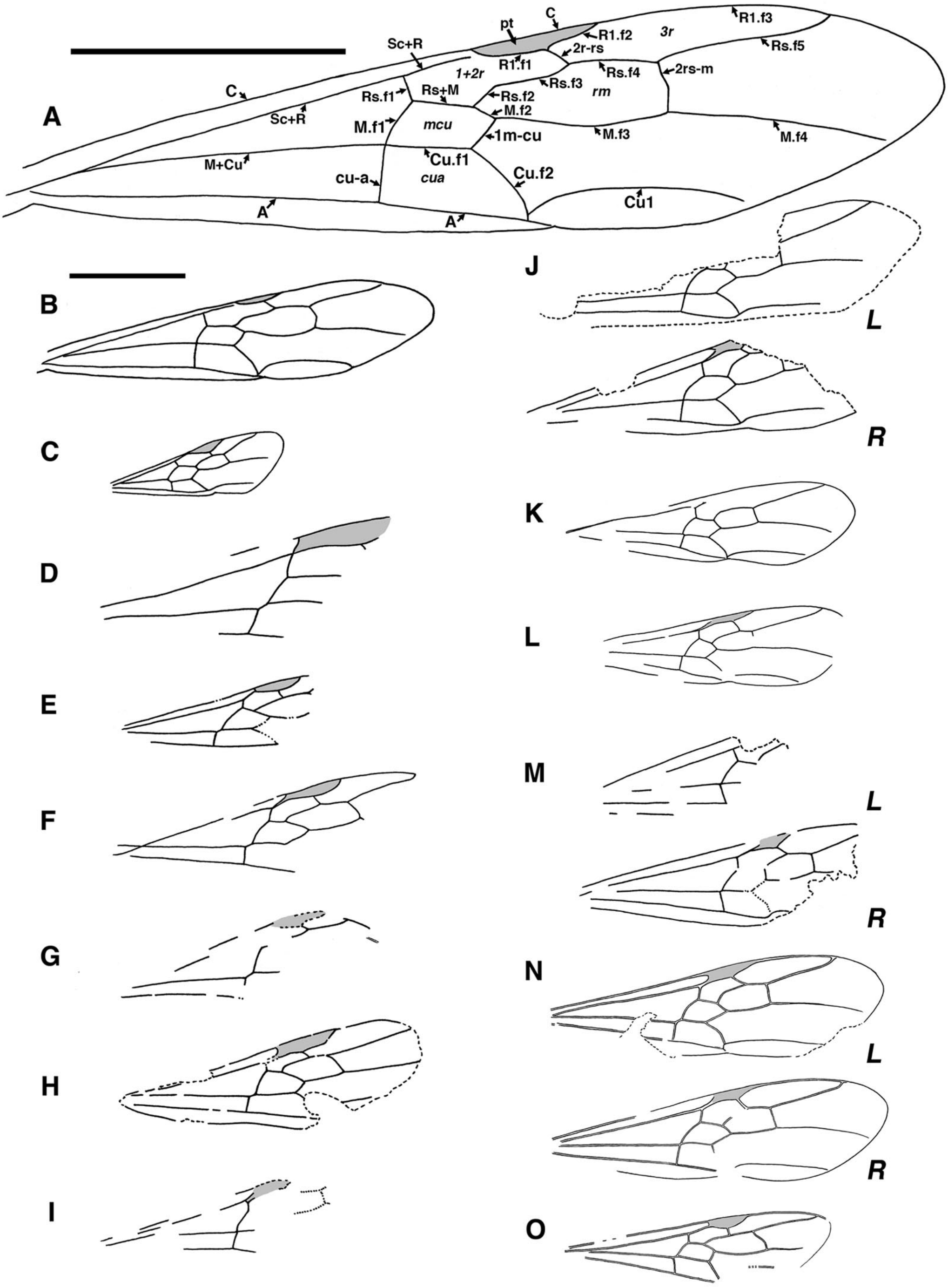

Fig. 16. Comparative forewings of Myrmeciinae (cell names in italics). Fenestrae (small gaps or weaknesses in veins where flexion lines cross) not indicated (not detected in fossils). (A) *Myrmecia* sp., MCZ specimen, with vein names (see materials and methods for abbreviations). (B) *Myrmecia* sp., same specimen as A. (C) *N. macrops*, male, redrawn from Taylor (1978). (D) *A. rostratus*, redrawn from Dlussky and Perfilieva (2003). (E) *A. piatnitzkyi*, redrawn from Viana and Haedo Rossi (1957). (F) *A. smekali*, redrawn from Dlussky and Perfilieva (2003). (G) *Y. rebekkae*, DK 83. (H) *Y. rebekkae*, CM No. 16-A3417, redrawn from Andersen and Rust (1999). (I) *Y. bartletti*, holotype. (J) *A. elongatus*, holotype. (K) *A. mastax* holotype. (L) *A. mastax* paratype. (M) *Y. orbiculata*, holotype. (N); *M.* incertae sedis (2003.2.9 CDM 033: Falkland male). (O) *M.* (?) *tabanifluviensis*, holotype. *L*. left wing; *R*, right wing. Scale bars = 5 mm: A, B–O.

Like *M.* (?) *goliath,* this species is tentatively assigned to the Myrmeciinae (and, therefore, to *Myrmeciites*) (see discussion below, Subfamily Placement).

The forewing of *M.* (?) *tabanifluviensis,* ≈12 mm in length, is smaller than that of any Okanagan Highlands and Danish species assigned to the Myrmeciinae; the forewing of *A. mastax* is the next smallest, at ≈13 mm.

Portions of this fossil are exceptionally preserved, particularly as visible when wetted with ethanol (water may degrade some Horsefly River specimens), e.g., fine-level details of tarsomeres and tarsal claws (Fig. 15C). Much of the lacustrine shale at Horsefly River is composed of varves (i.e., annual), each a couplet of light, diatomaceous laminae, and dark sapropel laminae, with diatom laminae hypothesized to represent late spring-summer deposition after yearly bloom events, and the sapropel laminae to represent winter deposition (Wilson 1977a, 1993; Wolfe and Edlund 2005). This fossil is preserved in a light diatom lamina, presumably on its edge, assuming regular thickness and a split along the interface between it and its adjoining sapropel layer. Wetting with ethanol shows detail that occurs minutely within the diatom layer (Fig. 15C). Diatom blooms have been associated with, and may be casual to the often exquisite fossil insect preservation at Florissant (Harding and Chant 2000, O'Brien et al. 2002) and are suggested as a taphonomic factor affecting bias in floating time of insects (further references and discussion in Archibald and Makarkin 2006) (for detailed taphonomic studies of the Horsefly River deposits, see Wilson 1977a, 1993; Barton and Wilson 2005, and references therein for each article).

Temperature seasonality is indicated as lessened at Eocene Horsefly, with MAT estimated by paleobotanical analyses as upper microthermal to mid-mesothermal ≈11–15°C by bioclimatic (nearest living relative) method, and an upper microthermal ≈7–13°C by leaf physiognomy, and the coldest month mean temperature ≈3–8°C by bioclimatic analysis, but constrained to >5°C by the presence of frost-intolerant biota such as palms (pollen) (Greenwood et al. 2005, Moss et al. 2005). However, because of counterclockwise rotation of North America during the Cenozoic, Horsefly River, today at ≈52° N latitude, may have been at a paleolatitude nearer 60° N (Wilson 1978), therefore, with photoperiod seasonality an increased factor. If the spring–summer hypothesis is correct for diatom blooms in this climatic regime, then, although the climate of Ypresian Horsefly differed from that of today, including lessened temperature seasonality, the mating flights of *M.* (?) *tabanifluviensis* were at a time during the late spring or summer, as is the usual case for ants in the modern world.

Systematic Placement

Subfamily Level

Assignment of Compression Fossils to the Myrmeciinae. Many of the body character states listed by Bolton (2003) and Ward and Brady (2003) as diagnostic of the subfamily are not likely to be preserved in compression fossils, e.g., details of the clypeus and metapleural gland opening. Dlussky and Rasnitsyn (2003) provided a set of body and forewing character states diagnostic for compression fossil Myrmeciinae, amended from Dlussky and Perfilieva (2003). Of those of the body, morphology of the tibial spurs and tarsal claws is visible on only one of the specimens considered here; a two-segmented waist, and the usual presence of ocelli are not valid for *Nothomyrmecia,* which they did not consider a member of the subfamily.

Ward and Brady (2003) supported assignment of the Argentine species *Archimyrmex piatnitzkyi* and *A. smekali* to the subfamily by a combination of their large, elongate and multidentate mandibles; large and (possibly) convex compound eyes; AIII markedly smaller than AIV; the notable constriction between AIII and AIV as in *Myrmecia* and *Prionomyrmex;* and overall habitus (large size, long appendages, evenly rounded propodeum in lateral aspect).

Like the above-mentioned authors, we assign genera (and species of the collective genus *Myrmeciites*) to the Myrmeciinae based on combinations of character states that are known to occur only within this taxon, rather than on the presence of individual apomorphic character states, unavailable for determination in the known compression fossils.

Considering *Nothomyrmecia* as a member of the subfamily (as by Bolton 2003), we find three major sets of morphological character states, somewhat modified and added to from those provided by the above-mentioned authors. Considered in combination, these enable compression fossil ants to be determined as myrmeciine.

Wing venation. The suite of myrmeciine forewing character states listed by Dlussky and Rasnitsyn (2003) includes cells 1 + 2r, 3r, rm, mcu, and cua closed; cells rm and mcu pentagonal; M.f2 longer than Rs+M; cu-a joining M+Cu within a vein's width proximad the branching of M.f1 and Cu.f1. Dlussky and Perfilieva (2003) further note that 1m-cu joins Cu basad of joining M and is parallel with M.f1. We revise this list as follows.

The basal vein-stub of 1r-rs (rarely, a more complete 1r-rs) is often present in extant myrmeciines and also many poneromorphs, in cells 1 + 2r, originating between Rs.f2 and Rs.f3. Brown and Nutting (1950) considered the presence of the 1r-rs rudiment as occurring too often in the myrmeciine specimens that they examined to be considered only an adventitious anomaly. When absent, there is still a distinct angle in Rs that marks the separation of Rs.f2 and Rs.f3, rendering cell rm hexagonal.

M.f2 is longer than Rs+M in *Archimyrmex*; however, it was the only genus of myrmeciine known as compression fossils at the time of Dlussky and Rasnitsyn's study. This is not always the case in *Myrmecia*, where M.f2 can be shorter than Rs+M; it is shorter in *Nothomyrmecia*.

In many species of *Myrmecia*, cu-a joins M+Cu within a vein's width proximad the branching of M.f1 and Cu.f1, and mcu is then pentagonal. In some, however, cu-a joins Cu.f1, distad M+Cu, rendering mcu hexagonal (18 spp.; B. Bolton personal communication). It joins at a greater distance proximad, within a distance less than half of the length cu-a of this branching in species of *Archimyrmex* (Fig. 16D–F). This joining, and consequent shape of mcu is variable in *Nothomyrmecia*. For example, cu-a is figured joining Cu.f1 several vein's widths distad M+Cu in a male, with mcu hexagonal (Taylor 1978: Figs. 2A; 16C); cu-a joins at this branching, with cell mcu five-sided, in the female *Nothomyrmecia* forewing that Taylor 1978 illustrated (see Fig. 2C) and in a male forewing examined by us at the MCZ.

Forewing venation in Myrmeciinae may then be characterized with the following traits: cells 1 + 2r, 3r, rm, mcu, and cua are closed; rm is hexagonal, and mcu is usually pentagonal, sometimes hexagonal; 1m-cu joins Cu basad joining M and is subparallel with M.f1; cu-a usually joins M+Cu within half its length proximad its branching to M.f1 and Cu.f1, but in some cases shortly distad this; and Cu1 is present.

This combination is also found in species of Ponerini and Platythyreini (Ponerinae) (Bolton 2003), and in *Paraponera clavata* (F.), the sole extant species of the subfamily Paraponerinae (unpublished data, MCZ specimens). The forewing of the African *Pachycondyla tarsata* seems practically indistinguishable from those of the Myrmeciinae. Forewings of the ponerines *Platytheria punctata* (Fr. Smith) (Brown and Nutting 1950: Fig. 1), *Pachycondyla harpax* (F.) (Creighton 1950: plate 6, Fig. 4), and *Odontomachus clarus* Roger (Creighton 1950: plate 10, Fig. 4, there named *O. hematoda* subsp. *clarus*) bear many of these character states, differing in details from those of the Myrmeciinae. Forewings of *Paraponera clavata* are only separable from those of the Myrmeciinae by minor differences, e.g., the gap between cu-a and the branching of Cu and M is slightly greater: just over a half cu-a length. Some Cerapachyinae (species of *Cerapachys* Fr. Smith, *Acanthostichus* Mayr, and *Cylindromyrmex* Mayr) further share this venation, and it occurs in some Myrmicinae [e.g., *Messor galla* (Mayr)] and Pseudomyrmecinae (*Tetraponera aethiops* Fr. Smith and relatives) (B. Bolton personal communication).

This forewing venation occurs in the extinct, Cretaceous subfamilies Armaniinae (Albian-Turonian) (considered by some authors as a formicoid family, Armaniidae, e.g., Grimaldi and Engel 2005, Wilson and Hölldobler 2005), and in some species of Sphecomyrminae (Albian-Campanian). Wings of the Sphecomyrminae differ from this pattern, however, by their lack of Cu1. The Armaniinae is generally regarded as the likely sister taxon to all other ants (or to ants, depending on one's view of its status).

The above-mentioned combination of forewing character states found in Myrmeciinae is plesiomorphic and is therefore not in itself phylogenetically informative. Their forewings are, however, useful in examining the subfamily relationships of species in the same manner that such plesiomorphic character states of the Myrmeciinae as bidentate pretarsal claws and two metatibial spurs have been included in its diagnosis to distinguish these ants in combination with other traits (Bolton 2003, Ward and Brady 2003).

Shape of AIII and its relative size to AIV. The relative sizes of AIII and AIV and aspects of the shape of AIII are useful to separate myrmeciines from all ponerines and from species of almost all other poneromorph subfamilies. Furthermore, these characters are likely to be usually well preserved and easily distinguishable in ants preserved in shale (i.e., compression fossils) as well as in amber.

Maximum AIII height is markedly less (≤ 0.80) than that of AIV in Myrmeciinae (AIII/AIV height in specimens measured: *Myrmecia* = 0.49; *Nothomyrmecia* = 0.73; *Prionomyrmex* = 0.76) (Fig. 17H, J, and K; Bolton 2003, Ward and Brady 2003). In species of the Ponerinae, AIII is about equal to substantially greater in height than AIV (Fig. 17M–Q). In lateral aspect, AIII invariably has a strongly vertical anterior dorsal surface followed by a distinct (sometimes very rounded) angle and subsequent flat dorsal surface rendering a blocklike shape in profile (weakly so in *Harpegnathos* Jerdon), whereas AIII is always cone/bell-shaped in Myrmeciinae (constricted at the posterior margin to form a postpetiole in *Myrmecia, Prionomyrmex,* and *Archimyrmex*).

The only members of the poneromorph subfamilies with AIII markedly smaller than AIV are *Paraponera* (Paraponerinae) and a few species of the Proceratiini (Proceratiinae) (Bolton 2003). In *Paraponera*, AIII is bell-shaped and may be either more or <0.80 AIV height in specimens measured by us ($n = 10$); there is a constriction between AIII and AIV, similar to that in *Prionomyrmex* in particular (Fig. 17J and L); and a notably strong sting is present (hence, its name "bullet ant"). Although *Paraponera* shares many of the character states with the Myrmeciinae discussed above, petiole morphology is, however, strongly dissimilar; furthermore, it differs in its massive head, about twice the maximum width of the mesosoma, and humeral teeth on the pronotum. One fossil species is known, *Paraponera dieteri* Baroni Urbani, from early Miocene Dominican amber, morphologically close to *P. clavata* (Wilson 1985, Baroni Urbani 1993). This species shows remarkable stability of its morphology, including that of its unmistakable petiole, at least to the early Miocene. Baroni Urbani (1993), p. 8, notes that *Paraponera* demonstrates a low evolutionary rate, having changed only "the tiniest imaginable" amount in this time. In the Okanagan Highlands and Danish ants considered here, there is no indication whatsoever of this petiole shape; their heads do not reach this large relative size; none bear these humeral teeth on the pronotum; there is no known paraponerine that lacks a constriction between AIII and AIV. Therefore, we confidently exclude the fossil ants considered here from the Paraponerinae. The Proceratiini are readily distinguishable from the Myrmeciinae by their highly reduced eyes and anterior-facing gastric terminus.

The condition of AIII markedly smaller than AIV is also found in the unrelated, aberrant monotypic genus *Aneuretus* Emery, currently placed in its own formicomorph subfamily, the Aneuretinae; it is easily separable from the Myrmeciinae, differing strongly in many characters (Bolton 1994: Figs. 3 and 4).

Grimaldi et al. (1997) placed the Late Cretaceous (≈97 Ma: Turonian) genus *Brownimecia* Grimaldi, Agosti and Carpenter from New Jersey amber in the Ponerinae (as then defined), based primarily on the slight constriction between AIII and AIV, finding this also suggestive of Myrmeciinae (Grimaldi and Engel 2005). Furthermore, AIII is bell-shaped, and its maximum height seems slightly but not distinctly less than that of AIV. This genus clearly differs from the Myrmeciinae in other characters and is currently considered to constitute the monotypic subfamily Brownimeciinae, likely close to the poneromorph group of subfamilies (Bolton 2003).

The Cretaceous Armaniinae also bear a bell-shaped AIII, < 0.80 the maximum height of AIV (cf. *Armania robusta* Dlussky; Dlussky 1984: Fig. 1). Myrmeciines are easily separated from them by a number of character states, e.g., the Armaniinae have a notably short female scape, a distinctive petiole shape, and bidentate mandibles without masticatory margin. The maximum height of AIII seems about equal to that of AIV in Sphecomyrminae, which is also otherwise distinct from Myrmeciinae by a suite of character states, e.g., the short female scape, and many others (Wilson et al. 1967, Wilson 1987).

Presence of a sting combined with lack of constriction between AIII and AIV. *Nothomyrmecia* has both a sting and no constriction between AIII and AIV, a condition it shares with few other extant ants (i.e., *Aneuretus*, *Asphinctopone* Santschi, *Anochetus* Mayr, and *Odontomachus* Latreille), none of which are closely related. In some ponerines, however, the constriction between AIII and AIV is sufficiently weak that its presence could likely not be confidently established in compression fossils. However, in these, the shape and relative size of AIII is distinctly ponerine as described above. Some genera of other subfamilies also bear stings and have little constriction between these segments, e.g., *Apomyrma* Brown, Gotwald and Lévieux (Apomyrminae); *Dorylus* F. (Dorylinae); and *Cheliomyrmex* Mayr (Ecitoninae); however, in those cases, other morphological characters of the head, mesosoma, wing, petiole, or a combination differ strongly from those of the Myrmeciinae.

Species of the extinct, Eocene Formiciinae (easily distinguished, e.g., head small, less than half length, width of mesosoma; legs short relative to mesosoma; M.f1 and 1m-cu convergent anteriorly, not parallel); and the Cretaceous Armaniinae and Sphecomyrminae also lack a constriction between AIII and AIV and bear a sting.

Ypresiomyrma. *Y. orbiculata.* Assignment of *Y. orbiculata* to the Myrmeciinae is confident by a combination of wing venation; mandibles large, elongate-triangular and multidentate; AIII bell-shaped, distinctly smaller than AIV (AIII/AIV height = 0.70), without a constriction between AIII and AIV; with a well-developed sting; the compound eye apparently large (convexity cannot be confirmed as preserved); and general habitus, including petiole morphology, and large size.

Forewing morphology of *Y. orbiculata* (Figs. 2, 16M) agrees with the combination of character states consistent within the subfamily (above). The closed cells 1 + 2r, rm, and mcu are present (3r cannot be confirmed closed, wing apex not preserved); cell rm is hexagonal and mcu pentagonal; cu-a joins M+Cu here within a vein's width proximad the branching of M.f1 and Cu.f1; 1m-cu is faintly preserved but is apparently subparallel with M.f1, joining Cu proximad its connection with M; and cell cua is apparently closed (Cu.f2 is faintly preserved).

The propodeum is rounded in lateral aspect, without spines or projections, as in all Myrmeciinae except *Prionomyrmex*, which bears small, blunt, paired propodeal teeth. Petiole morphology is close to that of *P. janzeni.*

Y. bartletti. The only specimen of this species is more poorly preserved, in low contrast to the surrounding matrix. Only portions of the forewing are preserved, and some of the gaster caudad AIII is slightly deformed. Preserved morphology agrees with that of the Myrmeciinae: elongate-triangular mandibles (as in *Nothomyrmecia, Prionomyrmex*); cu-a joins Cu at, or extremely close to the separation of M+Cu; cell rm is closed (crossvein 2rs-m present); the petiole is close in shape to that of *P. longiceps* (cf. Mayr 1868: Fig. 75); and AIII is bell-shaped; and a sting is present and well developed.

Although the correct size of AIV in life cannot be determined, because it is somewhat crushed, the shape of AIII, and its size in proportion to the preserved general morphology conforms to that of Myrmeciinae, and in particular to other species of *Ypresiomyrma.* Compound eye morphology cannot be determined by low-contrast preservation. The great overall similarity of all preserved characters to other species of *Ypresiomyrma* further makes placement in this genus, and therefore the Myrmeciinae, confident.

Y. rebekkae. Rust and Andersen (1999) supported assignment of this species to the extant ponerine genus *Pachycondyla* by its large, robust mandibles and the positions of the compound eyes and antennae, similar in particular to some extant African species of the genus. In our opinion, this species is clearly not a member of the genus *Pachycondyla* and not a ponerine.

AIV has sharply defined and distinct presclerites, over half the length of AIII, as in Myrmeciinae, the poneromorph subfamilies, and Cerapachyinae (Baroni Urbani et al. 1992, Rust and Andersen 1999). This is visible on the paratype Danekræ 93 (Figs. 5B, 17B) due to postmortem expansion of the gaster. Rust and Andersen (1999) excluded Cerapachyinae by pygidium morphology in this subfamily, it is large and flattened dorsally, with short spines or teeth (Bolton 2003). Details of the pygidial morphology are not or are only indistinctly preserved on almost all of the fossils of *Y. rebekkae* that we examined, although it seems smoothly rounded in lateral aspect in Danekræ

93, as in poneromorphs and Myrmeciinae (Fig. 5). This species is clearly excluded from the Cerapachyinae by many aspects of body morphology, which differ strongly (cf. Bolton 1994: Figs. 7–19). Rust and Andersen (1999) excluded the Myrmeciinae by mandibular dentition. *Myrmecia,* however, possesses comparably coarse dentition.

The preserved forewing venation conforms to that of the Myrmeciinae, although, as noted above, not excluding some Ponerinae, including *Pachycondyla.* Based on Fig. 3A of Rust and Andersen (1999) of specimen CM 16-A3417 (in a private collection, not examined by us), the most complete specimen (their Fig. 6B and C is a reconstruction bearing hypothetical morphology of missing portions), this includes: cells 1 + 2r, rm, 3r, and mcu are closed (cua is not confirmed closed or open, above); rm is hexagonal and mcu pentagonal. The crossvein cu-a joins M+Cu within a vein's width proximad the branching of M.f1 and Cu.f1 in CM 16-A3417. The crossvein 1m-cu is subparallel with M.f1, joining Cu basad its connection with M. M.f2 is longer than Rs+M, as in *Archimyrmex,* and Rs.f2 and Rs.f3 are angled as in *Myrmecia* (not in *Archimyrmex*).

This species is clearly excluded from the Ponerinae, and from almost all poneromorph subfamilies by AIII morphology, and from the remainder (*Paraponera* and some Proceratiini) as noted above; and further from Ponerinae by petiole morphology. AIII is bell-shaped and distinctly smaller than AIV (AIII/AIV height: Paratype Danekræ 94 = 0.75), without constriction between AIII and AIV (above; Figs. 4–6, 17B). The petiole of *Y. rebekkae* is moderate in size, with a low, rounded node. Those of ponerines tend to be tall, meeting or exceeding the height of the vertical anterior surface of AIII (Fig. 17M–Q); the convergently similar *Harpegnathos* is an exception. The petiole of *Y. rebekkae* is close to that of *Prionomyrmex* in particular. Species of *Pachycondyla* have a tall node, block-shaped, sometimes tall and sharply triangular but never low with a rounded node, as in this ant.

Avitomyrmex. *A. elongatus.* The forewings of the holotype are quite complete and well preserved; they bear all of the myrmeciine traits listed above. AIII is bell-shaped, distinctly smaller than AIV (although known only in dorsal aspect), with no constriction between them. The presence or absence of a sting cannot be determined.

A. mastax. The wings, AIII, and AIV are as in *A. elongatus;* the propodeal dorsum is curved in lateral profile, without spines or projections. The petiole has a low, rounded node. By their small size (about half head length), mandible morphology is, however, furthest from those of modern myrmeciines.

A. systenus. This species is known only from the worker caste. The propodeal dorsum is curved in lateral profile, without spines or projections; AIII is distinctly smaller than AIV (holotype: AIII/AIV height = 0.66), without a constriction between them, the waist is single-segmented; the petiole has a low, rounded node; there is a prominent sting.

Macabeemyrma. *M. ovata.* The sole specimen assigned to this genus lacks wings. Although the elongate head and mandible morphology readily distinguish *M. ovata* from species of *Ypresiomyrma,* their otherwise strong resemblance indicates a close phylogenetic relationship between them. The waist is single-segmented; the petiole has a low, rounded node and is broadly attached to AIII; AIII is bell-shaped, distinctly smaller than AIV (AIII/AIV height = 0.75), joined without a constriction. The presence or absence of a sting cannot be determined by preservation. The compound eyes of the poorly preserved only specimen are faintly suggested, but not confirmed. If this represents the true eye morphology and position, then *Macabeemyrma* resembles *Myrmecia* in this way.

Myrmeciites **Species.** *M. herculeanus.* This species is assigned to Myrmeciinae by similarity of the mandible length, propodeum, petiole, and AIII morphology. It is large, close in size to that of species of *Ypresiomyrma.* Petiole morphology is particularly similar to that of *Prionomyrmex janzeni.* AIII is almost completely preserved; it is distinctly bell-shaped (somewhat similar to that of *Archimyrmex*), as in Myrmeciinae, and the portions of AIV preserved indicate that it is most likely larger than AIII. The presence or absence of a sting cannot be determined by preservation.

M. incertae sedis (2003.2.9 CDM 033). We assign the male ant from Falkland to the Myrmeciinae based a combination of forewing characters, and AIII and AIV morphologies. Its forewings are the most clearly preserved of these fossils, bearing all of the venational traits found in the Myrmeciinae discussed above. AIII is bell-shaped in dorsal aspect, smaller than AIV. If we have delimited the anterior and posterior margins of these segments correctly, their dorsal midline length AIII/AIV is ≈0.80, but this is difficult to determine with certainty. Ward and Brady (2003), however, give the ratio ≤0.80 as characteristic of myrmeciine workers and queens. Myrmeciine antennal character states listed by them for males are not determinable on this fossil.

M. incertae sedis (SR05-03-01). Known only from a wingless queen (possibly a worker). The mandibles are long, approximately two-thirds head capsule length; the compound eyes are prominent, set well back from the clypeal margin, ≈two-thirds length of head capsule; the petiole is damaged and in part obscured, but evident morphology does not disagree with Myrmeciinae and does not seem ponerine; AIII is somewhat damaged, but is bell-shaped, definitely not shaped as in Ponerinae; AIII is smaller than AIV (AIII/AIV height, AIII height measured from height of anterior margin of AIV postsclerite = 0.79), without a constriction between them (single-segmented waist); there is a prominent sting.

M. (?) *goliath.* Although much of this specimen is preserved in fine detail, portions of the mandibles, mesosoma, petiole, and gaster are poorly and fragmentarily preserved, rendering comparison with the other ants discussed here difficult. Although the subfamily position of this ant is not confirmed, the re-

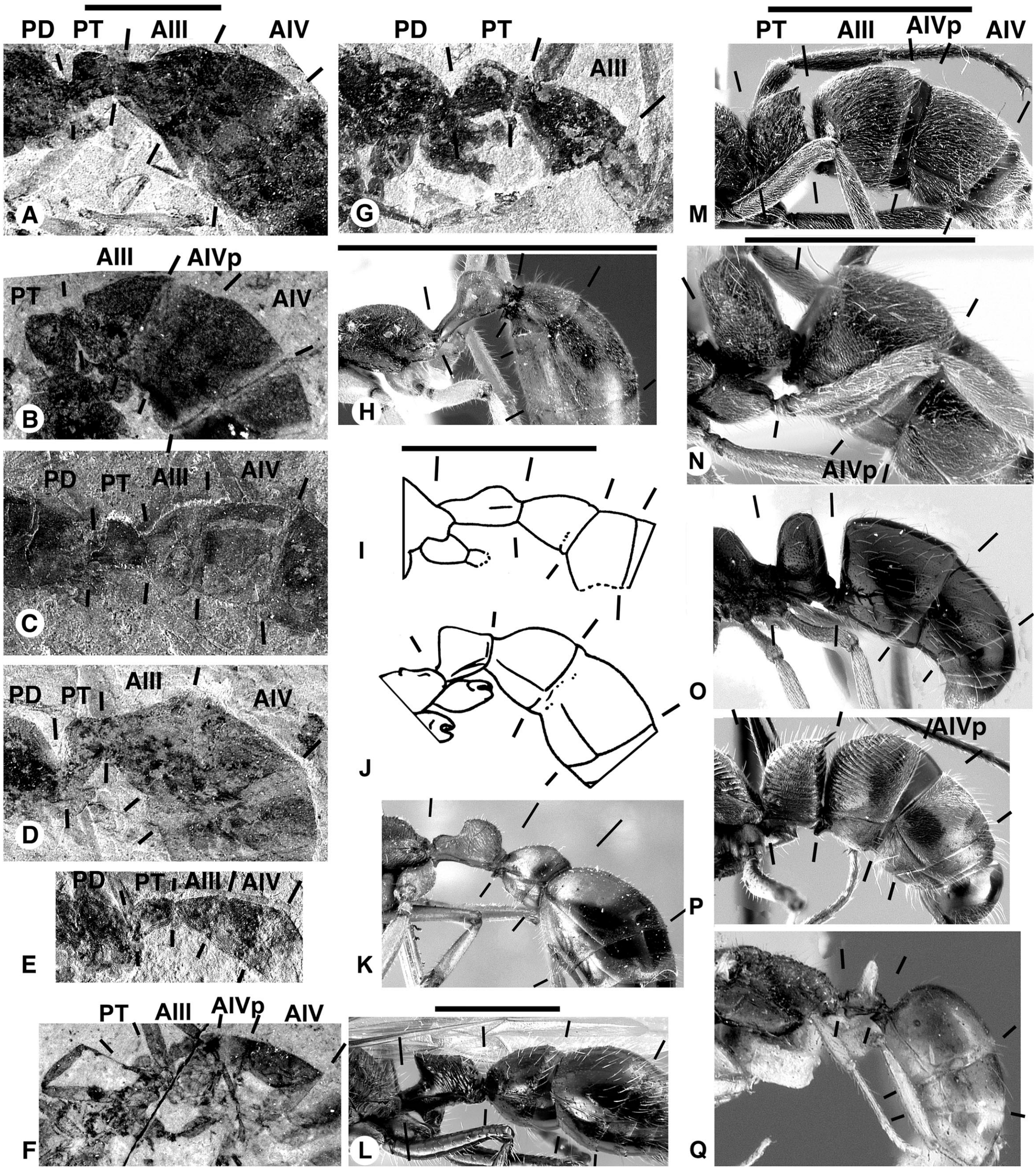

Fig. 17. Comparative lateral aspects of the petiole, AIII and AIV of species of Myrmeciinae (A–K), Paraponerinae (L) and Ponerinae (M–Q). (A) *Y. orbiculata*, holotype. (B) *Y. rebekkae*, paratype. (C) *Y. bartletti*, holotype. (D) *M. ovata*, holotype. (E) *M. systenus*, holotype. (F) *M. incertae sedis*. (G) *M. herculeanus*, holotype. (H) *N. macrops*. (I) *A. rostratus* (redrawn from Dlussky and Rasnitsyn 2002). (J) *P. janzeni* (redrawn from Baroni Urbani 2000). (K) *Myrmecia nigriscapa* Roger. (L) *Paraponera clavata* (Paraponerinae). (M) *Pachycondyla tridentata* F. Smith (Ponerinae). (N) *Pachycondyla leewenhoeki* (Forel) (Ponerinae). (O) *Thaumatomyrmex mandibularis* [Baroni Urbani and de Andrade] (Ponerinae). (P) *Diacamma rugosum* (LeGuillou) (Ponerinae). (Q) *Anochetus modicus* Brown (Ponerinae). Pinned specimens in MCZ collection; pAIV, presclerites of AIV; A–G, H, I–K, L, to scales, each = 5 mm; M–Q to scale = 2 mm.

semblance of its general habitus to that of the Okanagan Highlands myrmeciine species indicates that it is best tentatively placed with them, expecting that future, more complete specimens will clarify its position.

M. (?) *tabanifluviensis.* This species is also tentatively placed in the Myrmeciinae by incomplete preservation. Aside from its distinctive character states which separate it as a species, those others evident on the only known fossil are plesiomorphic within the

Formicidae: wing venation bearing all of the generalized character states listed above; bifurcate tarsal claws with a submedian tooth in addition to the apical tooth on the mid and hind legs (foreleg claws not known); and two metatibial spurs.

The condition of pretarsal claws with submedial teeth is known in the Myrmeciinae, Pseudomyrmecinae, and is found widely in the poneromorph group, in the Sphecomyrminae, and is variable in Vespidae. There are two metatibial spurs in the Myrmeciinae, most Pseudomyrmecinae, some poneromorphs, Sphecomyrminae and in the Vespidae. In *M. tabanifluviensis,* one spur seems significantly shorter than the other, as is found, for example, in derived *Myrmecia* of the *urens* species group (Ogata 1991). It cannot be determined whether the larger spur is pectinate.

The gaster is poorly preserved; however, the strongly suggested form of AIII in dorsal aspect seems narrower than that of Ponerinae and conforms to the myrmeciine condition. So far, no other subfamily of ants bearing these traits is known from the Okanagan Highlands assemblage.

Cretaceous Taxa

Myanmyrma. *M. gracilis,* from Burmese amber (≈100 Ma: late Albian), has been recently discussed as a possible myrmeciine (Engel and Grimaldi 2005, Grimaldi and Engel 2005, Wilson and Hölldobler 2005). Engel and Grimaldi (2005) treated this ant as subfamily incertae sedis, discussing it as either "poneroid" or as a tentative member of the myrmeciomorph group?. We agree with the caution shown in treating this ant as incertae sedis; however, we a find possible myrmeciomorph affinity unlikely, because supporting character states are few and not decisive, coupled with the poor preservation of the specimen (distorted, in cloudy amber with frass pellets, woody fragments). Indeed, the very short female scape is unprecedented in the Myrmeciinae and is only known in the most basal ants, the Sphecomyrminae and Armaniinae.

Wilson and Hölldobler (2005) suggested that three recently described Late Cretaceous (≈91 Ma: Turonian) genera from Botswana (Dlussky et al. 2004) might also be myrmeciines. These include *Orapia* Dlussky, Rasnitsyn and Brothers (two species: *O. rayneri* and *O.* [?] *minor,* tentatively placed in the genus), *Afropone* Dlussky, Rasnitsyn and Brothers (two species: *A. oculata* and *A. orapa*), and *Afromyrma* Dlussky, Rasnitsyn and Brothers (one species, *A. petrosa*).

Orapia. The genus *Orapia* was assigned to the Armaniinae, based primarily on petiole morphology and a very short female scape, with support by the apically directed base of vein Rs.f1, and the presence of the rudiment of crossvein 1r-rs (Dlussky et al. 2004).

The scape seems, however, only partially preserved and somewhat difficult to interpret on the specimens as illustrated and could be damaged or displaced, obscuring its true morphology. The first funicular segment (second antennal segment, pedicel) is usually short in female Armaniinae, about as long as wide, shorter than subsequent flagellomeres (diagnosis: Dlussky 1984); the length of what seems to be the pedicel in the holotype of *O. rayneri* is about twice its width, similar to the shape of the following few flagellomeres.

In Armaniinae, there is only a weak constriction (particularly as apparent in dorsal aspect) between the petiole and AIII. The diagnoses of the taxon provided by Dlussky (1984), p. 65: "petiolus massive, its maximum width at point of articulation with segment III of abdomen" (cf. Dlussky 1984: particularly Figs. 7 and 8), and by Bolton (2003), p. 73: "waist of one poorly separated segment (petiole), posteriorly very broadly articulated with abdominal segment III (first gastral)" clearly excludes *Orapia* from the Armaniinae, as the petiole in this genus is widest before joining with AIV; there is a marked constriction between these segments when viewed in dorsal aspect (cf. Dlussky et al. 2004: Figs. 5 and 6).

The form of Rs.f1 seems similar to that found in some Myrmeciinae, and as the authors note, the rudiment of 1r-rs does occur in individuals of *Myrmecia.* Brown and Nutting (1950) found this stub in Myrmeciinae not rare (above); they considered this an atavism, which would thus not be surprising to find occurring consistently in Turonian members. The preserved forewings of *Orapia* seem consistent with both the Armaniinae and Myrmeciinae (and others discussed above).

Dlussky et al. (2004) note that hind wing venation differs from that of all known armaniines, as (in their hind wing vein nomenclature) rs-m is close to the length of 1M, rather than much shorter; in this way *Orapia* further resembles the Myrmeciinae (*Myrmecia* spp. examined, and cf. hind wings of Armaniinae in Dlussky 1984: Fig. 8a and e; of *Nothomyrmecia* in Taylor 1978: Fig. 2).

AIII is bell-shaped, perhaps less maximum AIV height (but figures indicate not reliably measurable); there is a lack of constriction between AIII and AIV; and a sting is present. *Orapia* resembles both the Myrmeciinae and the Armaniinae in these ways.

The mandibles, however, differ significantly from those found in Myrmeciinae; they are falcate, without teeth or masticatory margin, and their bases are set widely apart. As Dlussky et al. (2004) note, the wide-set bases are similar to the condition seen in the armaniine *Khetania* Dlussky (Dlussky 1999: Fig. 1d). Unlike those of *Orapia,* the mandibles of Armaniinae, however, are bidentate. Falcate mandibles occur rarely in the Myrmicinae (*Chimaeridris* Wilson, *Strongylognathus* Mayr) and Formicinae (*Polyergus* Latreille) (Wilson 1989, Bolton 1994), indicating that this morphology may reflect particular adaptations relative to life habit (slave-making or specialized predation) rather than bear phylogenetic significance. *Brownimecia* also possesses falcate mandibles.

O. rayneri resembles no species of Armaniinae or Myrmeciinae by the quadrate shape of its head capsule and eye placement just posterior to the mid-point, unusually close to the mid-line.

Orapia seems most similar to both the Armaniinae and the Myrmeciinae; however, the ways in which it differs from these groups seem too strong for assignment to either, and we suspect that it might be best placed in its own subfamily.

Afropone. *Afropone* was placed in the Ponerinae, defined then more broadly. It can, however, be readily excluded from that subfamily as currently delimited by Bolton (2003) as well as from all other poneromorphs except *Paraponera* and some Proceratiini by AIII morphology, which is bell-shaped and distinctly smaller than AIV (height apparently ≈0.80; cf. Dlussky et al. 2004: Fig. 12) (*Paraponera* and those Proceratiini also are excluded, as noted above). They note that species of *Afropone* are similar to some Myrmeciinae by petiole morphology and further resemble species of the Myrmeciinae (and other subfamilies) by the amount of constriction between AIII and AIV, and by the position of cu-a; and further, that it differs from Ponerinae by the very large eyes of the species *A. oculata.* Large compound eyes with their anterior margin close to the clypeal posterior margin are found in *Myrmecia* and also occur elsewhere, e.g., in the aptly named formicine genus *Gigantiops* Roger.

The forewings of *Afropone* show some important disagreements with those of the Myrmeciinae: cell mcu is four sided, and cell rm is open as preserved (lacking 2rs-m), although Dlussky et al. (2004) infer that it is closed by the comparative morphology of its otherwise generalized venation. Forewing venation is consistent within the known Myrmeciinae; the form of the cell mcu (and lack of 2rs-m, if real) in *Afropone* seems to be a significant departure from that distinctive pattern. Like *Orapia, Afropone* seems to not fit well into any currently defined subfamily and might belong to its own.

Afromyrma. Dlussky et al. (2004) assigned the genus *Afromyrma* to the Myrmicinae, primarily by waist morphology, and supported by their triangular mandibles, which bear a well-developed masticatory margin. AIII is substantially smaller than AIV in this ant, to a degree not resembling myrmeciine morphology. *Afromyrma* does resemble myrmicines, although it also resembles pseudomyrmecines. This genus is enigmatic, because the characters evident on its single fossil are few.

We do not consider any known Cretaceous genus to belong to the Myrmeciinae.

Phylogenetic Analysis

All parsimony tree topologies from our analyses show support for a monophyletic Myrmeciinae when the new fossil orthotaxa *Ypresiomyrma, Avitomyrmex,* and *Macabeemyrma* are included. Furthermore, they support the findings of Ward and Brady (2003) of *Prionomyrmex* and *Archimyrmex* as myrmeciines when analyzed with our modified version of MORPH1. Analysis of the "*Ypresiomyrma*" data set resulted in two most parsimonious trees (L = 171; consistency index = 0.678; retention index = 0.667) (strict consensus tree with bootstrap values: Fig. 18A). In our "*Avitomyrmex*" analysis, we recovered two most parsimonious trees (L = 171; consistency index = 0.684; retention index = 0.669) (strict consensus tree with bootstrap values; Fig. 18B). The "*Macabeemyrma*" data set analysis also resulted in two most parsimonious trees (L = 170; consistency index = 0.682; retention index = 0.669) (strict consensus tree with bootstrap values; Fig. 18C). In these individual fossil genus analyses, the parsimony tree topologies show moderate to high support (77–91% bs) for their placement within the Myrmeciinae.

We recovered 173 most parsimonious trees for our "Fossil Genera" data set, which included all three new (orthotaxa) genera and *Archimyrmex* (L = 173; consistency index = 0.676; retention index = 0.680) (strict consensus tree with bootstrap values: Fig. 18D). In this analysis, although the topology of the individual generic analyses was maintained, less support was recovered. Higher support could not be expected when all four compression fossil genera were included, considering the limited number of characters that could be coded for each.

Because *Y. rebekkae* exhibits all character states coded for the genus *Ypresiomyrma,* analyses that use this data set represent both *Ypresiomyrma* genus and *Y. rebekkae* species analyses. No analysis recovered evidence of a generic relationship of *Y. rebekkae* to *Pachycondyla* as proposed by Rust and Andersen (1999); *Y. rebekkae* consistently groups with the myrmeciine taxa in both the "*Ypresiomyrma*" and the "Fossil Genera" analyses.

Although there is minimal parsimony bootstrap evidence (67% bs) for the fossil genera *Avitomyrmex, Macabeemyrma,* and *Ypresiomyrma* to be most closely related to the extant species *Nothomyrmecia macrops,* we do not feel confident in placing them in the tribe Prionomyrmecini (Fig. 18D).

Tribe Level

The single-segmented waist, more generalized mandible shape and dentition (where known), and compound eye placement and morphology of the Okanagan Highlands and Danish species are suggestive of primitive character states within the Myrmeciinae (except mandible and possibly eye morphologies in *Macabeemyrma*).

Some character states evident in species of this assemblage are included in those considered diagnostic of tribal affinity, e.g., AIII and AIV joining without constriction, eyes placed at mid-head, and the elongate-triangular mandibles of *Ypresiomyrma* indicate placement of that genus in the Prionomyrmecini (Bolton 2003, Ward and Brady 2003). We do not, however, assign *Ypresiomyrma, Avitomyrmex, Macabeemyrma,* or species of *Myrmeciites* to a tribe, not only because few of these characters are preserved but also, and more importantly, because the generalized mor-

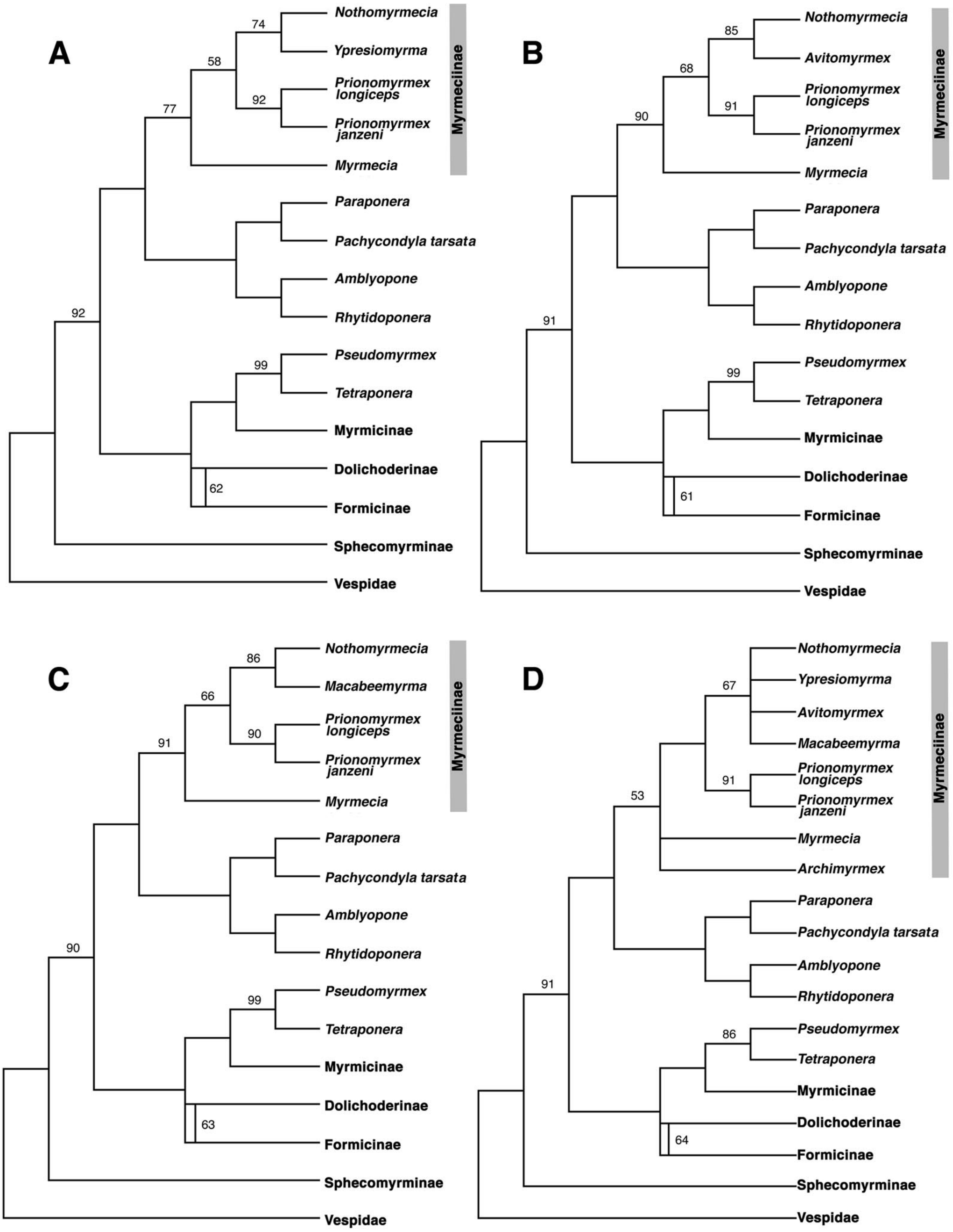

Fig. 18. Trees generated from phylogenetic analysis. Values above the branches represent bootstrap percentages >50%. (A) Strict consensus tree calculated from the two equally parsimonious trees resulting from the analysis of the *Ypresiomyrma* + modified MORPH1 data set. As *Y. rebekkae* showed all character states evident in this *Ypresiomyrma* set, this analysis represents that species, as well as the genus. (B) Strict consensus tree calculated from the two equally parsimonious trees resulting from the analysis of the *Avitomyrmex* + modified MORPH1 data set. (C) Strict consensus tree calculated from the two equally parsimonious trees resulting from the analysis of the *Macabeemyrma* + modified MORPH1 data set. (D) Strict consensus tree calculated from the 173 equally parsimonious trees resulting from the analysis of the "Fossil Genera" + modified MORPH1 data set (above three genera + *Archimyrmex*).

phology of these ants could be present in stem-group members of either lineage. Furthermore, these ants could possibly represent a natural tribe-level taxon (or taxa) of their own relative to those currently recognized. Given present knowledge, these possibilities cannot be distinguished.

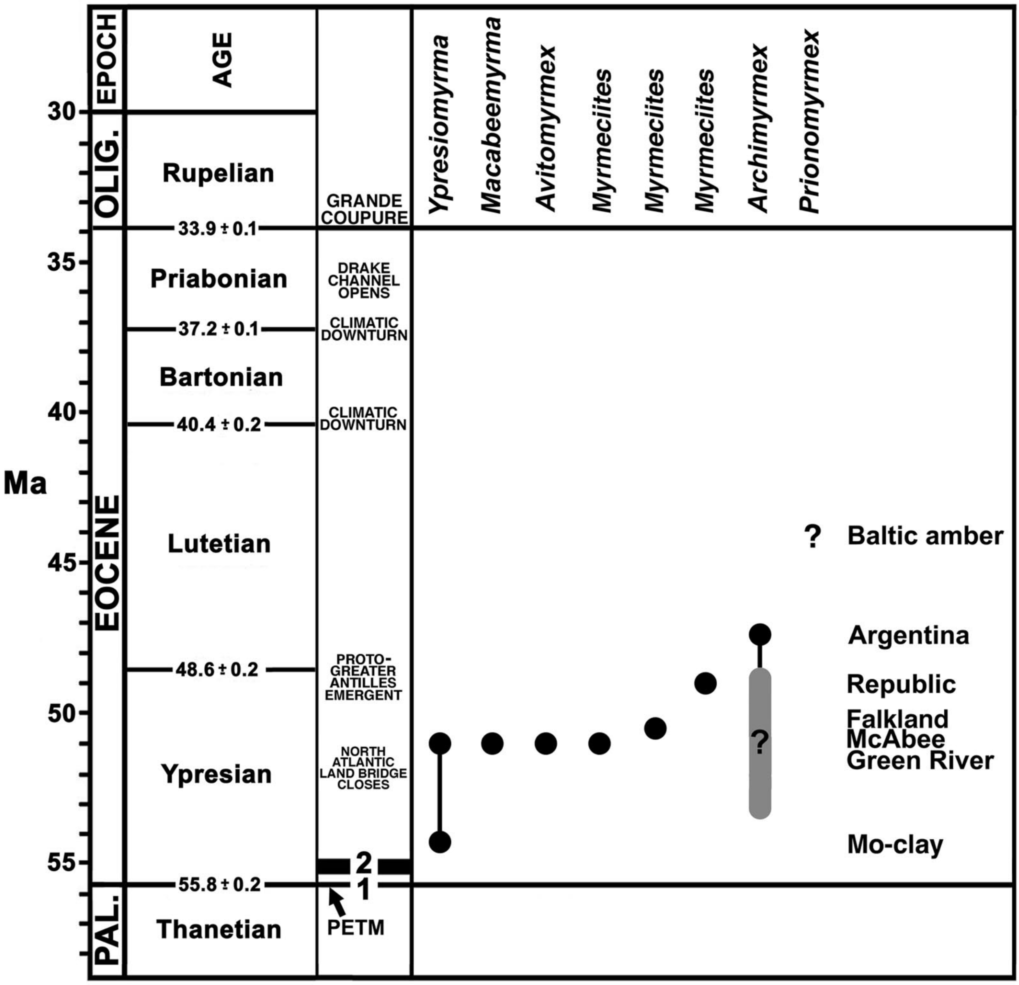

Fig. 19. Stratigraphic ranges of fossil Myrmeciinae genera (orthotaxa) and species of the collective genus *Myrmeciites*, and climatic/geographic events. The age of the Green River Formation is determined (gray line); however, those of myrmeciine-bearing localities within the formation are not known. The age of Baltic amber is discussed in the text. *Myrmeciites* (?) species not included (McAbee, Horsefly River). "1" and "2" indicate cross-North Atlantic mammalian dispersal events that predate Mo-Clay, Green River, and Okanagan Highlands times (Woodburne and Swisher 1995), PETM, Paleocene-Eocene Thermal Maximum. See text for further discussion.

Life Habit

For ants in particular, overall morphology is often an accurate predictor of life habit (Kaspari and Weiser 1999). Wheeler (1915), p. 27, wrote of *P. longiceps* that "the long, strong claws and remarkable mandibles of the worker indicate that *P. longiceps* was a predaceous, and in all probability, an arboreal ant." The morphology syndrome of all of the fossil ants described here is, like that of *Prionomyrmex,* consistent with a life habit found in the extant myrmeciines. Like extant myrmeciines, the fossil species are large in size, with large eyes (where known), a prominent sting, large mandibles, and long legs. The life habit of the modern Myrmeciinae consistently includes soil nesting (although some species of *Myrmecia* in north Queensland have arboreal nesting habits; Brown 1953); active arthropod predation (*Myrmecia* also collects plant nectar); foraging singly (they do not recruit nest mates to food sources, nor lay scent trails) on the soil surface or on trees and low vegetation; and they are all probably visual, using their eyes for predation and navigation (*Myrmecia,* diurnal, by the sun; *Nothomyrmecia,* nocturnal, by the moon) (Haskins and Haskins 1950, Wilson 1971, Hölldobler and Taylor 1983, Hölldobler and Wilson 1990). We expect these behaviors to have been the case as well in these fossil species.

By foraging in vegetation, it would be predicted that the McAbee Myrmeciinae, or their close relatives, should be present in apparently roughly coeval Hat Creek amber, some 30 or so km distant, because arboreal insects would be expected to be selected for in resins. None, however, have been found there so far. *Prionomyrmex* specimens are ≈0.1% of Baltic amber ants (Dlussky and Rasnitsyn 2003). Myrmeciinae might be underrepresented in amber producing coal swamps by lack of well-drained soil to nest in.

Biogeography

Ward and Brady (2003) proposed a biogeographic history of the Myrmeciinae, when its fossil record was restricted to species of *Prionomyrmex* and the Argentine species of *Archimyrmex.* Given those occurrences, coupled with the extant range of *Myrmecia,* basal in their phylogeny, and their molecular clock analysis, they inferred a Cretaceous Gondwanan origin, with a subsequent range extension in the early Paleogene from Africa across the Tethyan Sea to Europe.

The currently known fossil record indicates an origin in the Northern Hemisphere (Baroni Urbani 2005), a northern range in the Ypresian, and dispersals initially cross-North Atlantic, and then into the Southern Hemisphere. Crossing the Tethys from Africa into Europe around Fur Formation time could have involved reasonable distances between islands. Molecular data indicates that the Pseudomyrmecinae and Myrmeciinae diverged between the Ypresian and the Albian (101 Ma, latest Early Cretaceous) (Ward and Brady 2003, Ward and Downie 2005). The lower end of this estimate is, however, after Gondwana had begun to separate, with entrance into Africa involving the crossing of some distance of water (Scotese 1991, McLoughlin 2001). The next available routes for the Myrmeciinae between Europe and Australia occurred after their presence is established in the Northern Hemisphere and before their known presence in the Southern Hemisphere (below).

In considering the lack of a myrmeciine fossil record before the early Ypresian, it should be borne in mind that much of the Cretaceous ant record is known from amber (see summaries in Grimaldi et al. 1997, Grimaldi and Agosti 2000, Dlussky and Rasnitsyn 2003, Engel and Grimaldi 2005), where factors such as those mentioned above (see Life Habit), and their large size relative to the small size of the amber pieces in many deposits may produce bias against the presence of this subfamily in these fossil assemblages. Furthermore, Paleocene ants are little known: possible ant fragments from Alberta, Canada (Mitchell and Wighton 1979); 10 specimens, including Ponerinae, Aneuretinae, Dolichoderinae, and Formicinae in Sakhalin amber, Russia (Dlussky 1988); and two wings (probably formicine) from Primorye, Russia (Dlussky and Rasnitsyn 2003).

Eocene Dispersal. *Europe–North America* (*Ypresian*). The earliest occurrence of the subfamily is of *Ypresiomyrma rebekkae* in Ypresian Denmark, about a million years after the Paleocene–Eocene boundary. There, they are morphologically "primitive," bearing a single-segmented waist and robust mandibles with coarse teeth. About 3 million years later, in the mid-Ypresian, they are found in far-western North America in the Okanagan Highlands, with these "primitive" traits, including species of *Ypresiomyrma;* and around this time, *Archimyrmex rostratus* occurs in Colorado in the United States, with a more derived, two-segmented waist.

They share this cross-North Atlantic biogeographic pattern with other insect, plant, and mammal taxa in the Ypresian. In the Thanetian (late Paleocene) into the Ypresian, the northern Atlantic had not yet completely tectonically opened. Regional North Atlantic flood basalt volcanism and coincident sea-level drop joined North America and northern Europe via Greenland by a continuous terrestrial link in the latest Thanetian through likely much of the Ypresian. With mild climatic conditions into high latitudes in the Eocene (Basinger et al. 1994), this was a time of notable intercontinental dispersal of biota between Europe and North America, and also across the Bering land bridge, connecting North America and East Asia (Woodburne and Swisher 1995, Knox 1998, Beard and Dawson 1999, Manchester 1999, Hooker 2000, Tiffney 2000, Tiffney and Manchester 2001, Bowen et al. 2002, Archibald 2005, Archibald and Makarkin 2006). Discrete mammalian dispersal events between Europe and North America have been delimited (Woodburne and Swisher 1995), two of which preceded the Mo-clay, Baltic amber, Okanagan Highlands, and Green River times: the first associated with the Paleocene-Eocene Thermal Maximum (PETM), a sharp temperature spike at the Paleocene–Eocene boundary coincident with the carbon isotope excursion; and the second shortly after (see Fig. 19: PETM, and interchange events 1 and 2) (further review and discussion in Archibald and Makarkin 2006). The Mo-clay Fur Formation also shares the mecopteran genus *Cimbrophlebia* Willmann (Cimbrophlebiidae) (S.B.A., current research), and the neuropteran genera *Protochrysa* Willmann and Brooks (Chrysopidae) (V. N. Makarkin and S.B.A., current research) with the McAbee and *Palaeopsychops* Andersen (Polystoechotidae) with Horsefly River, Republic and Quilchena (also Okanagan Highlands) (Archibald and Makarkin 2006). Dispersal between Europe and North America could have been in either direction, and possibly more than once.

North America–South America (Lutetian). Archimyrmex species with a two-segmented waist and apparently "primitive" (but poorly preserved) mandibles then appear in early Lutetian Patagonia, South America. South America was a significant distance from North America at that time, and the Isthmus of Panama did not connect them until the Pliocene. However, the proto-Greater Antilles were sufficiently emergent at ≈49 Ma, around the close of Okanagan Highlands and Green River Formation times, in a position near that occupied by the Isthmus of Panama today (Graham 2003). Although it did not form an almost continuous land bridge with highlands until around the Eocene–Oligocene boundary, too late to account for the North America-South America crossing of *Archimyrmex*, in the latest Ypresian they were a sustained series of islands across the North America-South America gap, allowing for dispersal of insects whose climatic tolerances did not preclude low-latitude lowland heat. Such dispersal along an island chain is suggested by the distribution of ponerines in Melanesia (Wilson 1959).

Northern Europe (Middle Lutetian?). Two species of *Prionomyrmex* occur in Baltic amber (see above), also possessing a derived, two-segmented waist, and with derived, elongate mandibles, and teeth reduced to denticles.

Modern range. The post-Eocene record of the Myrmeciinae is restricted to the modern Australian region: *Myrmecia,* with a two-segmented waist and distinctive elongate-linear mandibles bearing coarse teeth; and *Nothomyrmecia,* with a single-segmented waist and teeth reduced to denticles.

North-South Dispersal. Hennig (1960) pointed out the danger in assuming a gondwanan origin of a taxon that has an exclusively southern modern distribution, without examining its fossil record. Darlington (1965) explained the current distribution of major Australian ground beetle groups (Coleoptera: Carabidae) as possibly originating in the Northern Hemisphere, crossing low latitudes into South America and Australia, and with subsequent extinctions in low and northern latitudes leaving their extant Southern Hemisphere distribution. Such a modern distribution would leave an apparent, but false solely Gondwanan history. The fossil record of Eomeropidae (Mecoptera) is exclusively Holarctic, found in China in the Jurassic, and in East Asia and North America (*Eomerope* Cockerell) in the Paleogene, indicating dispersal across Beringia. Today they are confined to Chile, which may provide a subset of those environmental conditions necessary for that taxon that were more widely expressed in the early Paleogene (Archibald et al. 2005). The Lutetian flora of Messel, Germany, resembles the modern assemblage of the Australian region at the family level, and also contains common genera (Burrows 1998).

Wheeler (1915) discussed a suite of ant genera in Baltic amber that today range in the Indo-Malaysian and Australian region. Dlussky (1996) revised the ant genera of Baltic amber; those found today in Australia are (extant distributions in parentheses, from Shattuck 1999): *Anonichomyrma* Donisthorpe (New Guinea, the Solomon Island and Australia, a single species in Malaysia, Sulawesi and Sumatra); *Iridomyrmex* Mayr (sensu Shattuck 1992: India east to China and south to Australia and New Caledonia); *Ochetellus* Shattuck (Japan south through Burma and the Philippines to Fiji, New Caledonia and Australia, a single species in Mauritius); *Oecophylla* Fr. Smith (Africa and India east through south-east Asia and into northern Australia); *Pseudolasius* Emery (throughout the Old World Tropics except Madagascar, one species in Australia); *Vollenhovia* Mayr (India, Sri Lanka east to Korea, south through Indonesia, Fiji, Vanuatu, New Caledonia and Australia); *Tetraponera* (tropical regions from Africa east to New Guinea and Australia) and *Rhytidoponera* Mayr (eastern Indonesia, New Guinea, Solomon Island, New Caledonia and Australia).

A subset of other Ypresian insects found in the Okanagan Highlands shows a similar biogeographic pattern, e.g., *Megymenum* Guérin (Hemiptera: Dinidoridae) (southeast Asia and Australia); the cockroach subfamily Diplopterinae (Blattodea: Blaberidae) (a single species in Australia and the southwest Pacific, recently introduced widely through low latitudes); and termites of the family Mastotermitidae (a single species in Australia north of the tropic of Capricorn and introduced in New Guinea) (Archibald and Mathewes 2000, Greenwood et al. 2005).

Like ants, the fossil record of termites indicates an initial diversification beginning in the Early Cretaceous, with an radiation and rise to ecological importance in the early Paleogene (Thorne et al. 2000). The Mastotermitidae possess a set of distinctly plesiomorphic character states, and, like the Myrmeciinae, are considered "primitive" Although the fossil record of the Mastotermitidae is more extensive than that of the Myrmeciinae, possibly reaching into the Cretaceous (review in Thorne et al. 2000: equivocal records from the English Weald Clay and French amber), they show a similar temporal-biogeographic pattern in that they were cosmopolitan in the Eocene (Okanagan Highlands, Canada; Tennessee, United States; Queensland, Australia; and Bembridge marls, England) and are today restricted to the Australian region (Okanagan Highlands, Wilson 1977b; others, see reviews by Emerson 1965, Thorne et al. 2000). (They are also known from the Oligocene of France, England, Mexico, and Poland; the Miocene of Croatia, the Dominican Republic, and Germany; and the Miocene-Pliocene of Brazil, reviewed in above-mentioned references.) Although they differ from the Myrmeciinae in having an Eocene record in Australia, Emerson (1955) inferred a northern origin from their fossil distribution.

Climate Change and Distribution. Cenozoic climate after the Ypresian is characterized by a global decline in MAT (Zachos et al. 2001) and equability (increase in seasonality), and an increase in the latitudinal thermal gradient, all contributing to lower winter temperatures in middle and high latitudes. This change in global climate, combined with the opening of dispersal corridors, may have driven a subset of a cosmopolitan insect assemblage that flourished through mid- to higher latitudes of North America, Asia, and Europe in the warm and more climatically uniform Cretaceous-early Paleogene world, to restrict their ranges to lower latitudes likely by the cooler Oligocene, with a cold-intolerant subset of insects then restricted to lower latitudes, including southern Asia.

Species of *Myrmecia* occupy regions of a variety of Australian climates, from warmer to cooler regions. Based on the molecular phylogeny of Ogata (1991), the basal species groups have a warm-region distribution, with cool region *Myrmecia* species groups among the more derived (A. N. Andersen, personal communication), suggesting a radiation of the genus from warm into cooler habitats. The mallee habitat of Eyre Peninsula in south Australia where *Nothomyrmecia* is found has a mediterranean climate, with mid-mesothermal MAT values (≈16–18°C) and cool winters without severe frosts (Commonwealth of Australia 2005).

The Pseudomyrmecinae, strongly supported by molecular data as the sister taxon to the Myrmeciinae, today range largely in tropical and subtropical regions, i.e., low and lower-middle latitudes with megathermal to upper mesothermal MAT (Ward and Downie 2005). Ward and Downie (2005) inferred a Gondwanan, Paleotropical (most likely Indo-Australian, if *Tetraponera* Fr. Smith is paraphyletic) origin of the subfamily, based on the current ranges of their basal living species and of the extant Myrmeciinae. The pre-Neogene fossil record of the Pseudomyrmecinae, is, however, exclusively from the mid- to northern Holarctic: four species of *Tetraponera* from Baltic amber (Dlussky 1996), one from Eocene Ukrainian Rovno amber (Dlussky and Perkovsky 2002), and one species of *Pseudomyrmex* Lund from late Priabonian (34.07 ± 0.10 Ma: Evanoff et al. 2001) Florissant, CO (Carpenter 1930: there called *Pseudomyrma*). Twelve species of *Pseudomyrmex* have been reported from low latitudes, all from Miocene Dominican amber (Ward 1992), following the series of climatic events discussed below.

Climatic equability. Wheeler (1910, 1915) found it difficult to explain syninclusions of ant genera in individual pieces of Baltic amber that are today restricted to both cool northern circumpolar regions and to megathermal low latitudes. The "tropical–temperate" mix of early Paleogene biota, particularly noted in cooler MAT higher latitudes and uplands such as the Okanagan Highlands is now known to be associated with Eocene climatic regime that is today restricted to higher altitudes in low latitudes, i.e., cool MAT values, yet seasonably equable with mild winters, allowing biota that are cold winter intolerant to inhabit microthermal regions (Wing and Greenwood 1993, Greenwood and Wing 1995, Archibald and Farrell 2003). For example, palms ranged well into middle latitude regions in the Eocene, including upper microthermal areas of the Okanagan Highlands (above-mentioned studies and Erwin and Stockey 1994, Greenwood et al. 2005, Moss et al. 2005). In the upper microthermal-lower mesothermal Eocene Canadian arctic (paleolatitude ≈78° N), crocodilians, varanid lizards, and large nonburrowing tortoises have been found, all restricted to or most diverse in high MAT regions today (Estes and Hutchinson 1980, McKenna 1980, Basinger et al. 1994). The decrease in equability (increase in seasonality), i.e., lowering of winter temperatures, may have been as important a factor in Cenozoic biotic sorting as declining MAT values.

Climatic downturns in the later Eocene. Paleobotanical indicators provide evidence for a significant drop in terrestrial MAT around the Lutetian–Bartonian boundary, and marine data indicates of another climatic downturn around the Bartonian-Priabonian boundary ("the most fundamental biotic division of the Cenozoic"; Prothero 1994: 151), associated with the extirpation of thermophilic plankton taxa from mid- and high latitudes (Keller 1983, Prothero 1994). The presence of thermophilic biota (some plants, e.g., palms; some insects) at upper microthermal to mid-mesothermal late Priabonian Florissant, CO, is consistent with sufficiently equable conditions for mild winters that preclude severe frost at this MAT value existing in higher elevation mid-latitudes after the Lutetian–Bartonian and Bartonian–Priabonian climatic downturns (Leopold and Clay-Poole 2001, Moe and Smith 2005).

Early Oligocene Grande Coupure. A precipitous drop in global MAT immediately after the Eocene–Oligocene boundary (early Rupelian) is coincident with a large-scale turnover of mammal, reptile, and amphibian taxa in Europe, often referred to as the *Grande Coupure,* or "Great Break" (Rage 1986, Hooker 2000). This event is determined from multiple biotic and isotopic indicators as a rapid, extreme climatic transition from the "greenhouse" world of the Cretaceous and early Paleogene to the "icehouse" world of the Oligocene through the present (Prothero 1994, and references therein). Wolfe (1992) estimated about a 12–13°C drop in MAT in northwestern United States.

The increased separation of Australia and Antarctica at this time is associated with the initiation of the circumpolar current, sequestering cold south polar waters, lessening pole to equator oceanic heat transport, and the development of the psychrosphere (segregation of cold, deep oceanic waters) (reviewed by Prothero 1994). Although there may have been some local Antarctic glaciation in the late Priabonian, continental ice sheets formed and rapidly expanded in the Rupelian (Zachos et al. 2001). δ^{18}O values from foraminifera indicate an increase in the thermal gradient between low and high latitudes (Keller 1983). Data from leaf physiognomy indicates a concomitant sharp increase in seasonality (Wolfe 1978).

Dispersal to Australia. *Via Antarctica.* An early route to Australia is possible from North America via South America and Antarctica, then into Australia, before the Rupelian Grande Coupure. The Drake Channel between South America and Antarctica opened ≈36 Ma (early Priabonian), some 11 Ma after *Archimyrmex* was in South America, leaving a wide window of opportunity for entrance into Antarctica, forested and unglaciated at that time (reviewed by Woodburne and Chase 1996). Rifting of Australia and Antarctica commenced in the Cretaceous, with the south Tasman Rise submerged by ≈64 Ma (earliest Paleocene), separating very slowly until ≈49 Ma, at moderate speed until ≈45 Ma, and more rapidly thereafter; with enough distance for initiation of the circumpolar current only by the Eocene-Oligocene boundary; Tasmania remained linked with Australia by land into the Neogene (Veevers et al. 1991, and studies above). Interchange of mammals between Australia and Patagonia via Antarctica is indicated at least into the mid-Ypresian, ≈52 Ma, with the possibility of sweepstakes dispersal until the early Rupelian climatic events (Woodburne and Chase 1996).

Via Southeast Asia. Also possible is a later, northern route from southeast Asia, as Australia moved closer to the Indonesian region in the Neogene. Routes to

Southeast Asia were available either from North America across Beringia and through Asia in the early Ypresian, or from Europe through Asia after the early Rupelian. The onset of extensive Antarctic glaciation in the early Rupelian is associated with eustatic sea level drop, opening dispersal corridors. The Obik Sea closed at this time, which had previously separated Asia from Europe in the region roughly occupied by the Ural Mountains today; this may have affected Grande Coupure biotic overturn by Europe-Asia interchange as much as climatic downturn (Hooker 2000). *Fagus* (beech) species may have entered Europe at this time from Asia (Denk 2004).

As the Australian Plate moved northward, Australia apparently remained largely isolated, with weak opportunities for biotic interchange with Asia until their mid-Miocene convergence, and consequent substantial island emergence between them (portions of Sulawesi, New Guinea, others) ≈10–15 Ma (de Jong 2001, Austin et al. 2004). Hesperiid genera (Lepidoptera) likely dispersed between Australia and Asia at this time (de Jong 2001). Murid rodents appear in the continent in the Pliocene (Woodburne and Chase 1996). The distributions of ponerines in Indonesia, Australia, New Guinea and the southwestern Pacific are consistent with an eastward expansion from Southeast Asia through New Guinea, many of which apparently entered northern Queensland by this route (Wilson 1959).

Range Restriction from Biotic Factors. Extirpation of the Myrmeciinae outside of the Australian region may have been due at least in part to climatic change; however, this would leave portions of its former range with apparently suitable conditions. Large-scale biotic change associated with these climatic and tectonic events also must be considered.

General post-Eocene biotic change. Eocene communities in which the Myrmeciinae had flourished underwent significant change after the Grande Coupure, when they disappear from the fossil record. In Rupelian North America, forests contained less thermophilic elements, more closely resembling those of modern temperate regions; there was a drying trend, closed canopies shifted toward more open habitats, including wooded grasslands; an increase in Pinaceae in northern high latitudes; an increase in smaller, drier fruits; an increase in mammal size, and a decrease in arboreal mammals (Graham 1999, Collinson 2000, Myers 2003).

Cenozoic ant community change. Ward and Brady (2003) considered that competition with other ants that are aggressive and more behaviorally sophisticated might today reduce the presence of *Myrmecia* in northern Australia, rather than differing climate. Dominant ants often actively exclude potential competitor ant taxa from their territories (Hölldobler and Lumsden 1980). A succession of exposures to new, competitive groups during the explosive Cenozoic radiation of ants may in part explain the limited modern range of the Myrmeciinae.

Major components of the Cenozoic radiation of ants include: the expansion of lineages, as the modern complement of subfamilies are further assembled and their internal lineages expand; increase in the amount of ants within the greater insect assemblage and within the landscape; and change in the relative dominance of groups within Formicidae with differing ecological roles. Individual components have received recent discussion by various authors cited above, e.g., Grimaldi and Agosti (2000), Dlussky and Rasnitsyn (2003), Grimaldi and Engel (2005), and Wilson and Hölldobler (2005).

Ants seem to become a common community element beginning in the Ypresian, e.g., the Green River Formation (Dlussky and Rasnitsyn 2003) and are well represented in the Okanagan Highlands (the earliest Ypresian *Y. rebekkae* may be relatively numerous in the Mo-clay by specific taphonomic factors?). Dlussky and Rasnitsyn (2003) recognize a significant change in ant assemblages after the Eocene, likely during the early Oligocene, with a decrease in the high representation of Dolichoderinae evident in both amber and shale during the Eocene, and an increase in representation of Formicinae and Myrmicinae in the Miocene.

Scant data are available for modern relative subfamily abundance. Although Winkler samples from worldwide forest communities show Dolichoderinae much reduced and Myrmicinae dominant (Ward 2000), these data are not, however, comparable with those from fossil assemblages, because these traps sample forest floor communities, with different patterns of taxon dominance than those preserved in fossil assemblages. Amber likely samples more in the manner of canopy fogging, selecting for arboreal insects, and shales (lacustrine and marine) like Malaise traps, selecting for winged insects transported over bodies of water. Large-scale Malaise and fogging data comparable with these fossil ant assemblages are not currently available.

Recent estimations indicate that the origin of the Formicidae was in the Early Cretaceous, between ≈120 and 140 Ma (Aptian to Valanginian) (Grimaldi and Agosti 2000, Brady 2003) and that the Pseudomyrmecinae and Myrmeciinae diverged between the Ypresian and the Albian (latest Early Cretaceous) (Ward and Brady 2003). The Myrmeciinae are morphologically and behaviorally "primitive"; although there is currently no fossil record of the subfamily older than the Eocene, it would not be surprising if they are found deep into the Late Cretaceous.

An alternative possibility, which would explain their absence from the Cretaceous fossil record, is that they arose later, perhaps closer to the upper end of Ward and Brady's estimate, i.e., in the later Paleocene, with *Y. rebekkae* an early member. If this were so, then they originated, diversified, and spread between northern Europe, North America, and South America in the short time before the early Lutetian, as behaviorally "primitive," highly visual predators in a world of unbroken northern forests, differing ant communities, and globally equable climate, opportunistically expanding their range as dispersal corridors opened. They may have an almost exclusively Eocene fossil record, outside of a possibly undiscovered record in the Australian region, if they were extirpated elsewhere by later Eocene and Rupelian ecological and climatic change to the modern icehouse world and change in the structure of ant communities somewhere around this time.

Further fossil occurrences, combined with advances in paleogeography, geochronology, paleoclimatology and paleoecology, allowing finer-level understanding of change through time are needed to add light to the history of the Myrmeciinae, as well as that of the Formicidae.

Notes

After the acceptance of this manuscript, the subsequent study of Moreau et al. (2006) estimates an origin of the Myrmeciinae at between 108.3 ± 3.0 and 127.2 ± 2.2, older than that estimated by Ward and Brady (2003), cited in the text here. Although this implies the possibility of an origin of the subfamily before the breakup of Gondwana, still, we find a northern origin and southward dispersal most likely by the temporal-geographic occurrences of their fossil representatives, e.g., of *Archimyrmex* in Ypresian North America and Lutetian South America. Also, Perkovsky et al. (2006) present further arguments for a later Ecocene age of Baltic amber.

Appendix

See Appendix 1 for morphological data sets.

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Appendix 1. Morphological data sets

Taxon	1 10 20 30 40 50 60 70
Modified MORPH1 (Ward and Brady 2003)	
Myrmecia	11110011100110101110100p000111000000100000p11000000010111000001010111010010
Nothomyrmecia	1000011111101110111010?1001111000000100000111000011000100000001010111010011
Prionomyrmex longiceps	1?00111111?011100110???1000?1???1??0?0000?011????00?1011????0??????????????10
Prionomyrmex janzeni	1?001111111011100 1?????000??1?0?1??010???0011????00?1011???00??????????????10
Pseudomyrmex	10000001000000001110p1100p001011110p10001010p11000000110110100001010000101110
Tetraponera	10000001000000011100p100p001011110p1010101011100000001101101000010100?0101110
Paraponera	1000001100000110001000?11100100000?010000101110010011pp1101000?0?00?0000010
Amblyopone	10000011p000011110010101010010000100 01p0100101001000010110100010000?0000010
Rhytidoponera	100000110000011pp0pp0111100010000 11100p0100111011 0010p0110100010100000000010
Myrmicinae	100000110000011110010 11p10p01001p111011011p1101100011011010000100000000 0110
Dolichoderinae	100000p100000p111p01000p00101001p1110110110110000 0000p0000010111010000001 1p
Formicinae	100000010000pp111001000p001010010p1101101101110000000100000011000000000001p
Sphecomyrminae	1?000000000000000 10p???000p0100?0000000100011???000?00000?000??????????????10
Vespidae	0000000p000p000000010000--110--00000000000p0000000000000000000000000000 0p0-
Pachycondyla tarsata	10000?11110001100010???10010101100 00?0001101110?100?01011010001???????0?010
Compression Fossil Genera added	
Ypresiomyrma	1??????111?0??1?????????????????????0?????00??011???????0110????0??????????????1
Avitomyrmex	1??????11??0??1?????????????????????0?????0???011???????0p10???????????????????11
Archimyrmex	1??????11??0?01?????????????????????0??0??0???111???????101?????????????????????0
Macabeemyrma	1???????1????????????????????????????0?????????011???????0010???????????????????1

MORPH1 was adapted from Ward and Brady (2003) as in text. Morphological data sets for the four compression fossil genera are as follows: *Ypresiomyrma*, *Avitomyrmex*, *Macabeemyrma*, and *Archimyrmex*, as in text. ?, unknown; p, polymorphic; -, inapplicable.