



RESEARCH ARTICLE - ANTS

Fossil Ants (Hymenoptera: Formicidae) of the Middle Eocene Kishenehn Formation

JS LAPOLLA¹, DE GREENWALT²

1 - Towson University, Towson, Maryland, USA

2 - National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

Article History

Edited by

Evandro N. Silva, UEFS, Brazil

Received 24 November 2014

Initial acceptance 19 February 2015

Final acceptance 11 March 2015

Keywords

Cenozoic, Coal Creek Member, Extinct, *Crematogaster*, Montana.

Corresponding author

John S. LaPolla

Department of Biological Sciences

8000 York Road, Towson University

Towson, Maryland, USA

E-Mail: jlapolla@towson.edu

Abstract

A broad range of interesting fossil insects have been discovered recently in Kishenehn Formation shale (middle Eocene, ca. 46 myo) in northwestern Montana, among them a diversity of ant species. Two hundred forty-nine ant fossils were examined in this study, with 152 them assignable at least to subfamily. Here, twelve fossil ant species are formally described. These include a new genus of Dolichoderinae (*Ktunaxia*, gen. nov.), and the oldest known species from two extant genera: *Crematogaster* (*C. aurora*, sp. nov.) and *Pseudomyrmex* (*P. saxulum*, sp. nov.). The Eocene is of particular interest for understanding ant evolution because it is during this period that many present-day speciose and ecologically dominant clades of ants apparently emerged. In order to understand the evolution of ants, and in particular their march to the terrestrial dominance observed in modern times, it is critical to understand the tempo of ant diversity during the Eocene. The Kishenehn provides another window into Eocene ant diversity; its relevance to some of the other major Eocene ant fossil deposits is discussed.

Introduction

A series of spectacular fossil discoveries over the past decade have firmly established that ants were both morphologically and behaviorally diverse as far back as the mid-Cretaceous around 100 million years ago (LaPolla et al., 2013). This is particularly interesting because the oldest definitive ant specimens are from the Albian (100-112 mya) and it therefore implies that once ants evolved they rather quickly diversified into a wide range of behavioral and ecological roles. The Cretaceous ant fauna was unique in many ways including a composition that consisted of both stem-groups, such as the extinct Sphecomyrminae, and crown-groups. But one of the most interesting attributes of Cretaceous ants is that, despite their diversity, they were apparently relatively minor members of Mesozoic insect communities. This changes dramatically in the Eocene when ants begin to comprise a larger percentage of the known insects from various Eocene fossil deposits (LaPolla et al., 2013). The importance of the Eocene to ant evolution has been corroborated in several recent molecular phylogenetic studies (Brady et al., 2006; Ward et al., 2014), with the period

representing a time of intense diversification for many extant, speciose clades. In many ways, the Eocene represents the beginning of the modern ant fauna both in terms of its taxonomic composition and the ecological dominance ants display among the terrestrial insects. It is therefore imperative to understand the diversity of various Eocene ant communities if we are to better understand the tempo of ant evolution during this critical time period.

The Coal Creek Member (estimated to be ca. 46 million years old) of the Kishenehn Formation located in northwestern Montana (Fig 1) has recently been the focus of several paleontological studies (Huber & Greenwalt, 2011; Greenwalt et al., 2015; Greenwalt et al. 2013; Shockley & Greenwalt, 2013; Greenwalt & Rust, 2014) based on a large and growing collection of fossils at the National Museum of Natural History (Washington, DC). The paleoclimate of the Kishenehn Basin 46 million years ago was tropical, with a mean annual temperature as much as 15°C higher than the region's current temperatures (Wolfe, 1995; Zachos et al., 2001; Huber & Caballero, 2011), and characterized by low temperature seasonality, similar to extant tropical forests



(Archibald et al., 2010, 2013). Among the fossils discovered in the Kishenehn were over two hundred specimens identified as ants (Hymenoptera: Formicidae). We here describe some of these ants and discuss the deposit's significance in understanding ant evolution in the Eocene.

Materials and Methods

This study is based on the examination of 249 compression fossil ant specimens from the lacustrine oil shale of the Kishenehn Formation. Of the 249 specimens examined, 97 of them, while assignable to the Formicidae, could not be identified further. Therefore the study presented is based on the 152 specimens that could at least be assigned to subfamily level. All collection sites contain exposures of the middle sequence of the Coal Creek member of the Kishenehn Formation exposed along the Middle Fork of the Flathead River in northwestern Montana between Paola and Coal Creeks (Fig 1). The middle sequence of the Coal Creek member has been estimated to be 46.2 ± 0.4 million years old (Lutetian) by $^{40}\text{Ar}/^{39}\text{Ar}$ analysis and 43.5 ± 4.9 million years old by fission-track analysis (Constenius, 1996). These dates are supported by biostratigraphic correlations with mammalian and molluscan fossils as well as palynology (Constenius et al., 1989; Pierce & Constenius, 2014).

Fossils were immersed in 95% ethanol for examination and photography. Specimens were photographed with an Olympus SZX12 microscope equipped with a Q-Color5 Olympus camera. Image-Pro Plus 7.0 software (Media Cybernetics, Inc., Bethesda, Maryland) was used to capture and record the images and measurements. Diagnosis sections are provided to allow for distinction between the species described here and other North American Eocene species and are not intended as global diagnoses.



Fig 1. Eocene fossil sites containing insects: (1) Horsefly (sites 1 – 4 are all Okanagan Highlands), (2) McAbee, (3) Falkland, (4) Republic, (5) Kishenehn, (6) Ruby River, (7) Green River (There are several Green River localities; shown is the Piceance Creek Basin site where most ant fossils have been collected), (8) Florissant, (9) Malvern (amber deposit).

Morphological terminology for measurements and indices employed throughout are defined as (modified from LaPolla et al., 2011a, 2011b, and as defined below):

EL (Eye Length): maximum length of compound eye in full-face view.

FrWL (Forewing Length): the maximum length of the forewing from basal articulation through distal tip.

GL (Gaster Length): the length of the gaster in lateral view from the anteriormost point of the first gastral segment (third abdominal segment) to the posteriormost point.

HL (Head Length): the length of the head proper, excluding the mandibles; measured in full-face view from the midpoint of the anterior clypeal margin to a line drawn across the posterior margin from its highest points.

HW (Head Width): the maximum width of the head in full-face view.

WL (Weber's Length): in lateral view, the distance from the posteriormost border of the metapleural lobe to the anteriormost border of the pronotum, excluding the neck.

ML2 (Mesosomal Length): in dorsal view, the distance from the posteriormost border of the propodeum to the anteriormost border of the pronotum, excluding the neck.

PetL (Petiole Length): the length of the petiole, in lateral view, from the anterior margin of the peduncle to the posterior margin of the petiole.

PPetL (Postpetiole Length): the length of the postpetiole, in lateral view, from the anterior margin of the peduncle to the posterior margin of the postpetiole.

PetH (Petiole Height): the maximum height of the petiole, in lateral view, measured at a right angle to the PetL.

PPetH (Postpetiole Height): the maximum height of the postpetiole, in lateral view, measured at a right angle to the PPetL.

PFL (Profemur Length): the length of the profemur from its margin with the trochanter proximally to its margin with the tibia distally.

PW (Pronotal Width): the maximum width of the pronotum in dorsal view.

SL (Scape Length): the maximum length of the antennal scape excluding the condylar bulb.

TerL (Tergite Length): maximum length, in lateral view, of gastral tergite from anterior to posterior margin. The tergite that is measured is indicated by the Roman numeral preceding TerL, for example TerLI would indicate gastral tergite 1.

TL (Total Length): $HL + WL + GL$

CI (Cephalic Index): $(HW/HL) \cdot 100$

SI (Scape Index): $(SL/HW) \cdot 100$

Forewing venation naming system (Fig 15a) follows recent work by Bolton (in prep). All specimens from this study are deposited in the National Museum of Natural History in Washington, DC.

Note on Collective Names

In the paleomyrmecological literature (as in all paleontological literature) there have been described so-called collective or form genera. Dlussky & Rasnitsyn (2003) used the potentially confusing term “formal genera”, but it is synonymous with the collective or form genus concept. Dlussky & Rasnitsyn (2003) provide an extensive review of the topic. In the paleomyrmecological literature the term form genus is often applied to compression or imprint fossils where preservation is poor and genus level assignment is difficult in order to reflect uncertainty in genus placement. In such cases, a genus may be created even though it is likely a synonym of an already described genus (often an extant genus). We find this distinction unnecessary, if a certain criterion is met (see below), because placement within a genus is always a hypothesis and even among extant species there may be considerable uncertainty in generic placement. Here we treat all genera as proper genera (i.e., as orthotaxa) if a type-species has been designated for it (following Bolton, 2014). Therefore, despite the fact Dlussky & Rasnitsyn (2003) considered the following to be form genera, they all have type-species and therefore we treat them as proper genera: *Camponotites*, *Eoformica*, *Ponerites*, *Proiridomyrmex*, and *Solenopsites*.

Results and Discussion

Synopsis of *Formicidae* Species Known from the Kishenehn Formation

Dolichoderinae

- Dolichoderus dlusskyi*, sp. nov.
- Ktunaxia jucunda*, gen. & sp. nov.
- Proiridomyrmex rotundatus*, sp. nov.
- Protazteca eocenica*, sp. nov.

Formicinae

- Camponotites* spp.
- Formica annosa*, sp. nov.
- Lasius glom*, sp. nov.

Myrmicinae

- Crematogaster aurora*, sp. nov.
- Solenopsites abdita*, sp. nov.

Ponerinae

- Ponerites kishenehne*, sp. nov.

Pseudomyrmecinae

- Pseudomyrmex saxulum*, sp. nov.

Incertae sedis within Formicidae

- Eoformica pinguis* (Scudder, 1877)
- Eoformica brevipetiola*, sp. nov.
- Eoformica latimedia*, sp. nov.

Dolichoderinae

Dolichoderus dlusskyi, sp. nov. (Fig 2)

Holotype worker, compression (dorsal view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609584.

Diagnosis: Head morphology of *Dolichoderus dlusskyi* differs from *Dolichoderus kohlsi* in that *D. dlusskyi* possesses a distinctly longer than wide head and scapes that surpass the posterior margin.

Worker Description. This species is only known from the holotype, which is a worker. Compression fossil in dorsal orientation. Head and mesosoma reddish brown, gaster dark brown; legs yellowish-brown. Head rectangular, distinctly longer than wide; eyes relative small, placed at midline of head; antennal segment number cannot be determined; scapes surpass posterior margin by at least one funicular segment length; posterolateral corners distinct and round; posterior margin straight. Orientation and preservation of specimen makes characters of the mesosoma difficult to observe; propodeum bispinate; petiole difficult to see but appears to be large with distinct node; gaster oval.

Measurements (n=1): TL: 4.21; HL: 1.02; HW: 0.82; EL: .07; SL: 0.97; ML2: 1.32; PW: 0.78; GL: 1.87; CI: 80.4; SI: 118.3

Etymology: Named to honor Russian paleomyrmecologist Gennady Dlussky, who for over 40 years made numerous, important contributions to paleomyrmecology. With his passing in May, 2014 not only was an immense working knowledge of fossil ants lost, but so was a generous colleague.

Comments: *Dolichoderus* is quite well represented in the fossil record with over 40 fossil species known. It is particularly diverse in Baltic amber. Three species are known from the Florissant (Carpenter, 1930) and Dlussky & Rasnitsyn (2002) described a species from the Green River. At Green River *Dolichoderus kohlsi* is the second most abundant species known (about 25% of all fossil ant specimens) (Dlussky & Rasnitsyn, 2002). By contrast, *Dolichoderus dlusskyi* is known from a single worker specimen among the Kishenehn ant fossils.

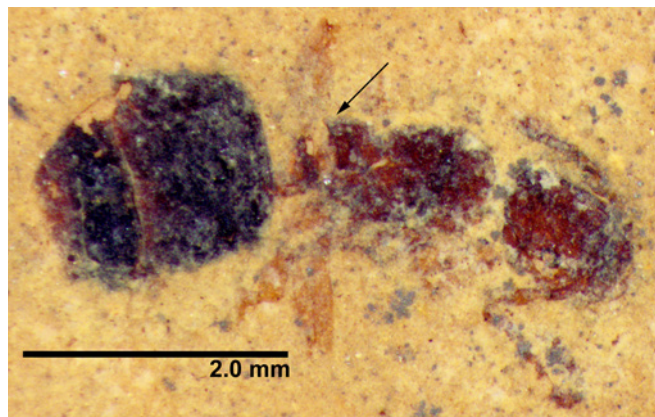


Fig 2. Holotype worker, *Dolichoderus dlusskyi* (USNM# 609584). Arrow indicates propodeal spine.

The placement of this species within *Dolichoderus* is based on the bispinate propodeum clearly observed on the holotype specimen.

***Ktunaxia*, gen. nov.**

Type species: *Ktunaxia jucunda*

Generic diagnosis (only known from a single specimen): scapes short not surpassing posterior margin; funiculus 10-segmented, incassate; all funicular segments beyond apical are very short and broad; mandible with nearly straight masticatory margin; basal margin angle sharply defined; basal margin apparently lacking denticulation.

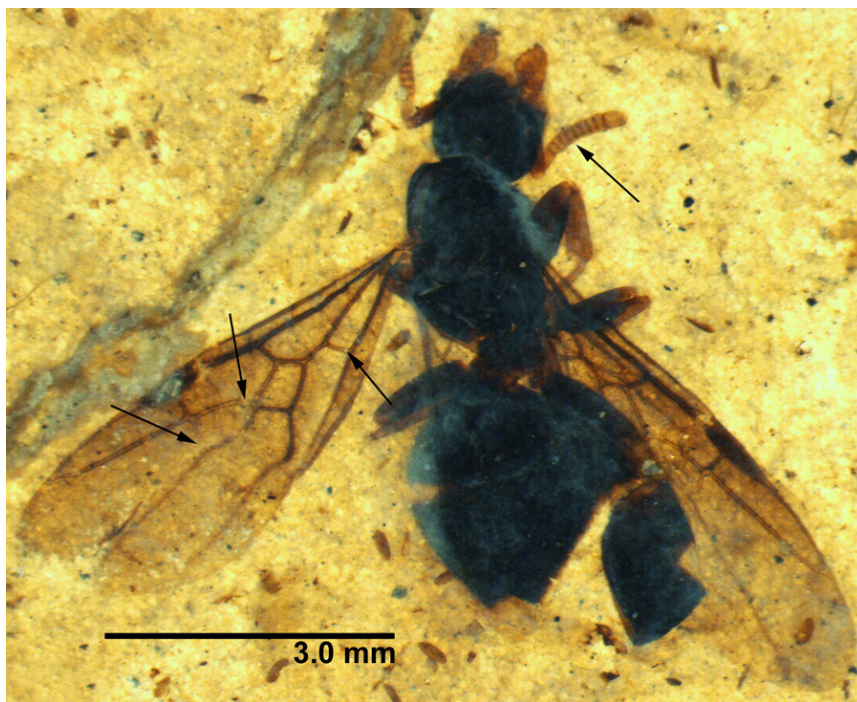
Etymology: Derived from Ktunaxa, the indigenous people of southeastern British Columbia, Idaho, Montana, and Washington.

Comments: This genus is placed within the Dolichoderinae based on overall forewing venation, especially the presence of fenestrae present in the Rs-f2-3, 2rs-m, and cu-a veins (Fig 15b). The fenestra in the Rs-f2-3 vein is particularly helpful in placing this genus within the Dolichoderinae because a fenestra is never present in this vein in formicines, which could be another potential subfamily placement for this genus. *Ktunaxia* is unique among the Dolichoderinae with regard to its short and stocky funiculus, a feature not observed among other dolichoderine genera, extinct or extant.

***Ktunaxia jucunda*, sp. nov.** (Figs 3 & 15b)

Holotype queen, compression (dorsal view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609585.

Diagnosis: This species is morphologically unique among known Eocene dolichoderines.



Queen Description. This species is only known from the holotype, which is an alate queen. Overall specimen is very dark, making many features of the body difficult to impossible to see. Head is distinctly wider than long; posterior margin apparently concave medially; posterolateral corners broadly rounded; scapes short, not surpassing posterior margin; funiculus 10-segmented; all funicular segments beyond apical are very short and broad; mandible with nearly straight masticatory margin; basal margin angle sharply defined; basal margin apparently lacking denticulation; masticatory margin with 5 or 6 teeth, all but apical and 2nd teeth are small; apparently denticles lacking. Unable to observe most features of the mesosoma; petiole apparently with small node; gaster largely missing beyond tergite 2; forewing venation as in Fig 15b.

Measurements (n=1): HL: 0.9; HW: 1.16; SL: 0.88; ML2: 1.93; PW: 1.26; FrWL: 5.45; TerLI: 1.0; CI: 128.8; SI: 75.9

Etymology: The specific epithet derives from the Latin *jocus* meaning jest or sport.

Comments: As this is the only species in the genus, comments for it are in the genus description comments.

***Proiridomyrmex rotundatus*, sp. nov.** (Figs 4 & 5)

Holotype queen, compression (dorsal view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609586; paratype queens: USNM# 609587; USNM# 609588; USNM# 609589.

Diagnosis: Differs from *P. vetulus* with eyes that are placed closer to the clypeal margin of the head and a much wider and rounder gaster.

Queen Description. Compression fossils in dorsal and lateral orientations. Overall brown, with slightly lighter antennae, legs, and segmental margins. Head wider than long, roughly heart-shaped; mandibles triangular with multiple teeth or denticles eyes placed towards clypeal margin; antennae 12-segmented; scape surpasses posterior margin; posterolateral corners rounded with distinct angles; posterior margin straight. Pronotum in lateral view rounded towards mesonotum; propodeum apparently with short dorsal face and steep, longer declivous face; petiole difficult to see but appears to be small; gaster distinctly distended in all specimens; for those in lateral view with a distinct rounded shape.

Measurements (n=1 [holotype]): TL: 5.68; HL: 0.87; HW: 1.01; EL: 0.168; WL: 1.55; PW: 0.99; GL: 3.26; CI: 116.

Fig 3. Holotype queen, *Ktunaxia jucunda* (USNM# 609585). Arrows on wings indicate fenestrae present; arrow on antennae indicates the stocky, 10-segmented funiculus.

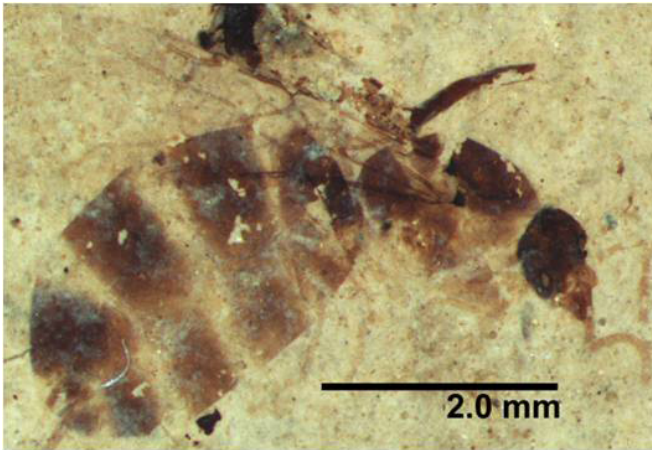


Fig 4. Holotype queen, *Proiridomyrmex rotundatus* (USNM# 609586).

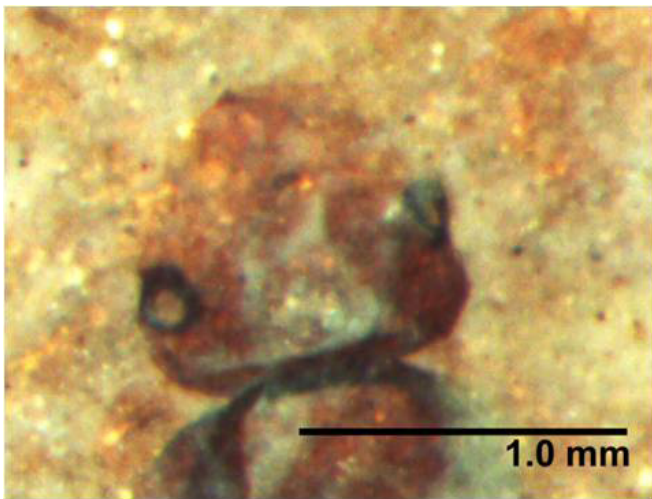


Fig 5. Head of paratype queen, *Proiridomyrmex rotundatus* (USNM# 609587).

Etymology: The specific epithet derives from the Latin *rotundatus* meaning round.

Comments: *Proiridomyrmex* was first described for a species found in the Green River Formation (Dlussky & Rasnitsyn, 2002) and the description here is the second species known from the genus. The placement of *P. rotundatus* in *Proiridomyrmex* is based on the heart-shaped head, rounded propodeum, and inclined petiole, all of which match the diagnosis provided by Dlussky & Rasnitsyn (2002). A partial portion of the forewing can be seen in one specimen (Fig 4), but it is very poorly preserved and both forewings appear to be on top of each other making it impossible to follow most of the venation. However, a fenestra is seen in Rs-f2-3, which would be expected for a dolichoderine (see comments for *Ktunaxia*).

***Protazteca eocenica*, sp. nov. (Figs 6 & 15c)**

Holotype queen, compression (dorsal view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609590.

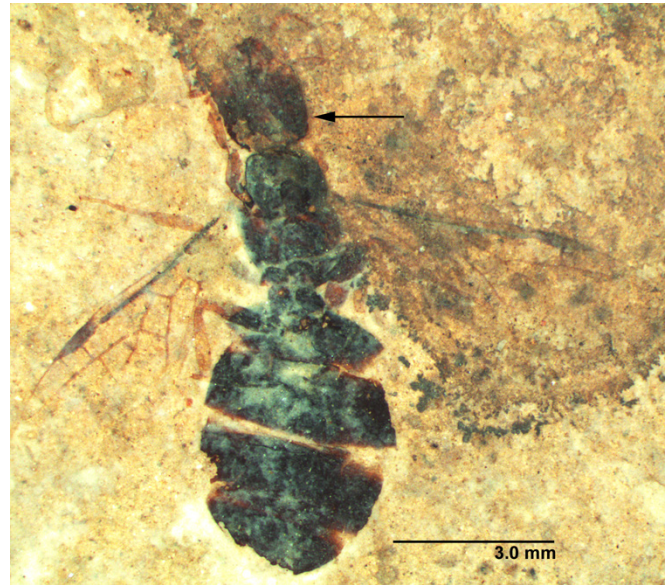


Fig 6. Holotype queen, *Protazteca eocenica* (USNM# 609590). Arrow indicates rectangular head, characteristic of the genus.

Diagnosis: Smallest species in genus (less than 10 mm in total length).

Queen Description. This species is only known from the holotype, which is an alate queen. Compression fossil in dorsal orientation. Overall dark brown, with slightly lighter antennae, mandibles, and legs. Head rectangular, distinctly longer than wide; eyes small and placed towards clypeal margin; antennal segment number cannot be determined (at least 10 segments can be seen clearly, but 12 are probably present); scape does not reach posterior margin; posterior margin straight with angular posterolateral corners; mandibles triangular with long masticatory margin and apparently many small teeth or denticles. Orientation of specimen makes characters of the mesosoma and gaster difficult to see; pronotal anterior margin appears to be rectangular with distinct angles present giving mesosoma a box-like appearance; petiole appears to present a small node; forewing venation as in fig. 15c.

Measurements (n=1): TL: 9.21; HL: 1.5; HW: 1.54; EL: 0.3; SL: 0.92; WL: 2.66; PW: 1.48; FrWL: 6.88; GL: 5.05; CI: 102.7; SI: 59.7

Etymology: The specific epithet derives from the Latin *eo* meaning early and the Greek *kainos* meaning new.

Comments: The extinct genus *Protazteca* was known prior to this study only from the Eocene/Oligocene boundary of Florissant, where one species, *P. elongata*, comprises over 26% of all fossil ants studied by Carpenter (1930). Three other species were also described from the Florissant. The discovery of *P. eocenica* extends the temporal range of the genus well into the mid-Eocene. It is the smallest species known in the genus (all other species are over 10 mm in total length). *Protazteca* in the Kishenehn is known only from a single queen, and therefore was apparently not nearly as abundant as it was by the time of the deposition of the

Florissant (Eocene/Oligocene boundary, ca. 34 myo). The placement of *P. eocenica* with *Protazteca* is based on the rectangular head that is distinctly longer than wide, coupled with short scapes (not reaching the head's posterior margin) that are positioned close to the clypeus.

Formicinae

Camponotites spp.

Nearly 9% of all identifiable Kishenehn ant specimens are *Camponotites*. Despite this fact, we do not formally describe a species from the Kishenehn because, although the specimens are clearly *Camponotites*, their preservation is very poor and therefore even a rudimentary description is impossible. It is unclear if the Kishenehn specimens represent one species or several. The use of the generic name *Camponotites* has been discussed extensively by Dlussky & Rasnitsyn (1999, 2002) and Dlussky et al. (2011). It seems likely that *Camponotites* is in fact *Camponotus*, but the fossils of *Camponotites* examined to date lack critical morphological features for such a decision to be made.

Formica annosa, sp. nov. (Figs 7 & 15d)

Holotype male, compression (lateral view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609591; paratype male: USNM# 609592.

Diagnosis: Shorter scape (SL= 1.2 mm) than *F. robusta* (SL= 1.5 mm).

Male Description. Compression fossils in lateral orientation. Overall dark brown, with slightly lighter areas on segmental margins and legs. Head appears to be rectangular, being much wider than long (exact width cannot be measured due to incomplete preservation); eyes large, twice as long as wide. Pronotum small and collar-like, succeeded by much larger and rounded mesonotum; propodeum with long and steep declivitous face. Petiole with large node; genitalia difficult to observe but parameres apparently triangular; forewing venation as in Fig 15d.

Measurements (n=1 [holotype]): EL: 0.45; SL: 1.24; WL: 2.14; FrWL: 4.22; PFL:0.86; GL: 3.35

Etymology: The specific epithet derives from the Latin *annosus* meaning full of years, long-lived.

Comments: *Formica* species are well represented in the fossil record with over 60 species from a variety of fossil deposits, but largely from Baltic amber. It is quite clear that the genus was well established and diverse in the Eocene, and has remained so to the present. There are three species known from the Florissant (Carpenter, 1930), however no *Formica* were reported from the Green River (Dlussky & Rasnitsyn, 2002). From the Florissant the only described *Formica* male is that of *Formica robusta*. *F. annosa* has a longer forewing and shorter scape than *F. robusta*. The other two Florissant

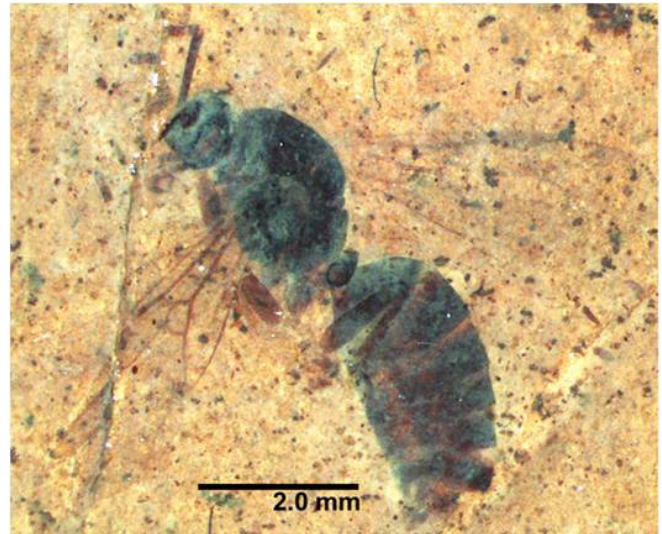


Fig 7. Holotype male, *Formica annosa* (USNM# 609591).

Formica species (*F. cockerelli* and *F. grandis*) are known only from queens, but the queens of these species are larger than we might expect the queen of *F. annosa* to be (although presently the queen caste remains unknown).

Lasius glom, sp. nov. (Figs 8 & 15e)

Holotype male, twisted compression (lateral view) from the Kishenehn (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609593; paratype male USNM# 609594.

Diagnosis: Weber's length greater than in *L. peritulus* (WL= 1.5 vs. 1.2).

Male Description. Overall specimens are dark brown. Head apparently wider than long (exact width is impossible to measure on available specimens); compound eyes distinctly breaking outline of head; number of teeth cannot be determined, but at least one distinct tooth present on basal angle, apparently separated by a short diastema and a longer apical tooth present; posterior margin rounded; posterolateral corners distinctly rounded; scapes and antennae obscured and with missing sections; unable to observe most features of the mesosoma, but overall rounded dorsally; with short but steep declivitous face; petiole cannot be seen; parameres of genitalia visible and triangular in shape with rounded apex; forewing venation as in fig. 15e.

Measurements (n=1 [holotype]). EL: 0.2; WL: 1.46; GL (including paramere): 1.68.

Etymology: The specific epithet derives from the Old English *glom* meaning twilight.

Comments: The genus *Lasius* is well represented in Cenozoic ant fossil deposits (with our description here there are now 24 species and subspecies known). In Baltic amber *Lasius schiefferdeckeri* comprises more than 10% of all ant fossils and in the Florissant *Lasius peritulus* comprises about 25% of all ant fossils (Dlussky & Rasnitsyn, 2002). *Lasius glom* differs from *L. peritulus* in possessing a larger

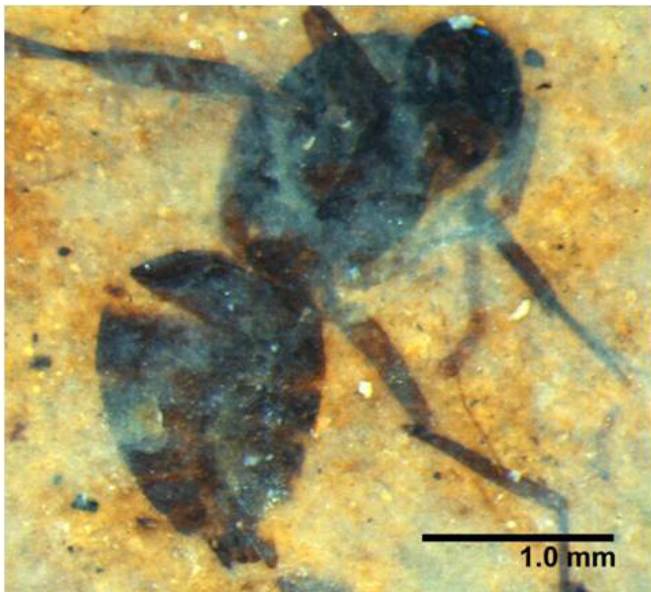


Fig 8. Holotype male, *Lasius glom* (USNM# 609593).

mesosoma and gaster. Interestingly, *Lasius* was not reported from the Green River (Dlussky & Rasnitsyn, 2002) and in this study it is rare, being known only from two male specimens.

Myrmicinae

Crematogaster aurora, sp. nov. (Fig 9)

Holotype queen, compression (lateral view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609595; paratype queen USNM# 609596

Diagnosis: Presence of a 2-segmented club on antennae, and petiole with distinct subpetiolar process directed anteriorly. (Note: this is the only *Crematogaster* species known from the Eocene.)

Queen Description. Dark brown overall, with lighter brown antennae, legs, petiole, postpetiole, and segmental margins. Head longer than wide (exact width is impossible to measure on available specimens); posterior margin apparently straight; posterolateral corners broadly rounded; scapes short, not surpassing posterior margin by length of at least 2 funicular segments; funiculus segmentation cannot be determined, but last three segments progressively longer, forming a 2-segmented club; mandibles obscured in both specimens. Unable to observe most features of the mesosoma; declivity steep, with two small spines directed slightly entad; petiole without node, longer than postpetiole; petiole with distinct subpetiolar process directed anteriorly; postpetiole short, without node, with smaller subpetiolar process than on petiole; postpetiole narrowly attached to gaster.

Measurements (n=1 [holotype]). WL: 1.73; GL: 3.91; PetL (not including peduncle): 0.5; PetH: 0.35; PPetL: 0.4

Etymology: The specific epithet derives from the Latin *aurora* meaning dawn.

Comments: *Crematogaster aurora* is the oldest known species in the genus. The only other *Crematogaster* fossil species is a male specimen from Silician Amber (16-23 myo) (Emery 1891; LaPolla et al. 2013). The discovery here of *Crematogaster* in the Kishenehn is therefore a significant expansion of the temporal range known for the genus. It is also an interesting find from a biogeographic perspective since the larger clade that *Crematogaster* belongs to is centered in the Paleotropics (Ward et al., 2014) and proposed sister groups to the genus have been Old World genera (Bolton, 2003; Blaimer, 2012). Ward et al. (2014) estimated an age of 28.1-42.4 myo (median age estimate 34.7 myo) for the genus. Clearly the discovery of *C. aurora* suggests that the genus is at least 46 myo and is probably older since *C. aurora* is definitively a crown-group *Crematogaster*.

The species likely belongs in the subgenus *Orthocrema* (B. Blaimer, pers. comm.). This placement is based on three

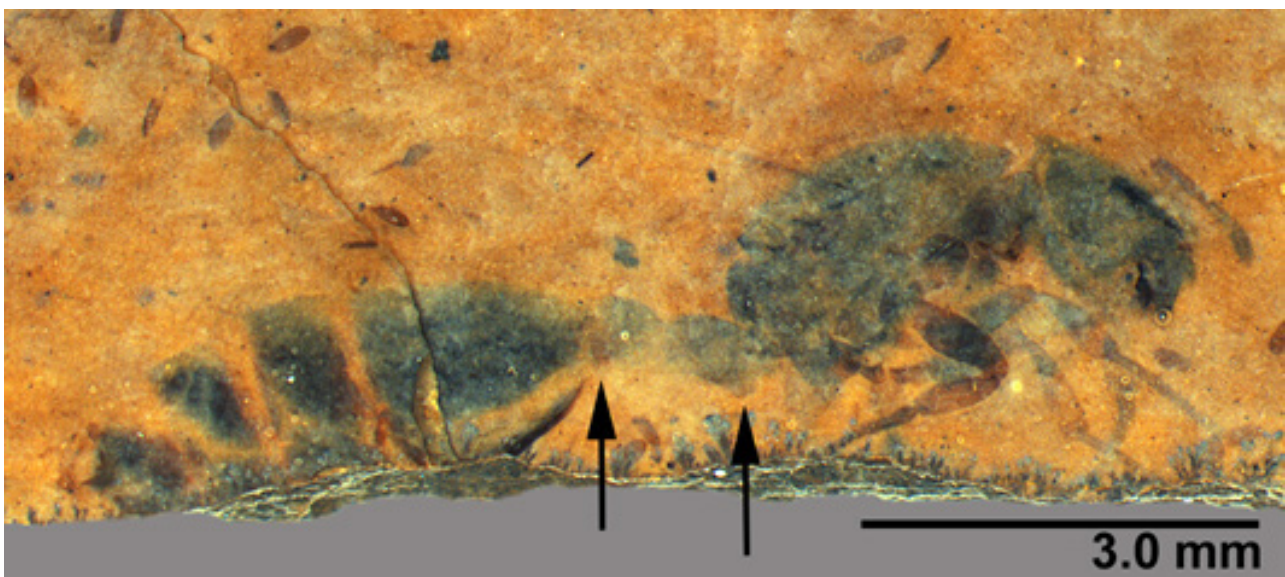


Fig 9. Holotype queen, *Crematogaster aurora* (USNM# 609595). Arrows indicate the subpetiolar processes found on both the petiole and postpetiole.

characteristics of the fossil species: 1) the presence of a 2-segmented antennal club; 2) a mesosoma that is elongated and more dorsally flattened; 3) a slender and elongate gaster.

Solenopsites abdita, sp. nov. (Fig 10)

Holotype queen, compression (lateral view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609597. Paratype queens USNM# 609598, USNM# 609599, USNM# 609600, USNM# 609601, USNM# 609602, USNM# 609603.

Diagnosis: Weber's length greater than *S. minutus* (2.2 mm vs. 1.2 mm).

Queen Description. Dark brown overall, with lighter brown antennae, legs, petiole, postpetiole, and segmental margins. Head longer than wide (width is impossible to measure on available specimens); shape of posterior margin cannot be determined; posterolateral corners apparently broadly rounded; scapes apparently short, not surpassing posterior margin; funiculus segmentation cannot be determined; mandibles obscured in available specimens. Mesosoma oval, with short pronotum, relatively flat dorsum; declivitous face of propodeum slightly convex and steep, unarmed; petiole without node, about the same length as postpetiole; postpetiole without node, narrowly attached to gaster.

Measurements (n=1 [holotype]). WL: 2.2; FrWL: 5.87; GL: 3.26; PetL: 0.55; PetH: 0.32; PPetL: 0.58; PPetH: 0.36

Etymology: The specific epithet derives from the Latin *abditus* meaning hidden, concealed.

Comments: The genus *Solenopsites* was created by Dlussky & Rasnitsyn (2002) to accommodate those myrmicines that probably belong in *Solenopsis* but, due to their condition, are impossible to confidently place within that genus. That said, the shape of the petiole and postpetiole of *Solenopsites* is very distinctive and unlike any other fossil myrmicine.

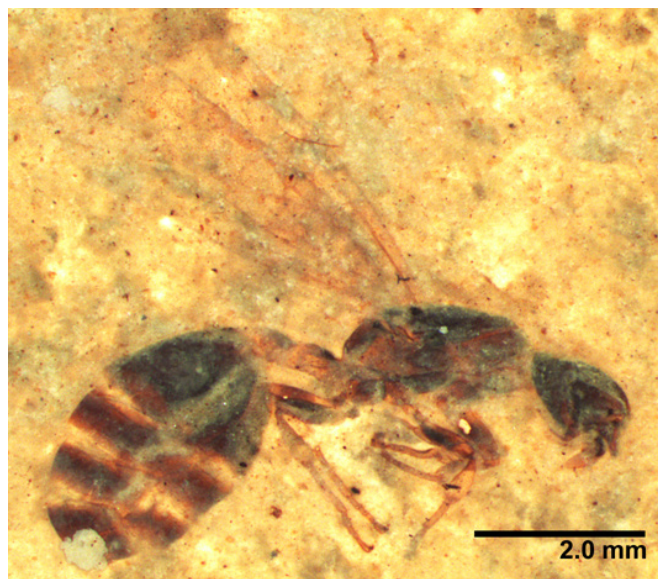


Fig 10. Holotype queen, *Solenopsites abdita* (USNM# 609597).

The Green River species, *Solenopsites minutus*, has a much smaller mesosoma than *S. abdita*. At 4.6% of all fossil ant specimens, *S. abdita* is one of the more common of the ant fossils from the Kishenehn. Unfortunately despite the fact the outline of forewings could be seen in two specimens the venation was so faint we were unable to illustrate them.

Ponerinae

Ponerites kishenehne, sp. nov. (Fig 11)

Holotype queen, compression (lateral view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609604.

Diagnosis: Short mesosoma (WL= 1.4 mm).

Queen Description. Compression fossil in lateral orientation. Overall brown. Head longer than wide; posterior margin apparently straight; posterolateral corners appear to be distinct, broadly rounded; eyes small (EL= 0.15); scapes short, appearing to not surpass posterior margin; funiculus incassate, apparently 8-segmented; all funicular segments beyond apical are very short and broad; mandible apparently with wide masticatory margin. Unable to observe most features of the mesosoma; propodeum likely with steep declivitous face; petiole large with node extending to at least mesosomal and gastral dorsums; gaster distended with a distinct sting present.

Measurements (n=1). EL: 0.15; WL: 1.4; PetL: 0.31; PetH: 0.5; TerLI: 0.66; TerLII: 0.66

Etymology: The epithet reflects the fossil deposit from which this species is known.

Comments: We report here only an 8-segmented antennae, which would make this species unusual among

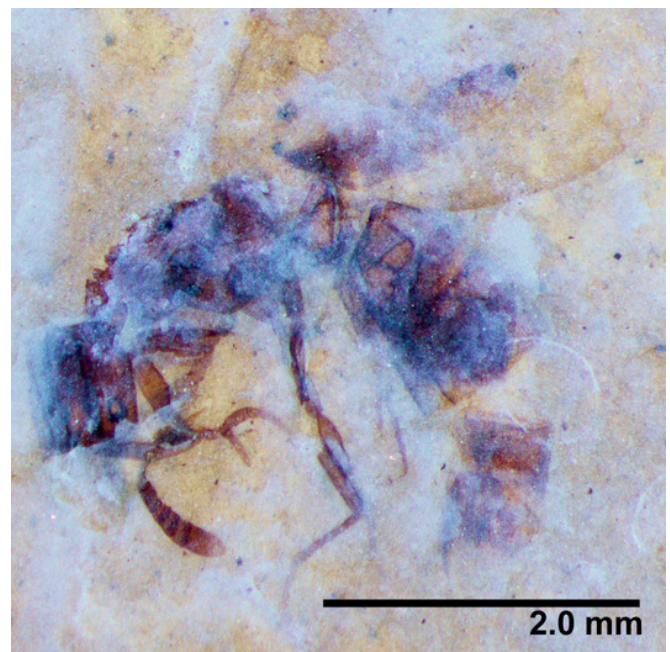


Fig 11. Holotype queen, *Ponerites kishenehne* (USNM# 609604).

ponerines, but caution is warranted because the funiculus is only visible in one specimen and it is impossible to fully see the scape and in particular the funiculus-scape articulation; therefore, this species may have more antennal segments than reported here. This species is most similar morphologically to *P. coloradensis*, but *P. kishenehne* is overall smaller. This appears to be the smallest known species in the genus. As discussed in Dlussky & Rasnitsyn (2002), *Ponerites* is likely either *Ponera* or *Hypoponera* but the condition of the specimens prevents placement within an extant genus.

Pseudomyrmecinae

Pseudomyrmex saxulum, sp. nov. (Fig 12)

Holotype queen, compression (lateral view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM# 609605.

Diagnosis: Smaller than *P. extinctus* (WL: 1.81; FrWL: 4.09; GL: 2.98).

Queen Description. Compression fossil in lateral orientation. Overall dark brown, with lighter areas on segmental margins; tibiae and tarsi, where visible, appear much lighter brown to yellow. Head rectangular, much longer than wide (but width cannot be measured due to incomplete preservation); eyes large, twice as long as wide. Mesosoma with relatively flat dorsum; metanotal area groove depressed below level of mesonotal and propodeal dorsal margins. Petiole with long peduncle; dorsal margin of petiole broadly rounded, bulbous, with short declivitous face.

Measurements (n=1): EL: 0.42; WL: 1.81; FrWL: 4.09; PFL: 0.59; GL: 2.98; PetL: 0.7; PetH: 0.37; PPetL: 0.46; PPetH: 0.45; TerLI: 0.95; TerLII: 0.6

Etymology: The specific epithet derives from the Latin *saxum* meaning rock; *saxulum* is the diminutive form.

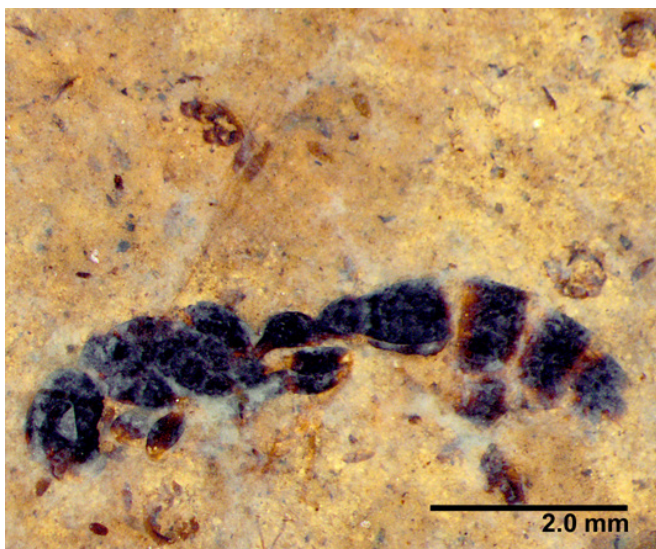


Fig 12. Holotype queen, *Pseudomyrmex saxulum* (USNM# 609605).

Comments: Known from a single specimen, *P. saxulum* now represents the oldest *Pseudomyrmex* species. *Pseudomyrmex extinctus* is from the Florissant, where it is apparently rare as well (or at least rarely preserved) since it is known from only two specimens. *Pseudomyrmex saxulum* was smaller than *P. extinctus* (the latter had a forewing 5 mm long, a petiole 1.2 mm long and a gaster 4.2 mm long). However, pseudomyrmecines were apparently diverse in the Eocene, with five *Tetraponera* species known from Baltic amber. There are eleven *Pseudomyrmex* species known from Miocene Dominican amber (Ward, 1992).

Incertae sedis within Formicidae

Eoformica Cockerell, 1921

Over 40% of the ant fossils studied by Dlussky & Rasnitsyn (2002) in the Green River deposit are *Eoformica pinguis*. *E. pinguis* also occurs in the Kishenehn (USNM# 609606, 609607, 609608, 609609), along with two new *Eoformica* spp. described below, but the three species combined comprise only slightly more than 5% of the fossil ants we examined. Unfortunately, because wings have never been preserved intact or with enough wing venation, it has not been possible to assign *Eoformica* to a subfamily, but the genus almost certainly belongs either in Dolichoderinae or Formicinae. We report here for the first time on the antennal segmentation for the two new species in this genus (both appear to have 10 funicular segments). Dlussky & Rasnitsyn (2002) provide an overview of the genus and its appearance in various fossil deposits.

Eoformica brevipetiola, sp. nov. (Fig 13)

Holotype male, compression (dorsolateral view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM#609610. Paratype male USNM# 609611.

Diagnosis: Distinctly short petiole (PetL: 0.305-0.393).

Male Description. Head wider than long; posterior margin appears to be slightly convex; posterolateral corners broadly rounded; scapes appear to surpass posterior margin by at least first 3-4 funicular segments; funicular segment count appears to be 10; mandibles long and slender, edentate. Details of the mesosoma are difficult to ascertain, but overall shape in lateral view is very distinct: robust, about as long as high, giving mesosoma a globular appearance; petiole distinctly short in length.

Measurements (n=2). EL: 0.405; SL: 0.94; WL: 1.88-2.7; GL: 1.62-2.4; PetL: 0.305-0.393

Etymology: The specific epithet derives from a combination of the Latin *brevis* meaning short and *petiolus* meaning stalk.

Comments: In overall appearance this species is rather similar to the Green River species, *E. globularis*, but a

major difference is in the length of the petiole (Dlussky & Rasnitsyn 2002), with *E. brevipetiola* possessing a distinctly short petiole. As in *E. globularis*, *A. brevipetiola* has a robust, bulky mesosoma. In the holotype the funicular segment count appears to be 10 segments (10 segments also appear to be present in *E. latimedia* as described below), which makes it the first time *Eoformica* funicular segments could be counted.

Eoformica latimedia, sp. nov. (Fig 14)

Holotype male, compression (lateral view) from the Kishenehn Formation (USA: Montana: Middle Fork of the Flathead River between Paola and Coal Creeks) (Eocene: Lutetian) USNM#609612. Paratype males USNM# 609613, USNM# 609614.

Diagnosis: Petiole distinctly wide (PetW= 1.0).

Male Description. Head wider than long; posterior margin appears to be slightly convex; posterolateral corners angular; scapes appear to surpass posterior margin; funicular segment count appears to be 10; mandibles long and slender, but with wide masticatory margin, apparently edentate. Details of the mesosoma are difficult to ascertain, but overall shape in lateral view is robust and wide; petiole distinctly wide in dorsal view.

Measurements (n=1). HL:1.0; WL: 3.03; GL: 3.38; PetL: 0.673; PetW: 1.0

Etymology: The specific epithet derives from a combination of the Latin *latus* meaning broad, wide and *medius* meaning the middle.

Comments: The wide petiole makes this a distinctive species within *Eoformica*. The species, like *E. brevipetiola*, is not abundant among fossil Kishenehn ants, being known from only three specimens.

Taxonomic Composition and Comparison to other Eocene Deposits

With completion of this study the Eocene ant fauna in North America is now represented by three relatively diverse

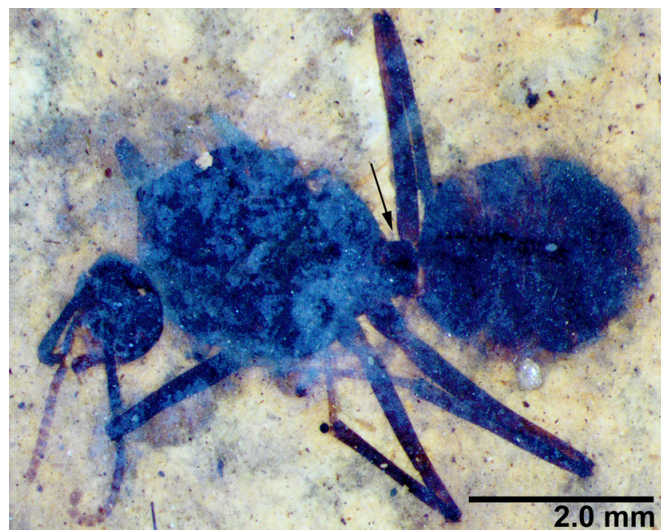


Fig 13. Holotype male, *Eoformica brevipetiola* (USNM# 609610).

fossil deposits: Green River (ca. 48 myo), Kishenehn (ca. 46 myo), and the Florissant (ca. 34 myo). There are two other Eocene deposits in North America that have yielded fossil ant species: Arkansas Amber (Wilson, 1985) and the Okanagan Highlands (Archibald et al., 2006) (Fig 1), but the taxonomic breadth of these deposits appears to be fairly limited. The Florissant has yielded by far the richest source of North American Eocene ants with 32 species described by Carpenter (1930).

As is the case with all Eocene ant deposits, the Dolichoderinae represent by far the greatest proportion of ant fossils in the Kishenehn (Fig 16). Both temporally and geographically the Green River Formation is closest to the Kishenehn. However, with regard to the ant fauna the two deposits possess some interesting differences. The Kishenehn is unique among other larger Eocene deposits in that we did not discover any species in particularly high abundance, as is the case in not only the Green River but also in Baltic Amber and the Florissant. In fact, no species comprises more than 10% of all the fossil ants examined (the highest number was among *Camponotites* spp., which comprises 9.2% of all Kishenehn ants). For example, in Green River, 40% of all specimens were *Eoformica pinguis* and 25% were *Dolichoderus kohlsi* (Dlussky & Rasnitsyn, 2002). The Kishenehn also possesses a higher percentage of formicines (ca. 26% vs. 4%) and myrmicines (ca. 13% vs 4%) than Green River. Formicine numbers approach those seen in Baltic amber and the Florissant (Fig 16). Two subfamilies that were prevalent in the Green



Fig 14. Holotype male, *Eoformica latimedia* (USNM# 609612)

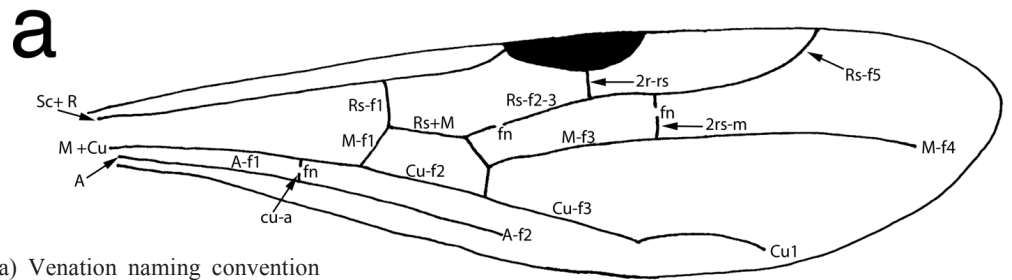
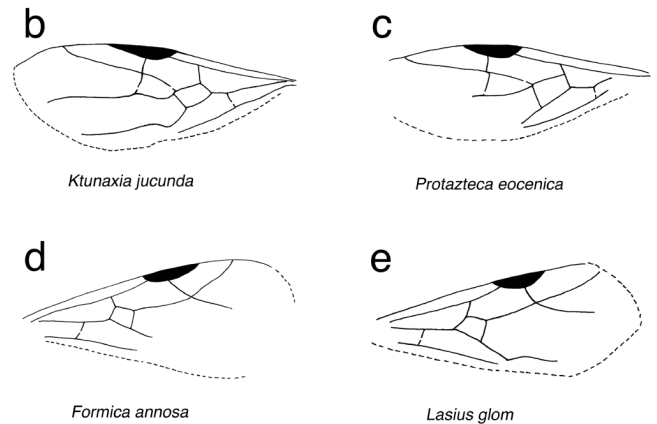


Fig 15a-e. Forewing venation. a) Venation naming convention follows recent work by Bolton (in prep). Upper figure indicates the maximum venation seen in a dolichoderine and includes all of the venation terms employed in this study; Sc+R= subcostal + radial; M+Cu= medial + cubital; A= anal; fn= fenestra in vein. b) *Ktunaxia jucunda* (USNM# 609585); c) *Protazteca eocenica* (USNM# 609590); d) *Formica annosa* (USNM# 609591); e) *Lasius glom* (USNM# 609594).



River were not found in the Kishenehn: Aneuretinae and Myrmeciinae. The Myrmeciinae are the second largest subfamily among Green River ants representing over 13% of specimens studied. Certainly both of these subfamilies were widespread in North America in the Eocene, being found not only in Green River but also in the Florissant, although only one aneuretine specimen is known from Florissant, so they were evidently rare or rarely fossilized (Fig 16). The absence of these subfamilies in the Kishenehn is therefore curious. The Kishenehn is well known for containing particularly small insects (in general insect rock fossils are of larger species) (Greenwalt et al., 2015), and certainly several of the ants described here are small as well.

The Kishenehn and Green River share six genera with each other (*Camponotites*, *Dolichoderus*, *Eoformica*, *Ponerites*, *Proiridomyrmex* and *Solenopsites*) but with regard to other taxa the Kishenehn is more similar to the Florissant. Like the Florissant, the Kishenehn possesses *Formica*, *Lasius*, *Protazteca*, and *Pseudomyrmex*. In fact, for both *Protazteca* and *Pseudomyrmex*, the Kishenehn species now represent the oldest known species within those genera. *Protazteca* is known only from a single specimen in the Kishenehn (although there are several other specimens that may be *Protazteca* but their state of preservation makes it impossible identify them with certainty), whereas one species, *P. elongata*, in the Florissant represents over 26% of all ants studied in that deposit (Carpenter, 1930).

The Kishenehn ant fossils offer a unique insight into the Eocene North American ant fauna. Not only were the oldest records for two extant genera (*Crematogaster* and *Pseudomyrmex*) discovered as part of this study, but the bizarre new dolichoderine genus *Ktunaxia* was described as well. With completion of this study 78 fossil ant species are now known from North American Cenozoic fossil deposits. This is obviously well below the actual number of ants that have lived across the Cenozoic in North America. Continued sampling of the Kishenehn fossil beds will hopefully continue to yield new and interesting ant discoveries that will further refine our view of ant evolution, particularly in the critically important Eocene.

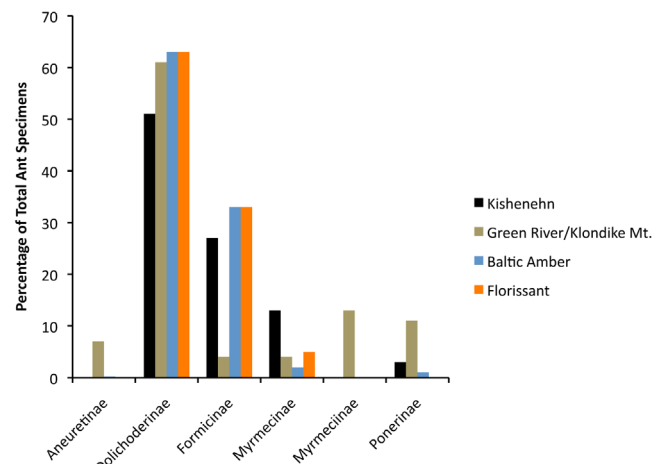


Fig 16. Percentage of total ant fossils that are assigned to major subfamilies for four of the largest Eocene deposits that contain ant fossils.

Acknowledgments

As ant rock fossils can be particularly difficult to interpret, we benefited from the thoughtful discussion and opinions of the following people: Bonnie Blaimer, Barry Bolton, Brendon Boudinot, Vincent Perrichot, Ted Schultz, Jeffrey Sosa-Calvo, James Trager, and Phil Ward. We would also like to thank Ted Schultz and two anonymous reviewers whose suggestions significantly improved the manuscript. Of course we remain solely responsible for any errors that inevitably remain. This study was supported in part by the National Science Foundation under grant DEB-0743542 to JSL. This is contribution number 329 of the Evolution of Terrestrial Ecosystems Consortium of the USNM.

References

- Archibald, S.B., Greenwood, D.R., & Mathewes, R.W. (2013). Seasonality, montane beta diversity, and Eocene insects: Testing Janzen's dispersal hypothesis in an equable world. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 371: 1-8.
- Archibald, S.B., Bossert, W. H., Greenwood, D.R., & Farrell, B. D. (2010). Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology*, 36: 374-398.
- Archibald, S.B., Cover, S.P., & Moreau, C.S. (2006). Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Annals of the Entomological Society of America*, 99: 487-523.
- Blaimer, B.B. (2012). Acrobat ants go global—Origin, evolution and systematics of the genus *Crematogaster* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution* 65: 421-436.
- Brady, S.G., Schultz, T.R., Fisher, B.L. & Ward, P.S. (2006). Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences USA*, 103: 18172–77.
- Bolton, B. (2014). An online catalog of the ants of the world. Available from <http://antcat.org>. (accessed 28 January 2015).
- Bolton, B. (2003). Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71:1-370.
- Carpenter, F.M. (1930). The fossil ants of North America. *Bulletin of the Museum of Comparative Zoology*, 70: 1-66.
- Constenius, K.N. (1996). Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. *Geological Society of America Bulletin*, 108: 20-39.
- Constenius, K.N., Dawson, M.R., Pierce, H.G., Walter, R.C., & Wilson, M.V.H. (1989). Reconnaissance paleontologic study of the Kishenehn Formation, northwestern Montana and southeastern British Columbia. In: D.E. French and R.F. Grabb (eds.), 1989 Field Conference Guidebook: Montana Centennial Edition, Vol. 1., 189-203. Geological Resources of Montana.
- Dlussky, G.M. & Rasnitsyn, A.P. (2002). Ants (Hymenoptera: Formicidae) of formation Green River and some other Middle Eocene deposits of North America. *Russian Entomological Journal* 11: 411-436.
- Dlussky, G.M., Hans-Volker, K., Brauckmann, C., Gröning, E., & Reich, M. (2011). Two ants (Insecta: Hymenoptera: Formicidae: Formicinae) from the Late Pliocene of Willershausen, Germany, with a nomenclatural note on the genus *Camponotites*. *Paläontologische Zeitschrift*, 85: 449-455.
- Emery, C. (1891). Le formiche dell'ambra Siciliana nel Museo Mineralogico dell'Università di Bologna. *Mem. R. Accademia delle Scienze dell'Istituto di Bologna*, 5: 141–165.
- Greenwalt, D. & Rust, J. (2014). A new species of *Pseudotettigonia* Zeuner 1937 (Orthoptera: Tettigoniidae) with an intact stridulatory field and a revision of the subfamily Pseudotettigoniinae. *Systematic Entomology*, 39: 256-263.
- Greenwalt, D., Goreva, Y., Siljeström, S., Rose, T. & Harbach, R.E. (2013). Hemoglobin-derived porphyrins preserved in a Middle Eocene blood-engorged mosquito. *Proceedings of the National Academy of Sciences USA*, 110(46):18496-18500.
- Greenwalt, D.E., Rose, T.R., Siljeström, S.M., Goreva, Y.S., Constenius, K.N., & Wingerath, J.G. (2015). Taphonomic studies of the fossil insects of the Middle Eocene Kishenehn Formation. *Acta Palaeontologica Polonica*, 60: In press.
- Huber, M. & Caballero, R. (2011). The early Eocene equable climate problem revisited. *Climate of the Past Discussions*, 7: 603-633.
- Huber, J.T. & Greenwalt, D. E. (2011). Compression fossil Mymaridae (Hymenoptera) from Kishenehn oil shales, with description of two new genera and review of Tertiary amber genera. *ZooKeys*, 130: 473-494.
- LaPolla, J.S., Dlussky, G.M. & Perrichot, V. (2013). Ants and the fossil record. *Annual Review of Entomology*, 58: 609-630.
- LaPolla, J.S., Brady, S.G. & Shattuck, S.O. (2011a). Monograph of *Nylanderia* (Hymenoptera: Formicidae) of the World: An introduction to the systematics and biology of the genus. *Zootaxa*, 3110: 1-9.
- LaPolla, J.S., Hawkes, P.G., & Fisher, B.L. (2011b). Monograph of *Nylanderia* (Hymenoptera: Formicidae) of the World, Part I: *Nylanderia* in the Afrotropics. *Zootaxa*, 3110: 10-36.
- Pierce, H.G. & Constenius, K.N. (2014). Terrestrial and aquatic mollusks of the Eocene Kishenehn Formation, Middle Fork Flathead River, Montana. *Annals of the Carnegie Museum*, 82: 305-329.
- Scudder, S.H. (1877). The first discovered traces of fossil insects in the American Tertiaries. *Bulletin of the U.S. geological and geographical survey of the territories*, 3: 741-762.
- Shockley, F.W., & Greenwalt, D.E. (2013). *Ptenidium kishenehnsis*, a new fossil described from the Kishenehn oil shales (Coleoptera: Ptiliidae), with a checklist of previously known fossil ptiliids. *Proceedings of the Entomological Society of Washington*, 115: 173-181.
- Ward, P.S., Brady, S.G., Fisher, B.L. & Schultz, T.R. (2015). The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology*, 40: 61-81.
- Ward, P.S. (1992). Ants of the genus *Pseudomyrmex* (Hymenoptera, Formicidae) from Dominican amber, with a synopsis of the extant Antillean species. *Psyche*, 99: 55-85.
- Wilson, E.O. (1985). Ants from the Cretaceous and Eocene amber of North America. *Psyche*, 92: 205-216.
- Wolfe, J.A. (1995). Paleoclimatic estimates from Tertiary leaf assemblages. *Annual Review of Earth and Planetarian Sciences*, 23: 119-142.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms and aberrations in global climate 65 Ma to present. *Science*, 292: 686-693.