Article

Fossil ants (Hymenoptera: Formicidae) of the early Oligocene Canyon Ferry Reservoir deposit

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Abstract

The early Oligocene (*ca*. 32.0 Ma) Canyon Ferry Reservoir deposit is known to contain an extraordinary number of well-preserved plant and animal fossils. Among those are 111 fossil ant specimens that were examined and assigned to five genera: *Dolichoderus*, *Liometopum*, *Camponotus*, *Lasius*, and *Manica* from three subfamilies: Dolichoderinae, Formicinae, and Myrmicinae. Two new fossil species are described. *Liometopum greenwalti* **sp. nov.** is the third fossil species known from this genus in North America and is morphologically distinct from the other two fossil species that are known from the Florissant deposit. The three fossil *Liometopum* species are compared to the three extant North American species. *Manica iviei* **sp. nov.** is the first fossil species in this genus known from North America and only the second fossil species described. This species possesses a broad ventral postpetiolar process which among North American extant species is only present in *Manica hunteri*. The Canyon Ferry ants represent the only definitively Oligocene-aged fossil deposit that contains ants in North America and therefore offer a unique view into a time when the modern-day ant communities of the continent were emerging.

Keywords: Cenozoic, impression fossils, *Liometopum*, *Manica*, Montana, paper shale

Introduction

Ants have an incredibly species-rich fossil record (nearly 800 described species) that stretches back to the mid-Cretaceous (LaPolla *et al*., 2013; Barden, 2017; Bolton, 2023). This extensive fossil record helps reveal the tempo of ant evolution over the last one hundred million years. For example, based on fossils it is likely that it was in the Eocene that ants began their rise in numerical dominance they display in most terrestrial ecosystems today (Barden, 2017). It can also be seen that during the Oligocene and Miocene not only do ants continue to increase in abundance, but diversification also accelerates and many extant ant genera appear during these periods (Grimaldi & Agosti, 2000; Dlussky & Rasnitsyn, 2002; LaPolla *et al*., 2013; Barden, 2017). Therefore, the continued study of ant fossils allows for further refinement and understanding of ant evolution and their ecological impacts over an evolutionary time scale.

While there are three species-rich North American Eocene rock fossil deposits that contain ants: Florissant (Carpenter, 1930), Green River (Dlussky & Rasnitsyn, 2002), and Kishenehn (LaPolla & Greenwalt, 2015), there is only one Oligocene North American deposit known to contain ants. The Florissant is from the late Eocene (Priabonian (38.0–33.9 Ma; Meyer (2003) reported an age of 34.07 Ma) but has at various times been attributed to the earliest Oligocene. The Florissant is one of the most ant species-rich rock deposits known for ants, with 33 species (Carpenter, 1930), and is by far the richest ant-containing fossil deposit in North America (Barden, 2017). That leaves the Quesnel lacustrine shale deposits from Canada as the only Oligocene deposit containing ants (Scudder, 1877). There are four ant fossils species described from Quesnel. One of those species, however, *Calyptites antediluvianum*, is likely not an ant (Bolton, 2003). The other three species were minimally described by Scudder (1877) making it difficult to assess them based on the literature and therefore need to be re-evaluated to be sure they are even ants, and if they are ants, that their generic designations are correct.

In 2002, CoBabe *et al*. revealed a deposit of paper shales from Canyon Ferry Reservoir in Montana (USA) that contained a high diversity of both plant and insect fossils. Among the insect fossils, CoBabe *et al*. (2002) noted ant specimens were present. The deposit has been dated from the Rupelian (32.0 ± 0.1 Ma), making it definitively within the early Oligocene. Those ant specimens are described here.

Material and methods

This study is based on the examination of 111 compression fossil ant specimens from paper shales recovered from the Canyon Ferry Reservoir deposit. Of those specimens, 88 were identifiable to genus, while 23 specimens remained that could only be identified as being ants. All specimens are deposited in the Museum of the Rockies, Montana State University, Bozeman, Montana, USA. All specimens are given a unique code that begins with MOR-IV followed by a number identifying the specific specimen.

Geological setting and palaeoenvironment
The geological and geographic details of the Canyon Ferry Reservoir deposit where all the fossils discussed in this study are from are provided by CoBabe *et al*. (2002). The deposit is estimated to be from the early Oligocene (base of the fossil-bearing section dated radiometrically as Rupelian, 32 ± 0.1 Mya) (CoBabe *et al*., 2002). At the time of deposition, Canyon Ferry Reservoir was likely a warm, moist environment with an area of shallow water or a wet meadow associated with a lake (Jennings, 1920).

Morphological terminology
Morphological terminology for measurements and indices employed throughout are defined as:

EL (Eye Length): maximum length of the 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.

GW (Gaster Width): the maximum width of the gaster in lateral view or dorsal view depending on specimen preservation.

GonoL (Gonopod Length): the length of the gonopod from its base to the apex

GonoW (Gonopod Width): the maximum width of the gonopod in lateral view or dorsal view depending on specimen preservation.

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.

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

PetL (Petiole Length): the maximum length of the petiole, in lateral view.

PetW (Petiole Width): in dorsal view, maximum width 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.

PPetW (Postpetiole Width): in dorsal view, maximum width of the postpetiole.

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

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

TL (Total Length): HL+WL+GL

CI (Cephalic Index): (HW/HL) × 100

SI (Scape Index): (SL/HW) × 100

All measurements are given in millimeters (mm).

Forewing venation naming system follows Perfilieva *et al*., 2017 and Bolton (pers. comm.).

Imaging
Photographs were taken with a JVC KY-F75U digital camera attached to a Leica MS5 stereomicroscope, processed with Synchroscopy Automontage, and modified in Adobe Photoshop 23.2.0.

Why there are no part and counterpart of specimens described here
As specimens from the Canyon Ferry Reservoir deposit are compressions on paper shales they are extremely delicate. The collection took place in bulk samples so many pieces fell apart before they could be properly stored. Specimens were retrieved from these bulk samples and set aside for later study. As a result, the specimens reported here are only one part of the fossil and presumably, the counterpart was destroyed during the sampling process (M. Ivie, pers. comm.).

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Family Formicidae Latreille, 1809
Subfamily Dolichoderinae Forel, 1878
Tribe Dolichoderini Forel, 1878
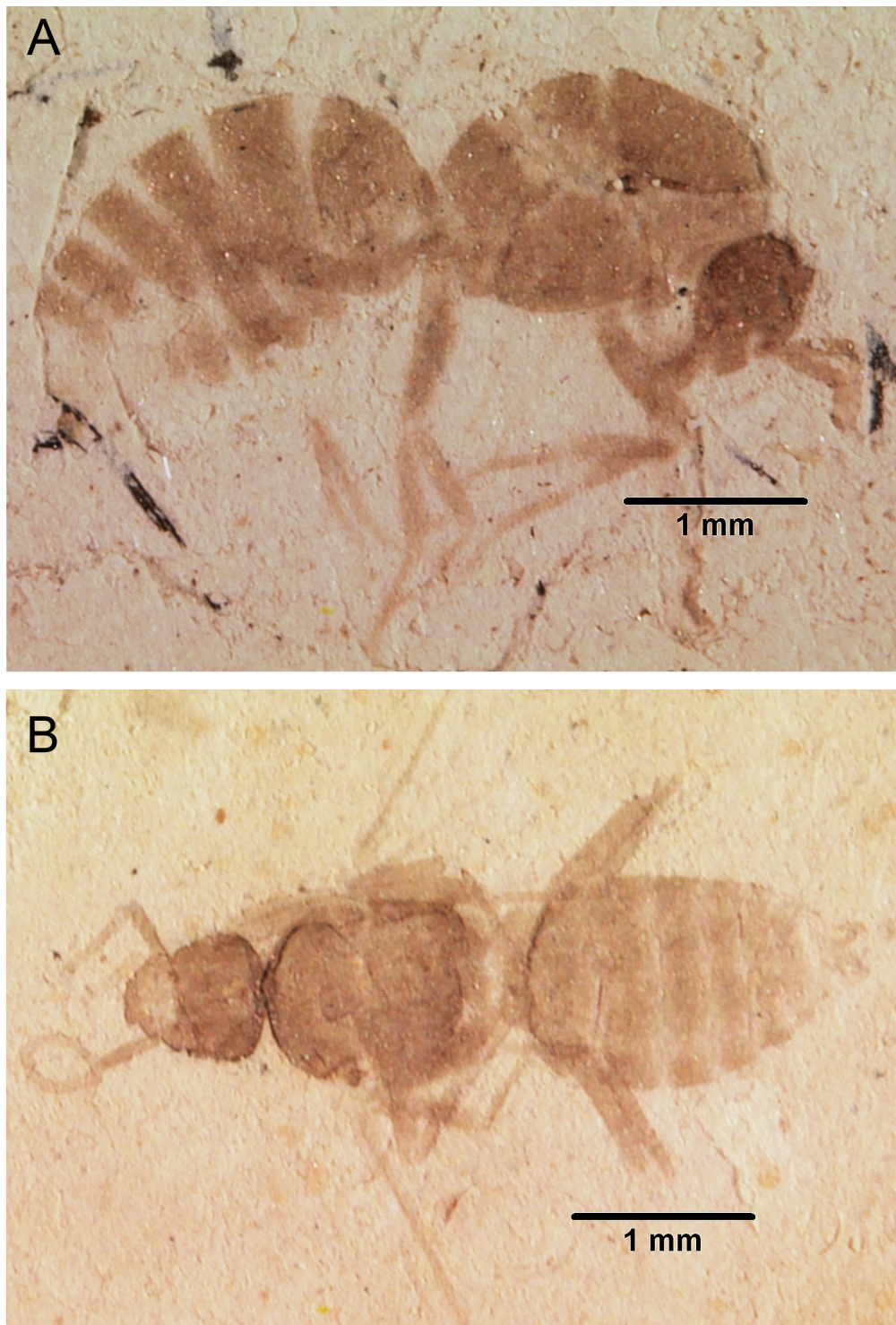**Genus *Dolichoderus* Lund, 1831**

FIGURE 1. *Dolichoderus* sp. **A**, Male in lateral view, MOR-IV-2684. **B**, Male in dorsal view, MOR-IV-2750B.

Dolichoderus sp.
(Fig. 1A, B)

Material. MOR-IV-212; MOR-IV-368; MOR-IV-637; MOR-IV-788; MOR-IV-2684; MOR-IV-2750A–B; MOR-IV-2760; MOR-IV-2761; MOR-IV-2762; MOR-IV-2763; MOR-IV-2764A–B (2 specimens); MOR-IV-2765; MOR-IV-2766; MOR-IV-2767; MOR-IV-2768; MOR-IV-2769; MOR-IV-2770; MOR-IV-2771; MOR-IV-2772; MOR-IV-2773; MOR-IV-2774A–B (2 specimens); MOR-IV-2801; MOR-IV-2802; MOR-IV-2803.

Remarks. The shape and structure of the propodeum leads to placement within *Dolichoderus*. The declivitous face of the propodeum is concave and there is a distinct propodeal angle present (Fig. 1A) both of which indicate the specimens are *Dolichoderus*.

A diverse array of fossil *Dolichoderus* species are known from a variety of deposits, the Baltic amber being

particularly species-rich. Among North American fossil species, three species are known from the Florissant (Carpenter, 1930), one species from the Kishenehn (LaPolla & Greenwalt, 2015), and Dlussky & Rasnitsyn (2002) described a species from the Green River Formation where it made up nearly 25% of ant fossils from that deposit. As in Green River, the apparently single *Dolichoderus* species from Canyon Ferry comprises around 29% of specimens identified to genus. Despite the fact 26 specimens were examined, the preservation of the specimens is such that a new species is not described. In part, this is because it would be difficult to be certain it is, in fact, different from species found within the Florissant. It does appear based on size and the shape of the propodeum in lateral view (which displays a distinct angle as in Fig. 1A) that all the specimens comprise a single Canyon Ferry species. All the specimens examined are thought to be males; figure 1B shows what appear to be the gonopods in dorsal view.

Tribe Tapinomini Emery, 1913
Genus *Liometopum* Mayr, 1861

***Liometopum greenwalti* sp. nov.**
(Figs 2A, B, 6)
http://zoobank.org:act:B1571268-450C-4A36-80F7-CCE382B51856

Type material. Holotype queen (compression fossil in dorsal view) MOR-IV-1465; 3 paratype queens: MOR-IV- 1047, MOR-IV-1107, MOR-IV-1156.

Other material. MOR-IV-176AB; MOR-IV-210; MOR-IV-318; MOR-IV-347; MOR-IV-434; MOR-IV-500; MOR-IV-537; MOR-IV-548; MOR-IV-900; MOR-IV-901; MOR-IV-956; MOR-IV-1199; MOR-IV-1576; MOR-IV-2233; MOR-IV-2752; MOR-IV-2753; MOR-IV-2754; MOR-IV-2756AB; MOR-IV-2757; MOR-IV-2758; MOR-IV-2774; MOR-IV-2775; MOR-IV-2776; MOR-IV-2777; MOR-IV-2778; MOR-IV-2778; MOR-IV-2780.

Etymology. Named in honor of Dale Greenwalt, research associate at the National Museum of Natural History. Dale has been greatly supportive of my efforts to understand North America's Cenozoic fossil ant diversity and made me aware of the Canyon Ferry Reservoir deposit and the presence of ants within it.

Diagnosis. Parallel-sided head with forewing radiomedial cell maintaining a rectangular shape across its entire length.

Type locality and horizon. Canyon Ferry Reservoir deposit; early Oligocene.

Description. Queen. Head rectangular, slightly wider than long, in one specimen slightly longer than wide; sides of head appear parallel-sided with some slight narrowing anteriorly; posterolateral corners rounded; posterior margin appears to be straight; scape appears to just reach posterior margin; mandible triangular, robust with long masticatory margin and prominent, long apical tooth (best visible in MOR-IV-1107); many small teeth only slightly visible on specimen holotype and paratype MOR-IV-1156. Mesosoma only visible in lateral view on specimen MOR-IV-1156; pronotum band-like, with prominent, but relatively low mesonotum; propodeal declivitous face rounded; petiole reaches about half the height of declivitous face, with rounded apex; forewing venation as in Fig. 6. Gaster intact but except for segmental margins other details are not visible.

Measurements (in mm). Holotype: HL: 1.64; HW: 1.75; ML2: 2.63; PW: 1.85; FrL: 7.69; GL: 4.41; GW: 2.24. Paratypes: MOR-IV-1107: HL: 1.64; HW: 1.73; SL: 1.28; ML: 2.4; MW: 1.82; PetW: 0.671. MOR-IV-1156: HL: 1.65; HW: 1.48; SL: 1.35; EL: 0.345; ML: 2.87; MW: 1.69; PetH: 0.65; PetW: 0.35; GL: 4.3; GW: 2.66.

Remarks. The presence of fenestrae within the forewing veins rs-m and 2-3 RS identify these specimens as dolichoderines and the presence of three closed cells (1+2r, rm, and mcu) allows for placement within *Liometopum* (Fig. 6). Additionally, the structure of the mandibles with numerous teeth (at least 7 are present) and the apical tooth being just slightly longer than the subapical tooth further suggests placement within *Liometopum*.

Within North America, there are two fossil species known, both from the ant-rich Florissant deposit (Carpenter, 1930). There are three extant North American *Liometopum* species. Given the relatively close age of the Florissant deposit and the Canyon Ferry Reservoir, it was important to establish that the species described here differed from the two previously described Florissant species. *Liometopum miocenicum* Carpenter, 1930 is overall a much larger species (HL: 3.8; HW: 3.3; SL: 2.0 as reported in Carpenter, 1930) and has a distinctly triangular head. The head shape contrasts starkly with the more parallel-sided head of *L. greenwalti*. The radiomedial cell of the *L. miocenicum* forewing narrows toward the M-f2 cross-vein whereas in *L. greenwalti* the radiomedial cell maintains a more rectangular shape across its entire length.

It is worth noting that, among Florissant ants, *L. miocenicum* is one of the most common ants, with all three castes known from fossils. Similarly, *L. greenwalti* was the single most common ant fossil encountered among specimens identified to genus (nearly 36% of all identified ants). *Liometopum* is absent among Kishenehn ants (LaPolla & Greenwalt, 2015).

The separation of *L. greenwalti* from *L. scudderi* Carpenter, 1930 is based on again having a more parallel-sided head, whereas *L. scudderi* possesses a distinctly triangular head as in *L. miocenicum*. The scape of *L.*
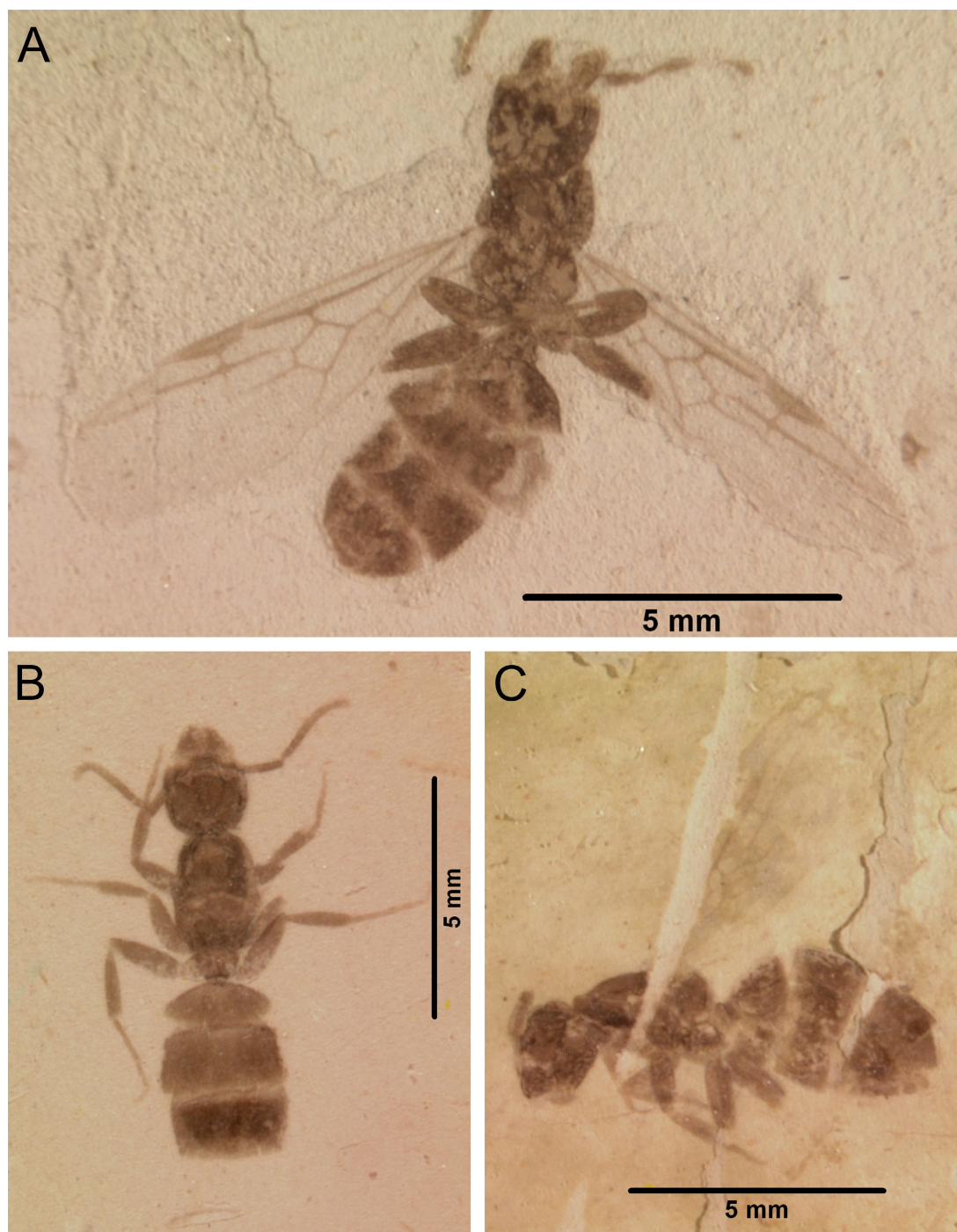
FIGURE 2. *Liometopum greenwalti* **sp. nov. A**, Holotype queen in ventral view (?), MOR-IV-1465. **B**, Paratype queen in dorsal view, MOR-IV-1107. **C**, Paratype queen in lateral view, MOR-IV-1156.

greenwalti (SL: 1.35) is also longer than that of *L. scudderi* (SL: 0.9 as reported in Carpenter, 1930).

Among extant North American *Liometopum* species, the radiomedial cell of the forewing in *L. greenwalti* is closest to that of *L. occidentale* Emery, 1895 in terms of the overall shape. While the radiomedial cell does slightly narrow toward the M-f2 cross-vein (much more so than seen in *L. greenwalti*), it is much less than seen in the other two extant North American species, *L. apiculatum* Mayr, 1870 and *L. luctuosum* Wheeler, 1905.

Subfamily Formicinae Latreille, 1809
Tribe Camponotini Forel, 1878
Genus *Camponotus* Mayr, 1861
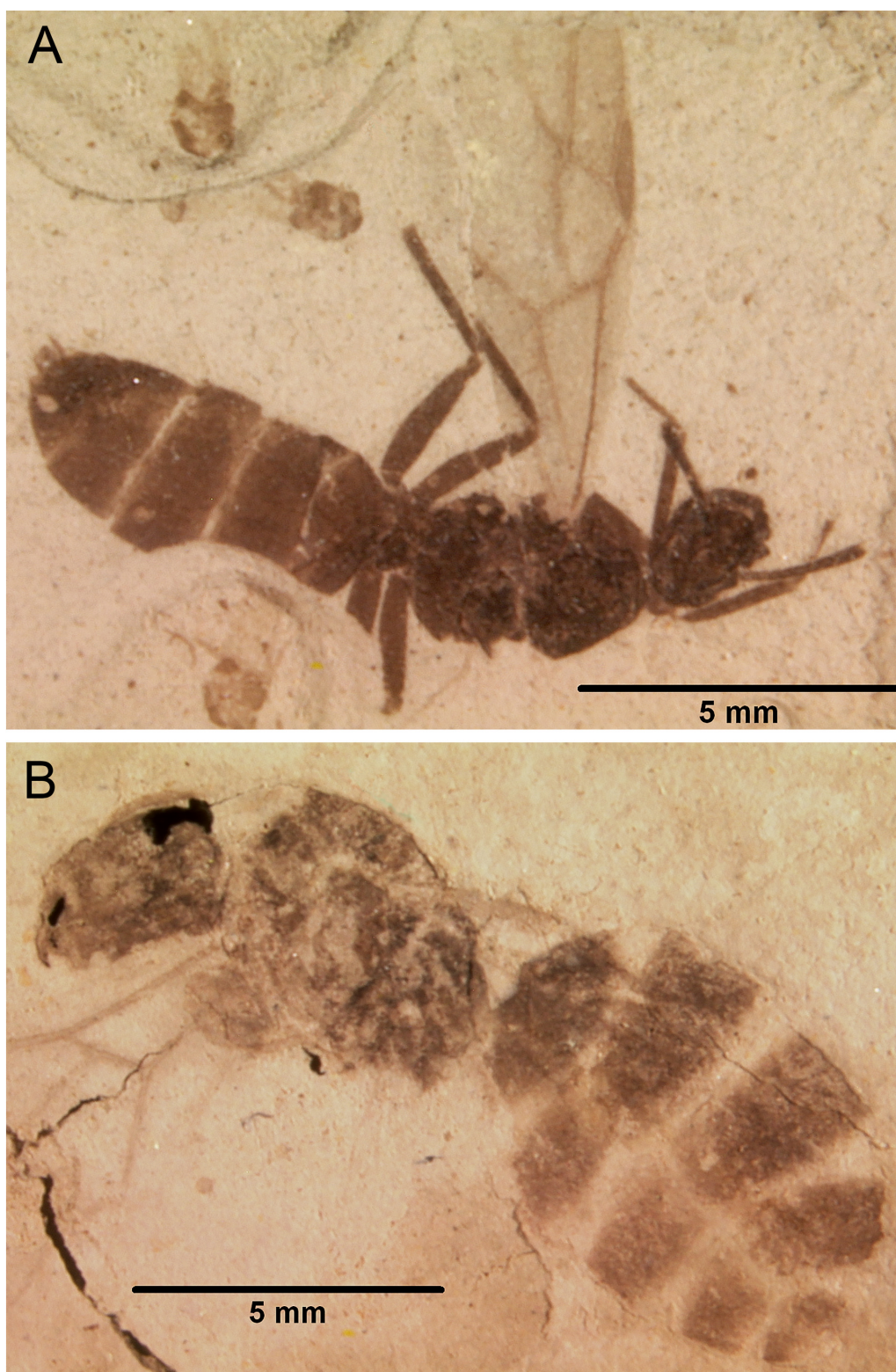
***Camponotus* sp.**
(Figs 3A, B, 6)

FIGURE 3. *Camponotus* sp. **A**, Male in dorsal view, MOR-IV-504. **B**, Queen in lateral view, MOR-IV-1102A.

Material. MOR-IV-504; MOR-IV-1102A; MOR-IV-1151.

    Remarks. The large size of these specimens (Fig. 3), coupled with the pattern of forewing venation (with cell 1+2r present and cell mcu lost) (Fig. 6) led to their placement within *Camponotus*. The only other comparable-sized formicine genus would be *Formica*, but they possess a mcu cell. Nonetheless, many of the head and mesosomal morphological characters that would lend more confidence to placing the fossils within *Camponotus* are not visible so taxonomic assignment within the genus is tentative. The uncertainty around all fossil *Camponotus* (Antropov *et al*., 2014) has led to the creation of the morphogenus *Camponotites* Dlussky, 1981, but see

LaPolla & Greenwalt (2015) for further commentary regarding the necessity of this genus construction.

Despite the fact that only three *Camponotus* specimens were discovered, two of the specimens are males and one is a queen (Fig. 3A, B). None of the specimens are particularly well preserved, but part of a wing was able to be illustrated (Fig. 6). Carpenter (1930) reported *Camponotus* as relatively rare among Florissant fossils, with only 12 specimens discovered out of many thousands examined. In contrast, about 9% of all Kishenehn ant fossils were *Camponotites* (LaPolla & Greenwalt, 2015).

Tribe Lasiini Ashmead, 1905
Genus *Lasius* Fabricius, 1804

Lasius sp.
(Figs 4A, B, 6)

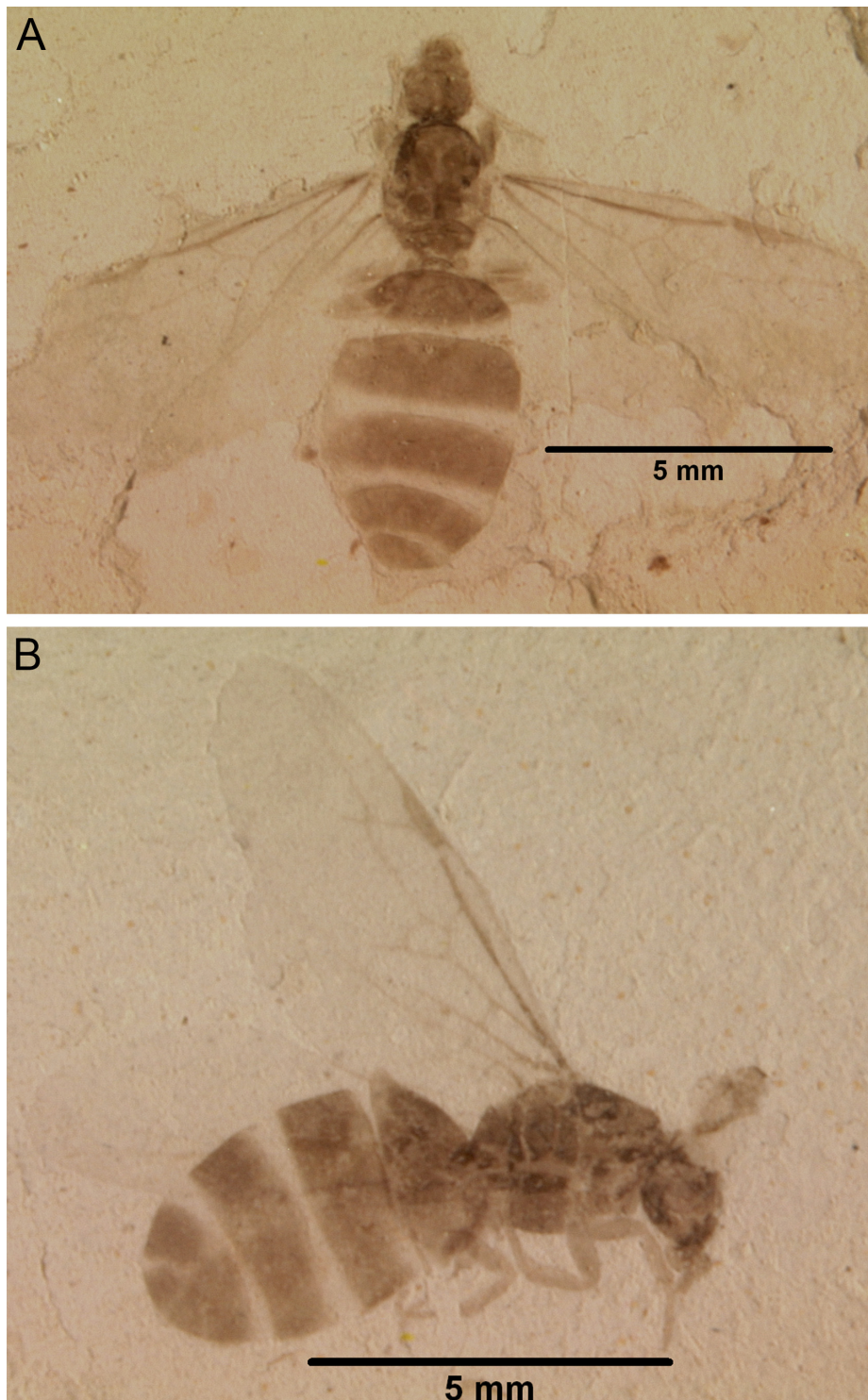**Material.** MOR-IV-194A–B (2 specimens); MOR-IV-

FIGURE 4. *Lasius* sp. **A**, Queen in dorsal view, MOR-IV-476. **B**, Queen in lateral view, MOR-IV-1178.

342; MOR-IV-394; MOR-IV-397; MOR-IV-938; MOR-IV-476; MOR-IV-851; MOR-IV-975; MOR-IV-1017; MOR-IV-1178; MOR-IV-1346; MOR-IV-1362A–B (2 specimens); MOR-IV-1559; MOR-IV-1575; MOR-IV-2733; MOR-IV-2804.

Remarks. As noted recently by Boudinot *et al.* (2022), the morphological features used to identify extant *Lasius* species are not visible on the impression fossil *Lasius* species, making comparisons between extant and fossil species challenging. Placement of the Canyon Ferry specimens in *Lasius* is based on wing venation (presence of the mcu cell for example) (Fig. 6) and the overall gestalt matching with *Lasius*. Interestingly, Boudinot *et al.* (2022) found crown-group *Lasius* emerging in the Oligocene or early Miocene (mean age 24.9 Ma). Both *Lasius peritulus* Cockerell, 1927 from Florissant and *Lasius glom* LaPolla & Greenwalt, 2015 were considered *incertae sedis* within the genus and were considered to likely belong to stem lineages. The same limitations noted for those species regarding morphological features and species identification would apply to the species here from Canyon Ferry, which is also older than the crown-group *Lasius* reported by Boudinot *et al.* (2022).

Lasius peritulus is one of the most encountered ant fossils in the Florissant, comprising about 25% of all ant fossils (Dlussky & Rasnitsyn, 2002). Similarly, just over 20% of specimens identified to genus were *Lasius* among Canyon Ferry ants, although all of the *Lasius* in Canyon Ferry appear to be queens and males remain unknown. Both males and queens of *Lasius peritulus* are known. All the specimens represent a single species based on the overall size and shape of the head and mesosoma. In fact, based on the specimens examined it is possible the Canyon Ferry *Lasius* could in fact be *L. peritulus*. While the scape length is shorter in the one specimen where scapes could be measured (MOR-IV-476) among the Canyon Ferry specimens compared to *L. peritulus* (0.61 *vs*. 0.9 in the holotype of *L. peritulus*), other measurements conform to those observed in *L. peritulus*.

Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835
Tribe Myrmicini Lepeletier de Saint-Fargeau, 1835
Genus *Manica* Jurine, 1807

Manica iviei **sp. nov.**
(Figs 5, 6)
http://zoobank.org:act:80FA9674-15BC-44FC-BC45-74E28202E76A

Type material. Holotype queen (compression fossil in dorsal view) MOR-IV-2723; 1 paratype queen: MOR-IV-974.

Other material. MOR-IV-188; MOR-IV-230; MOR-IV-456; MOR-IV-685; MOR-IV-2233; MOR-IV-2723; MOR-IV-2751; MOR-IV-2759.
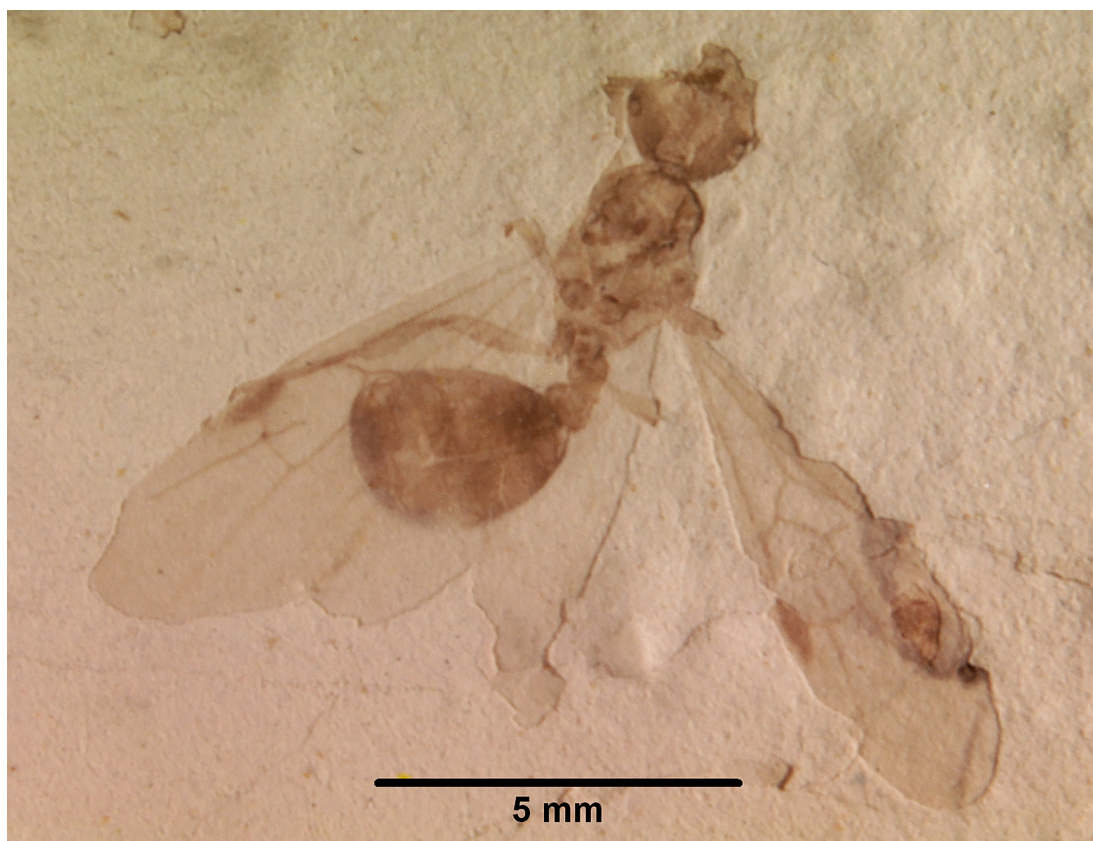

FIGURE 5. Holotype *Manica iviei* **sp. nov.** queen in ventral view, MOR-IV-2723.
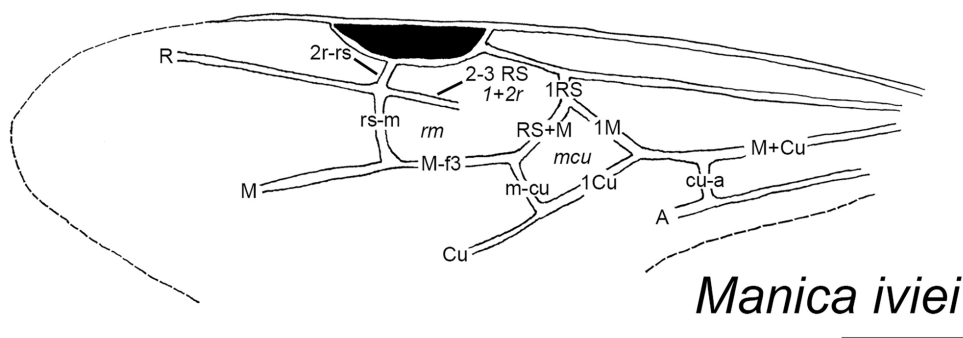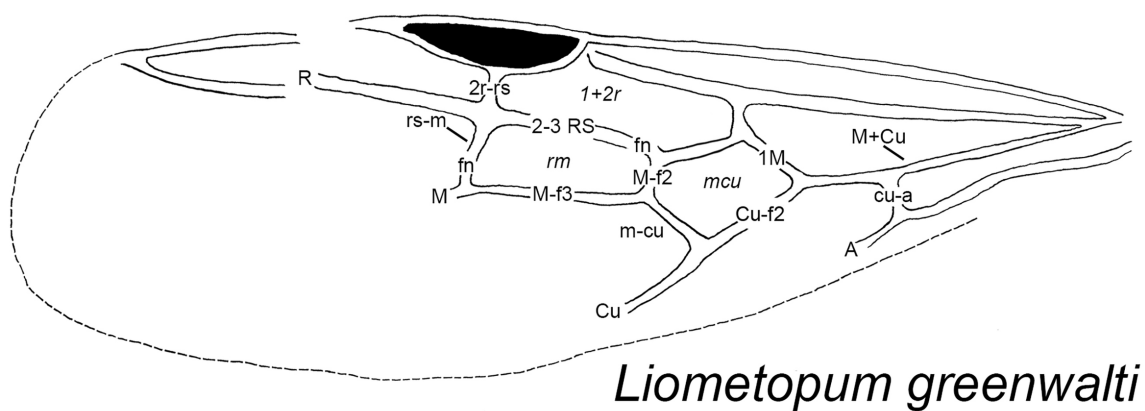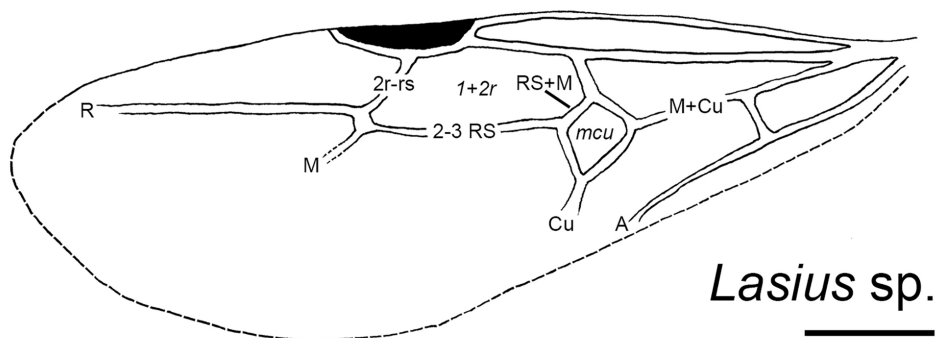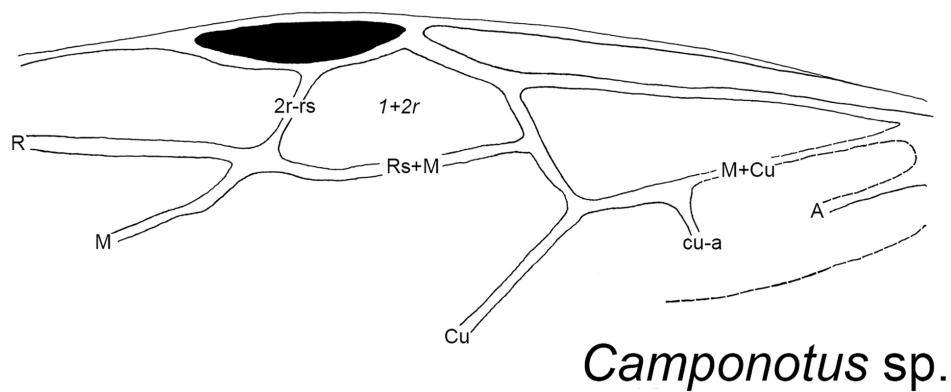
FIGURE 6. Forewing venation. Venation naming convention follows Perfilieva *et al*. (2017) and Bolton (pers. comm.). R= radial, M= medial, Cu= cubital, A= anal, fn= fenestra in vein. *Liometopum greenwalti* (queen) (holotype MOR-IV-1465); *Camponotus* sp. (male) (MOR-IV-504); *Lasius* sp. (queen) (MOR-IV-1178); *Manica iviei* (queen) (paratype MOR-IV-974). Scale bars = 1 mm.

Etymology. Named in honor of Mike Ivie, associate professor at Montana State University. Mike was instrumental in making the wider community aware of the great diversity of insect fossils found within the Canyon Ferry Reservoir deposit. He was also an extremely generous host to me while I examined the collection in June 2018.

Diagnosis. Presence of a broad ventral postpetiolar process.

Type locality and horizon. Canyon Ferry Reservoir deposit; early Oligocene.

Description. Queen.

Measurements (in mm). Holotype: HL: 1.41; HW: 1.71; EL: 0.249; ML: 2.53; MW: 1.85; WingL:7.92; PetH: 0.58; PetW: 0.535; PPetL: 0.498; PPetW: 0.701; GL: 3.02; GW: 2.16. Head distinctly wider than long; sides of head convex, giving head an over rounded appearance; posterolateral corners rounded with apparently slightly convex posterior margin; eyes relatively small compared to the size of the head; mandible robust with near right angle at mandibular basal angle followed by the long masticatory margin; individual teeth not visible. Mesosoma is only visible in dorsal view and few details of it are visible; petiole with slight node visible, slightly longer than postpetiole; postpetiole cylindrical; forewing venation as in Fig. 6. Gaster intact but difficult to see details other than faint segmental margins.

Remarks. This is the first known fossil *Manica* species from North America. The incomplete 2-3RS vein leads to a combined 1+2r cell and rm cell (Fig. 6) which is seen in both *Manica* and *Myrmica* species. However, in *Myrmica* the propodeum is armed with either teeth or spines, and in *Manica* it is not, thus placement of this fossil species in *Manica* (which does not appear to possess propodeal teeth or spines) and not *Myrmica*. *Manica* has a Holarctic distribution with four extant North American *Manica* species, which includes one social parasite (Fisher & Cover, 2007). It is difficult to discuss similarities or differences between the extant species and the fossil species described here since much of the key characteristics among extant species have to do with cuticular sculpturing and color which are not visible on the fossil specimens. That said examination of the postpetiole (Fig. 5) suggests the presence of a broad ventral postpetiolar process which among North American extant species is only present in *M. hunteri*. The ventral postpetiolar process is also found in the Palaearctic species *M. rubida* and *M. yessensis* and in the recently discovered Baltic amber fossil species *M. andrannae* (Zharkov *et al*., 2023).

Unidentified Formicidae
Several specimens examined could be identified as ants, but could not be assigned further to either subfamily or genus. Below is the list of unidentified Canyon Ferry ant fossils.

MOR-IV-256; MOR-IV-306; MOR-IV-376; MOR-IV-392; MOR-IV-437; MOR-IV-994; MOR-IV-2781; MOR-IV-2783; MOR-IV-2784; MOR-IV-2785; MOR-IV-2786; MOR-IV-2789; MOR-IV-2790; MOR-IV-2791; MOR-IV-2792; MOR-IV-2793; MOR-IV-2794; MOR-IV-2795; MOR-IV-2796; MOR-IV-2797; MOR-IV-2798; MOR-IV-2799.

Discussion

The Canyon Ferry ants are notably modern in their composition of genera. The five genera present are all found living together in various Rocky Mountain ant communities today (Wheeler, 1917; Creighton, 1950; Fisher & Cover, 2007). While it is certainly the case that the Canyon Ferry ants represent a fraction of the actual ant species that would have been present 32 Ma, the lack of any extinct genera or genera that are no longer found in the broader region is interesting. It may in fact point to North American ant communities becoming remarkably stable since the Oligocene.

Stability in the abundance of the three most speciose extant subfamilies extends across the Kishenehn, Florissant and Canyon Ferry (Fig. 7), although the composition of genera within those subfamilies varies considerably between the fossil deposits. In both the Kishenehn and Florissant there are several extinct genera present. Entire subfamilies have disappeared from North America as well that were present in the Paleocene and Eocene. For example, Green River (Eocene, 51 Ma) had both Aneuretinae (although see LaPolla and Barden (2018) who suggest the species ascribed to Aneuretinae in that deposit may be incorrect) and Myrmeciinae (Carpenter, 1930; Dlussky & Rasnitsyn, 2002; Dlussky & Perfilieva, 2003) present. Today Aneuretinae is restricted to a single species found in Sri Lanka and the Myrmeciinae are only found in Australia. Within the Florissant there are two species of Agroecomyrmecinae, whereas today that subfamily in the New World is only found in the Neotropics (Radchenko & Khomych, 2022). Therefore, the transition from the Eocene to the Oligocene in North America may have been an inflection point in what genera make up modern-day ant communities.

The Eocene-Oligocene transition is particularly important in the history of the Cenozoic for many groups of organisms, as it was a time when the earth went from greenhouse to icehouse climate states (Toumoulin *et al*., 2022). It was also marked by an extinction event (often referred to as the Grande Coupure), especially noted for turnover in the Eurasian mammalian fauna (Costa *et al*., 2011). Therefore, could the Eocene-Oligocene transition have brought about the advent of modern-day North American ant communities in terms of their composition of genera? The lack of other North American Oligocene
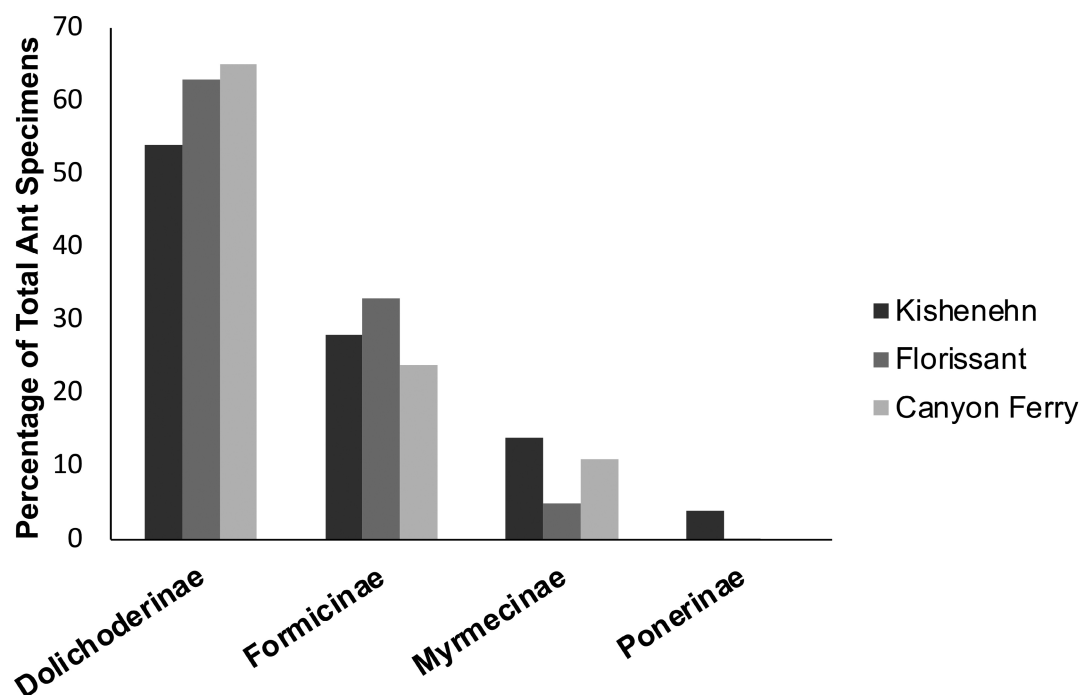
FIGURE 7. Percentage of total ant fossils identified to at least subfamily for three North American deposits that contain ant fossils.

and Miocene deposits that contain ants makes it difficult to answer. We now have two ant-containing deposits spanning the Eocene-Oligocene transition, the Florissant and Canyon Ferry. Examining the genera present in the Florissant, 8 of the 19 known are extinct (*ca.* 42% of total genera). Of the extant genera, *Iridomyrmex*, has two described species in the Florissant, even though the genus is only found in Asia and Australia today. However, Heterick & Shattuck (2011) considered both species as an unidentifiable taxon. The remaining Florissant genera are all common components of extant Rocky Mountain ant communities.

Outside of North America, Dominican amber has thirty-four genera, and all but one are extant. So, while there have been considerable changes in the species composition of the ants found on Hispaniola today compared to the Miocene, almost all of the genera are either still found on the island or if not on Hispaniola today, are found elsewhere in the Neotropics (Arillo & Ortuño, 2005). The Miocene age Radoboj deposit from Croatia (18.2 Ma; Dlussky & Putyatina, 2014; Barden, 2017) is one of the richest ant rock fossil localities from that time period. It was found by Dlussky and Putyatina (2014) to have thirty-four species from fifteen genera. Several of these genera are extinct, however, they are considered "formal genera" by Dlussky & Putyatina (2014), which means they may be from modern genera but the key characters necessary for placing them in such genera could not be seen in the fossils. Interestingly, while

there are genera present in this deposit that now have strictly tropical distributions (for example, *Oecophylla* and *Gesomyrmex*), two genera, *Lasius* and *Formica*, are dominant numerically (Dlussky & Putyatina, 2014). These same two genera also are the dominant genera found in Europe today. Two other Miocene rock fossils deposits that could be useful for determining how modern ant communities evolved are Oeningen from Switzerland (12.2 Ma; Barden, 2017) and Shanwang from China (15.5 Ma; Barden, 2017), but both are in need of taxonomic revision before proper comparisons can be made. The recently discovered mid-Miocene Zhangpu amber (14.7 Ma) from southeastern China contains numerous ants (Wang *et al.*, 2021) and once these are more fully examined and described will likely be a valuable source of information on Miocene ant diversity.

The rise of ants to the dominant members they are in most extant terrestrial ecosystems is documented in ant fossil deposits from around the world and across geological periods. As noted by Barden (2017) the fact that today there are usually just a few genera that make up the bulk of ant biomass in various habitats around the world, is a trend that also seems to hold true in most ant fossil deposits from the Oligocene onward, as demonstrated in this study as well with the numerical dominance of *Liometopum* and *Dolichoderus*. Continued study and discovery of Oligocene-aged and younger ant fossils will allow an ever-increasingly clear view of how ant communities have evolved over time.

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