

Early Miocene Formicidae (Amblyoponinae, Ectatomminae, ?Dolichoderinae, Formicinae, and Ponerinae) from the Foulden Maar Fossil Lagerstätte, New Zealand, and their biogeographic relevance

Uwe Kaulfuss¹ and Gennady M. Dlussky^{2†}

¹University of Otago, Department of Geology, PO Box 56, Dunedin 9054, New Zealand (uwe.kaulfuss@otago.ac.nz)

²Moscow State University, Biological Faculty, Moscow 199991, Russia

Abstract.—The fossil record of Australasian Formicidae is extremely sparse. It currently comprises two ants in the subfamilies Ponerinae and Dolichoderinae from Plio/Pleistocene strata in Victoria, Australia, 14 as-yet undescribed ants from Cape York amber, and one ant in the subfamily Amblyoponinae from the early Miocene Foulden Maar in southern New Zealand. Here, we report on a diverse myrmecofauna preserved as compression fossils from Foulden Maar and describe Amblyoponinae gen. et sp. indet., *Rhytidoponera waipiata* n. sp., *Rhytidoponera gibsoni* n. sp., *Myrmecorhynchus novaeseelandiae* n. sp., and *Austroponera schneideri* n. sp. Further isolated wings are designated as Formicidae sp. A, B, and C, the former resembling a member of subfamily Dolichoderinae. Fossils of *Austroponera* and *Myrmecorhynchus* are reported for the first time, whereas *Rhytidoponera waipiata* n. sp. and *R. gibsoni* n. sp. are the first Southern Hemisphere fossil records of this genus.

The fossil taxa from Foulden Maar establish the subfamilies Ectatomminae, Formicinae, Ponerinae and, possibly, Dolichoderinae in the Australasian region in the early Miocene and provide evidence that the few native ants in the extant New Zealand fauna are the surviving remnant of taxonomically different, possibly more diverse, warm-temperate to subtropical myrmecofauna.

Introduction

Ants (Formicidae) are among the ecologically most important insects, occurring in many terrestrial habitats in all zoogeographic regions, with their highest diversity in tropical forest habitats (Hölldobler and Wilson, 1990; Grimaldi and Engel, 2005). The family currently is composed of 471 genera and almost 14,000 species placed in 16 extant and four extinct subfamilies (Bolton, 2014). The fossil record indicates that ants evolved in the Early Cretaceous between 110 and 130 Ma, and that a diversification of ant subfamilies representing most of the extant genera and their rise to ecological dominance took place in the Eocene (Grimaldi and Agosti, 2000; Dlussky and Rasnitsyn, 2007; LaPolla et al., 2013). The Cenozoic record is extensive (except for the Paleocene) and includes three-dimensionally preserved ants from various amber deposits, such as Eocene Baltic (Dlussky and Rasnitsyn, 2009) and Indian amber (Rust et al., 2010), and Miocene Mexican (Solórzano Kraemer, 2007) and Dominican amber (summarized in Arillo and Ortuno, 2005). In addition, there are Cenozoic compression and impression fossils from various localities, such as the Okanagan Highlands in British Columbia, Canada, and Washington State, USA (Ypresian; Archibald et al., 2006); the Green River Formation, USA (Ypresian; Dlussky and Rasnitsyn, 2002), the Fur Formation in Denmark (Ypresian; Rust

and Andersen, 1999; Archibald et al., 2006); Florissant, Colorado, USA (Eocene/Oligocene; Carpenter, 1930); and others (overview in LaPolla et al., 2013). However, all of these localities are in the Northern Hemisphere and comparatively little is known about the Cenozoic myrmecofauna in the Southern Hemisphere, making new finds such as those described here from New Zealand important for reconstructing the past diversity and geographic range of Formicidae.

The Southern Hemisphere record of fossil ants is very patchy. The South American record includes the myrmeciines *Archimyrmex piatnitzkyi* (Viana and Rossi, 1957) and *A. smekali* (Rossi de Garcia, 1983) from the Paleocene–Eocene of Argentina (Dlussky and Perfilieva, 2003) and an undescribed ant fossil in mid-Miocene amber from Peru (mentioned in Perichot et al., 2014). The few sub-Saharan Africa fossils include the formicine *Oecophylla leakeyi* Wilson and Taylor, 1964 from the Miocene of Kenya, and a single ant from the Eocene Mahenge maar in Tanzania (Harrison et al., 2001). The record for Australasia, a region with a generally highly diverse extant ant fauna, is similarly poor, with a few published records from mainland Australia: *Hypoponera (Ponera) scitula* (Clark, 1934a) and *Iridomyrmex* Mayr, 1862 from Plio–Pleistocene copal at Allendale, Victoria (Hills, 1957; Oke, 1957); several formicid genera from the Miocene “Upper Site” locality at Riversleigh (Archer et al., 1991); and 14 as-yet undescribed ants from the fossiliferous Cape York amber (Hand et al., 2010), for which a

† Professor G.M. Dlussky passed away on May 1, 2014

recent study suggested a origin in Southeastern Asia rather than Australia, and a maximum Eocene age (Sonibare et al., 2014). The sole record from New Zealand is a member of the Amblyoponinae recently reported from the early Miocene Foulden Maar, Otago (Kaulfuss et al., 2014a). In this paper, we describe a diverse fossil myrmecofauna, preserved as compression fossils, from Foulden Maar (Fig. 1), which allows a first evaluation of early Miocene ant diversity in New Zealand and the wider Australasian region. It enables comparisons with the extant fauna in Australasia and with the Northern Hemisphere Cenozoic record.

The Recent New Zealand ant fauna currently comprises 37 established species in 23 genera, placed in the subfamilies Amblyoponinae Forel, Proceratiinae Emery, Heteroponerinae Bolton, Ponerinae Lepeletier de Saint-Fargeau, Ectatomminae Emery, Myrmicinae Lepeletier de Saint-Fargeau, Dolichoderinae Forel, and Formicinae Latreille (with the Ectatomminae and Dolichoderinae comprising only introduced species). More than two-thirds of the established species are exotic or introduced, mainly from Australia and the Pacific islands, and only one genus, *Huberia* Forel, 1890, and 11 species are considered endemic: *Stigmatomma saundersi* (Forel, 1892), *Discothyrea antarctica* Emery, 1895a, *Heteroponera brounii* (Forel, 1892), *Austroponera castanea* (Mayr, 1865), *A. castaneicolor* (Dalla Torre, 1893), *Huberia brounii* Forel, 1895, *H. striata* (F. Smith, 1876), *Monomorium antarcticum* (F. Smith, 1858), *M. antipodum* Forel, 1901, *M. smithii* Forel, 1892, and *Prolasius advenus* (F. Smith, 1862) (Don, 2007).

The small stock of both native and introduced ants in New Zealand has been referred to as depauperate or meagre in comparison to species numbers in Australia and the southwest Pacific region (e.g., Brown, 1958a; Harris and Berry, 2001; Gibbs, 2006). For example, 1275 ant species are known from Australia (Shattuck, 1999) and 1222 species from the Melanesian region, with ~800 species in New Guinea (Janda

et al., 2008), 187 species on Fiji (Sarnat and Economo, 2012), and 125 species in the New Caledonian fauna (Ward, 1985). However, Don (2007) considered 11 endemic species in New Zealand as a realistic number with respect to its temperate climate, its isolated position in the south Pacific, and a general decline of ant diversity with increasing latitude. It has been recognized that the native ant fauna in New Zealand might be the remnant of a more diverse fauna in the past (Watt, 1975; Gibbs, 2006; Don, 2007) and the early Miocene fauna described herein from Foulden Maar suggests that this was indeed the case.

Material and methods

Photomicrographs of specimens were taken with a Nikon Coolpix 4500 camera attached to a Leica Wild MZ8 binocular microscope. Wetting the specimens with ethanol enhanced the visibility of anatomical structures and specimen images are composites of close-up photographs. For the preparation of drawings, we traced enlarged photographs, while checking anatomical structures of each specimen visually under the microscope. The resulting draft drawings were then scanned and digitalized. Solid, thick lines in the drawings indicate boundaries of visible sclerites, dashed lines trace supposed sclerite boundaries, thin solid lines show structures other than sclerite boundaries, e.g. deformation folds and elements of sculpture, and areas highlighted in grey denote the preserved, even if chemically modified, original sclerites. The drawings are based on the more complete parts and were finalized with morphological details preserved on the counterparts (where available). Measurements of anatomical structures were taken with an ocular micrometer and are given in millimeters as preserved, unless otherwise stated. Our nomenclature of the wing venation (Fig. 2) follows Rasnitsyn (1980) and Dlussky (2009); other terminology is adopted from Bolton (1994) and classification and synonymy from Bolton (2003) and Bolton (2014). Fossils described herein are stored in the Department of Geology, University of Otago (OU); catalog numbers for each specimen are provided below.

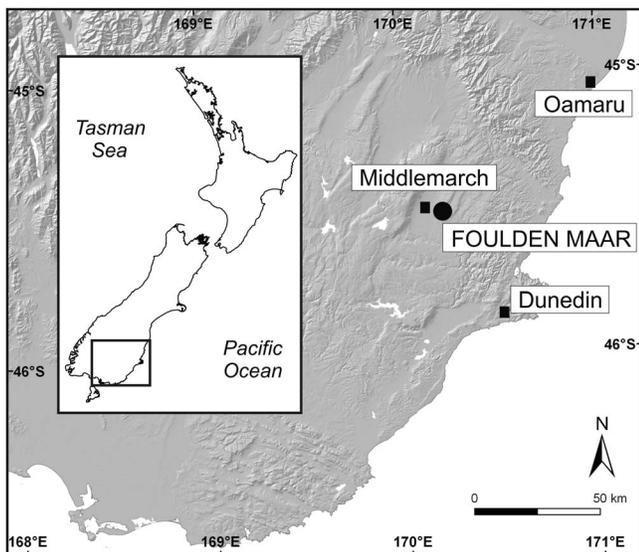


Figure 1. Map showing the location of the Foulden Maar fossil lagerstätte in southern New Zealand.

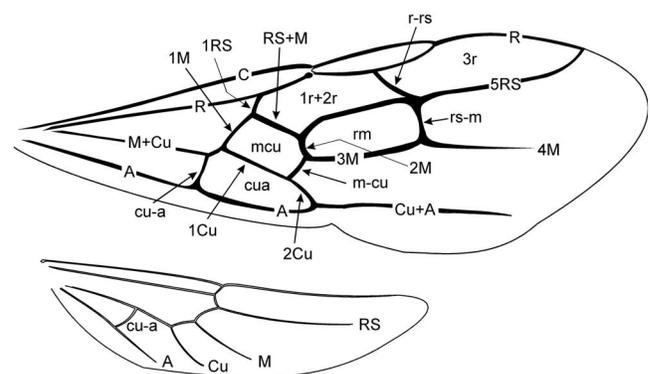


Figure 2. Illustration of the wing nomenclature used by Dlussky (2009). Wings of a gyne of *Gnamptogenys europaea* (Mayr, 1868), neotype SIZK, no. UA-822, late Eocene, Rovno amber. Designations: C, R, RS, M, Cu, A: longitudinal veins; 1RS, RS + M, 2M, etc.: longitudinal vein sections; r-rs, r-m, m-cu, etc.: cross-veins; 1r + 2r, rm, 3r, m-cu, cua: cells.

Locality and age

Foulden Maar is a maar-type fossil lagerstätte in the early to mid-Miocene Waipiata Volcanic Field in Otago, southern New Zealand (NZ Map Grid Infomap I43 reference 929166: 45.5271° S, 170.2218° E) (Fig. 1). Fossils at the site are preserved in finely laminated diatomite deposited in a ~1000 m diameter maar lake (Lindqvist and Lee, 2009) and include mainly micro- and macrofloral remains such as pollen, spores, seeds, fruits, flowers, leaves, fern fronds. The flora is indicative of an evergreen Lauraceae-dominated rainforest growing around the paleolake under a warm-temperate to subtropical climate, including some forest openings near the lake margin (Pole, 1996; Bannister et al., 2005, 2012; Lee et al., 2012, Mildenhall et al., 2014). Arthropod fossils found at the site include representatives of the Araneae, Plecoptera, Isoptera, Hemiptera, Coleoptera, Hymenoptera, Trichoptera and Diptera, making Foulden Maar the most informative site for terrestrial fossil arthropods in New Zealand (Kaulfuss et al., 2014b). Insect taxa previously described in detail include diaspid scale insects (Harris et al., 2007), the termite *Stolotermes kupe* Kaulfuss, Harris and Lee, 2010, the flat-bug *Aneurys* sp. (Aradidae) (Kaulfuss et al., 2011) and a winged ant in the subfamily Amblyoponinae (Kaulfuss et al., 2014a).

The earliest Miocene age of Foulden Maar is based on radiometric dating of volcanics (Ar^{40}/Ar^{39} age of 23.2 Ma for the maar eruption; Lindqvist and Lee, 2009) and on the palynological assemblage within the diatomite, which represents the uppermost *Rhoipites waimumuensis* Zone to lower early *Proteacidites isopogiformis* Zone (New Zealand local stages: late Waitakian–early Otaian) (Mildenhall et al., 2014). The Foulden Maar diatomite represents a Southern Hemisphere mid-latitude lowland ecosystem under an ocean-influenced, seasonal warm-temperate to subtropical climate, following a period of major marine transgression in the Oligocene.

Systematic paleontology

Family Formicidae Latreille, 1809
Subfamily Amblyoponinae Forel, 1893
Genus and Species indet.
Figure 3.1, 3.2

Description.—Part and counterpart of gyne in dorsal view, head not preserved; body length (without head) 8.7 mm, estimated total body length about 10 mm, mesosoma length 3.3 mm; mesosoma width 1.4 mm, petiole length 1.37 mm, petiole width 1.05 mm.

Mesosoma elongate, 2.3 times longer than wide, with nearly parallel sides. Legs comparatively short and thick. Middle tibia with two spurs; first and second segments of middle tarsus both with a pair of long setae. Petiole a little longer than wide, with short anterior peduncle, without free posterior surface, broadly attached to first gastral segment, separated from gaster only by constriction. Second gastral segment a little wider and about as long as first segment. Tip of gaster acute, indicating the probable presence of a sting. Wings fragmentary preserved; wing venation indistinct.

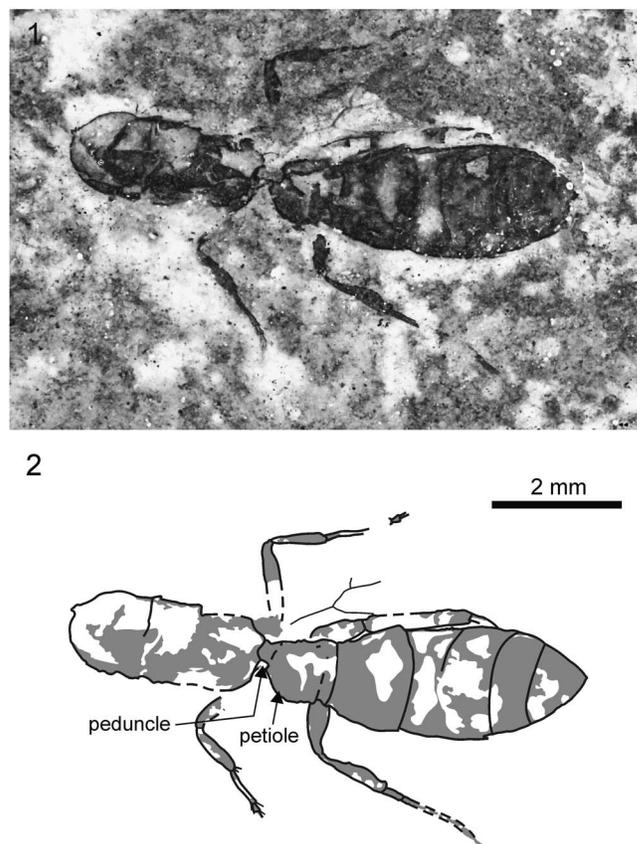


Figure 3. Amblyoponinae gen. et sp. indet., gyne, OU44898; (1) photograph; (2) line drawing.

Material.—Specimen OU44898; gyne, dorsoventrally compressed, head not preserved; deposited in the Department of Geology, University of Otago.

Occurrence.—Foulden Maar diatomite, Waipiata Volcanic Field, Otago, New Zealand; early Miocene.

Remarks.—The assignment of the fossil as an amblyoponine ant is based on the construction of the petiole and the general habitus; two features that have been regarded traditionally as reliable for the subfamily Amblyoponinae (Brown, 1960). Genera of Malagasy Amblyoponinae were revised by Yoshimura and Fisher (2012), who reassigned species of *Amblyopone* sensu lato into *Xymmer* Santschi, 1914, *Amblyopone* Erichson, 1842 sensu stricto and *Stigmatomma* Roger, 1859, based on male morphological characters, which are not applicable to the gyne from Foulden Maar, as are morphological characters of workers (e.g. Brown, 1960; Taylor, 1987). Two extant members of Amblyoponinae are present in the New Zealand fauna: the endemic *S. saundersi* (Forel, 1892) and the introduced *A. australis* Erichson, 1842; only gynes of the latter species approach the size of the fossil. In the absence of morphological characters such as the structure of mandibles and wing venation, we assign the fossil to tribe Amblyoponini without placement into an extinct or extant genus.

Published fossil Amblyoponinae include a winged male without generic placement from Foulden Maar (Kaulfuss et al.,

2014a), *Casaleia inversa* (Dlussky, 1981) (Kyrgyzstan, Middle Miocene), *C. longiventris* (Heer, 1849) (early Miocene, Croatia), *Myopopone sinensis* Zhang, 1989 (Shanwang, China, early Miocene) and, from the Eocene Messel pit in Germany *Stigmatomma groehni* (Dlussky, 2009), *S. electrinum* (Dlussky, 2009), and *C. eocenica* (Dlussky and Wedmann, 2012). Two of these species, *C. eocenica* and *C. longiventris*, were based on gynes, which can be readily distinguished from the gyne described here by a smaller body size and a much shorter and wider gaster (*C. eocenica*) and a wider petiole and first gastral segment, differing proportions of the gastral segments (in dorsal aspect) and a less pointed tip of the gaster (*C. longiventris*).

Subfamily Ectatomminae Emery, 1895

Genus *Rhytidoponera* Mayr, 1862

Rhytidoponera waipiata new species

Figure 4.1–4.3

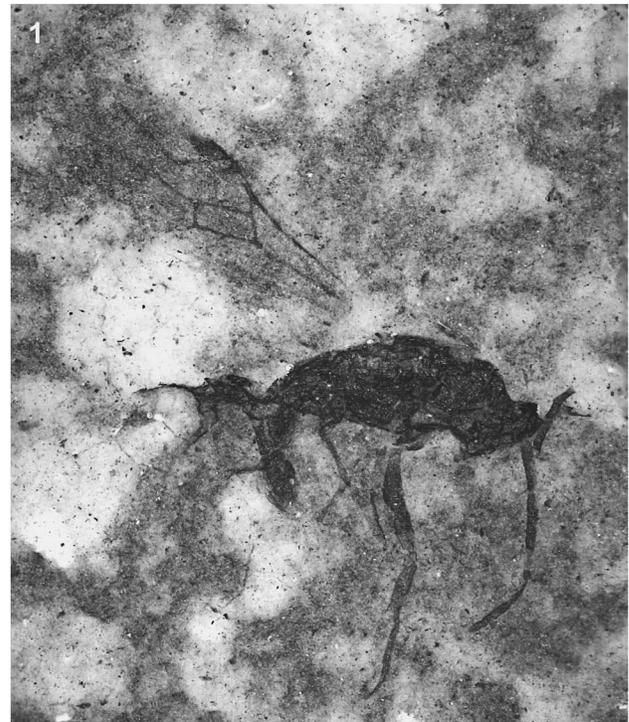
Diagnosis.—Gyne: Body length about 6 mm; petiole 1.8 times longer than high, with short peduncle and low node, somewhat angulated in side view; forewing with closed cells 1 + 2r, 3r, rm and mcu; cross-vein cu-a meets M + Cu near cell mcu, proximal to section 1M, at a distance less than cu-a length. May be distinguished from *R. kirghizorum* Dlussky, 1981 (Kyrgyzstan, Miocene) by body size (3.8 mm in *R. kirghizorum*) and form of the petiole (rounded in side view in *R. kirghizorum*).

Description.—Part and counterpart of winged gyne, partly preserved in lateral view; length of preserved compression 4.7 mm, estimated total body length about 6 mm. Outlines of head and mouth parts obscure, head apparently longer than wide; mandibles rather short and apparently triangulate. Scape 1.2 mm long, longer than head (in living ant extending more than one-third of its length beyond the posterior corners of the head), funicular joints longer than thick. Mesosoma elongate, 2.5 times longer than high (2.8 mm/1.1 mm); dorsum of propodeum gradually rounded in lateral view. Legs rather long, tibial spur visible only on fore tibia. Pretarsal claws (visible on a fragment of middle leg) with median tooth. Petiole 1.9 times longer than high (0.77 mm/0.41 mm), with short peduncle and low node, somewhat angulate in side view. Helcium projects from about mid-height of anterior face of first gastral segment; dorsum of first gastral tergite gradually rounded above the helcium. First gastral sternite anteriorly with sharp angle. Head, mesosoma and petiole with coarse sculpture, visible as rows of grooves along sutures (partially filled by sediment).

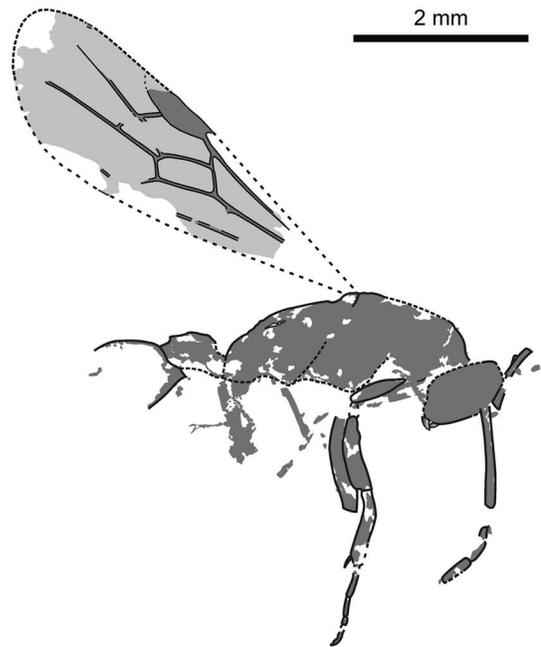
Wing with veins and knots partly preserved. Cells 1 + 2r, rm and mcu closed, cells 1r and cua probably closed. Cell mcu pentagonal, but vein section 2M very short. Cross-veins 2r-rs and r-m meeting RS almost at one point; cross-vein cu-a close to cell mcu: vein section 2M + Cu shorter than cu-a.

Etymology.—The species name refers to the Waipiata Volcanic Field, New Zealand, where the fossil was found.

Type.—Holotype OU44899 (part and counterpart); a laterally compressed gyne; deposited in the Department of Geology, University of Otago.



2



3

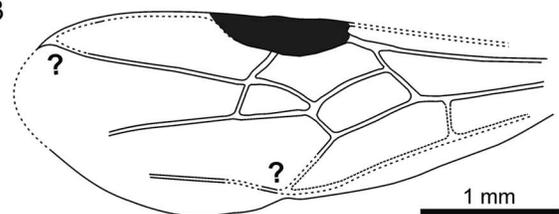


Figure 4. *Rhytidoponera waipiata* n. sp., gyne, holotype, OU44899; (1) photomicrograph; (2) line drawing of the holotype; (3) reconstruction of forewing.

Occurrence.—Foulden Maar diatomite, Waipiata Volcanic Field, Otago, New Zealand; early Miocene.

Remarks.—The distal position of the cross-vein cu-a is a character found in Myrmeciinae, Dorylinae and poneromorph subfamilies. The new species cannot belong to Myrmeciinae since they have longer mandibles (0.7–1.2 times as long as head). Dorylinae have wingless gynes (except most ants in the former subfamily Cerapachyinae) and differ in general wing venation. The poneromorph subfamily-group includes Amblyoponinae, Ectatomminae, Heteroponerinae, Paraponerinae, Ponerinae and Proceratiinae. Paraponerinae include the sole genus *Paraponera* F. Smith, 1858, with one extant and one extinct species from the Neotropical Region. The new species differs from *Paraponera* in many habitual characters. In Amblyoponinae, the helcium projects from a very high position on the anterior face of abdominal segment III and in Ponerinae the helcium projects from a very low position on the anterior face of abdominal segment III, the latter with a high vertical anterior face above the helcium. Proceratiinae have an extremely large abdominal segment III. These characters are not found in the new species, which may therefore belong to Ectatomminae or Heteroponerinae. These subfamilies include the genera *Ectatomma* F. Smith, 1858; *Gnamptogenys* Roger, 1863; *Rhytidoponera* Mayr, 1862; *Typhlomyrmex* Mayr, 1862; *Acanthoponera* Mayr, 1862; *Aulacopone* Arnoldi, 1930; and *Heteroponera* Mayr, 1887. The new species can be excluded from *Ectatomma*, *Typhlomyrmex*, and *Acanthoponera* because these genera are only known from the Neotropical Region. The known species of *Gnamptogenys*, *Aulacopone* and *Heteroponera* differ from the new species in having rather short legs and scapes, a more compact mesosoma, and often an angulated propodeum. Only some Australian *Rhytidoponera* have relatively long legs and a long scape, elongated mesosoma, and a long propodeum with a gradually rounded dorsum. We therefore assign the new species to the genus *Rhytidoponera*, subfamily Ectatomminae.

The only described extinct species of *Rhytidoponera* is *R. kirghizorum* Dlussky, 1981 reported from the Miocene of Chon-Tuz, Kotchkorka District, Kyrgyzstan. It differs from *R. waipiata* n. sp. by its smaller size (3.8 mm) and by the form of the petiole (rounded in side view).

Rhytidoponera gibsoni new species
Figure 5.1, 5.2

Diagnosis.—May be distinguished from gynes of *R. waipiata* n. sp. by the more robust mesosoma, shorter appendages, and the shape of the petiole with concave anterior and posterior and flat dorsal faces of petiole.

Description.—Gyne in lateral view; total body length 11.6 mm, gaster enormously long (probably swollen due to water drift before burial). Head 1.75 mm long, 1.3 times longer than wide. Mesosoma 3.3 mm long, robust, less than twice as long as high. Dorsal and declivous sides of propodeum form rounded obtuse angle. Declivous side several times longer than dorsal side of propodeum. Legs rather short and thick. Petiole 1.1 times longer

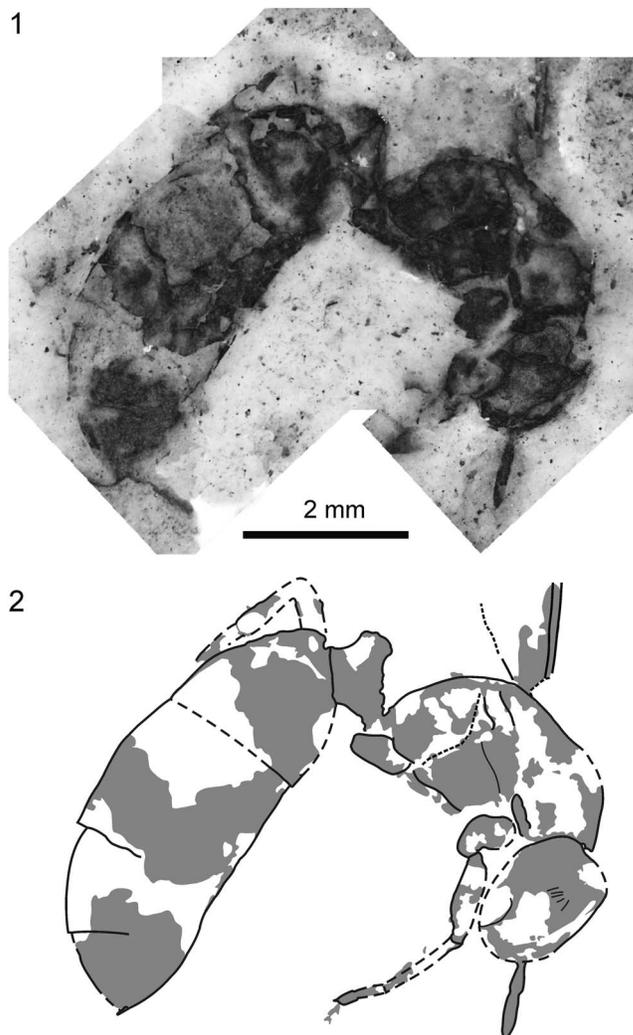


Figure 5. *Rhytidoponera gibsoni* n. sp., gyne, holotype, OU44900; (1) photomicrograph; (2) line drawing.

than high (1.12 mm/1.03 mm), with concave anterior and posterior sides and flat dorsal side. Tip of gaster acute with short sting.

Etymology.—The species name honors the Gibson family on whose property the Foulden Maar lagerstätte is located.

Type.—Holotype OU44900; a laterally compressed gyne; deposited in the Department of Geology, University of Otago.

Occurrence.—Foulden Maar diatomite, Waipiata Volcanic Field, Otago, New Zealand; early Miocene.

Remarks.—Although most key characters of *Rhytidoponera* are not preserved in the fossil, we assign the new species to this genus because its general habitus and particularly the distinctive petiole is very similar to some extant species of *Rhytidoponera*. *Rhytidoponera gibsoni* n. sp. differs from *R. waipiata* n. sp., described above, by the more robust mesosoma, shorter appendages, and by the shape of the petiole. Gynes of *Gnamptogenys europaea* (Mayr, 1868) in Baltic amber resemble *R. gibsoni* in the position of the helcium and by the robust

mesosoma. However, their propodeum is distinctly angulated and the petiolar node is rounded in side view.

Subfamily Ponerinae Lepeletier de Saint-Fargeau, 1835
 Tribe Ponerini Lepeletier de Saint-Fargeau, 1835
 Genus *Austroponera* Schmidt and Shattuck, 2014
Austroponera schneideri new species
 Figure 6.1, 6.2

Diagnosis.—Worker: A ponerine ant morphologically very similar to extant *Austroponera*, in particular *A. castanea* (Mayr, 1865) but may be distinguished from the latter by a more slender constitution and the slightly more posterior position of the eyes.

Description.—Worker, laterally compressed, middle and hind legs and most parts of antennae absent. Body length 5.8 mm, body without coarse sculpture. Mesosoma length 1.7 mm, petiole length 0.47 mm, petiole height 0.55 mm. Head length including mandibles 1.2 mm (1.0 mm without mandibles). Eyes nearly round, small, situated laterally, at about mid-length of head. Gena twice as long as maximum diameter of eye. Scape protruding slightly beyond the occipital margin of head. Middle segments of funiculus about as long as thick. Promesonotal dorsum slightly convex in side view, without distinct promesonotal groove. Mesopleural suture absent. Metanotal groove distinct. Propodeum angular in side view, with slightly convex dorsum, rounded angle, and nearly straight declivity;

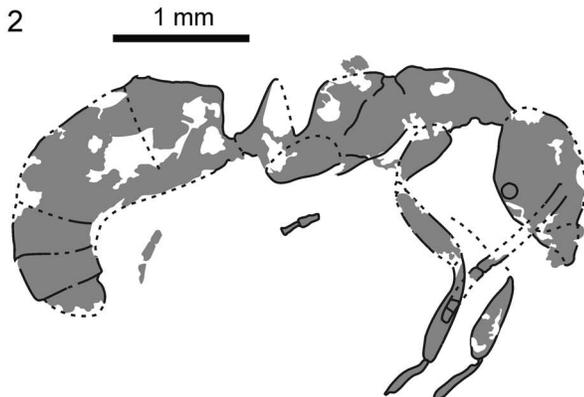


Figure 6. *Austroponera schneideri* n. sp., worker, holotype, OU44901; (1) photomicrograph; (2) line drawing.

propodeal declivity nearly as long as propodeal dorsum. Petiole nearly triangular in side view, 1.2 times higher than long, dorsal tip rounded. Mesosoma and petiole without specialized structures such as spines, teeth, tubercles, etc. Helcium projecting from a very low position on the anterior face of first gastral (III abdominal) segment, the latter having a high vertical anterior face above the helcium.

Etymology.—In honor of Jörg W. Schneider, emeritus professor at the Freiberg University of Mining and Technology, Germany.

Type.—Holotype OU44901; a laterally compressed worker; deposited in the Department of Geology, University of Otago.

Occurrence.—Foulden Maar diatomite, Waipiata Volcanic Field, Otago, New Zealand; early Miocene.

Remarks.—The position of the helcium and the form of the first gastral segment undoubtedly indicate that this species belongs to the tribe Ponerini. Its habitus is very similar to *Austroponera* Schmidt and Shattuck, 2014, particularly to the New Zealand endemic *A. castanea* (Mayr, 1865) (formerly *Pachycondyla castanea*) (Brown, 1958a, fig. 1; Schmidt and Shattuck, 2014, fig. 41). We therefore attribute the new species to *Austroponera*, although key characters of the genus (features of the clypeal margin and the mandibles, shape of the propodeal spiracle, etc.) are not discernable in the fossil. The new fossil species differs from *A. castanea* by a more slender constitution and the slightly more posterior position of the eyes. No other fossil species of *Austroponera* are known.

Subfamily Formicinae Latreille, 1809
 Genus *Myrmecorhynchus* André, 1896
Myrmecorhynchus novaeseelandiae new species
 Figure 7.1–7.3

Diagnosis.—Male: waist with one segment (petiole). Antennae 13-segmented, geniculate, scape long, protrudes beyond the occipital margin of the head, all funicular segments longer than thick. Propodeum gradually rounded in side view. Forewing with closed cells 1 + 2r, 3r and mcu; closed cell rm absent. Vein sections 5RS and 4M with joint start (rs-m lost); cross-vein cu-a displaced to the base of wing.

Description.—Part and counterpart of laterally compressed male. Body length about 6 mm, mesosoma length 2.2 mm, head length about 0.75 mm, head width about 0.85 mm. Head rounded, a little wider than long, mandibles presumably long, more than one-third of head length (outline of mandibles not visible). Antennae 13-segmented, geniculate, scape long, protrudes beyond the occipital margin of the head, all funicular segments longer than thick. Scutum overhangs pronotum. Propodeum gradually rounded in side view. Petiole indistinct. Genital parameres nearly as long as wide, with rounded tip.

Forewing 4.8 mm long, with closed cells 1 + 2r, 3r and mcu; closed rm absent. Pterostigma well developed. Vein sections 5RS and 4M with jointed start (rs-m lost). Cell 3r 4 times longer than wide. Cell 1 + 2r nearly three times longer than wide. Cell mcu trapezoid (RS + M appreciably shorter than

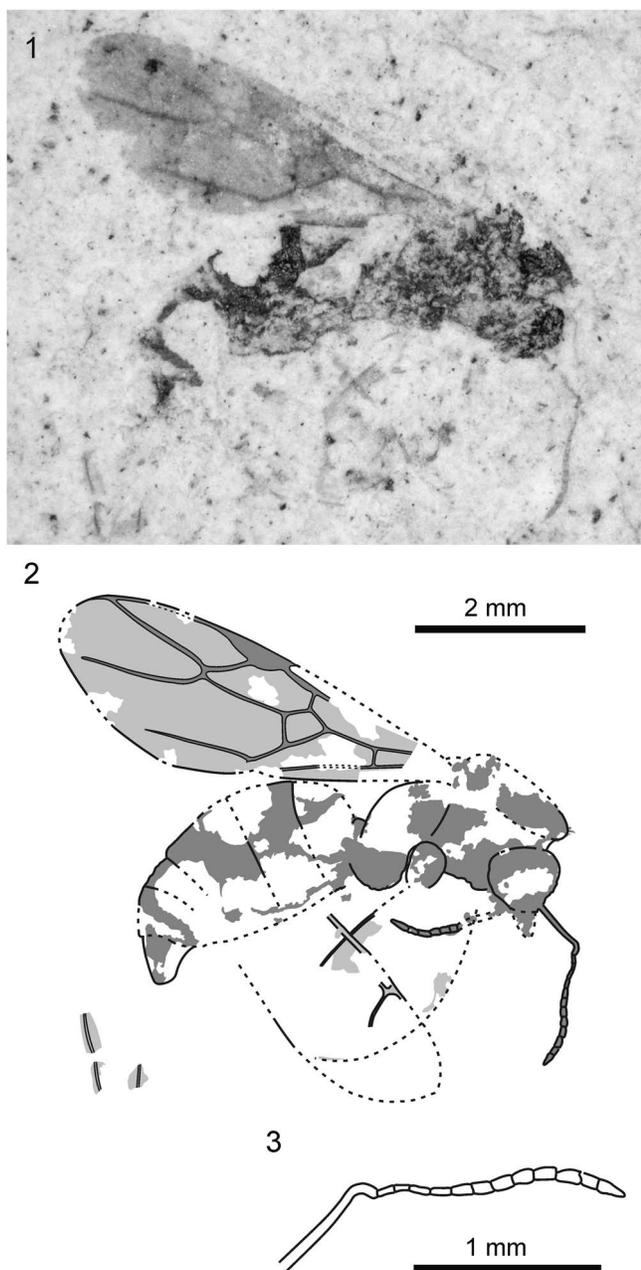


Figure 7. *Myrmecorhynchus novaeseelandiae* n. sp., male, holotype, OU44569; (1) photomicrograph; (2) line drawing; (3) line drawing of left antenna.

1Cu). Vein 1RS shorter than 1M. Cross-vein cu-a displaced to the base of wing; vein section 2M+Cu longer than 1Cu and three times as long as cu-a.

Etymology.—*Novaeseelandiae* refers to New Zealand, where this species was once native.

Type.—Holotype OU44569 (part and counterpart); a laterally compressed winged male; deposited in the Department of Geology, University of Otago.

Occurrence.—Foulden Maar diatomite, Waipiata Volcanic Field, Otago, New Zealand; early Miocene.

Remarks.—The wing venation of the new species is usual among genera of Formicinae. Some members of Dolichoderinae and Myrmicinae have a similar venation, but male representatives of these subfamilies possess antennae with a short scape. The six extant formicine species known from New Zealand are the endemics *Prolasius advenus* (F. Smith, 1862) and *Camponotus (Colobopsis) newzealandicus* Donisthorpe, 1940 and the introduced *Anoplolepis gracilipes* (F. Smith, 1857) and three species of *Paratrechina* Motschoulsky, 1863 (Brown, 1958a; Taylor, 1987; Don, 2007). All species of these genera have forewings without a closed cell mcu, so the new species cannot belong to these taxa.

Native species of the following 18 formicine genera are known in the extant Australasian fauna: *Calomyrmex* Emery, 1895a; *Camponotus* Mayr, 1861; *Echinopla* F. Smith, 1857; *Opisthopsis* Dalla Torre, 1893; *Polyrhachis* F. Smith, 1857 (tribe Camponotini Forel); *Acropyga* Roger, 1862; *Prolasius* Forel, 1892; *Stigmacros* Forel, 1905; *Teratomyrmex* McAreavey, 1957 (Lasiini Ashmead); *Melophorus* Lubbock, 1883 (Melophorini Forel); *Myrmecorhynchus* André, 1896; *Notoncus* Emery, 1895b; *Pseudonotoncus* Clark, 1934b (Myrmecorhynchini Wheeler); *Notostigma* Emery, 1920 (Notostigmatini Bolton); *Oecophylla* F. Smith, 1860 (Oecophyllini Emery); *Paratrechina* Motschoulsky, 1863; *Plagiolepis* Mayr, 1861; and *Pseudolasius* Emery, 1887 (Plagiolepidini Forel) (Taylor, 1987). Winged *Teratomyrmex* and *Pseudonotoncus* are not known. Amongst the remaining genera, the cell mcu is present only in *Opisthopsis*, *Myrmecorhynchus* and *Notoncus*, while wings of representatives of other genera are lacking this cell (Emery, 1925). In *Opisthopsis*, the cell mcu is either triangulate (*O. haddoni* Emery, 1893, *O. major* Forel, 1902) or absent (male of *O. respiciens moestus* Wheeler, 1918). In *Notoncus*, the cell mcu is present in gynes but absent in males. Only in *Myrmecorhynchus* both gynes and males have a trapezoid cell mcu (Clark, 1934a). Similar wing venations occur in Formicini Latreille (*Formica* Linnaeus, 1758; *Cataglyphis* Förster, 1850, etc.) and some Lasiini (*Lasius* Fabricius, 1804; *Acanthomyops* Mayr, 1862; *Myrmecocystus* Wesmael, 1838). However, all representatives of these genera inhabit the Northern Hemisphere, and there are no reasons to suppose that they were present in the Australasian region in the early Miocene. Similar wing venations are also present in *Gesomyrmex* Mayr, 1868 and *Dryomyrmex* Wheeler, 1915. The native range of extant *Gesomyrmex* extends from the highlands of southern Borneo north into western India. In the Eocene, they also lived on the territory of modern Europe (Dlussky et al., 2009). *Dryomyrmex* is known exclusively from late Eocene Baltic amber (Wheeler, 1915). The new species can be excluded from these genera because of the following differences: males of *Gesomyrmex* have much larger eyes and very short 8–11 segmented antennae. Only the gynes of *Dryomyrmex* are known and they possess 11-segmented antennae. Usually, in all known ants whose females have less than 12 antenna segments, males have less than 13 segments. We therefore consider the new species as a member of the genus *Myrmecorhynchus*. An additional argument in favor of *Myrmecorhynchus* is the similar length of mandibles in the new species, whereas males of the majority of other ants exhibit shorter mandibles.

Formicidae incertae sedis
Formicidae species A
Figure 8.1, 8.2

Description.—Forewing, visible length 3.7 mm. Closed cells 1+2r, 3r and mcu; closed rm absent. Pterostigma well developed. Vein sections 5RS and 4M with separate start (rs-m present). Cell 3r 3.8 times longer than wide. Cell 1+2r nearly 2.5 times as long as wide. Cell mcu trapezoid (RS+M appreciably shorter than 1Cu). Vein section 1RS nearly as long as 1M. Cross-vein cu-a displaced to the base of wing; vein section 2M+Cu a little longer than 1Cu, and 2.2 times as long as cu-a.

Material.—Specimen OU44903; a partly preserved forewing; deposited in the Department of Geology, University of Otago.

Occurrence.—Foulden Maar diatomite, Waipiata Volcanic Field, Otago, New Zealand; early Miocene.

Remarks.—The cross-vein cu-a displaced to the base of the forewing is a character found in Formicinae, Dolichoderinae, and Myrmicinae (Dlussky, 1981). However, in Formicinae the vein sections 5RS and 4M initiate jointed (cross-vein rs-m absent) and most Myrmicinae possess an open cell 3r. Thus, the fossil wing could belong to a representative of Dolichoderinae. It is very similar to forewings of the extant *Tapinoma ambiguum* Emery, 1925, but as all species of the *Tapinoma erraticum* group, including *T. ambiguum*, inhabit the Palearctic Region, this similarity is likely to represent convergence.

Formicidae Species B
Figure 9.1–9.3

Description.—Forewing, partly preserved in two fragments. Pterostigma well developed. Cells 1+2r, 3r, rm and mcu closed. Cell 3r 4.4 times longer than wide. Cross-vein rs-m more distal than r-rs, so cell rm pentagonal. Cell mcu pentagonal, 1.8 times longer than wide. Section 2M+Cu nearly as long as cross-vein cu-a.

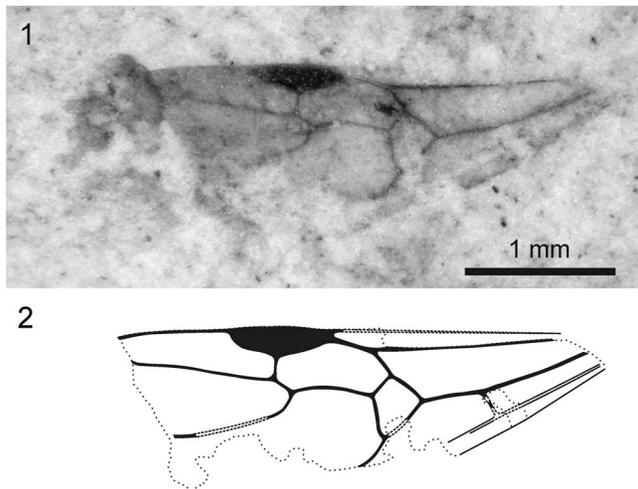


Figure 8. Formicidae species A, isolated forewing, OU44903; (1) photomicrograph; (2) line drawing.

Material.—Specimen OU44904; a partly preserved forewing; deposited in the Department of Geology, University of Otago.

Occurrence.—Foulden Maar diatomite, Waipiata Volcanic Field, Otago, New Zealand; early Miocene.

Remarks.—The position of cross-vein cu-a in this wing is typical for members of the poneromorph subfamilies. The only fossil poneromorph ant with preserved wing venation from New Zealand is *Rhytidoponera waipiata*, described above.

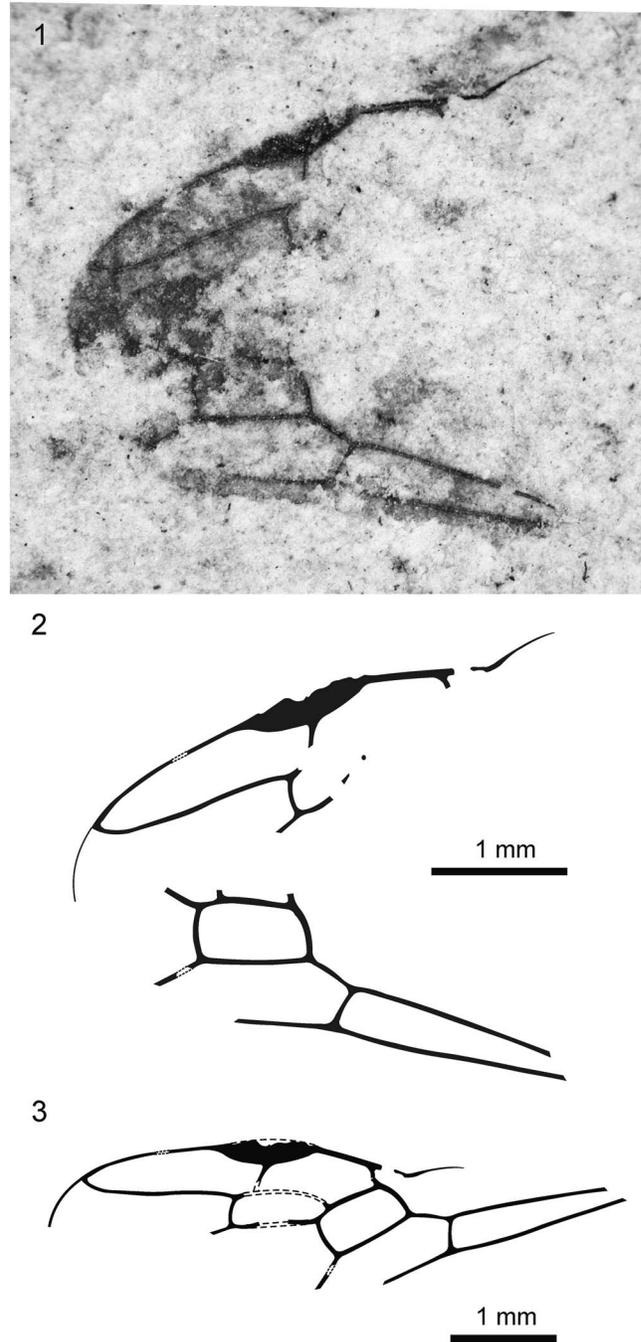


Figure 9. Formicidae species B, isolated forewing, OU44904; (1) photomicrograph; (2) line drawing; (3) reconstruction of the wing. The wing has been torn and opened up; the lower part in (1) and (2) is the hind portion of the wing that has been displaced downward and to the left.

The described wing cannot belong to *R. waipiata* since wings of this species have a shorter cell *rm* (this character is not quite authentic since the cell *rm* was reconstructed in both specimens) and cross-veins *r-rs* and *rs-m* starting from *RS* at the same point while in Formicidae species B *rs-m* initiates distinctly more distally than *r-rs*.

Formicidae Species C
Figure 10.1, 10.2

Description.—Forewing, 7.7 mm long, with closed cells 1 + 2r, 3r and *mcu*; closed *rm* absent. Pterostigma well developed. Vein sections 5RS and 4M with joint start (*rs-m* lost). Cell 3r 3.3 times longer than wide. Cell 1 + 2r nearly 2.6 times longer than wide. Cell *mcu* trapezoid (*RS* + *M* appreciably shorter than 1Cu). Vein 1RS nearly as long as 1M. Cross-vein *cu-a* displaced to the base of wing: vein section 2M + Cu a little shorter than 1Cu and nearly twice as long as *cu-a*.

Material.—Specimen OU44902; an isolated forewing; deposited in the Department of Geology, University of Otago.

Occurrence.—Foulden Maar diatomite, Waipiata Volcanic Field, Otago, New Zealand; early Miocene.

Remarks.—The wing venation of the fossil is usual in the subfamily Formicinae. The wing differs from those of *Myrmecorhynchus novaeseelandiae* n. sp., described above, by its larger size, the proportions of cells 1 + 2r and 3r, and the comparatively short vein section 2M + Cu. The two native genera of extant Formicinae in New Zealand, *Camponotus* and *Prolasius*, both have forewings without a closed cell *mcu*.

Discussion

Comparison with the fossil record of Formicidae.—The ants described here represent the first fossil myrmecofauna from New Zealand and provide a preliminary account of early

Miocene (23 Ma) ant diversity in New Zealand and Australasia. Until now, the published record of fossil Formicidae from Australasia comprised the subfamilies Ponerinae and Dolichoderinae in Plio-Pleistocene copal from Allendale, Victoria, Australia (Hills, 1957; Oke, 1957). The few pre-Pleistocene ant fossils have not yet been described (Archer et al., 1991; Hand et al., 2010) and those from the Cape York amber may represent a fauna from southeastern Asia (Sonibare et al., 2014). Including the recently published record of an *Amblyopone*-like ant (Kaulfuss et al., 2014a), the taxa from Foulden Maar now establish the subfamilies Amblyoponinae, Ectatomminae, Formicinae and Ponerinae in early Miocene (23 Ma) Australasia, with a presence in warm-temperate to subtropical New Zealand (approx. 45°S), shortly after a period of major marine transgression of the Zealandian subcontinent at ca. 25 Ma (New Zealand paleogeography and paleoclimate summarized in Lee et al., 2001; Buckley et al., 2014, and references therein). Members of the subfamily Dolichoderinae were probably also present in the early Miocene fauna, as indicated by the isolated wing of Formicidae sp. A, but this needs to be confirmed by more complete fossils. Fossil records of Amblyoponinae from Croatia, Kyrgyzstan, China, and Foulden Maar in southern New Zealand indicate a wide geographic distribution of this subfamily during the Miocene epoch (Fig. 11), whereas in the Eocene amblyoponines are only known from Germany.

On the genus level, the formicine *Myrmecorhynchus novaeseelandiae* n. sp. and the ponerine *Austroponera schneideri* n. sp. are the first fossil records globally, thus extending the fossil age of these two genera back to the early Miocene. *Myrmecorhynchus* is here reported from outside Australia for the first time, demonstrating a wider distribution of this genus within the Australasian region in the past. *Rhytidoponera* is a large genus containing 104 extant species native to New Guinea, the Solomon Islands, New Caledonia, Australia, and eastern Indonesia (Bolton, 2014; Shattuck, 1999). The only previously known fossil of *Rhytidoponera*, a poorly preserved gyne described as *R. kirghizorum* from the middle-upper Miocene of Kyrgyzstan (Dlussky, 1981; stratigraphic position in Prokofiev, 2007) indicates that the genus was formerly present in the Palearctic region. *Rhytidoponera waipiata* n. sp. and *R. gibsoni* n. sp. from Foulden Maar extend the fossil age of this genus back to ~23 Ma and indicate that the geographic range of *Rhytidoponera* included southern New Zealand in the early Miocene. *Ectatomma (Rhytidoponera) europaeum* (Mayr, 1868) described from Baltic amber was allocated to *Gnamptogenys europaea* within Ponerinae (Brown, 1958b).

Comparison with the Recent Australasian ant fauna.—Amblyoponinae, Ectatomminae, Dolichoderinae, Formicinae, and Ponerinae are diverse and widely distributed in warm temperate to tropical regions in modern Australasia (Ward, 1985; Janda et al., 2008; Bolton, 2014) but they are low-diverse or absent in cooler climates on the isolated New Zealand land mass in the Southern Pacific. For instance, there are no native species of Ectatomminae and Dolichoderinae in New Zealand, although introduced species are now established or doubtfully established (Don, 2007). Subfamilies Amblyoponinae and Formicinae are represented in New Zealand by only one native species each, and Ponerinae include merely two species. It has been suggested

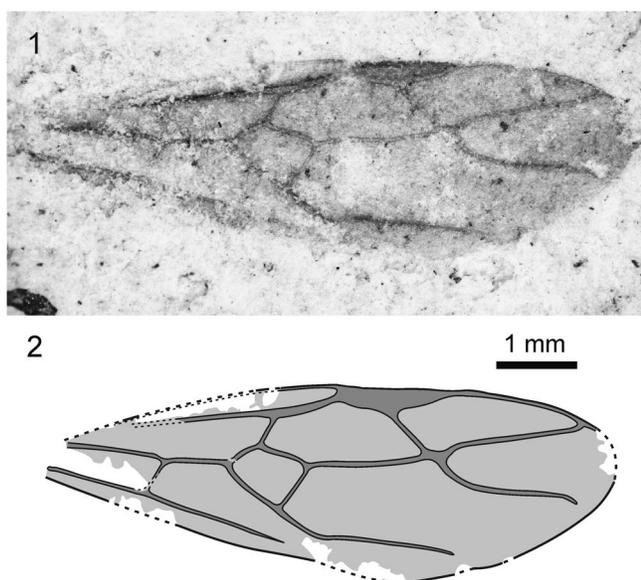


Figure 10. Formicidae species C, isolated forewing, OU44902; (1) photomicrograph; (2) line drawing.

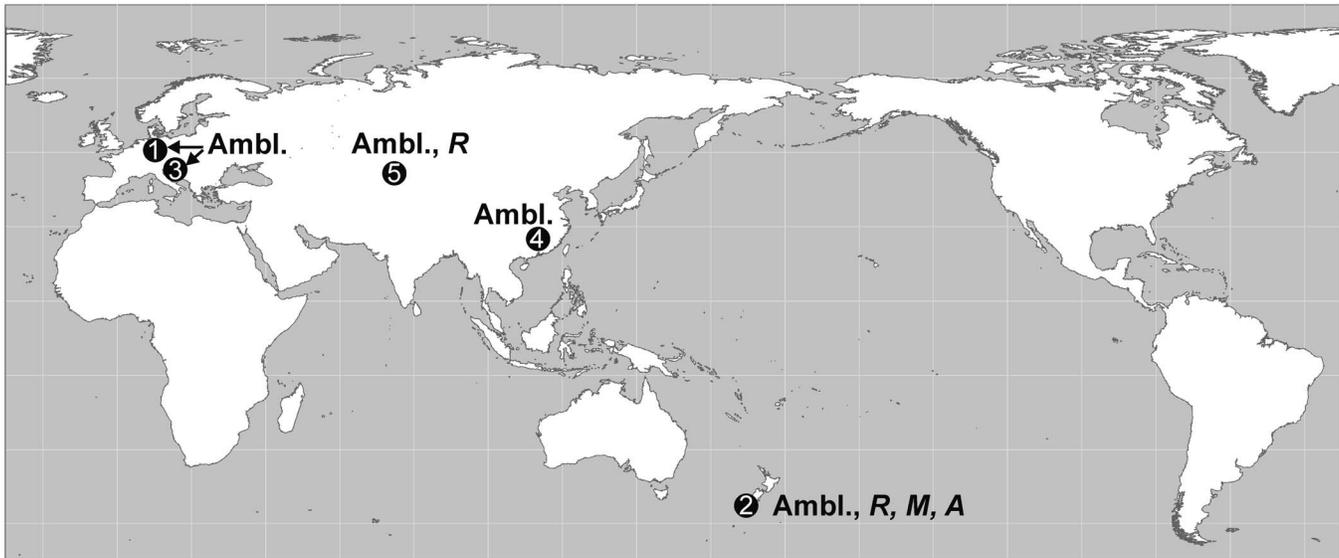


Figure 11. World map showing the occurrence of published fossil members of subfamily Amblyoponinae (Ambl.) and extinct species of *Rhytidoponera* (R), *Myrmecorhynchus* (M) and *Austroponera* (A) in one Eocene and four Miocene localities. (1) Messel Maar, Germany, Eocene (Lutetian): Amblyoponinae: *Stigmatomma groehni*, *S. electrinum* and *Casaleia eocenica*; (2) Foulden Maar, New Zealand, early Miocene: Amblyoponinae gen. et. sp. indet., *Rhytidoponera waipiata* n. sp., *Rhytidoponera gibsoni* n. sp., *Myrmecorhynchus novaeseelandiae* n. sp., *Austroponera schneideri* n. sp.; (3) Radoboj, Croatia, early Miocene: Amblyoponinae: *Casaleia longiventris*; (4) Shanwang Formation, China, middle Miocene: Amblyoponinae: *Myopopone sinensis*; (5) Kotchkorka District, Kyrgyzstan, middle Miocene: Amblyoponinae: *Casaleia inversa*, *Rhytidoponera*: *R. kirghizorum*.

that the few ants native to New Zealand are the relict of a more diverse fauna in the past (Watt, 1975; Gibbs, 2006; Don, 2007) but fossil evidence was missing until now. The small fossil myrmecofauna from Foulden Maar demonstrates for the first time that the early Miocene fauna indeed contained taxa that are now extinct in New Zealand, including *Rhytidoponera* and subfamily Ectatomminae in general, the formicine *Myrmecorhynchus*, now confined to Australia, as well as possibly subfamily Dolichoderinae. Similarly, Amblyoponinae seem to have been more diverse in the early Miocene fauna, with two fossil taxa at Foulden Maar but only one native species, *Stigmatomma saundersi*, in the modern fauna. This confirms previous suggestions of a long establishment of Amblyoponinae in New Zealand, which were based on the wide distribution of the extant *S. saundersi* on the North and South Islands and offshore islands such as Three Kings and Chatham Islands (Brown, 1958a, 1973; Don, 2007).

Only one genus, the ponerine *Austroponera* Schmidt and Shattuck 2014, is present in the taphocoenosis at Foulden Maar and in the modern New Zealand fauna. It is a small genus containing two species in northern parts of New Zealand (*A. castanea* and *A. castaneicolor*) and one species, *A. rufonigra* (Clark, 1934a), in Australia. *Austroponera schneideri* n. sp. described herein provides rare fossil evidence for the antiquity dating back to at least 23 Ma of some New Zealand insect genera, as has previously been shown for the bibionid *Dilophus* Meigen, 1803 from the Eocene (Harris, 1983), the termite *Stolotermes* and the aradid *Aneurus* Curtis, 1825 from the early Miocene (Kaulfuss et al., 2010, 2011) and at least two Miocene beetle genera yet to be described in detail (Kaulfuss et al., 2014b).

In the absence of post-early Miocene Formicidae fossils in New Zealand, the timing of extinction of the above mentioned

ant subfamilies and genera is currently not assessable. A major diversity decline and extinction due to late Miocene to Pliocene climate cooling and Pleistocene glacial cycles has been shown for many subtropical floral elements such as eucalypts, *Araucaria*, the *Brassospora* group of *Nothofagus* and Casuarinaceae, accompanied by a simultaneous appearance of temperate and alpine plants in New Zealand (McGowran et al., 2000; Lee et al., 2001, 2012; Gibbs, 2006). For invertebrates, molecular evidence indicates radiation of many groups, such as weta, cicadas, grasshoppers, cockroaches, and snails, in response to newly formed alpine habitats during the Pliocene, and local extinction of many groups during Pleistocene glacial cycles (Watt, 1975; Gibbs, 2006; Goldberg et al., 2008 and references therein). Climate variables such as temperature, rainfall, and humidity are key factors in ant distribution (Hölldobler and Wilson, 1990; Kaspari et al., 2000). Thus, it is very likely that climate cooling since the late Miocene was also a main factor for the complete loss (Ectatomminae, Dolichoderinae, *Myrmecorhynchus*) or local extinction (north shift of *Austroponera*) of the early Miocene, warm-temperate to subtropical ant fauna in New Zealand.

The effect of major late Oligocene (ca. 25 Ma) marine transgression on the New Zealand ant fauna (and other terrestrial arthropods) is very poorly known (Buckley et al., 2014), mainly due to the lack of fossils. Our results show that some ant genera from Foulden Maar are no longer present in New Zealand, which suggests that the early Miocene myrmecofauna at 23 Ma, shortly after the maximum marine transgression, was taxonomically different and possibly more diverse. We thus conclude that the previous assumption that the small extant New Zealand myrmecofauna might reflect the failure of ants to re-colonize New Zealand after the Oligocene marine transgression (Cranston, 2009) is no longer valid.

Acknowledgments

Our thanks go to the Gibson family and Featherston Resources Ltd. for allowing us access to the fossil site at Foulden Maar. We are grateful to B. Barratt, A.C. Harris, M. Solórzano Kraemer, S. Martin, R. Debbie, and M. Archer for helpful information and literature on living and fossil ants; K. Perfilieva for help in the interpretation of wing venations; the Queensland Museum for providing photographs of Australian ant specimens; and the Department of Botany, Otago University for providing photographic equipment. D.E. and W.G. Lee and Vincent Perrichot provided helpful and constructive comments on the manuscript. Our study has been funded by the Russian Foundation for Basic Research (grant nos. 08-04-00701 and 11-04-00421), and the University of Otago, Division of Science Scholarship, and the Marsden Fund by the Royal Society of New Zealand (awarded to D.E. Lee, University of Otago).

References

- André, E., 1896, Fourmis nouvelles d'Asie et d'Australie: *Revista de Entomologia*, v. 15, p. 251–265.
- Archer, M., Hand, S., and Godthelp, H., 1991, *Australia's Lost World. Prehistoric Animals of Riversleigh*, Bloomington, Indiana University Press, 264 p.
- Archibald, S.B., Cover, S.P., and Moreau, C.S., 2006, Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmecinae): *Annals of the Entomological Society of America*, v. 99(3), p. 487–523.
- Arillo, A., and Ortuno, V.M., 2005, Catalogue of fossil insect species described from Dominican amber (Miocene): *Stuttgarter Beiträge zur Naturkunde B*, v. 352, 68 p.
- Arnoldi, K.V., 1930, Studien über die Systematik der Ameisen, IV, *Aulacopone*, eine neue Ponerinengattung (Formicidae) in Russland: *Zoologischer Anzeiger*, v. 89, p. 139–144.
- Bannister, J.M., Lee, D.E., and Raine, J.I., 2005, Morphology and palaeoenvironmental context of *Fouldenia staminosa*, a fossil flower with associated pollen from early Miocene Otago, New Zealand: *New Zealand Journal of Botany*, v. 43, p. 515–525.
- Bannister, J.M., Conran, J.G., and Lee, D.E., 2012, Lauraceae from rainforest surrounding an early Miocene maar lake, Otago, southern New Zealand: *Review of Palaeobotany and Palynology*, v. 178, p. 13–34.
- Bolton, B., 1994, *Identification guide to the ant genera of the world*, Cambridge, Harvard University Press, 222 p.
- Bolton, B.G., 2014, An online catalog of the ants of the world: <http://www.antcat.org/> (accessed July 2014).
- Brown, W.L., 1958a, A review of the ants of New Zealand (Hymenoptera): *Acta Hymenopterologica*, v. 1(1), p. 1–50.
- Brown, W.L., 1958b, Contributions toward a reclassification of the Formicidae, II, Tribe Ectatommini (Hymenoptera): *Bulletin of the Museum of Comparative Zoology at Harvard College*, v. 118, p. 175–362.
- Brown, W.L., 1960, Contribution towards a reclassification of the Formicidae, III, Tribe Amblyoponini (Hymenoptera): *Bulletin of the Museum of Comparative Zoology*, v. 122, p. 145–230.
- Brown, W.L., 1973, A comparison of the Hylean and Congo-West African rain forest ant faunas, in Meggers, B.J., Ayensu, E.S., and Duckworth, W.D., eds., *Tropical Forest Ecosystems in Africa and South-America: A Comparative Review*, Washington DC, Smithsonian Institute Press, p. 161–185.
- Buckley, T.R., Krosch, M., and Leschen, R.A.B., 2014, Evolution of New Zealand insects: summary and prospectus for future research: *Austral Entomology*, v. 54, p. 1–27.
- Carpenter, F.M., 1930, The fossil ants of North America: *Bulletin of the Museum of Comparative Zoology at Harvard College*, v. 70, p. 1–66.
- Clark, J., 1934a, New Australian ants: *Memoirs of the National Museum of Victoria*, v. 8, p. 21–47.
- Clark, J., 1934b, Ants from the Otway Ranges: *Memoirs of the National Museum of Victoria*, v. 8, p. 48–73.
- Curtis, J., 1825, *British Entomology*, v. 2: London, R. Taylor, p. 51–98.
- Cranston, P.S., 2009, Biodiversity of Australasian insects, in Footitt, R., and Adler, P., eds., *Insect Biodiversity: Science and Society*, Chichester, Wiley-Blackwell, p. 83–106.
- Dalla Torre, K.W., 1893, *Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus*, v. 7, Formicidae (Heterogyna), Leipzig, W. Engelmann, 289 p.
- Dlussky, G.M., 1981, Miocene ants (Hymenoptera, Formicidae) of the USSR, in Vishnjakova, V.N., Dlussky, G.M., and Pritykina, L.N., eds., *New fossil insects from the territory of the USSR*, Moscow, Nauka Press, Moscow, p. 64–83. [in Russian]
- Dlussky, G.M., 2009, The ant subfamilies Ponerinae, Cerapachyinae, and Pseudomyrmecinae (Hymenoptera, Formicidae) in the late Eocene Ambers of Europe: *Paleontological Journal*, v. 43(9), p. 1043–1086.
- Dlussky, G.M., and Rasnitsyn, A.P., 2002, Ants (Hymenoptera: Formicidae) of Formation Green River and some other Middle Eocene deposits of North America: *Russian Entomological Journal*, v. 11(4), p. 411–436.
- Dlussky, G.M., and Perfilieva, K.S., 2003, Paleogene ants of the genus *Archimyrmex* Cockerell, 1923 (Hymenoptera, Formicidae, Myrmecinae): *Paleontological Journal*, v. 37(1), p. 39–47.
- Dlussky, G.M., and Rasnitsyn, A.P., 2007, Paleontological record and stages of ant evolution: *Uspehi Sovremennoj Biologii*, v. 127(2), p. 118–134. [in Russian]
- Dlussky, G.M., and Rasnitsyn, A.P., 2009, Ants (Insecta: Vespida: Formicidae) in the upper Eocene amber of Central and Eastern Europe: *Paleontological Journal*, v. 43(9), p. 1024–1042.
- Dlussky, G.M., and Wedmann, S., 2012, The poneromorph ants (Hymenoptera, Formicidae: Amblyoponinae, Ectatomminae, Ponerinae) of Grube Messel, Germany: high biodiversity in the Eocene: *Journal of Systematic Palaeontology*, v. 10, p. 725–753.
- Dlussky, G.M., Wappler, T., and Wedmann, S., 2009, Fossil ants of the genus *Gesomyrmex* Mayr (Hymenoptera, Formicidae) from the Eocene of Europe and remarks on the evolution of arboreal ant communities: *Zootaxa*, v. 2031, p. 1–20.
- Don, W., 2007, *Ants of New Zealand*, Dunedin, Otago University Press, 239 p.
- Donisthorpe, H., 1940, Descriptions of new species of ants (Hym., Formicidae) from various localities: *Annals and Magazine of Natural History*, v. 11(5), p. 39–48.
- Emery, C., 1887, *Catalogo delle formiche esistenti nelle collezioni del Museo Civico di Genova, parte terza, formiche della regione Indo-Malese e dell'Australia*: *Annali del Museo Civico di Storia Naturale Giacomo Doria*, v. 5(25), p. 427–473.
- Emery, C., 1893, *Formicides de l' Archipel Malais*: *Revue Suisse de Zoologie*, v. 1, p. 187–229.
- Emery, C., 1895a, Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna: *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, v. 8, p. 257–360.
- Emery, C., 1895b, Descriptions de quelques fourmis nouvelles d'Australie: *Annales de la Société Entomologique de Belgique*, v. 39, p. 345–358.
- Emery, C., 1920, *Le genre Camonotus* Mayr. Nouvel essai de la subdivision en sous-genres: *Revue de Zoologie Africaine*, v. 8, p. 229–260.
- Emery, C., 1925, *Hymenoptera Fam. Formicidae. Subfam: Formicinae: Genera Insectorum*, v. 183, 302 p.
- Erichson, W.F., 1842, Beitrag zur Insecten-Fauna von Vandiemensland, mit besonderer Berücksichtigung der geographischen Verbreitung der Insecten: *Archiv für Naturgeschichte*, v. 8(1), p. 83–287.
- Fabricius, J.C., 1804, *Systema Piezatorum secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus*, Brunswick, C. Reichard, 439 p.
- Förster, A., 1850, Eine Centurie neuer Hymenopteren. Zweite Dekade: Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens, v. 7, p. 485–500.
- Forel, A., 1890, *Aenicetus-Typhlata* découverte de M. Wroughton. Nouveaux genres de Formicides: *Annales de la Société Entomologique de Belgique*, v. 34, p. 102–113.
- Forel, A., 1892, Die Ameisen Neu-Seelands: *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, v. 8, p. 331–343.
- Forel, A., 1895, Nouvelles fourmis de diverses provenances, surtout d'Australie: *Annales de la Société Entomologique de Belgique*, v. 39, p. 41–49.
- Forel, A., 1901, Variétés myrmécologiques: *Annales de la Société Entomologique de Belgique*, v. 45, p. 334–382.
- Forel, A., 1902, Fourmis nouvelles d'Australie: *Revue Suisse de Zoologie*, v. 10, p. 405–548.
- Forel, A., 1905, *Miscellanea myrmécologiques II*: *Annales de la Société Entomologique de Belgique*, v. 49, p. 155–185.
- Gibbs, G., 2006, *Ghosts of Gondwana. The History of Life in New Zealand*, Nelson, Craig Potton, 232 p.
- Goldberg, J.S., Treweek, A., and Paterson, A.M., 2008, Evolution of New Zealand's terrestrial fauna: a review of molecular evidence: *Philosophical Transactions of the Royal Society B*, v. 363, p. 3319–3334.
- Grimaldi, D., and Agosti, D., 2000, A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants: *PNAS*, v. 97(25), p. 13678–13683.

- Grimaldi, D., and Engel, M.S., 2005, Evolution of the insects: Cambridge University Press, 755 p.
- Hand, S., Archer, M., Bickel, D., Creaser, P., Dettmann, M., Godthelp, H., Jones, A., and Wicks, D., 2010, Australian Cape York Amber, in Penney, D., ed., Biodiversity of Fossils in Amber from the Major World Deposits, Manchester, Siri Scientific Press, p. 69–79.
- Harris, A.C., 1983, An Eocene larval insect fossil (Diptera: Bibionidae) from North Otago, New Zealand: Journal of the Royal Society of New Zealand, v. 13, p. 93–105.
- Harris, A.C., Bannister, J.M., and Lee, D.E., 2007, Fossil scale insects (Hemiptera, Coccoidea, Diaspididae) in life position on an angiosperm leaf from an early Miocene lake deposit, Otago, New Zealand: Journal of the Royal Society of New Zealand, v. 37(1), p. 1–13.
- Harris, R.J., and Berry, J.A., 2001, Confirmation of the establishment of three adventive ants (Hymenoptera: Formicidae) in New Zealand: *Cardiocondyla intutor* Forel, *Ponera leae* Forel, *Mayriella abstinens* Forel: New Zealand Entomologist, v. 24, p. 53–56.
- Harrison, T., Msuya, C.P., Murray, A.M., Jacobs, B.F., Báez, A.M., Mundil, R., and Ludwig, K.R., 2001, Paleontological investigations at the Eocene locality of Mahenge in North-Central Tanzania, East Africa, in Gunell, G.F., ed., Eocene Biodiversity: Unusual occurrences and rarely sampled habitats: Topics in Geobiology, v. 18, p. 40–74.
- Heer, O., 1849, Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Zweiter Theil: Heuschrecken, Florfliegen, Aderflügler, Schmetterlinge und Fliegen, Leipzig, W. Engelmann, 264 p.
- Hills, E.S., 1957, Fossiliferous Tertiary resin from Allendale, Victoria: Proceedings of the Royal Society of Victoria, v. 69, p. 15–20.
- Hölldobler, B., and Wilson, E.O., 1990, The Ants: Cambridge, Massachusetts, Harvard University Press, 228 p.
- Janda, M., Alpert, G., and Borowiec, M., 2008, Checklist of ants described and recorded from New Guinea and associated islands: <http://www.new-guineants.org/> (accessed July 2014).
- Kaspari, M., Alonso, L., and O'Donnell, S.O., 2000, Three energy variables predict ant abundance at a geographical scale: Proceedings of the Royal Society, B, v. 267, p. 485–489.
- Kaulfuss, U., Harris, A.C., and Lee, D.E., 2010, A new fossil termite (Isoptera, Stolotermitidae, Stolotermes) from the early Miocene of Otago, New Zealand: Acta Geologica Sinica, v. 84, p. 705–709.
- Kaulfuss, U., Wappler, T., Heiss, E., and Larivière, M.-L., 2011, *Aneurys* sp. from the early Miocene Foulden Maar, New Zealand: the first Southern Hemisphere record of fossil Aradidae (Insecta: Hemiptera: Heteroptera): Journal of the Royal Society of New Zealand, v. 41, p. 279–285.
- Kaulfuss, U., Harris, A.C., Conran, J.G., and Lee, D.E., 2014a, An early Miocene ant (subfam. Amblyoponinae) from Foulden Maar: the first fossil Hymenoptera from New Zealand: Alcheringa, v. 38 (doi, p. 10.1080/03115518.2014.928181).
- Kaulfuss, U., Lee, D.E., Barratt, B.I.P., Leschen, R.A.B., Larivière, M.-C., Dlussky, G.M., Henderson, I.M., and Harris, A.C., 2014b, A diverse fossil terrestrial arthropod fauna from New Zealand: evidence from the early Miocene Foulden Maar fossil lagerstätte: Lethaia, (doi, p. 10.1080/03115518.2014.928181).
- LaPolla, J.S., Dlussky, G.M., and Perrichot, V., 2013, Ants and the fossil record: Annual Review of Entomology, v. 58, p. 609–630.
- Lee, D.E., Lee, W.G., and Mortimer, N., 2001, Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to paleogeography and climate: Australian Journal of Botany, v. 49, p. 341–356.
- Lee, D.E., Conran, J.G., Lindqvist, J.K., Bannister, J.M., and Mildenhall, D.C., 2012, New Zealand Eocene, Oligocene and Miocene macrofossil and pollen records and modern plant distributions in the Southern Hemisphere: Botanical Review, v. 78, p. 235–260.
- Lindqvist, J.K., and Lee, D.E., 2009, High-frequency paleoclimate signals from Foulden Maar, Waipiata Volcanic Field, southern New Zealand: an early Miocene varved lacustrine diatomite deposit: Sedimentary Geology, v. 222, p. 98–110.
- Linnaeus, C., 1758, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, Tomus I, Editio decima, reformata: Stockholm, L. Salvii, 824 p.
- Lubbock, J., 1883, Observations on ants, bees, and wasps, part X, with a description of a new genus of honey-ant: Journal of the Linnean Society of London, Zoology, v. 17, p. 41–52.
- Mayr, G., 1887, Südamerikanische Formiciden: Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, v. 37, p. 511–632.
- Mayr, G.L., 1861, Die europäischen Formiciden, Nach der analytischen Methode bearbeitet, Wien, Gerolds Sohn, 80 p.
- Mayr, G.L., 1862, Myrmecologische Studien: Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, v. 12, p. 649–776.
- Mayr, G.L., 1865, Formicidae, in Reise der Österreichischen Fregatte “Novara” um die Erde in den Jahren 1857, 1858, 1859, band II, abtheilung 1, Wien, Gerolds Sohn, 119 p.
- Mayr, G.L., 1868, Die Ameisen des baltischen Bernsteins: Beiträge zur Naturkunde Preussens, v. 1, p. 1–102.
- McAreevey, J.J., 1957, Revision of the genus *Stigmacros* Forel: Memoirs of the National Museum of Victoria, v. 21, p. 7–64.
- McGowran, B., Archer, M., Bock, P., Darragh, T.A., Godthelp, H., Hageman, S., ...Warne, M., 2000, Australasian palaeobiography: the Palaeogene and Neogene record, in Wright, A.J., Young, G.C., Talent, J.A., and Laurie, J.R., eds., Palaeobiogeography of Australian faunas and floras: Association of Australian Palaeontologists Memoir, v. 23, p. 405–470.
- Meigen, J.W., 1803, Versuch einer neuen Gattungstheilung der europäischen zweiflügeligen Insekten: Magazin für Naturkunde, v. 2, p. 259–281.
- Mildenhall, D.C., Kennedy, E.M., Lee, D.E., Kaulfuss, U., Bannister, J.M., Fox, B., and Conran, J.G., 2014, Palynology of the early Miocene Foulden Maar, Otago, New Zealand: diversity following destruction: Review of Palaeobotany and Palynology, v. 204, p. 27–42.
- Motschoulsky, V.I., 1863, Essai d'un catalogue des insectes de l'île Ceylan: Bulletin de la Société Impériale des Naturalistes de Moscou, v. 36, p. 1–153.
- Oke, C.G., 1957, Fossil insecta from Cainozoic Resin at Allendale, Victoria: Proceedings of the Royal Society of Victoria, v. 69, p. 29–31.
- Perrichot, V., Antoine, P.-O., Salas-Gismondi, R., Flynn, J.J., and Engel, M.S., 2014, The genus *Macroteleia* Westwood in Middle Miocene amber from Peru (Hymenoptera, Platygastridae s.l., Scelioninae): ZooKeys, v. 426, p. 119–127.
- Pole, M., 1996, Plant macrofossils from the Foulden Hills Diatomite (Miocene), Central Otago, New Zealand: Journal of the Royal Society of New Zealand, v. 26(1), p. 1–39.
- Prokofiev, A.M., 2007, Redescription of a Fossil Loach *Triplophysa opinata* (Yakowlew, 1959) from the Miocene of Kirgizia (Balitoridae: Nemacheilinae): Journal of Ichthyology, v. 47(1), p. 26–31.
- Rasnitsyn, A.P., 1980, The origin and evolution of hymenopterous insects: Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR, v. 174, p. 1–192. [in Russian]
- Roger, J., 1859, Beiträge zur Kenntniss der Ameisenfauna der Mittelmeerlande I: Berliner Entomologische Zeitschrift, v. 3, p. 225–259.
- Roger, J., 1862, Einige neue exotische Ameisen-Gattungen und Arten: Berliner Entomologischer Anzeiger, v. 6, p. 233–254.
- Roger, J., 1863, Die neu aufgeführten Gattungen und Arten meines Formiciden-Verzeichnisses nebst Ergänzung einiger früher gegebenen Beschreibungen: Berliner Entomologische Zeitschrift, v. 7, p. 131–214.
- Rossi de Garcia, E., 1983, Insectos fósiles en la Formación Ventana (Eoceno): Provincia de Neuquén: Revista de la Asociación Geológica Argentina, v. 38, p. 17–23.
- Rust, J., and Andersen, N.M., 1999, Giant ants from the Paleogene of Denmark with a discussion of the fossil history and early evolution of ants (Hymenoptera: Formicidae): Zoological Journal of the Linnean Society, v. 125, p. 331–348.
- Rust, J. et al., 2010, Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India: PNAS, v. 107(43), p. 18360–18365.
- Santschi, F., 1914, Formicides de l'Afrique occidentale et australe du voyage de Mr. le Professeur F. Silvestri: Bollettino del Laboratorio di Zoologia Generale e Agraria della Reale Scuola Superiore d'Agricoltura, v. 8, p. 309–385.
- Sarnat, E.M., and Economo, E.P., 2012, Ants of Fiji, Berkeley, University of California Press, 384 p.
- Schmidt, C.A., and Shattuck, S.O., 2014, The Higher Classification of the Ant Subfamily Ponerinae (Hymenoptera: Formicidae), with a Review of Ponerine Ecology and Behavior: Zootaxa, Monograph, v. 3817, p. 1–242.
- Shattuck, S.O., 1999, Australian ants, their biology and identification: CSIRO Monographs on Invertebrate Taxonomy, v. 3, p. 226 p.
- Smith, F., 1857, Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by Wallace, A.R.: Journal of the Proceedings of the Linnean Society of London, Zoology, v. 2, p. 42–88.
- Smith, F., 1858, Catalogue of Hymenopterous Insects in the collection of the British Museum, part VI, Formicidae, London, British Museum, 216 p.
- Smith, F., 1860, Catalogue of hymenopterous insects collected by Mr. A. R. Wallace in the islands of Bachian, Kaisaa, Amboyna, Gilolo, and at Dory in New Guinea: Journal of the Proceedings of the Linnean Society of London, Zoology, v. 5(17b), p. 93–143.
- Smith, F., 1862, Descriptions of new species of Australian Hymenoptera, and of a species of Formica from New Zealand: Transactions of the Entomological Society of London, v. 11(2), p. 53–62.
- Smith, F., 1876, Descriptions of new species of hymenopterous insects of New Zealand, collected by C. M. Wakefield, Esq., principally in the

- neighbourhood of Canterbury: Transactions of the Entomological Society of London, v. 24, p. 473–487.
- Solórzano Kraemer, M.M., 2007, Systematic, palaeoecology, and palaeobiogeography of the insect fauna from Mexican amber: *Palaeontographica*, Abt. A, v. 282, p. 133.
- Sonibare, O.O., Agbaje, O.B., Jacob, D.E., Faithfull, J., Hoffmann, T., and Foley, S.F., 2014, Terpenoid composition and origin of amber from the Cape York Peninsula, Australia: *Australian Journal of Earth Sciences*, v. 61(7), p. 979–985.
- Taylor, R.W., 1987, A checklist of the ants of Australia, New Caledonia and New Zealand (Hymenoptera: Formicidae): CSIRO Division of Entomology Report, v. 41, 92 p.
- Viana, M.J., and Rossi, J.A.H., 1957, Primer hallazgo en el hemisferio sur de Formicidae extinguidos y catalogo mundial de los Formicidae fosiles: *Ameghiniana*, v. 1, p. 108–113.
- Ward, P.S., 1985, Taxonomic congruence and disparity in an insular ant fauna: *Rhytidoponera* in New Caledonia: *Systematic Zoology*, v. 34, p. 140–151.
- Watt, J.C., 1975, The terrestrial insects, in Kuschel, G., ed., *Biogeography and ecology in New Zealand*, Den Haag, W. Junk Publishers, p. 507–535.
- Wesmael, C., 1838, Sur une nouvelle espèce de fourmi du Mexique: *Bulletin de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles*, v. 5, p. 766–771.
- Wheeler, W.M., 1915, The ants of the Baltic Amber: *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg*, v. 55, p. 1–142.
- Wheeler, W.M., 1918, The ants of the genus *Opisthopsis* Emery: *Bulletin of the Museum of Comparative Zoology*, v. 62, p. 341–362.
- Wilson, E.O., and Taylor, R.W., 1964, A fossil ant colony: new evidence of social antiquity: *Psyche*, v. 71, p. 93–103.
- Yoshimura, M., and Fisher, B.L., 2012, A revision of male ants of the Malagasy Amblyoponinae (Hymenoptera: Formicidae) with resurrections of the genera *Stigmatomma* and *Xymmer*: *PLoS ONE*, v. 7(e33325), 1–18.
- Zhang, J., 1989, Fossil insects from Shangwang, Shandong, China, Jinan, Shandong Science and Technology Publishing House, 459 p.

Accepted 18 April 2015