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ORIGINAL PAPER

A dance fly (Empididae: *Hilarempis* Bezzi) from the Foulden Maar Fossil-Lagerstätte (Early Miocene, New Zealand)

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Abstract

New Zealand has a diverse and highly endemic fauna of dance flies (Empididae) with much of its diversity found in the tribe Hilarini. Here we report the first fossil of a dance fly from New Zealand from lacustrine diatomites of the earliest Miocene Foulden Maar Fossil-Lagerstätte in Otago. *Hilarempis otagoensis* sp. nov. is described from a single male specimen and assigned to the tribe Hilarini based on characters of the wing venation. This new species represents the first fossil record of the predominantly southern temperate genus *Hilarempis* Bezzi and the second fossil record of the subfamily Empidinae from the Southern Hemisphere. The articulated preservation suggests that *Hilarempis otagoensis* sp. nov. lived among riparian vegetation on the shore of the Foulden Maar palaeolake and probably drowned while skimming the water surface in search for prey or nuptial gifts.

Keywords Fossil Empidoidea · Empidinae · Hilarini · Australasia · Miocene · Maar lake · Diptera

Introduction

The Empidoidea (Diptera) include more than 12.000 species of mostly predatory flies that are grouped into five to nine families and numerous subfamilies (Sinclair and Cumming 2006; Pape et al. 2011; Wahlberg and Johanson 2018). The fossil record indicates that empidoid flies existed in the Jurassic and that families and subfamilies diversified during the Early Cretaceous (Grimaldi 1999, Grimaldi and Cumming 1999, Grimaldi and Engel 2005). The Empididae (dance flies) is divided into several subfamilies, including the Clinocerinae, Empidinae and Hemerodromiinae (Sinclair and Cumming 2006). About 55 fossil species of Empidinae have been described, mainly from Cenozoic sites of the Northern Hemisphere, and most are placed in the extant genera *Rhamphomyia* Meigen and *Empis* Linnaeus of the tribe Empidini (e.g. Statz 1940; Förster 1891; Evenhuis 1994). The oldest and only Mesozoic records of Empidinae are *Turonempis styx* Grimaldi and Cumming and *Emplita casei* Grimaldi and Cumming (tribe Empidini) from New Jersey amber (Turonian) and *Empis orapaensis* Waters (tribe Empidini) from the Cenomanian/Turonian of Botswana, with the latter species representing the sole Southern Hemisphere fossil record of Empidinae (Grimaldi and Cumming 1999, Waters 1989). Fossils of the tribe Hilarini are extremely rare and exclusively represented by species of *Hilara* Meigen from the Palearctic Region (e.g. Meunier 1908, 1915; Gil Collado 1926; Theobald 1937; Evenhuis 1994).

Here we describe a fossil specimen of *Hilarempis* Bezzi, a hilarine genus with 110 extant species that occur mainly in southern temperate areas (Rafael 2012). The specimen comes from the Foulden Maar Fossil-Lagerstätte in southern New Zealand. The geographically isolated islands of New Zealand exhibit a diverse extant Empidoidea (exclusive of Dolichopodidae) fauna of 41 genera and at least 300 (plus many undescribed) species, with all of the described species being endemic to the islands (MacFarlane et al. 2010). Much

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of their overall diversity, life history and ecology remain to be studied in detail (MacFarlane et al. 2010, and references therein). The tribe Hilarini (Empidinae) is particularly well represented in New Zealand (47 species in 6 genera) and the most speciose genera are *Hilara* (15 spp.) and *Hilarempis* (19 spp.), both with as yet numerous undescribed species (MacFarlane et al. 2010; Bickel 2023). Despite this great extant diversity, no fossil representatives of Empididae were previously reported from New Zealand.

Locality and methods

Locality

The specimen described herein was collected at the Foulden Maar Fossil-Lagerstätte, Otago, southern New Zealand (45.5269°S, 170.2191°E). Laminated (varved) and highly fossiliferous diatomite at this locality accumulated in a small (~2000 m diameter) and deep (100–200 m) maar lake over a period of at least 130.000 years in the earliest Miocene (Lindqvist and Lee 2009; Kaulfuss 2017). Anoxic conditions on the profundal lakebed facilitated exquisite preservation of a diverse fossil flora (leaves, flowers and inflorescences, fruits and seeds) and fauna (freshwater sponges, spiders, insects, fish) from a lake/rainforest ecosystem (Bannister et al. 2012; Mildenhall et al. 2014; Kaulfuss et al. 2015; Lee et al. 2016; 2022; Selden and Kaulfuss 2018). The forest growing around the palaeolake, i.e. the palaeohabitat of the *Hilarempis* specimen described herein, was a Lauraceae-dominated rainforest growing under warm-temperate to subtropical climate, very similar to modern simple notophyll vine forests of eastern Australia (Bannister et al. 2012; Mildenhall et al. 2014). The open lake edge vegetation included some quick-growing tree species in the *Mallotus-Macaranga* complex on the lakeshore and aquatic plants such as bur reeds, bulrushes and flaxes growing in shallow, swampy areas (Lee et al. 2010; Mildenhall et al. 2014)

Data from $^{40}Ar/^{39}Ar$ dating, pollen biostratigraphy and sediment magnetic properties indicate that Foulden Maar erupted in the latest Oligocene at ~23.3 Ma and that sedimentation of the ~190 m thick lacustrine crater sequence lasted at least 130.000 years until the earliest Miocene (Lindqvist and Lee 2009, Mildenhall et al. 2014, Fox et al. 2015, Kaulfuss 2017). The *Hilarempis* specimen was collected in the uppermost 10 m of the preserved diatomite section, which correspond to the latest uppermost *Rhoipites waimumuensis* to lower early *Proteacidites isopogiformis* Zone (Aquitanian; New Zealand local stages: late Waitakian–early Otaian). The fossil locality is registered as I43/f8503 in the New Zealand Fossil Record File (https://fred.org.nz/) administered by the Geoscience Society of New Zealand and GNS Science.

Methods

The fossil specimen was studied and photographed with a Nikon SMZ1000 stereomicroscope equipped with a Canon T3 camera. Wetting the fossil with ethanol enhanced the contrast and visibility of anatomical details. Photomicrographs taken at up to 15 focal planes were stacked using Photoshop CS5.1 software (Adobe Systems Inc.). Terms used for adult structures follow those of Cumming and Wood (2017).

Systematic Palaeontology

Order Diptera
Family Empididae Latreille, 1804
Subfamily Empidinae Latreille, 1804
Tribe Hilarini Collin, 1961
Genus *Hilarempis* Bezzi, 1905
Type species *Hilarempis nudifacies* Bezzi, 1905

Hilarempis otagoensis sp. nov.
(Figs. 1–3)

Studied material: OU47068, male, Geology Museum, Department of Geology, University of Otago.
Etymology: The specific epithet refers to the Otago region where the specimen was found.
Type locality and horizon: Foulden Maar near Middlemarch, Otago, New Zealand; earliest Miocene (Aquitanian, New Zealand local stages: late Waitakian–early Otaian).
Description: Male. Both wings, left halter, thorax, abdomen with genitalia and one leg (possibly midleg) visible. Thorax apparently darker than abdomen (Fig. 1).
Wing 3.27 mm long, broad with angular anal lobe; Sc evanescent, ending beyond origin of R_{2+3}; apical section of R_1 expanded; radial fork broad, with R_4 bell-shaped; cell dm shorter than length of M_1 (Figs. 2–3).
Midleg (?) with femur and tibia subequal in length; apical third of tibia with setae, shorter than width of tibia; length of tarsomere 1 subequal to length of tarsomeres 2 and 3 combined; apical tarsomeres missing.
Male terminalia upright, typical Hilarini-type; smaller than width of abdomen, higher than long; phallus tubular.
Remarks: The fossil is assigned to the tribe Hilarini, which is defined in part by the apically thickened (or swollen) vein R_1, which is clearly visible in the fossil. Some diagnostic characters for tribal classification and differentiation of genera within Empidinae are wing venation (vein Sc complete/incomplete), male basitarsus I swollen/ unmodified, presence/ absence of laterotergal setae, the setae on tibia I of

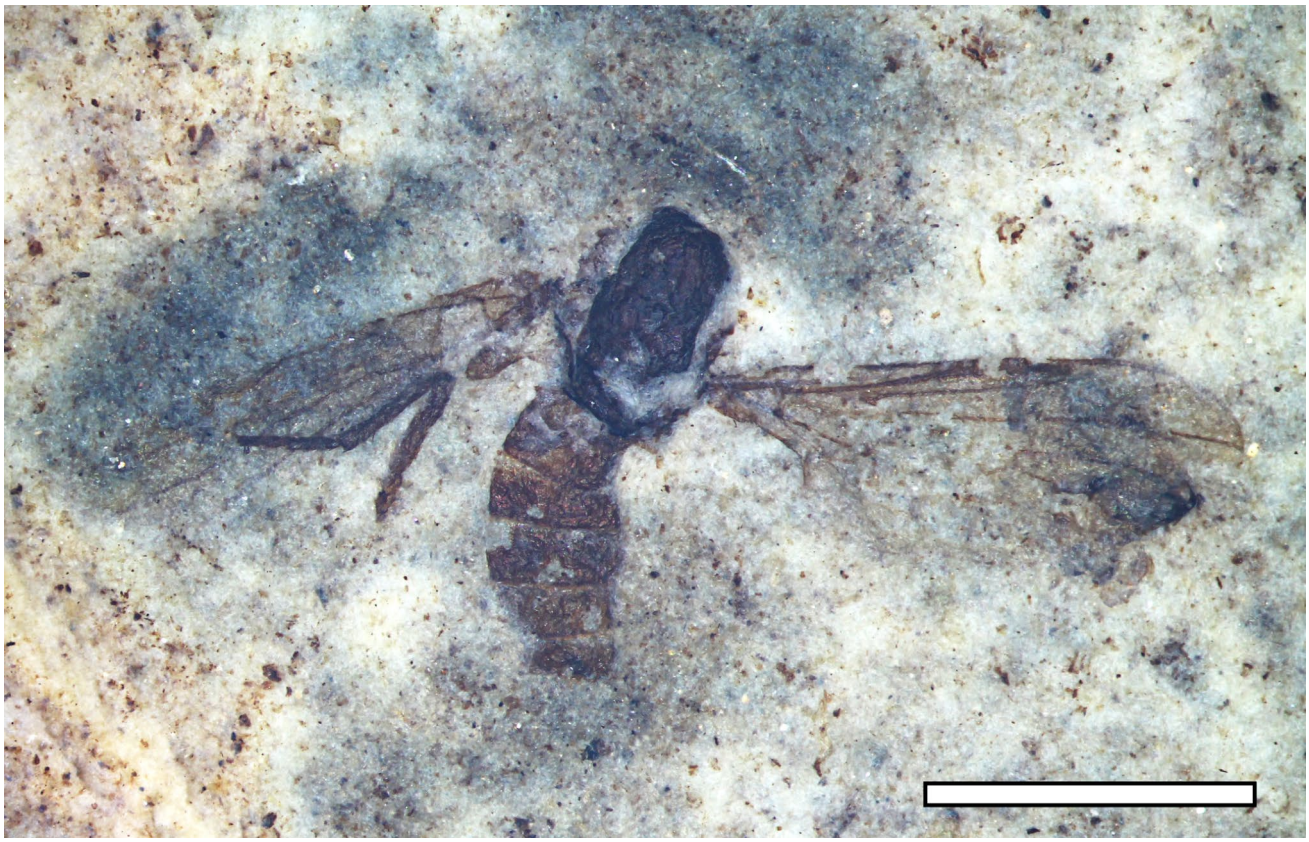

Fig. 1 Habitus of *Hilarempis otagoensis* sp. nov. from Foulden Maar, male, specimen OU47068. Scale bar = 2 mm

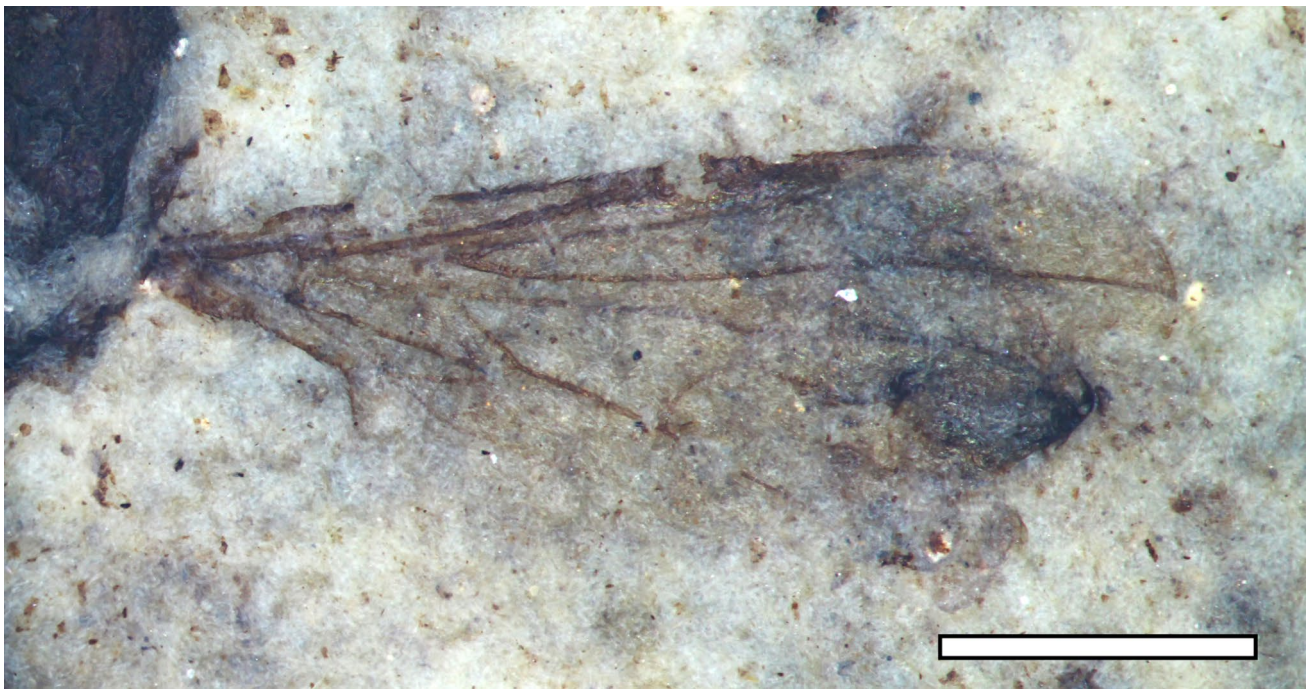

Fig. 2 *Hilarempis otagoensis* sp. nov. from Foulden Maar, close-up of wing. Scale bar = 1 mm

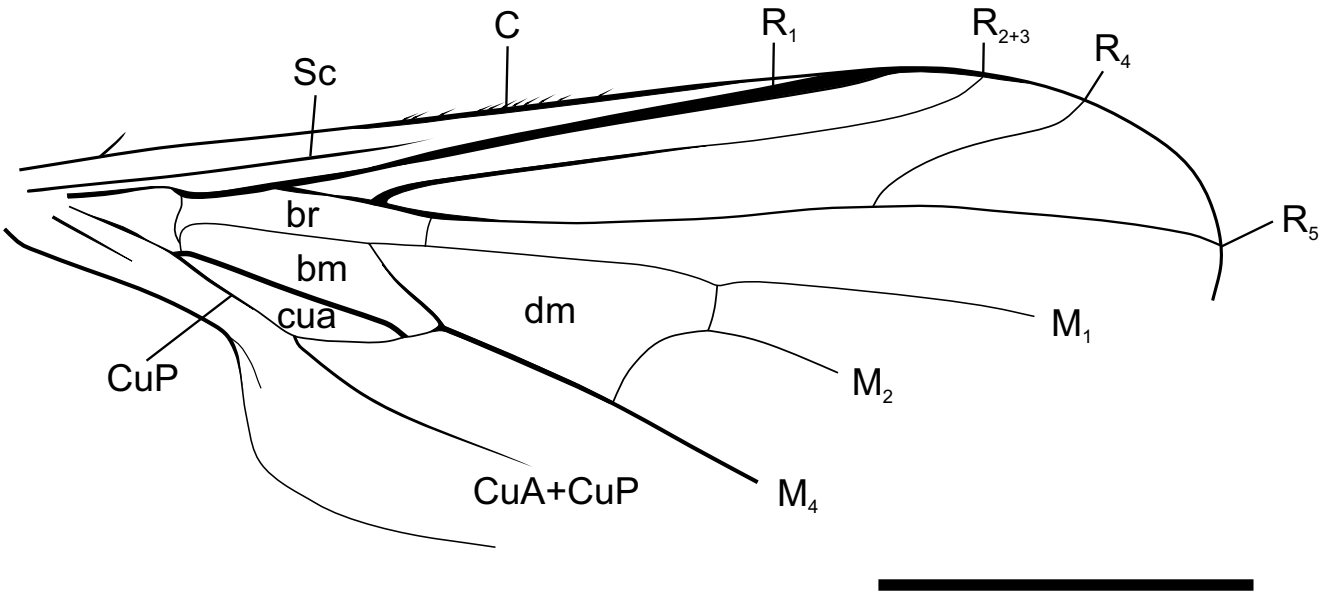

Fig. 3 *Hilarempis otagoensis* sp. nov. from Foulden Maar, line drawing of wing. Veins: *C* costa; *CuA* anterior branch of cubitus; *CuP* posterior branch of cubitus; *M* media; *R* radius; *Sc* subcosta. Cells: *cua* anterior cubital; *bm* basal medial; *br* basal radial; *dm* discal medial. Scale bar = 1 mm

both sexes, structure of hypopygium and genitalia and morphology of the antennae (Bickel 1996, Grimaldi and Cumming 1999, Sinclair and Cumming 2006). Taken individually many of these characters can be variable in expression and genera (and tribes) of Empidinae are ideally defined by a set of these characters (e.g. Bickel 1996). Although very few diagnostic characters are decipherable in the fossil from Foulden Maar, it readily falls within the rather broad definition of the genus *Hilarempis* based on the vein Sc being incomplete (Bickel 1996, Sinclair and Cumming 2006). It thus differs from the cosmopolitan genus *Hilara*, which has a complete vein Sc, with a strongly curved apex.

Discussion

New Zealand has a sparse but increasing fossil record of Diptera. From the Eocene at Livingstone, Otago, Harris (1983) described the march fly *Dilophus campbelli* Harris (Bibionidae), based on a larva, the only insect found at this site. Other fossil Diptera have been reported from late Oligocene and Early Miocene amber (Schmidt et al. 2018) and the mid-Miocene Hindon Maar Complex (Kaulfuss et al. 2018) in Otago, South Island. Families represented at these sites include Bibionidae, Cecidomyiidae, Ceratopogonidae, Chironomidae, Muscidae(?) and Mycetophilidae but detailed descriptions of individual taxa are not yet available. Diptera known from Foulden Maar include a few adult specimens resembling Tipulidae and Muscidae or Acalyptratae groups (Kaulfuss et al. 2015) and a fauna of pre-imaginal aquatic Chironomidae, Chaoboridae and brachyceran flies (Baranov et al. 2024).

Hilarempis otagoensis sp. nov. described here from Foulden Maar is the first fossil representative of dance flies (Empididae) from New Zealand and the first fossil record of this genus globally (Evenhuis 1994). Extant species of *Hilarempis* often form dense swarms over water, with males skimming the water surface looking for prey and nuptial gifts. A swarming behaviour can be assumed for males of the fossil *Hilarempis* species from Foulden Maar, based on its presence in lacustrine sediments of a small, isolated volcanogenic lake. Its more or less articulated preservation suggests that this species lived in the immediate surroundings of the lake, probably among riparian vegetation on the lakeshore. As most extant empidid flies (e.g. MacFarlane et al. 2010), both adults and larvae may have preyed on other insects, mainly other Diptera.

Hilarempis is a widespread genus but likely not monophyletic and it differs from the genus *Hilara* by a small venational change. Together with the limited diagnostic details preserved in the fossil this prevents any biogeographical comparisons. The new fossil provides unequivocal evidence for the presence of empidid flies in the tribe Hilarini in southern New Zealand in the earliest Miocene, concurring with the great diversity of this genus in the extant New Zealand fauna.

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Data availability This manuscript has no associated data. The material is housed at the Geology Museum, Department of Geology, University of Otago.

Declarations

Conflict of Interest The authors declare no conflict of interest.

References

Bannister, J. M., Conran, J. G., & Lee, D. E. (2012). Lauraceae rainforest surrounding an early Miocene maar lake, Otago, southern New Zealand. *Review of Palaeobotany and Palynology 178*, 13–34. https://doi.org/10.1016/j.revpalbo.2012.03.015

Baranov, V., Haug, J. T., & Kaulfuss, U. (2024). New records of immature aquatic Diptera from the Foulden Maar Fossil-Lagerstätte, New Zealand, and their biogeographic implications. *PeerJ 12*, e17014. https://doi.org/10.7717/peerj.17014

Bezzi, M. (1905). Empididae neotropicae Musei Nationalis Hungarici. *Annales Historico-Naturales Musei Nationalis Hungarici 3*, 424–460.

Bickel, D. J. (1996). *Thinempis*, a new genus from Australia and New Zealand (Diptera: Empididae), with notes on the tribal classification of the Empidinae. *Systematic Entomology 21*, 115–128. https://doi.org/10.1046/j.1365-3113.1996.d01-2.x

Bickel, D. J. (2023). Hilarini (Diptera: Empididae) from the Auckland Islands New Zealand, the homoplastic loss of the male silk-producing basitarsus in two insular species, and notes on the Empidoidea of the Subantarctic Islands. *Diversity 15*, 267. https://doi.org/10.3390/d15020267

Collin, J. E. (1961). *British Flies*, Volume 6, Empididae. New York: Cambridge University Press.

Cumming, J. M., & Wood, D. M. (2017). [Chapter] 3. Adult morphology and terminology. In A. H. Kirk-Spriggs & B. J. Sinclair (Eds.), *Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families* (pp. 89–133). Pretoria: South African National Biodiversity Institute.

Evenhuis, N. L. (1994). *Catalogue of the Fossil Flies of the World (Insecta: Diptera)*. Leiden: Backhuys Publishers.

Förster, B. (1891). Die Insekten des „Plattigen Steinmergels" von Brunstatt. *Abhandlungen zur Geologischen Specialkarte von Elsass-Lothringen 3*(5), 333–593.

Fox, B. R. S., Wartho, J., Wilson, G. S., Lee, D. E., Nelson, F. E., & Kaulfuss, U. (2015). Long-term evolution of an Oligocene/Miocene maar lake from Otago, New Zealand. *Geochemistry, Geophysics, Geosystems 16*, 59–76. https://doi.org/10.1002/2014GC005534

Gil Collado, J. (1926). Nota sobre algunos insectos fósiles de Ribesalbes (Castellón). *Boletín del Instituto Geológico de España 6*(3), 89–107.

Grimaldi, D. (1999). The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden 86*(2), 373–406.

Grimaldi, D. A., & Cumming, J. M. (1999). Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History 239*, 1–124.

Grimaldi, D., & Engel, M. S. (2005). *Evolution of the Insects* (pp.1-755). New York: Cambridge University Press.

Harris, A. C. (1983). An Eocene larval insect fossil (Diptera: Bibionidae) from North Otago, New Zealand. *Journal of the Royal Society of New Zealand 13*(3), 93–105. https://doi.org/10.1080/03036758.1983.10415323

Kaulfuss, U. (2017). Crater stratigraphy and the post-eruptive evolution of Foulden Maar, southern New Zealand. *New Zealand Journal of Geology and Geophysics 60*(4), 410–432. https://doi.org/10.1080/00288306.2017.1365733

Kaulfuss, U., Lee, D. E., Barratt, B. I. P., Leschen, R. A. B., Larivière, M.-C., Dlussky, G. M., Henderson, I. M., & Harris, A. C. (2015). A diverse fossil terrestrial arthropod fauna from New Zealand: evidence from the early Miocene Foulden Maar fossil Lagerstätte. *Lethaia 48*, 299–308. https://doi.org/10.1111/let.12106

Kaulfuss, U., Lee, D. E., Wartho, J.-A., Bowie, E., Lindqvist, J. K., Conran, J. G., Bannister, J. M., Mildenhall, D. C., Kennedy, E. M., & Gorman, A. R. (2018). Geology and palaeontology of the Hindon Maar Complex: a Miocene terrestrial fossil Lagerstätte in southern New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology 500*, 52–68. https://doi.org/10.1016/j.palaeo.2018.03.022

Latreille, P. A. (1804). Tableau méthodique des insectes. In Société de Naturalistes et d'Agriculteurs. *Nouveau dictionnaire d'histoire naturelle. Tome 24* (pp. 129–200). Paris: Déterville.

Lee, D. E., Bannister, J. M., Raine, J. I., & Conran, J. G. (2010). Euphorbiaceae: Acalyphoideae fossils from early Miocene New Zealand: *Mallotus–Macaranga* leaves, fruits and inflorescence with *in situ Nyssapollenites endobalteus* pollen. *Review of Palaeobotany and Palynology 163*, 127–138. https://doi.org/10.1016/j.revpalbo.2010.10.002

Lee, D. E., Kaulfuss, U., Conran, J. G., Bannister, J. M., & Lindqvist, J. K. (2016). Biodiversity and palaeoecology of Foulden Maar: an early Miocene Konservat-Lagerstätte deposit in southern New Zealand. *Alcheringa: An Australian Journal of Palaeontology 40*, 525–541. https://doi.org/10.1080/03115518.2016.1206321

Lee, D. E., Kaulfuss, U., & Conran, J. G. (2022). *Fossil treasures of Foulden Maar. Window into Miocene Zealandia*. Dunedin, New Zealand: Otago University Press.

Lindqvist, J. K., & 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 222*, 98–110. https://doi.org/10.1016/j.sedgeo.2009.07.009

MacFarlane, R.P., Maddison, P. A., Andrew, I. G., Berry, J. A., Johns, P. M., Hoare, R. J. B., Larivière, M.-C., Greenslade, P., Henderson, R. C., Smithers, C. N., Palma, R. L., Ward, J. B., Pilgrim, R. L. C., Towns, D. R., McLellan, I., Teulon, D. A. J., Hitchings, T. R., Eastop, V. F., Martin, N. A., Fletcher, M. J., Stufkens, M. A. W., Dale, P. J., Burckhardt, D., Buckley, T. R., & Trewick, S. A. (2010). Subphylum Hexapoda: Protura, springtails, Diplura, and insects. In D. P. Gordon (Ed.), *New Zealand Inventory of Biodiversity. Volume Two: Kingdom Animalia. Chaetognatha, Ecdysozoa, Ichnofossils* (pp. 233–467). Canterbury University Press.

Meunier, F. (1908). Monographie des Empidae de l'ambre de la Baltique et catalogue bibliographique complet sur les diptères fossiles de cette résine. *Annales des Sciences Naturelles, Zoologie (9)7*, 81–135, pls III–XII.

Meunier, F. (1915). Nouvelles recherches sur quelques insectes des Plâtrières d'Aix en Provence. *Verhandelingen der Koninklijke Akademie van Wetenschappen te Amsterdam 18*(5), 1–17.

Mildenhall, D. C., Kennedy, E. M., Lee, D. E., Kaulfuss, U., Bannister, J. M., Fox, B., & Conran, J. G. (2014). Palynology of the early Miocene Foulden Maar, Otago, New Zealand: Diversity following destruction. *Review of Palaeobotany and Palynology 204*, 27–42. https://doi.org/10.1016/j.revpalbo.2014.02.003

Pape, T., Blagoderov, V., & Mostovski, M. B. (2011). Order Diptera Linnaeus, 1758. Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. *Zootaxa 3148*, 222–229. https://doi.org/10.11646/zootaxa.3148.1.42

Rafael, J. A. (2012). Revision of Neotropical species of Empididae (Diptera) described by Mario Bezzi. VIII. The species described in *Hilarempis* Bezzi. *Zootaxa 3189*, 56–68. https://doi.org/10.11646/zootaxa.3488.1.3

Schmidt, A. R., Kaulfuss, U., Bannister, J. M., Baranov, V., Beimforde, C., Bleile, N., Borkent, A., Busch, A., Conran, J. G., Engel, M. S., Harvey, M., Kennedy, E. M., Kerr, P. H., Kettunen, E., Kiecksee, A. P., Lengeling, F., Lindqvist, J. K., Maraun, M., Mildenhall, D. C. et al. (2018). Amber inclusions from New Zealand. *Gondwana Research 56*, 135–146. https://doi.org/10.1016/j.gr.2017.12.003

Selden, P.A., & Kaulfuss, U. (2018). Fossil arachnids from the earliest Miocene Foulden Maar Fossil-Lagerstätte, New Zealand. Alcheringa: *An Australian Journal of Palaeontology 43*, 165–169. https://doi.org/10.1080/03115518.2018.1450446

Sinclair, B. J., & Cumming, J. M. (2006). The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa 1180*, 1–172. https://doi.org/10.11646/zootaxa.1180.1.1

Statz, G. 1940. Neue Dipteren (Brachycera et Cyclorhapha) aus dem Oberoligozän von Rott. *Palaeontographica Abt. A, 91*, 120–174.

Theobald, N. (1937). Les insectes fossiles des terrains oligocènes de France. *Bulletin Mensuel (Mémoires) de la Société des Sciences de Nancy 1*, 1–473.

Wahlberg, E., & Johanson, K. A. (2018). Molecular phylogenetics reveals novel relationships within Empidoidea (Diptera). *Systematic Entomology 43*(4), 619–636. https://doi.org/10.1111/syen.12297

Waters, S. B. (1989). A Cretaceous dance fly (Diptera: Empididae) from Botswana. *Systematic Entomology 14*, 233–241. https://doi.org/10.1111/j.1365-3113.1989.tb00280.x