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Hindon Maar of southern New Zealand  
(Hymenoptera, Colletidae)

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*Leioproctus (Otagocolletes) barrydonovani* n. subgen., n. sp. holotype OU46559, habitus of part.

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# A bee from the middle Miocene Hindon Maar of southern New Zealand (Hymenoptera, Colletidae)

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## ABSTRACT

The first fossil bee from Zealandia is described and figured from an excellent compression recovered from the middle Miocene Hindon Maar Fossil Lagerstätte of southern New Zealand. *Leioproctus* (*Otagocolletes*) *barrydonovani* n. subgen., n. sp. is represented by an impression of a nearly complete bee in dorsal view. The palaeohabitat of *L. barrydonovani* n. subgen., n. sp. was a *Nothofagus*/podocarp/mixed broadleaf forest and the species may have visited flowers of the araliaceous genus *Pseudopanax* K. Koch, today common throughout New Zealand. The fossil is compared with its modern congeners known in New Zealand.

## RÉSUMÉ

*Une abeille du miocène moyen du Hindon Maar, sud de la Nouvelle-Zélande (Hymenoptera, Colletidae).* La première abeille fossile de Zealandia est décrite et figurée à partir d'une excellente compression trouvée dans le gisement fossilifère du Miocène moyen du Hindon Maar au sud de la Nouvelle-Zélande. *Leioproctus* (*Otagocolletes*) *barrydonovani* n. sous-gen., n. sp. est représenté par une impression d'abeille presque complète en face dorsale. Le paléohabitat de *L. barrydonovani* n. sous-gen., n. sp. était une forêt mixte de *Nothofagus*/podocarpes/feuillus et l'espèce a peut-être visité des fleurs du genre araliacé *Pseudopanax* K. Koch, aujourd'hui commun dans toute la Nouvelle-Zélande. Le fossile est comparé avec ses congénères modernes de Nouvelle-Zélande.

## KEY WORDS

Anthophila,  
Langhian,  
*Leioproctus*,  
palaeontology,  
Zealandia,  
new subgenus,  
new species.

## MOTS CLÉS

Anthophila,  
Langhian,  
*Leioproctus*,  
paléontologie,  
Zealandia,  
sous-genre nouveau,  
espèce nouvelle.

## INTRODUCTION

The biota of New Zealand is a mosaic of ancient lineages interspersed among arrays of relative newcomers that have diversified since the Oligocene-Miocene. Indeed, in many respects the fauna is typical of an island biota, reflective of lineages dispersing to the landmass at various times since its breakup from Gondwana *c.* 80 mya and then speciating (Buckley *et al.* 2014). Some insect lineages have clearly thrived and evolved unique features within New Zealand (Buckley *et al.* 2014), but many are conspicuously and enigmatically depauperate given the complexity and scale of the landscape (e.g. Watt 1975), seemingly reflecting their late arrival to the islands. Indeed, some prominent and complex biological interactions are poorly represented within the modern New Zealand fauna such as specialized insect pollinators, which are few in New Zealand and generalist flies are the dominant pollinators (Didham 2005). In fact, although bees are the preëminent pollinators worldwide, their diversity in New Zealand is meagre, with only 42 species of which a mere 28 are endemic (Donovan 2007, 2016). This has led to a perception that bees are comparative newcomers to New Zealand and in the absence of any fossil record it has been challenging to determine the antiquity of the melittofauna.

It is therefore of significance to report the discovery of a fossil bee from the middle Miocene deposits of the Hindon Maar in Otago, New Zealand. The Konservat-Lagerstätte at Hindon Maar has been dated by palynological and radiometric methods to be 14.6 Myr-old, that is, it formed after major reduction of the New Zealand land area in the late Oligocene and shortly after the mid-Miocene Climate Optimum, but prior to late Miocene-Pleistocene climate-cooling episodes.

## GEOLOGICAL SETTING

The Hindon Maar Complex (HMC) is a middle Miocene Konservat-Lagerstätte near the township of Outram in Otago, southern New Zealand (45°45.62'S, 170°15.88'E; Fig. 1). As one of many eruptive centres of the late Oligocene-late Miocene Dunedin Volcanic Group, the HMC includes four closely spaced, partly eroded maar-diatreme volcanoes excavated into regional schist basement rocks. According to geological and geophysical investigations, three of the four maar craters are filled by fossiliferous lacustrine sediments (gyttja, diatomite, and spiculite), deposited in small (500–1000 m diameter) but probably deep lakes with anoxic conditions in the profundal zone (Kaulfuss *et al.* 2018). A diverse fossil biota recovered from temporary excavations is representative of lake and surrounding *Nothofagus/ podocarp/* mixed broadleaf forest ecosystems of a warm temperate climate. Fossil insects are relatively common at the HMC and are dominated by Coleoptera, in particular weevils, with representatives of Hemiptera, Thysanoptera, Diptera, Hymenoptera and Trichoptera also present. Of these, the hairy cicada *Paratettigarcta zealandica* Kaulfuss &

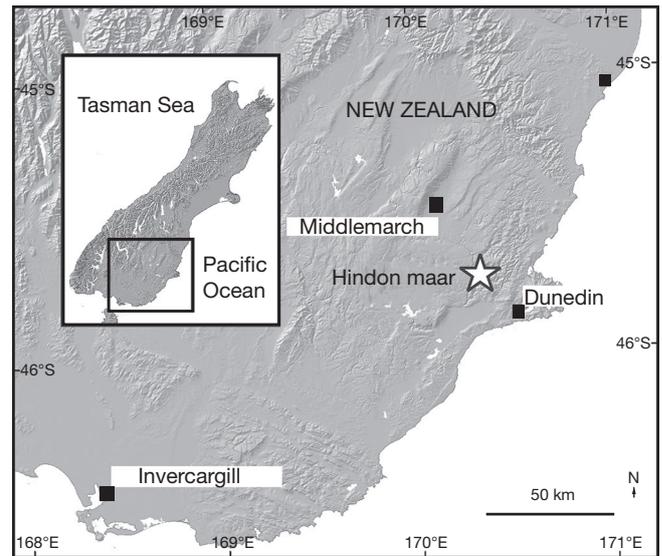


FIG. 1. — Map of the South Island of New Zealand showing the location of the Hindon Maar Konservat Lagerstätte.

Moulds, 2015 (Tettigarctidae; now extinct in New Zealand) is the only insect taxon hitherto described from the site (Kaulfuss & Moulds 2015).

The specimen of *Leioproctus* Smith, 1853 described herein was collected in a temporary excavation pit (informally named Pine Tree Pit) on private farmland in maar 1 (*vide* Kaulfuss *et al.* 2018: figs 1, 2). The fossil site is registered as 144/f0392 in the New Zealand Fossil Record File jointly administered by the Geoscience Society of New Zealand and GNS Science (<https://fred.org.nz/>).

The middle Miocene age (Langhian, New Zealand local stage: Lillburnian) of the HMC is based on palynomorphs from the lake sediments and a  $^{40}\text{Ar}/^{39}\text{Ar}$  date of  $14.603 \pm 0.093$  my obtained from basanite in one of the maars (Kaulfuss *et al.* 2018).

## MATERIAL AND METHODS

The single specimen studied herein is a compressed, articulated fossil bee preserved as part and counterpart in dark grey organic mudstone (gyttja) (Figs 2; 3). Head, mesosoma, and basal metasomal segments are visible from a dorsal aspect, with the forewings and, partially, the hind wings preserved, whereas appendages (antennae, palpi, legs) are mostly obscured or not preserved. An attempt to expose further anatomical details by preparation with fine needles and paintbrushes proved unsuccessful due to the strongly compressed nature of the fossil.

The specimen was studied and photographed with a Nikon SMZ1000 stereomicroscope equipped with a Canon T3 camera. Wetting the specimen with ethanol improved the contrast to the sediment matrix. Drawings were prepared from photomicrographs using Adobe Photoshop software (Fig. 4). Morphological terminology follows Engel (2001) and Michener (2007), while the classification followed here is that of Engel & Gonzalez (2022).



Fig. 2. — *Leioproctus (Otagocolletes) barrydonovani* n. subgen., n. sp. holotype OU46559, habitus of part. Scale bar: 1 mm.

## SYSTEMATIC PALAEOONTOLOGY

Tribe Neopasiphaeini Cockerell, 1930  
 Subtribe Neopasiphaeina Cockerell, 1930  
 Genus *Leioproctus* Smith, 1853

*Otagocolletes* n. subgen.

TYPE SPECIES. — *Leioproctus (Otagocolletes) barrydonovani* n. sp.

DIAGNOSIS. — The new subgenus is similar to *Nesocolletes* Michener, 1965 in the possession of a more pronounced malar space (i.e., at least longer than 0.5× the basal mandibular width), about as long as wide in the fossil, and the short and wholly declivitous basal area to the propodeum but differs in the more parallel-sided pterostigma, the distal origin of r-rs, the more abruptly tapered pterostigmal border within the marginal cell (more convex in *Nesocolletes*), the weakly and evenly arched 2rs-m, and shortened second medial cell (*vide etiam* Discussion, *infra*).

ETYMOLOGY. — The new subgeneric name is a combination of the Otago region, southern Māori dialect version of Ōtākou, and kollitís (κολλητήρ, meaning, “gluer” or “one who glues”). The gender of the name is masculine.

*Leioproctus (Otagocolletes) barrydonovani* n. sp.  
 (Figs 2-4)

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HOLOTYPE. — New Zealand • ♀; OU46558; Lacustrine mudstones from Hindon Maar (Langhian; I44/f0392 in the New Zealand Fossil Record File); Dunedin Volcanic Group, 10 km N of Outram, Otago, southern New Zealand; Department of Geology, University of Otago, Dunedin, New Zealand.

TYPE LOCALITY AND HORIZON. — Lacustrine mudstones from Hindon Maar (Langhian; I44/f0392 in the New Zealand Fossil Re-

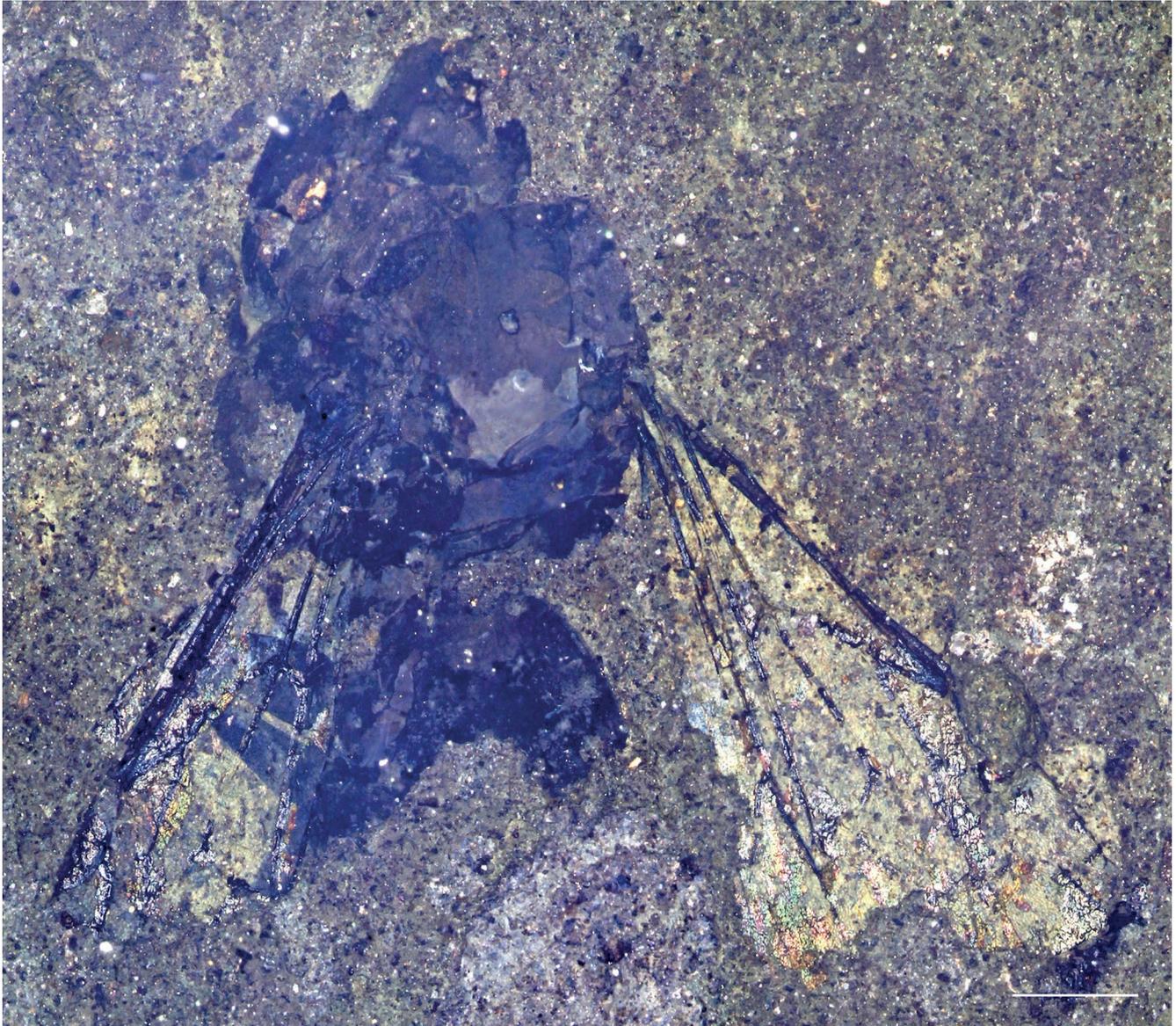


FIG. 3. — *Leioproctus (Otagocolletes) barrydonovani* n. sp. holotype OU46559, habitus of counterpart. Scale bar: 1 mm.

cord File), Dunedin Volcanic Group, 10 km N of Outram, Otago, southern New Zealand.

**ETYMOLOGY.** — The specific epithet honours the late Barry J. Donovan (1941-2022), authority on New Zealand's unique bee fauna (e.g. Donovan 2007) and a charming and generous man with whom we had the pleasure of working. This project was just starting with Barry when he passed away (van Toor *et al.* 2022). He is missed.

**DIAGNOSIS.** — As for the subgenus (*vide supra*).

#### DESCRIPTION

##### *Female*

**Body.** Total length as preserved (vertex to apex of fragment of tergum II) 6.4 mm; forewing length as preserved (base to torn apex as apical portion of membrane largely missing including apex of marginal cell) 5.6 mm; mesoscutum length 2.1 mm, mesoscutellum length 0.4 mm; metasoma width as preserved

2.7 mm. Integument nearly black as preserved (colouration taphonomically altered but likely dark brown to black in life). Sculpturing not discernible for most sclerites (ental surfaces exposed for many sclerites and thereby not depicting external sculpturing or pubescence), where evident seemingly closely punctate (e.g. small portions of mesoscutum, at least laterally, and metasomal terga but otherwise these sclerites internally exposed).

**Head.** Apparently broad (incomplete and in oblique posterior position so precise dimension impossible to determine but seeming broad based on upper width as preserved); gena narrower than compound eye; malar space apparently about as long as wide (the sclerite at the lower margin of the compound eye is not the base of the mandible and indicates a malar space that is 0.5× as long as wide, or even slightly

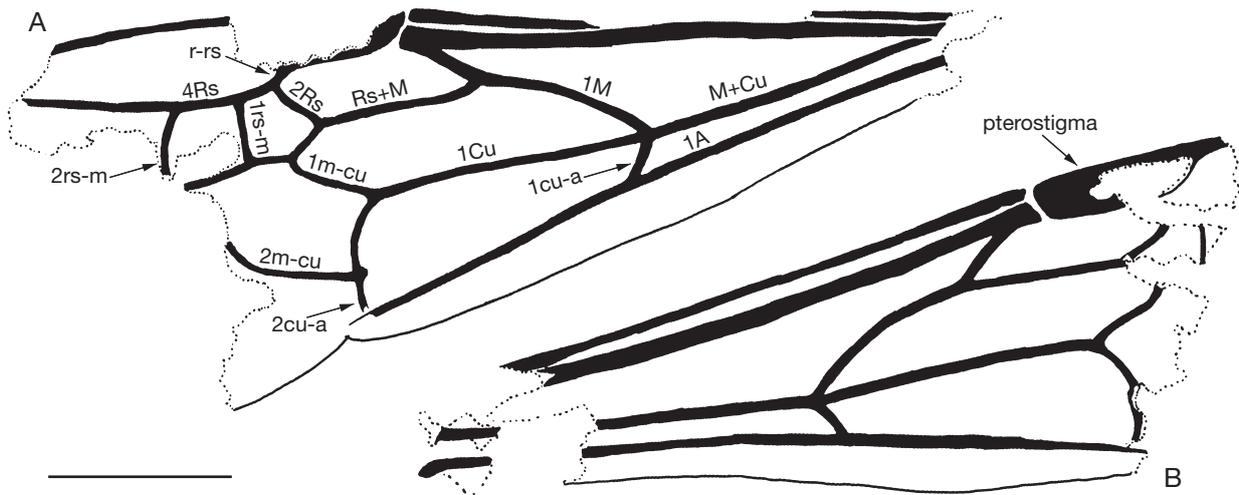


FIG. 4. — *Leioproctus (Otagocolletes) barrydonovani* n. sp. holotype OU46559, line drawings of left (A) and right (B) forewing as preserved. Scale bar: 1 mm.

more; this seems almost certainly the case in the part but is less clear in the counterpart as preserved); mesoscutellum longer than combined lengths of metanotum and basal area of propodeum; metanotum exceedingly short (as preserved), slightly shorter than basal area of propodeum; basal area of propodeum wholly declivitous (best observed on part), almost undifferentiated from posterior surface.

**Forewing.** All wing veins strong and tubular; marginal cell long (although incomplete as preserved the course of Rs and anterior wing margin demonstrate overall length) (Figs 2-4), longer than pterostigma; prestigma about as long as wide and perhaps about as long as pterostigmal base; pterostigma slender, roughly parallel-sided, not widening apically (Fig. 4), tapering within marginal cell, border within marginal cell distinctly convex (Fig. 4); basal vein (1M) faintly arched, confluent with 1cu-a; 1cu-a straight, oblique, sloping toward wing apex; 1Rs slightly longer than prestigma, oblique relative to Rs+M, much shorter than 1M; Rs+M nearly straight; first submarginal cell longer than individual lengths of second and third submarginal cells, slightly longer than combined lengths of remaining submarginal cells; prestigmal length of first submarginal cell slightly less than  $0.3\times$  pterostigmal length of cell; 1r-rs well distad pterostigmal midlength, near pterostigmal apex, shorter than 3Rs; second submarginal cell slightly narrowed anteriorly, 2Rs longer than 3Rs, 2Rs and 1rs-m not parallel; 1m-cu entering second submarginal cell at cell midlength, basad 1rs-m by 4-5 $\times$  vein width; 3Rs shorter than 4Rs; anterior border of third submarginal cell longer than anterior border of second submarginal cell; 2rs-m weakly curved distally; posterior border of third submarginal cell about as long as that of second submarginal cell, only slightly longer than anterior border of third submarginal cell; 2m-cu apparently entering third submarginal cell near apex (incomplete but

given that majority of posterior border of cell present and not in contact with 2m-cu indicates it must make contact near cell's apex); 2Cu much longer than 2cu-a.

#### Male

Unknown.

#### DISCUSSION

Among endemic bee lineages the wing venation is most consistent with *Leioproctus*, rather than *Hylaeus* Fabricius, 1793 or *Lasioglossum* Curtis, 1833 (Donovan 2007). The wings of *Hylaeus* have two submarginal cells and 1cu-a is typically orthogonal to M+Cu and A, while those of *Lasioglossum* have the distal wing veins weakened, none of which is the case in the current fossil. In fact, the venation of the fossil is remarkably similar to that of the three subgenera of *Leioproctus* native to New Zealand: *Nesocolletes*, *Maoricolletes* Engel in Engel & Gonzalez, 2022, and *Donovanapis* Engel in Engel & Gonzalez, 2022 (Donovan 2007; M.S.E. pers. obs.). Unfortunately, it is not possible to make a more refined placement given the absence of information on the malar space, clypeus, length of scape, metatrochanter, metatibial spurs, and male terminalia. The malar space is similar to that of *Nesocolletes* and unlike those of other New Zealand *Leioproctus* (Donovan 2007). The sclerite at the lower margin of the compound eye is not the base of the mandible and is a malar space that is  $0.5\times$  as long as wide, or even slightly more. This is almost certainly the case in the part but less clear in the counterpart. It will require more completely preserved material to better clarify its length (e.g. seemingly  $0.75\times$  basal width of mandible but perhaps even longer?), as well as the degree to which the clypeus extends below the lower tangent of the compound eyes. Also similar to *Nesocolletes* is the confluence of 1M and 1cu-a [at least in the type species,

*Leioproctus* (*Nesocolletes*) *fulvescens* (Smith, 1876)], 1M is faintly arched and long, Rs+M is straight, and 1m-cu enters the second submarginal cell near its middle. In addition, the basal area of the propodeum appears scarcely distinguished from the posterior surface and would therefore have been almost wholly declivitous, and without carinae. This is also in agreement with *Nesocolletes*, although the basal area of the propodeum is as long as or perhaps even slightly longer than the metanotum, while in extant species of this subgenus the basal area is shorter than the metanotum. Quite unlike *Nesocolletes*, however, the fossil has a nearly parallel-sided pterostigma with r-rs arising well distal the pterostigmal midlength. In *Nesocolletes* the pterostigma is parallel-sided in its basal half and then tapers more gradually from r-rs, which is near midlength, to its apex. In addition, 2rs-m in *Nesocolletes* is much more sinuate, with the third submarginal cell therefore more protruding posteriorly toward the wing apex, rather than the more evenly and weakly arched 2rs-m of the fossil. The fact that 2rs-m does not arch apically also means that the second medial cell is shortened, not extending as far apically as in modern *Nesocolletes*. In fact, these character-states also differ from all other New Zealand species of *Leioproctus*, distinguishing *Otagocolletes* n. subgen. from all of the extant subgenera and species.

The presence of a species of *Leioproctus s.l.* in the middle Miocene fauna of New Zealand poses some interesting ideas regarding the bee fauna of these islands. If the genus had invaded New Zealand before 14.6 mya, then it should have been sufficient time for the group to have more extensively diversified or to develop floral specializations with the endemic flora. The reality is, however, that there are merely 18 species of endemic *Leioproctus*, indicating that either there was a diversification that was subsequently winnowed considerably through extinction and driven by factors unknown, that some complex biotic processes or interactions prevented the lineage from more extensive speciation, or that the modern *Leioproctus* of New Zealand are unrelated to the fossil, at least subgenerically, and represent one or more later reintroductions between the mid-Miocene and Pleistocene (and thereby of sufficiently young age as to have not yet more thoroughly radiated). In fact, there are currently no data to indicate that the three groups of *Leioproctus* in New Zealand form a monophyletic group, and they themselves could represent multiple, younger invasions of the islands. If the fossil is representative of an early invasion of *Leioproctus s.l.* into New Zealand during or before the middle Miocene, then one would hypothesize that a greater number of species would have developed across the complex landscape and climates of the islands. In at least the same time frame, Hawaiian drosophilids radiated to nearly 600 species (Church & Extavour 2022) and cicadas flourished across New Zealand (Fleming 1975; Marshall *et al.* 2008), among many other examples of island diversifications of similar scope. Bees are not shy of diversification or specialization given similar lengths of time (e.g. Magnacca & Danforth 2006), and there is no *a priori* reason to expect them to have not diversified considerably across a heterogeneous landscape, with a rich and varied flora, and numerous localized environments. It would therefore seem to be a good null hypothesis to consider the

extant New Zealand endemic *Leioproctus* as a comparatively young clade or clades most probably derived from Australia (Donovan 2007), and that the fossil, rather than being related to *Nesocolletes*, is of an earlier lineage of *Leioproctus* that failed to take hold, with other bees of the genus arriving in more recent stages and giving us the melittofauna we are familiar with today. Phylogenetic analyses will be needed to test such a hypothesis along with continued excavations and the discovery of additional fossils.

The articulated preservation of *L. barrydonovani* n. subgen., n. sp. indicates little post-mortem transport by wind or water, suggesting that the *Nothofagus*/podocarp/mixed broadleaf forest surrounding the Miocene maar lake at Hindon was the habitat of this species. Extant New Zealand species of *Leioproctus* visit a range of host plants from various families, some of which have been found as macrofossils at the HMC: Araliaceae, Lauraceae, Loranthaceae, and Myrtaceae. At least one extant species, *L. (L.) pango* Donovan, 2007, is known to collect pollen from flowers of *Pseudopanax* K. Koch (Araliaceae), a genus of small trees and shrubs common throughout New Zealand (Donovan 2007). Among 48 fossilized flowers collected at the HMC all but two are Araliaceae flowers of an undescribed species of *Pseudopanax* (Kaulfuss *et al.* 2023). Although there is no direct evidence of the host plant(s) of *L. barrydonovani* n. subgen., n. sp. (no pollen was found attached to the fossil), the abundance of flowers of *Pseudopanax* in the same deposit might indicate that this Miocene bee species visited *Pseudopanax* sp., probably among other plants. Given the fine detail of preservation, the potential to recover *in situ* pollen is great should additional and more complete bees be uncovered in future excavations. Direct evidence of such floral associations has been recorded from other important Lagerstätten (e.g. Wappler *et al.* 2015; Grímsson *et al.* 2017; Wedmann *et al.* 2021; Geier *et al.* 2024; Engel unpubl. data), and the HMC and nearby Foulden Maar have considerable potential for glimpses into insect-plant interactions during the Miocene of Zealandia.

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### Author’s contributions

MSE composed the morphological descriptions and comparisons. Both authors drafted the manuscript as well as read, edited, and approved the final version.

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