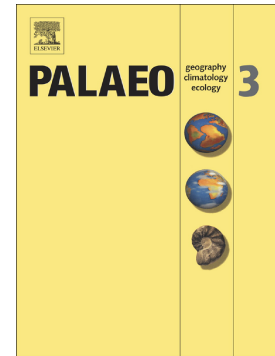


## Accepted Manuscript

Geology and palaeontology of the Hindon maar complex: A Miocene terrestrial fossil Lagerstätte in southern New Zealand

Uwe Kaulfuss, Daphne E. Lee, Jo-Anne Wartho, Elliot Bowie, Jon K. Lindqvist, John G. Conran, Jennifer M. Bannister, Dallas C. Mildenhall, Elizabeth M. Kennedy, Andrew R. Gorman



PII: S0031-0182(18)30052-X

DOI: doi:[10.1016/j.palaeo.2018.03.022](https://doi.org/10.1016/j.palaeo.2018.03.022)

Reference: PALAEO 8710

To appear in: *Palaeogeography, Palaeoclimatology, Palaeoecology*

Received date: 18 January 2018

Revised date: 10 March 2018

Accepted date: 19 March 2018

Please cite this article as: Uwe Kaulfuss, Daphne E. Lee, Jo-Anne Wartho, Elliot Bowie, Jon K. Lindqvist, John G. Conran, Jennifer M. Bannister, Dallas C. Mildenhall, Elizabeth M. Kennedy, Andrew R. Gorman , Geology and palaeontology of the Hindon maar complex: A Miocene terrestrial fossil Lagerstätte in southern New Zealand. The address for the corresponding author was captured as affiliation for all authors. Please check if appropriate. *Palaeo*(2018), doi:[10.1016/j.palaeo.2018.03.022](https://doi.org/10.1016/j.palaeo.2018.03.022)

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

## Geology and palaeontology of the Hindon Maar Complex: a Miocene terrestrial fossil *Lagerstätte* in southern New Zealand

Uwe Kaulfuss<sup>a,\*</sup>, Daphne E. Lee<sup>a,\*</sup>, Jo-Anne Wartho<sup>b</sup>, Elliot Bowie<sup>a</sup>, Jon K. Lindqvist<sup>a</sup>, John G Conran<sup>c</sup>, Jennifer M. Bannister<sup>d</sup>, Dallas C. Mildenhall<sup>e</sup>, Elizabeth M. Kennedy<sup>e</sup>, Andrew R. Gorman<sup>a</sup>

<sup>a</sup>Department of Geology, University of Otago, PO Box 56, Dunedin 9054, New Zealand

<sup>b</sup>GEOMAR Helmholtz Centre for Ocean Research Kiel, D-24148 Kiel, Germany

<sup>c</sup>ACEBB and SGC, School of Biological Sciences, Benham Bldg DX 650 312, The University of Adelaide, SA 5005, Australia

<sup>d</sup>Department of Botany, University of Otago, PO Box 56, Dunedin 9054, New Zealand

<sup>e</sup>GNS Science, PO Box 30-368, Lower Hutt, New Zealand

\*Corresponding authors.

*Email addresses:* uwe.kaulfuss@otago.ac.nz, daphne.lee@otago.ac.nz

### ABSTRACT

This paper highlights the geology, biodiversity and palaeoecology of the Hindon Maar Complex, the second Miocene *Konservat-Lagerstätte* to be described from New Zealand. The *Lagerstätte* comprises four partly eroded maar-diatreme volcanoes, with three craters filled by biogenic and highly fossiliferous lacustrine sediments. The exceptionally well-preserved and diverse biota from the site is derived from a mid-latitude Southern Hemisphere lake-forest palaeoecosystem, including many fossil taxa not previously reported from the Southern Hemisphere. The most common macrofossils are leaves of *Nothofagus*, but the flora also includes conifers, cycads, monocots (such as *Ripogonum* and palms), together with Lauraceae, Myrtaceae and Araliaceae leaves and flowers. The small maar lakes were surrounded by *Nothofagus*/podocarp/mixed broadleaf forest growing under humid, warm temperate to subtropical conditions. The fossil fauna comprises insects in the orders Odonata, Hemiptera, Thysanoptera, Coleoptera, Diptera, Hymenoptera and Trichoptera, and the fish assemblage includes a non-migratory species of the Southern Hemisphere *Galaxias* (Galaxiidae) and a



significant new record of the freshwater eel *Anguilla* (Anguillidae). The fossil assemblage also includes the first pre-Quaternary bird feathers from New Zealand and abundant coprolites derived from fish and volant birds, presumably waterfowl. Palynomorph analysis and a  $^{40}\text{Ar}/^{39}\text{Ar}$  age of 14.6 Ma obtained from basanite associated with the maar complex indicate that the Hindon Maar Complex is of mid-Miocene age (Langhian; New Zealand local stage: Lillburnian). It thus provides a new and unique perspective on Neogene terrestrial biodiversity and biogeography in the Australasian region, around the end of the mid-Miocene thermal optimum and prior to late Miocene–Pleistocene climate cooling episodes when many warm-temperate and subtropical forest components became extinct in New Zealand.

## ARTICLE INFO

### *Article history:*

Received

Received in revised form

Accepted

Available online

### *Keywords:*

maar lake

sedimentology

palaeoecology

fossil plants

fossil insects

Zealandia

## 1. Introduction

Fossil *Lagerstätten* are sedimentary deposits that exhibit exceptional fossil preservation and allow insights into past ecosystems, environments, biodiversity and evolution. Some of the most informative terrestrial *Lagerstätten* are associated with maars – small, but deep volcanic craters formed by phreatomagmatic eruptions and surrounded by a ring of tephra. Biogenic, laminated maar lake sediments may store

various environmental proxies and potentially provide annual records of temperature, seasonality and rainfall. Fossil *Lagerstätten* associated with maars are crucial for reconstructing past terrestrial biodiversity and the biogeography and evolutionary history of plant and animal groups (Kaiser et al. 2006, Lehmann and Schaal 2012, Lutz et al. 2010, Rasser et al. 2013). Fossils preserved in maars cover a wide range of terrestrial life forms, from microscopic algae to articulated mammals and typically preserve minute anatomical structures, cuticle, insect colour and soft tissues as the result of burial in an anoxic environment (Kaiser et al. 2006, Lehmann and Schaal 2012, Lutz et al. 2010, Rasser et al. 2013, Wuttke et al. 2015).

In the Southern Hemisphere, only one pre-Quaternary maar has been cored fully and studied palaeontologically: the Foulden Maar, in southern New Zealand, where a 110 m thick sequence of annually-laminated, fossiliferous diatomite is present (Kaulfuss 2017, Lindqvist and Lee 2009). Dated at 23 million years, this maar has yielded numerous well-preserved fossils and provided exceptional insights into Southern Hemisphere terrestrial biota and climate in the earliest Miocene (Lee et al. 2016a). In 2011, an aeromagnetic geophysical survey of an area near Hindon, about 25 km southeast of Foulden Maar (Fig. 1) revealed four further subcircular topographic basins associated with high magnetic intensity. Small-scale preliminary surface excavations carried out by our research team between 2014 and 2017 established that at least three of these basins contain lake sediments with remarkably well-preserved and diverse fossils. Preliminary examination of pollen samples suggested a Miocene age (D.C. Mildenhall, pers. comm. 2014), but abundant mummified leaves indicated a forest dominated by species of Nothofagaceae, in contrast to the Lauraceae-dominated mesothermal rainforest that surrounded Foulden Maar.

This paper reviews what is currently known of the geological setting, geophysical structure, sedimentology, age and biota of the Hindon Maar Complex (HMC). Fossils are abundant and include numerous insects, hundreds of entire leaves with cuticular preservation, flowers and cones with *in situ* pollen, many fish including examples with preserved soft parts and the first pre-Quaternary fossil bird feathers from New Zealand.

Detailed study of this new fossil biota and determination of the age and thickness and type of the Hindon Maar sediments will greatly enhance our understanding of the

terrestrial climate, environments and biodiversity of the mid-latitude Southern Hemisphere in the middle Miocene.

## 2. Geological setting

Late Oligocene to mid-Miocene intra-plate volcanism in the Waipiata Volcanic Field (WVF), southern New Zealand produced dozens of individual small-volume volcanoes over an area of ca. 5000 km<sup>2</sup> in a fluvial setting of the Dunstan Formation (Németh and White 2003; Coombs et al. 2008). Eastwards, towards the Pacific coast, the maar-diatremes, dykes, scoria cones, plugs and lava flows of WVF are adjoined by the Dunedin Volcano; a complex shield volcano that was intermittently active from 16–10 Ma (Coombs et al. 2008, Hoernle et al. 2006). Significant erosion since the Miocene has removed the upper structural levels of volcanoes and their syn-eruptive sedimentary substrates and regional metamorphic basement (Jurassic Otago Schist) is exposed in most parts of the WVF. Although numerous maar-diatremes are known within the WVF (Németh and White 2003), only a few are known to preserve fossiliferous lacustrine sediments: the earliest Miocene Foulden Maar (Kaulfuss 2017, Lindqvist and Lee 2009,) and three craters associated with the mid-Miocene Hindon Maar Complex (HMC) presented herein (Fig. 1).

## 3. Material and methods

### 3.1 Fieldwork methods

Aerial magnetic data of the field area (Fig. 1) were acquired by Glass Earth New Zealand Limited as part of a regional survey of the Otago region, using methods described by Henderson et al. (2016). Preliminary ground-based geophysical surveys of the Hindon Maar *Lagerstätte* were conducted by Bowie (2015). The seismic profile in Fig. 2B was acquired using a trailer-mounted, 250 kg hydraulic thumper as seismic source with four thumps recorded and stacked at each shot point. A 769 m-long reflection profile was recorded by a RAS-24 seismograph system. Each shot point was recorded by a 96-channel (470 m-long) spread with 8 m geophone and shot spacings. Shot positions were roughly centred on the spread to provide a nominal fold of 48 traces at each common depth point (CDP). Data were edited for noise, filtered (using a 5-15-

160-200 Hz trapezoidal filter), adjusted for normal moveout (using a velocity model based on semblance spectra and constant velocity gathers) and stacked.

Descriptions of lithofacies types at the maar complex are based on limited surface outcrops, shallow (<5 m) digger excavations and two drill cores provided by RSC Mining and Mineral Exploration Ltd. The 38.7 m-long core 1 was obtained near the centre of Maar 1 and the 29.6 m-long core 2 near the north-eastern margin of Maar 3 (Fig. 1). There are no natural exposures of fossiliferous maar-lake sediments.

### **3.2. $^{40}\text{Ar}/^{39}\text{Ar}$ dating methods**

See Supplementary File S1 for details of the  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology methods undertaken at the Ar-Ar dating laboratory in the GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany.

### **3.3 Palaeontological methods**

Fossils at the HMC are preserved as organic compressions and were collected as part and counterpart by splitting sediment blocks along bedding planes with a knife blade. About 2000 leaves, 200 insects and numerous fish fossils have been collected since 2015 and more than 250 leaf cuticles have been prepared to date. Cuticle slides were prepared by soaking leaf material in concentrated hydrogen peroxide, warming gently and rinsing gently in distilled water. Where possible, fine paintbrushes were used to remove debris and separate the upper and lower cuticle layers before staining with 0.1% crystal violet for ca. 60 s. If the cuticle fragmented during treatment, a 100  $\mu\text{m}$  cell strainer was used when rinsing and staining the fragments. Cuticle samples were then rewashed and slide mounted in thymol-glycerine jelly and cuticular structure photographed with a Leica digital camera attached to a Leica DM1000 LED microscope using LAS software from Leica Microsystems. Some cuticles were mounted on stubs for SEM microscopy.

Pollen grains were removed from fossil flowers using a fine paintbrush or needle and rinsed in water or 6% hydrogen peroxide to clear adhering organic detritus; the grains were then mounted in thymol-glycerine jelly on a slide for light microscopy and photography. The fossil pollen grains were studied using an Axioplan 2 Imaging Photomicroscope 20483 using a 40 $\times$  or 100 $\times$  objective, with and without oil immersion,

or mounted on a stub for scanning electron microscopy. Where anthers or pollen masses were not visible on the flower surface, whole or part flowers were cleared in dilute  $\text{H}_2\text{O}_2$  and then mounted in thymol-glycerine jelly for microscopic examination; in many cases pollen masses were found on the cleared flower parts.

Insects were prepared with a fine needle and photographed with a Canon T3 camera attached to a Nikon SMZ1000 stereomicroscope, some under ethanol to accentuate anatomical details. Photomicrographs taken at several depths of field were stacked using Photoshop CS5.1 software (Adobe Systems Inc.). Macrophotographs of fossils were taken with a Sony D80 DSLR camera.

References to authors of all extant plant genera and species mentioned in the text can be found at The International Plant Names Index (<http://www.ipni.org/>), for algae at AlgaeBase ([www.algaebase.org/](http://www.algaebase.org/)) and for animals at The Taxonomicon (<http://www.taxonomy.nl/taxonomicon>). Fossil palynomorph nomenclature and authorities follow Raine et al. (2011). The fossil sites are registered in the New Zealand Fossil Record File administered by the Geoscience Society of New Zealand and GNS Science (<http://www.data.gns.cri.nz/fred>). All specimens, apart from duplicates of pollen slides, are held in the collections of the Geology Museum (OU), University of Otago, Dunedin, New Zealand, some in a refrigerator to prevent or delay desiccation of the sediment matrix and disintegration of the fossil material.

#### **4. Results of geological and geophysical investigations**

##### ***4.1. Local geology and geophysics***

The Hindon Maar Complex is situated on private farmland near Hindon, 30 km west of Dunedin, Otago, southern New Zealand ( $45^{\circ}45.62'S$ ;  $170^{\circ}15.88'E$ ; Fig. 1). The complex includes four subcircular topographic basins (Fig. 2A), which coincide with positive aeromagnetic anomalies that indicate the presence of volcanic (clastic) material at some depth below the surface (Fig. 1). Ground-based geophysical surveys have established that the magnetic anomalies are associated with gravity minima (Bowie 2015), which is typically the case with maar-diatreme structures (Buness et al. 2006, Matthes et al. 2010, Mrlina et al. 2009). The two isolated maars in the northeast of the complex are  $500 \times 500$  m and  $1000 \times 500$  m wide, whereas two closely-spaced, originally possibly coalescent maars in the south are ca. 750 m wide (Fig. 1). At the

surface, the maars are surrounded by Otago Schist, the regional metamorphic basement; pyroclastic material of the original tephra rings is not preserved. A seismic reflection survey of Maar 1 (Fig. 2B) revealed a steep-sided, funnel-shaped structure excavated into Otago Schist basement to a depth of at least 400 m. Based on seismic observations at other maar-diatreme volcanoes (Buness et al. 2006), chaotic seismic facies in the lower part of the structure may represent pyroclastic material of the lower diatreme and the overlying distinctively stratified interval may be bedded pyroclastics of the upper diatreme. Velocity modelling of the seismic data suggests that the layered units (150–200 ms two-way travel time in Fig. 2B) have an average velocity of total thickness of about 1300–1400 m/s and, therefore, a thickness of 100–140 m. The <20 m thick post-eruptive sediments in Maar 1 (see drill core analysis below) do not account for the stratified interval in the seismic model.

#### 4.2 Lithology

The sedimentary and volcanic lithologies of the HMC were studied in two exploration wells (up to 39 m deep), several auger-holes (2.5 m deep) and temporary near-surface excavations (Fig. 2C). The general stratigraphy in the central parts of the maars consists of the following units (from top to base):

- highly fossiliferous, biogenic lake sediments (gyttja, spiculite, diatomite)
- siliciclastic gravity flow deposits (turbidites and debris flows beds)
- coherent basanite (in Maar 3 only)
- homogeneous or crudely stratified tuff breccia

The fine-grained, fossiliferous lacustrine sediments are the stratigraphically youngest maar units and are unconformably overlain by clayey to pebbly alluvium and loess. Essentially composed of amorphous and detrital organic material and siliceous microfossils, these non-calcareous sediments comprise gyttja (>50% organic material), spiculite (>50% sponge spicules) and diatomite (>50% diatoms). Black and dark brown, medium to coarsely laminated gyttja and spiculite are the prevailing sediments and contain low amounts of siliciclastic silt/sand (Fig. 3). Thin intervals of finely laminated diatomite occur sporadically throughout. Pyrite is commonly present as dispersed framboids or as replacement of plant material and fish bones. Sedimentary structures

related to currents, bioturbation or desiccation are absent, as are fossils of benthic organisms. Interbedded mm to cm thick, homogeneous or normally graded beds occur sporadically and are compositionally indistinguishable from the laminated sediments (Fig. 3C). Some of these beds contain laminated intraclasts.

The sum of sediment characters suggests cyclic, biogenic sedimentation under anoxic conditions, in the profundal zone of a stratified, possibly meromictic maar lake with sporadic sedimentation by turbidity currents. No calcareous-shelled fossils have been recorded, which may suggest that acidic conditions prevailed in the bottom waters of the lakes. The thickness of fossiliferous sediments in exploration wells is 8 m (Maar 1) and 7 m (Maar 3); their thickness in Maar 4 is uncertain. It is not possible to determine the original sediment thickness prior to erosion and no biogenic sediments were found in Maar 2, which appears to have been infilled completely by volcanoclastic (either primary or reworked) deposits. Underlying the biogenic sediments is an 8–10 m-thick, gently dipping siliciclastic sequence composed of massive and graded breccias and sandstones (Fig. 3). Interpreted as sub-aqueously emplaced debris flows and turbidites, these beds probably accumulated on the maar floor adjacent to steep walls of the freshly formed maar craters.

Massive and crudely stratified tuff breccias encountered in deeper parts of exploration wells (Fig. 3) are composed of basaltic glass, angular schist fragments and rounded quartz granules and pebbles. In contrast to the overlying sediments, these deeper beds show no signs of transport or particle sorting by gravity flows and are, by analogy with lithofacies successions described from maar-diatremes elsewhere (Goth et al. 2003, Kaulfuss 2017, Pirrung et al. 2003, White and Ross 2011), most plausibly interpreted as pyroclastic deposits of the upper diatreme. The abundant schist and quartz clasts in these deposits may, therefore, represent lithic fragments of a mixed syn-eruptive substrate comprising schist and unconsolidated quartz pebble conglomerates. The latter are completely eroded at the maar sites, but localised erosional remnants of quartz pebble conglomerate are preserved below basanite at nearby Fortification Peak (Fig. 1).

A coherent basanite body at least  $300 \times 140$  m in transverse dimensions occurring above pyroclastic beds in Maar 3 was  $^{40}\text{Ar}/^{39}\text{Ar}$  dated for this study. Because geophysical surveys have found no extra-crater dykes or vents, we interpret this

basanite as having been emplaced on the syn-eruptive maar floor at the end of the maar-forming eruption sequence, possibly due to a shift from phreatomagmatic to ‘dry’, effusive activity as (ground)water became exhausted. A second  $^{40}\text{Ar}/^{39}\text{Ar}$  date was obtained from Fortification Peak (Fig. 1), a small subaerial basanite plug 2 km to the west of Maar 1 that has been quarried extensively for aggregate.

## 5. Results of palynostratigraphy and radiometric dating

A key part of this study involves determination of the precise age of the HMC *Lagerstätte* to put the fossil biota into a stratigraphic and palaeoenvironmental context and to provide well-dated calibration points for molecular phylogenies of the fish, plants and insects. This was obtained by two independent methods: palynology and radiometric dating of volcanic rock (basanite) associated with the lake sediments.

### 5.1 Palynology

Hindon Maar was estimated initially to be of early Miocene age (Aquitainian/Burdigalian; 23.03–15.97 Ma), corresponding to the Otaian to Altonian New Zealand Stages (Raine et al. 2015), based on an assessment of the palynological assemblage (DC Mildenhall pers. comm. in Youngson, 1993). The only clues to age in several newly investigated palynological samples from Maars 1 and 3 were *Coprosma* J.R.Forst. and G.Forst. (Rubiaceae) pollen, which first appears in the late Oligocene of New Zealand, close to the 27 Ma Duntroonian/Waitakian boundary (Mildenhall 1980) and *Assamiapollenites incognitus* Pocknall and Mildenh., which first appears in Otaian sediments (Mildenhall and Pocknall 1989), extending through to at least the middle Pliocene (Waipipian: 3.6–2.6 Ma) of New Zealand (Pocknall and Mildenhall 1984; Mildenhall and Pocknall 1989). These indicate that the HMC is no older than early Miocene, but is potentially younger.

### 5.2. $^{40}\text{Ar}/^{39}\text{Ar}$ dating

Previously published K/Ar and  $^{40}\text{Ar}/^{39}\text{Ar}$  ages (Hoernle et al. 2006, Coombs et al. 2008) indicate that the Waipiata Volcanic Field was active from 25 to 11 Ma, which represents the time range in which the Hindon Maar Complex erupted. In this study, the groundmass of two basanite samples from Maar 3 and Fortification Peak (Fig. 1 and Supplementary File S2) were analysed by laser step heating, yielding plateau ages



comprising >99% of the total  $^{39}\text{Ar}$ . The sample from the Hindon Maar 3 (OU85802) yielded a plateau age of  $14.603 \pm 0.093$  Ma ( $2\sigma$ ; Mean Square Weighted Deviation (MSWD) = 1.5; probability (P) = 0.077; 99.93% of  $^{39}\text{Ar}$ ; steps 1–19) and a valid inverse isochron age of  $14.62 \pm 0.12$  Ma (95% confidence; MSWD = 1.18, P = 0.28, Spreading Factor (SF) = 86.6%; steps 1–19; Fig. 4), with an initial  $^{40}\text{Ar}/^{36}\text{Ar}$  ratio of  $293.8 \pm 5.3$ , which is within error of the atmospheric  $^{40}\text{Ar}/^{36}\text{Ar}$  ratio of 295.5 (Steiger and Jäger 1977). The  $^{36}\text{Ar}/^{39}\text{Ar}$  alteration index values indicate the presence of some alteration in this sample, but steps 8–17 originated from fresh material (S2), therefore we have confidence in this  $^{40}\text{Ar}/^{39}\text{Ar}$  age. The  $14.603 \pm 0.093$  Ma age indicates that the Hindon Maar Complex is of mid-Miocene age (Langhian; New Zealand local stage: Lillburnian, 15–11.5 Ma). Likely emplaced during the final maar-forming eruptions, this basanite provides a maximum age of 14.603 Ma for the fossiliferous maar lake sediments. By analogy with the sedimentation history in maars elsewhere (Pirrung et al. 2003, 2008), the fossiliferous sediment likely accumulated a few hundreds to thousands of years after cessation of volcanic activity. Age data for the three other maars of the HMC are not available, but it is likely that all four maars erupted within days or weeks of each other, as observed at the historically erupted Ukinrek Maars in Alaska (Kienle et al. 1980, Self et al. 1980).

The basanite groundmass sample from the nearby Fortification Peak (OU85803) yielded a plateau age  $17.941 \pm 0.094$  Ma ( $2\sigma$ ; MSWD = 1.5, P = 0.11; 99.72% of  $^{39}\text{Ar}$ ; steps 2–15) and a valid inverse isochron age of  $17.97 \pm 0.18$  Ma (initial  $^{40}\text{Ar}/^{36}\text{Ar}$  =  $294.2 \pm 7.5$ ; MSWD = 1.3, P = 0.20, SF = 84.6%; Fig. 4). The  $^{36}\text{Ar}/^{39}\text{Ar}$  alteration index values indicate the presence of alteration in the majority of this sample, as only step 14 indicates fresh material, therefore, this  $^{40}\text{Ar}/^{39}\text{Ar}$  age should be treated as a minimum estimate, as alteration may have resulted in some Ar loss. The  $17.941 \pm 0.094$  Ma age indicates that Fortification Peak is significantly older than the volcanic/phreatomagmatic episode that formed the HMC.

## 6. Systematic overview

### 6.1 Limnic microfossils

Limnic microfossils are ubiquitous throughout the lacustrine sequence and include sponge spicules, diatoms and golden and green algae. Slender, smooth or slightly

ornamented siliceous megascleres of the freshwater sponge *Spongilla* Lamarck were found in all sediment samples from Maars 1, 3 and 4 (Fig. 5A). Typically 0.2–0.3 mm long, these spicules are mostly pristine, although some have pitted surfaces that indicate some corrosion (silica dissolution). Microscleres and gemmuloscleres of *Spongilla* are comparatively rare; circular gemmules ca. 2 mm in diameter are sporadically present on laminae planes (Fig. 5B). In the palaeolakes, *Spongilla* probably lived attached to the substrate and macrophytes in the littoral zone and spicules were later distributed into the profundal sediments.

A preliminary study of the diatoms revealed an assemblage (Fig. 5C, D; Table 1) consisting of eight pennate taxa and at least two species of the centric diatom *Aulacoseira* Thwaites (pers. comm. M. Harper 2017). *Aulacoseira* is the dominant diatom in Maar 3, whereas various pennate species dominate in the sediments of Maars 1 and 4. More detailed studies are required to decipher the hydrological and environmental conditions that explain the different assemblages in the palaeolakes. Overall, the diversity of diatoms at the HMC is higher than that of the early Miocene diatomites at Foulden Maar, although the dominating taxon in the latter deposit, *Encyonema jordanii* (Grunow) Mills, appears to be absent from the HMC assemblages. However, the diatom flora is of low diversity compared to other Miocene freshwater deposits in southern New Zealand, for example the Miocene shales at the Nevis Valley (27 diatom taxa) and at Double Hill near Dunedin (32 taxa) (Harper et al. 2016). This may indicate that the restricted habitats and hydrological conditions in the deep maar lakes, possibly accompanied by volcanic disturbance, were not suitable for supporting high diatom diversity. Siliceous stomatocysts of golden algae (Chrysophyta) occur scattered throughout the sediments, either isolated or as clusters of cysts representing at least two morphotypes (Fig. 5E). Sediment samples studied by SEM also contain dispersed colonies of the green alga *Botryococcus braunii* Kützing (Fig. 5F).

## 6.2 Palynomorphs

Palynomorphs were difficult to extract from the humic matrix of highly degraded plant material and many of the spores and pollen grains appear to have been lost during processing, with mainly robust taxa recovered. Overall, the spores and pollen recovered were sparse and diversity was low, except for Nothofagaceae and Podocarpaceae (Supplementary File S3). Samples previously collected by Youngson (1993) were

dominated by *Nothofagus* Blume subgen. *Brassospora* Philipson and M.N. Philipson (23–40%) and subgen. *Fuscospora* R.S. Hill and J. Read (8–13%), Myrtaceae (24–30%) and both tri- and bi-saccate Podocarpaceae palynomorphs (9–13%). Fern spores were sparse, including various polypodiaceous spores. In the current study, the most common pollen types were *Nothofagus* subgen. *Brassospora* (52%), *Casuarina* L.-type (6%), *Nyssapollenites endobalteus* Mildenh. and Pocknall (4%), *Rhoipites* Wodehouse spp. (6%), *Nothofagus* subgen. *Fuscospora* (2%), Myrtaceae (2%), very small, smooth tricolp(or)ate grains identified as possible Cunoniaceae (4%) and various unidentifiable tricolpate and tricolporate grains (11%). Anther-derived pollen clumps from Casuarinaceae, Loranthaceae, Myrtaceae, Nothofagaceae and Euphorbiaceae (*Malloranga*) were also present, affecting pollen counts due to apparently uneven dispersal. Conifers were represented by *Podocarpidites* Cookson spp. (4%), *Dacrydiumites praecupressinoides* (Couper) Truswell (2%), *Podosporites parvus* (Couper) Mildenh. (1%) and rare *Araucariacites* Cookson and Couper, *Dacrycarpites* Cookson and K.M. Pike, *Microalatidites* Mildenh. and *Taxodiaceapollenites* Kremp ex Potonié pollen. As per Youngson's (1993) results, fern spores were relatively sparse, but four *Polypodiisporites* Potonié spp. (the dominant fern spores at the site), *Laevigatosporites ovatus* R.M. Wilson and L.R. Webster, *Monolites alveolatus* Couper, *Cyathidites* Couper sp., *Triletes* Reinsch sp. and *Verrucosisporites kopukuensis* (Couper) Stover were present. The palynomorph assemblage implies a mainly beech/podocarp source forest growing under humid mesothermal conditions.

### 6.3 Macrofloral assemblage

#### 6.3.1 Podocarpaceae

Podocarpaceae macrofossils (Fig. 6A–C) are represented by several genera: individual leaves of *Podocarpus* L'Hér. ex Pers. and leafy branchlets of *Prumnopitys* Phil., all with well-preserved cuticle, have been found. Several twigs with up to 12 attached small, flattened leaves (Fig. 6C) are referred to an undescribed extinct species of *Prumnopitys* and there are also shoots of the scale-leaved taxa *Dacrydium* Sol. ex Lamb and *Dacrycarpus* (Endl.) de Laub. There are also significant records of several small compressed, resiniferous Podocarpaceae pollenate cones (Fig. 6A). Pollen extracted from these cones resembles closely the dispersed fossil palynomorph

*Podocarpidites puteus* Mildenh. and Pocknall, which is considered to represent a species of *Podocarpus* (Mildenhall and Pocknall 1989, Raine et al. 2011).

### 6.3.2 *Cycad and ferns*

There is an incomplete section of a cycad leaf with excellent cuticular preservation that appears to be a new species of the extinct Australasian *Pterostoma* R.S.Hill (Zamiaceae); its affinities are the subject of ongoing research. A single, unidentified fern pinna has been collected to date (Fig. 6R)

### 6.3.3 *Monocots*

Although monocot leaf fossils other than palms tend to be uncommon (Greenwood and Conran, 2000), three taxa have been identified so far at Hindon: *Astelia* Banks and Sol. ex R.Br. (Asteliaceae), *Ripogonum* J.R.Forst. and G.Forst. (Ripogonaceae) (Fig. 6G) and *Typha* L. (Typhaceae) (Fig. 6D–E). Although monocot leaves are generally recognized by their elongate, linear to lanceolate shape and parallel venation, the *Ripogonum* macrofossils are differentiated by their ovate, reticulate-veined leaves with prominent suprabasal secondary veins and distinctive epidermal cell shapes (Conran et al. 2015, Kerr 2016). *Ripogonum* is a characteristic liana in modern New Zealand and Australian rainforests, whereas *Astelia* is a rhizomatous epiphytic or forest-floor herb and the emergent aquatic *Typha* probably fringed the lake edge.

Although no palm fronds have been found at the site as yet, there is a *Rhopalostylis* H.Wendl. and Drude-like flower with *in situ* *Arecipites* D.J.Nichols, H.T.Ames and Traverse pollen. Dispersed *Arecipites* pollen is also present in the maar sediments and a single, distinctive palm phytolith was retrieved from a diatom preparation (John Carter pers. comm., 2015); however, the affinities of these microfossils and most other New Zealand fossil palms are still uncertain (Pole 1993, Conran et al. 2015).

### 6.3.4 *Basal angiosperms and eudicots*

Many of the numerous basal angiosperm and eudicot leaves have excellent preservation of cuticular features (Fig. 6) whereas others, particularly those from weathered surface exposures, exhibit detailed venation without cuticular preservation. These leaves include representatives of at least 10 families (Table 2), including several taxa of Araliaceae (Fig. 6H–K), Euphorbiaceae (including *Malloranga dentata* Conran, D.E.Lee, and T.Reichg.), Lauraceae (*Cryptocarya* R. Brown, *Litsea* Lam. and other

genera) (Fig. 6M, N), Menispermaceae (Fig. 6O), Monimiaceae (*Laurelia* Juss.), Myrtaceae (Fig. 6L), Myrsinaceae and Sapindaceae (Fig. 6Q). However, the leaf assemblage is overwhelmingly dominated by several species of *Nothofagus* (Nothofagaceae) (Fig. 6P), with assessment of species abundance and comparisons to modern *Nothofagus*-forests being the subject of further research.

### 6.3.5 Flowers, fruits and seeds

Globally, flowers with *in situ* pollen are relatively uncommon in the pre-Quaternary fossil record (Balme 1995, Friis et al. 2011). So far at the HMC, we have collected 47 individual flower compressions ranging in diameter from 6–20 mm, most with petals, anthers and stamens preserved. All but two collected so far are assigned to Araliaceae based on flower structure and pollen type (Fig. 6J, K). Another represents an extinct genus of mistletoe with *in situ* pollen of *Cranwellia striata* (Couper) S.K.Srivast., making it only the second fossil Loranthaceae flower to be reported globally; the other is a mummified flower from Foulden Maar with *in situ* *Gothanipollis perplexus* Pocknall and Mildenh. pollen (Conran et al. 2014). Fruits and seeds recovered from the site include a winged Bignoniaceae seed, an Elaeocarpaceae-like endocarp (aff. *Phymatocaryon* F.Muell.), paniculate capsular Myrtaceae infructescences (Fig. 6L), Nothofagaceae cupules and several types of Araliaceae false berries.

### 6.4 Insects

Insect remains include articulated specimens, body fragments and isolated wings; many are yet to be studied in detail. Insects are typically preserved with wing patterns and structural colours and some beetles found in spiculite lithofacies preserve a three-dimensional aspect (Fig. 7), presumably because interlocking sponge spicules impeded strong compaction. Most insects represent terrestrial taxa from forest and forest floor habitats; insects with aquatic or semi-aquatic lifestyles are comparatively rare (Table 1).

#### 6.4.1 Odonata

A partially preserved wing from the HMC is the first fossil record of damselflies (Zygoptera) from New Zealand. Although the specimen requires further study, some venation characters, such as the position of the two antenodal cross-veins, a large and near rectangular quadrilateral cell and the appearance of vein A1, suggest an affiliation

with Argiolestidae; a family of 20 extant genera in the Old World tropics (Kalkman and Theischinger 2013) that is now extinct in New Zealand.

#### 6.4.2 Hemiptera

Hemiptera (10% of identified insects) include the only insect previously described from HMC. The primitive hairy cicada *Paratettigarcta zealandica* Kaulfuss and Moulds (Auchenorrhyncha: Tettigarctidae) was the first fossil cicada to be described from New Zealand (Kaulfuss and Moulds 2015). The two extant species of this mainly Mesozoic family are confined to Australia and *P. zealandica*, therefore, provides a rare example of an insect group that has become extinct in New Zealand since the mid-Miocene.

The suborder Heteroptera is represented by several taxa in Pentatomidae (stink bugs and shield bugs) (Fig. 7A, B), which have no previous fossil record for New Zealand. Additionally, there is one specimen of the flatbug *Aneurus* Curtis (Pentatomorpha: Aradidae), which has been documented from the early Miocene Foulden Maar (Kaulfuss et al. 2011) and persists with six extant species (in subgenus *Aneurodellus* Heiss) in mixed evergreen broadleaf/podocarp and southern beech (*Nothofagus*) forests in New Zealand.

Among Sternorrhyncha, an isolated wing with venation characters found in Psyllidae and Calophyidae (absence of vena spuria, common stem of veins M and CuA, long vein RP) provides the first fossil evidence for Psylloidea (jumping plant lice and psyllids) in New Zealand (Fig. 7C). Both Psyllidae (40 spp.) and Calophyidae (1 sp.) are represented in the modern New Zealand fauna, mainly by adventive species, including some host-specific gall formers (Macfarlane et al. 2010). Unfortunately, characters that would allow distinction between the two families, such as tarsal segments and antennae, are not preserved in the fossil. Suborder Sternorrhyncha is also represented by 18 individual whitefly (Aleyrodidae) puparia attached in life position on an angiosperm leaf. Fossil puparia are rare globally and, although the family has a long fossil record (Boykin et al. 2013), this is the first Southern Hemisphere record of fossil Aleyrodidae and has the potential to reveal biogeographic relationships of the extant whitefly fauna in New Zealand (14 spp., eight endemic).

### 6.4.3 *Thysanoptera*

Thysanoptera (thrips) are minute, slender, predatory or plant-feeding insects comprising about 6000 extant species worldwide and 121 species in New Zealand with an endemism level of 69% in suborder Tubulifera and 32% in suborder Terebrantia (Macfarlane et al. 2010). Although thrips have been reported from the Permian and Cretaceous of Australia (Jell 2004), the fossils from the HMC are the first Cenozoic records for the Australasian region. Most specimens appear to be wingless taxa in suborder Tubulifera, as indicated by their tube-shaped apical abdominal segment (Fig. 7D), but one winged specimen has the general habitus of suborder Terebrantia. Their relative abundance at the HMC (6% of insects) indicates that thrips were an important component of the Miocene forest ecosystem at the site.

### 6.4.4 *Coleoptera*

Beetles are the most abundant fossil insects at the HMC (69% of all insects). Despite their high diversity in modern and fossil faunas, it is possible that the group is over-represented at the HMC because many insect taphocoenoses in Cenozoic maars are taphonomically biased towards heavy, compact insects, such as beetles (Lutz et al. 2010, Wedmann et al. 2010). Currently, taxa in Hydrophilidae, Buprestidae, Elateridae, Curculionidae and possibly Chrysomelidae are recognised in the Hindon fauna. In addition, several isolated elytra have been recovered, but those are not determinable to family level. Most diverse and specimen-rich is Curculionidae (weevils), including cf. *Nyxetes* Pascoe (Curculioninae: Eugnomini), a monotypic, endemic genus from northern New Zealand, a cryptorhynchine weevil close to the flightless, endemic *Clypeolus* Broun and an apionine member of Rhadinocybini, now represented by four native New Zealand genera (S. Brown pers. comm., 2015). As in other lacustrine fossil *Lagerstätten*, most of the weevils are preserved as laterally compressed specimens (Fig. 7E, F), owing to toppling of their rounded bodies on the lake floor. Other beetles with a more flattened habitus are usually found as dorsoventrally compressed fossils.

### 6.4.5. *Diptera*

Diptera (flies and midges) currently comprise 5% of determined insects and are, except for an aquatic pupa, represented by isolated wings only. One of these is a calytrate fly (*Schizophora*) that can be placed tentatively into Muscidae (house flies),

based on the preserved venation, although the diagnostic wing base is missing in the specimen (Fig. 7H). The venation of a second wing is congeneric with, or very close to the march fly *Dilophus* Meigen (Nematocera: Bibionidae), the sole extant bibionid in New Zealand, with all eight species endemic (Harrison 1990). The only fossil Diptera described formally from New Zealand is *Dilophus campbelli* Harris from the Eocene of Otago (Harris 1983). This species was based on a final instar larva and cannot be compared taxonomically to the wing from the HMC, but both records suggest a long history for *Dilophus* in New Zealand, dating back to at least the Eocene.

Another dipteran fossil preserves traces of compound eyes, wing pads arising out of the thorax and an elongate abdomen (Fig. 7I) and strongly resembles the aquatic pupa (or pupal exuviae) of chironomid midges (Nematocera: Chironomidae). With 67 genera, Chironomidae are the most diverse nematocerans in the extant fauna, but the pre-Quaternary fossil record of chironomids from New Zealand is almost a complete blank. The poorly preserved specimen from the HMC does not provide any taxonomic information, other than that chironomid midges were present at the site in the mid-Miocene. However, four adult specimens discovered in Miocene amber from South Island (Schmidt et al. 2018) and several pupae collected recently at the Foulden Maar *Lagerstätte* (Kaulfuss, pers. obs.) will assist with an assessment of Miocene New Zealand chironomid diversity.

#### 6.4.6 Trichoptera

Caddisflies (Trichoptera) at Hindon are represented exclusively by larval stages (Fig. 7J, K). These are the most common aquatic insects in the maar lake sediments and account for 7% of all insects recovered at the site. Empty larval cases and cases with the larvae preserved are equally common, although larvae are mostly unidentifiable below order. Nevertheless, variable case size (6–18 mm long), shape (curved or straight) and building materials (plant fragments, mineral grains, or mixed) suggest the presence of several trichopteran taxa. One larva in a case made of small twigs and other plant material appears to have dark-banded legs (Fig. 7K) and is assigned tentatively to *Triplectides* Kolenati (stick caddis, Leptoceridae), which has three endemic extant species in New Zealand streams. However, this needs to be confirmed by a more detailed study and the same applies for the only other trichopteran fossils from New Zealand discovered recently at Foulden Maar (Kaulfuss, pers. obs.).



#### **6.4.7 Hymenoptera**

Insects attributable to the Hymenoptera currently comprise mostly unidentifiable body and wing fragments, which account for 5% of all insects. All the identified specimens belong to Apocrita and await detailed taxonomic study. This includes a partly preserved, winged specimen (Fig. 7G) with stout body and incomplete forewing veins resembling the general venation pattern present in Apidae (bees).

A further specimen is assigned to the parasitoid wasps Ichneumonidae, based on wing venation, but lacks preservation of anatomical details that would allow further placement within this diverse family (Fig. 7L). In addition to an unidentified (but different) ichneumonid from Foulden Maar (Kaulfuss et al. 2015), this is only the second fossil record of Ichneumonidae from New Zealand. Another apocritan specimen with long first antennal segments, slender and elongate mandibles, an oval abdomen tapering towards the thorax and parts of the wing venation preserved (Fig. 7M) is tentatively identified as a female ant alate (Formicidae). This fossil may eventually add to the Miocene diversity of Formicidae, which appears to have been taxonomically different and more diverse than the meagre extant fauna native to New Zealand (Kaulfuss and Dlussky 2016). Very distinctive, circular, 2 mm diameter leaf galls with radially arranged exit holes found on leaves closely resemble those produced by some species of chalcid wasps (Chalcidoidea), but this is not yet confirmed by body fossils.

#### **6.5 Plant-insect associations**

Insect herbivory patterns at the HMC were studied in detail by Möller et al. (2017). In a sample of 584 angiosperm leaves at the site, they found a very high proportion of insect-damaged leaves (73%) and a high diversity of 87 damage types representing all eight functional feeding groups. Damage types related to hole feeding, margin feeding, surface feeding and galling were most commonly observed, whereas mining, skeletonizing, piercing and sucking and oviposition were less common. Besides providing one of very few studies on insect herbivory in the Cenozoic of New Zealand, the high richness of insect herbivory found by Möller et al. (2017) also provides indirect evidence for a diversity of herbivorous insects at the HMC, with producers of many of the damage types currently not documented by insect body fossils.

## 6.6 Fish

Fish fossils are common at the HMC and are distributed and oriented randomly in the sediment; no mass-mortality layers were observed. They are found as articulated specimens with soft tissue, such as eyes and skin, preserved. Soft tissue is evident as dark shadows tracing body outlines, whereas eyes appear as dark black spots (Fig. 7O). Fish bones exhibit various degrees of pyritization, from non-pyritized to completely pyritized and show little signs of bone decalcification. Almost all fish fossils belong to *Galaxias* Cuvier in the Southern Hemisphere Galaxiidae (Teleostei). Comprising mainly diadromous species, Galaxiidae is present with c. 25 species in the modern fauna (DOC, 2017) and has also been reported from various Miocene freshwater deposits in New Zealand (McDowall and Pole 1997, Lee et al. 2007, Schwarzhans et al. 2012). The presence of c. 12 mm long galaxiid larvae, together with juveniles and adult specimens up to 180 mm body length, strongly suggests that *Galaxias* at the HMC was a lake-locked, non-migratory species.

The second fossil fish at the site is a species of *Anguilla* Schrank (Anguillidae), represented by three partly preserved specimens that have the elongate, slender body form, the continuous dorsal and anal fins and the vomerine tooth bands seen in freshwater eels. *Anguilla* fossils have only been reported previously from Cenozoic localities in Europe (e.g. Stinton 1975, Micklich 1985). The significance of finds of *Anguilla* in Miocene lake sediments in New Zealand (another unpublished fossil has also been found at the Foulden Maar) for the biogeographic and evolutionary history of freshwater eels will be discussed in a forthcoming publication.

## 6.7 Birds

Three well-preserved feathers (Fig. 7N) provide direct evidence for the presence of birds at the Hindon maar lakes and, although currently taxonomically unassigned, are the first pre-Quaternary avian feathers from New Zealand. A diverse mid-Miocene avifauna has been documented by isolated bones from the Manuherikia Group in Otago (Worthy et al. 2013) but despite this documented diversity and an abundance of likely bird-derived coprolites (see below), no avian fossils have been found at HMC to date. The same is true for the early Miocene Foulden Maar *Lagerstätte*, where the presence of waterfowl has been inferred from coprolites (Lindqvist and Lee 2009).

## 6.8 Coprolites

Coprolites are extremely abundant in the lacustrine sediments and occur either randomly distributed throughout, or as mass layers on individual bedding planes. Typically, the coprolites are 15–30 mm long and with elongate or coiled shape and mostly consist of quartz sand, mica and organic detritus (Fig. 7P–R). A less common type is 5–15 mm long and consists of organic material (seeds, plant and insect cuticle, amorphous material) and mineral grains. These smaller coprolites are most likely derived from fish, but the larger examples incorporating well-rounded quartz grains (which are otherwise not found in the sediments) are almost certainly from volant birds, such as waterfowl.

## 7. Discussion

### 7.1 Lacustrine sedimentation in a volcanic environment

Drill core and geophysical data demonstrate that the Hindon Maar fossil *Lagerstätte* in southern New Zealand is associated with four maar craters formed by phreatomagmatic eruptions within the late Oligocene to mid-Miocene Waipiata Volcanic Field. The organic and highly fossiliferous sediments of this *Lagerstätte* accumulated in central parts of small lakes within three 500–1000 diameter maar craters. The preservation of organic material, such as plant and insect cuticle, in the laminated lake sediments in combination with the absence of benthic fossils, bioturbation structures and current ripples argue for anoxic conditions at the water-sediment-interface and sedimentation under stratified (meromictic) lacustrine conditions. Fossils in the laminated sediments comprise diverse plants, insects, fish and bird feathers and there is no indication that specific taxa have been lost through diagenetic processes, except possibly for calcareous-shelled organisms.

The fine to coarse lamination in the lacustrine sediments may document annual sedimentation cycles, similar to those reported from the early Miocene diatomites at Foulden Maar (Lindqvist and Lee 2009) and other lacustrine maar sediments (Zolitschka et al. 2015 and references therein), but this has yet to be confirmed by detailed sedimentological studies. Interbedded, graded or massive beds are reworked lake sediments and document episodic mass flow events within the maar lakes. Because the sediments of the central lake facies provide no evidence for sediment input by

streams, the palaeolakes of the HMC may have been disconnected from the local drainage system, at least for the depositional period documented by the preserved (post-erosion) maar sediments. Massive or graded breccia and sandstones underlying the fossiliferous lithologies are interpreted as subaqueous gravity flow deposits within the freshly formed maar craters and rest on tuff and tuff breccia of steep-sided diatremes. Based on pollen stratigraphy and an  $^{40}\text{Ar}/^{39}\text{Ar}$  age of  $14.603 \pm 0.093$  Ma ( $2\sigma$ ) obtained from a basanite in one of the maars, we propose a mid-Miocene age (international stage: Langhian, New Zealand stage: Lillburnian) for the fossil biota of the Hindon Maar Complex.

## 7.2 *The floral assemblage*

Fossil plant diversity requires the recognition of the different taxa, association of dispersed parts of the same species (flowers, leaves, fruits etc.), where possible and the phylogenetic placement of these taxa to assess their importance for the evolution of the groups to which they belong. Given the relative paucity of definitively identified and well-dated plant fossils for many Southern Hemisphere families and genera, the diversity seen at Hindon and the generally excellent preservation of some floral organs (e.g., leaf cuticle; flowers and cones with *in situ* pollen) means that the site is of particular importance for understanding the vegetation prevailing in southern Zealandia in the mid-Miocene.

Only one fern macrofossil has been collected to date and the pteridophyte spore record is relatively sparse, with only 5–6 families recorded: Polypodiaceae (*Belvisia*), several spore morphotypes referable to Polypodiaceae/Davalliaceae, the tree ferns Cyatheaceae and Dicksoniaceae, the climbing fern *Lygodium* (Schizaeaceae) and generalist fern spore types. Fern fronds are generally rare at the Foulden Maar (Lee et al. 2016) and at most other localities; most likely a taphonomic bias reflecting the fact that most taxa do not drop their fronds at senescence (e.g. Drake and Burrows 1980). One cycad (Zamiaceae) has been collected: cycads are not represented in the modern New Zealand flora, presumably because of climate cooling from the late Miocene to Pleistocene. Conifers are represented by a dozen pollen morphotypes and foliage and/or polleniferous cones attributable to four podocarp genera: *Dacrycarpus*, *Dacrydium*, *Podocarpus* and *Prumnopitys*, all of which have a long record in New Zealand (Lee et al. 2016b) and are still key components of the modern flora. At least one palm species

grew close enough to the lake for flowers to fall into the water and the relative abundance of leaves of an undescribed species of the liana *Ripogonum* suggests it was also common in the lake-side forest.

Overall, the forests surrounding the Hindon maar lakes can be described as a *Nothofagus*/podocarp/mixed broadleaf forest ecosystem. About 50% of the several hundred leaves collected to date are from several broad-leaved species of *Nothofagus*, suggesting that these trees grew on the lake margins on relatively fertile soils. At least three species of Lauraceae are present, together with two or three Myrtaceae taxa. Araliaceae are also well-represented by leaves and flowers; the preponderance of small, well-preserved flowers indicating these trees were part of the understorey vegetation on the edge of the lakes. Apparent differences in the abundance of some pollen types at different stratigraphic levels within the maar (e.g. 2% to 30% Myrtaceae pollen) could suggest major shifts in local vegetation but this requires further investigation. Although some *Typha* leaf fragments are present, indicating it was present along the lake edges, it is not common as a macrofossil, possibly reflecting the narrow littoral zone generally seen around maars relative to most other lakes.

Despite very similar depositional environments, the plant fossils from the mid-Miocene HMC indicate a very different forest composition from that reconstructed for the earliest Miocene Foulden Maar. For example, there are abundant and diverse *Nothofagus* leaves at the HMC, but none have been collected in the thousands of leaves retrieved from Foulden Maar. Instead, the vegetation surrounding Foulden Maar was a highly diverse, Lauraceae-dominated mixed rainforest (Lee et al. 2016a), with many monocot taxa. Hindon hosts a new species of *Ripogonum*, not closely related to the several species present at Foulden Maar. At Foulden, at least 30 flower compressions representing a dozen families are present, half with *in situ* pollen (Conran et al. 2014). A similar number of pollen-bearing flowers are known from the HMC, but all but two are from the same species of Araliaceae.

Given the significance of the plant diversity already recognised at Foulden Maar (e.g. Bannister et al. 2012, Lee et al. 2016a), the presence of such a different, younger, warmer and potentially even richer flora at the HMC makes study of this new site critical for allowing a better understanding of the past floral diversity at a mid-latitude Southern Hemisphere site around the time of the mid-Miocene thermal maximum. A

similar, but much more detailed study carried out on the early middle Miocene flora of the Randeck Maar in Germany (Rasser et al. 2013), which has been the subject of detailed investigation for well over 100 years has yielded 168 plant taxa, including leaves, fruit and dispersed pollen. We expect that the Hindon Maar flora, which has been under investigation for just four years, will yield a similar number of taxa, eventually allowing some comparisons of mid-latitude N and S Hemisphere vegetation at the same key time periods.

### 6.3 *The faunal assemblage*

Fossil evidence for the evolutionary history of insects in New Zealand is very scant and the Hindon fauna encompasses the first insects reported from mid-Miocene strata. Previously documented faunas from Neogene strata include 16 families in seven insect orders from the early Miocene Foulden Maar (Kaulfuss et al. 2015) and amber inclusions from ten insect families in six orders recently discovered in early Miocene amber (Schmidt et al. 2018). In our preliminary study we have identified 20 families of insects in the orders Odonata, Hemiptera, Thysanoptera, Coleoptera, Diptera, Hymenoptera and Trichoptera (Fig. 8), which makes the HMC the most informative site for Neogene insect diversity in New Zealand. The fauna provides a unique window into insect diversity of a mesothermal *Nothofagus*/podocarp/mixed broadleaf forest prior to post-mid Miocene climate cooling. It also offers insights into the antiquity of some insect groups on the isolated New Zealand sub-continent.

Damselflies (Zygoptera), thrips (Terebrantia and Tubulifera), shield bugs (Pentatomidae), jumping plant lice (Psylloidea) and whiteflies (Aleyrodidae) from the site are the first fossil records from New Zealand. Most of the taxa identified to family or genus level are still present in the modern New Zealand fauna, with some now being confined to warm climates in northern parts of the islands and thus provide important evidence for the antiquity of some of New Zealand's insects. This includes the flatbug *Aneurys*, jumping plant lice in the Psyllidae or Calophyidae, the weevils *Nyxetes* and *Clypeolus* and caddisflies putatively assigned to *Triplectides*. However, argiolestid damselflies and the hairy cicada *Paratettigarcta* (Tettigarctidae) indicate that the mid-Miocene fauna also included insects that have become extinct in New Zealand. The low proportion of aquatic/semiaquatic taxa (6% of all insects) in the lacustrine sediments is typical for insect taphocoenoses in maar lake sediments (Lutz and Kaulfuss 2006,

Wedmann et al. 2010). Most likely, such taxa were buried in oxygenated near shore habitats, in sediment types that are less suitable for fossil preservation than the profundal laminites and that are often not encompassed by palaeontological excavations.

Compared to Oligocene/Miocene ambers in New Zealand, the insect assemblage from the HMC differs in a much higher proportion of Coleoptera, a lower proportion of Diptera, the presence of Odonata, Thysanoptera and Trichoptera, and the absence of Psocoptera and Lepidoptera; these differences may largely reflect taphonomic bias. There are also significant differences to the early Miocene insect fauna from the apparently very similar depositional and taphonomic setting at Foulden Maar. Ants and termites, for instance, are diverse at Foulden Maar (Kaulfuss and Dlussky 2016, Engel and Kaulfuss 2017) but are absent (termites) or represented by only one putative ant at the HMC. Hymenopterans are generally more abundant at Foulden (35%) than at Hindon (5%). By contrast, thrips constitute 6% of insects at the HMC but have not yet been found at Foulden Maar. Beetles are the most common insects at both sites, but their proportion of 69% at the HMC is significantly higher than that at Foulden Maar (46%). At a generic level, the only insect taxon common to both sites is the flat bug *Aneurys*; all other insects identified so far are site-specific. Further collecting and more detailed studies of the insect faunas from the lake sediments at Foulden and Hindon and from New Zealand amber are required to better understand whether these taxonomic differences reflect taphonomic bias or variations in local forest composition, climate or palaeogeographic factors.

With respect to fish, the presence of *Galaxias* in the mid-Miocene sediments at Hindon is not unexpected, given the documentation of this genus from other Miocene localities (Lee et al. 2007) and the diversity of extant galaxiids in New Zealand. The find of fossils of the freshwater eel *Anguilla* is far more significant because this genus has hitherto only been reported from fossil sites in Europe, with *Anguilla ignota* Micklich from the Eocene Messel maar in Germany as the oldest reported body fossil (Micklich 1985). Another discovery confirming the high palaeontological value of the HMC are bird feathers, suggesting the possibility that entire bird fossils and other vertebrates (e.g. reptiles and bats) may be present at Hindon, as in some international World Heritage maar sites, such as Messel in Germany.

## 8. Conclusions

The Hindon Maar Complex is the second fossil *Konservat-Lagerstätte* to be described from New Zealand and significantly expands palaeontological data obtained from the earliest Miocene Foulden Maar *Lagerstätte*. It allows a comparative analysis to the terrestrial biodiversity to the Foulden biota and other Miocene sites and to the extant New Zealand biota, under a warm temperate climate at a time of increased land area after maximum marine transgression in the Oligocene, before Pleistocene glacial episodes that shaped the composition of the modern New Zealand biota. Our study shows that the Hindon Maar Complex depicts a mid-Miocene inland lake and *Nothofagus*/podocarp/mixed broadleaf forest ecosystem in Southern Hemisphere mid-latitudes. Our preliminary excavations indicate that in terms of diversity and quality of preservation the site is a fossil *Lagerstätte* deposit of international significance. At least 35 families and 43 genera of plants (20 families from leaves, fruits and flowers), at least 20 insect families in seven orders, unidentified birds and two families of fish are currently recognized and this diversity is expected to increase markedly with ongoing fossil collecting.

## Acknowledgments

We thank the Neehoff family for kindly allowing access to the study site, Keith McLeod Excavation Ltd. for carrying out fossil excavations and RSC Mining and Mineral Exploration Ltd. for providing drill core data for lithofacies analysis. Seismic data were processed at the University of Otago with an academic licence for GLOBE Claritas. Dan Bickel, Samuel Brown, Margaret Harper, Ed Jarzembowski, Andrey Khalaim, Richard Leschen, Richard Rowe and Gary Taylor are thanked for help with taxonomic identifications of diatoms and insects. We particularly wish to thank Liz Girvan, Otago Centre for Electron Microscopy, University of Otago, for help with the Scanning Electron Microscopy. We also thank the editor and two anonymous reviewers for their constructive and helpful comments, which improved the manuscript.

## Funding

This work was supported in part by a Royal Society of New Zealand Marsden Grant (14-UOO-102); the Royal Society of New Zealand Hutton Fund (to UK 2016); and a University of Otago Research Grant.



## Supplementary data

Supplementary data to this article can be found online at <http://xxxxxxxxxx>

## References

- Balme, B.E., 1995. Fossil *in situ* spores and pollen grains: an annotated catalogue. Rev. Palaeobot. Palynol. 87, 81–323.
- Bannister, J.M., Lee, D.E., Conran, J.G., 2012. Lauraceae from rainforest surrounding an early Miocene maar lake, Otago, southern New Zealand. Rev. Palaeobot. Palynol. 178, 13–34.
- Bowie, E., 2015. The geophysical characterization of Hindon Maar. P.G. Dip.Sc. thesis. University of Otago, New Zealand (149 p).
- Boykin, L.M., Bell, C.D., Evans, G., Small, I., De Barro, P.J., 2013. Is agriculture driving the diversification of the *Bemisia tabaci* species complex (Hemiptera: Sternorrhyncha: Aleyrodidae)? Dating, diversification and biogeographic evidence revealed. BMC Evol. Biol. 13, 228.
- Buness, H.A., Wiederhold, H., Wonik, T., 2006. Seismic reflection patterns of two Tertiary maars in Germany. Z. Dt. Ges. Geowiss. 175, 339–353.
- Conran, J.G., Bannister, J.M., Lee, D.E., Carpenter, R.J., Kennedy, E.M., Reichgelt, T., Fordyce, R.E., 2015. An update of monocot macrofossil data from New Zealand and Australia. Bot. J. Linn. Soc. 178, 394–420.
- Conran, J.G., Lee, W.G., Lee, D.E., Bannister, J.M., Kaulfuss, U., 2014. Reproductive niche conservatism in the isolated New Zealand flora over 23 million years. Biol. Lett. 10, 20140647.
- Coombs, D.S., Adams, C.J., Roser, B.P., Reay, A., 2008. Geochronology and geochemistry of the Dunedin Volcanic Group, eastern Otago, New Zealand. N. Z. J. Geol. Geophys. 51, 195–218.
- DOC, 2017. Non-migratory galaxiids. <http://www.doc.govt.nz/nature/native-animals/freshwater-fish/non-migratory-galaxiids/>.
- Drake, H., Burrows, C.J., 1980. The influx of potential macrofossils into Lady Lake, north Westland, New Zealand. N. Z. J. Bot. 18, 257–274.

- Engel, M.S., Kaulfuss, U., 2017. Diverse, primitive termites (Isoptera: Kalotermitidae, *incertae sedis*) from the Miocene of New Zealand. *Austral Entomol.* 56, 94–103.
- Friis, E.M., Crane, P.R., Pedersen, K.R., 2011. Early flowers and angiosperm evolution., Cambridge University Press, Cambridge.
- Goth, K., Suhr, P., Schulz, R., 2003. Zwei Forschungsbohrungen in das verdeckte Maar von Baruth (Sachsen). *Z. Angew. Geol.* 1/2003, 9–17.
- Greenwood, D.R., Conran, J.G., 2000. The Australian Cretaceous and Tertiary monocot fossil record, in: Wilson, K.L., Morrison, D.A. (Eds.), *Monocots – systematics and evolution*. Commonwealth Scientific and Industrial Research Organisation, Melbourne, pp. 52–59.
- Harper, M.A., Lee, D.E., Holmes, A.M., Jones, D.T., 2016. Freshwater diatoms in Miocene sediments in Otago, in: Reisselmann, C., Roben, A. (Eds.) *Abstracts, New Zealand Geosciences Society Conference 2016*. Wanaka, GSNZ Misc. Publ. 145A, p. 32.
- Harris, A.C., 1983. An Eocene larval insect fossil (Diptera: Bibionidae) from North Otago, New Zealand. *J. Roy. Soc. N. Z.* 13, 93–105.
- Harrison, R.A., 1990. *Bibionidae (Insecta: Diptera)*. Fauna of New Zealand 20. Auckland, DSIR Plant Protection, 28 pp.
- Henderson, S.M., Martin, A.P., Coote, J.A., 2016. Glass Earth regional gold exploration program in Otago – area selection to mining within ten years, in: Christie, A.B. (Ed.), *Mineral deposits of New Zealand: exploration and research*. Aust. IMM. M. 31, pp. 141–147.
- Hornibrook, N. de B., 1992. New Zealand Cenozoic Marine Paleoclimates: A review based on the distribution of some shallow water and terrestrial biota, in: Tsuchi, R., Ingle, J.C. Jr. (Eds.), *Pacific Neogene. Environment, Evolution, and Events*. Tokyo, University of Tokyo Press, pp. 83–106.
- Hoernle, K., White, J.D.L., van den Bogaard, P., Hauff, F., Coombs, D.S., Werner, R., Timm, C, Garbe-Schönberg, D., Reay, A., Cooper, A.F., 2006. Cenozoic intraplate volcanism on New Zealand: Upwelling induced by lithospheric removal. *Earth Planet. Sc. Lett.* 248, 350–367.
- Jell, P.A., 2004. The fossil insects of Australia. *Memoirs of the Queensland Museum* 50(1), 1–124.

- Kaiser, T.M., Ansorge, J., Arratia, G., Bullwinkel, V., Gunnell, G.F., Herendeen, P.S., Jacobs, B., Mingram, J., Msuya, C., Musolff, A., Naumann, R., Schulz, E., Wilde, V., 2006. The maar lake of Mahenge (Tanzania) – unique evidence of Eocene terrestrial environments in sub-Sahara Africa. *Z. Dt. Ges. Geowiss.* 157, 411–431.
- Kalkman, V.J., Theischinger, G., 2013. Generic revision of Argiolestidae (Odonata), with four new genera. *Int. J. Odonatol.* 16, 1–52.
- Kaulfuss, U., 2017. Crater stratigraphy and post-eruptive evolution of the Foulden Maar, southern New Zealand. *N. Z. J. Geol. Geophys.* 60, 410–432.
- Kaulfuss, U., Dlussky, G.M., 2016. Early Miocene Formicidae (Amblyoponinae, Ectatomminae, ?Dolichoderinae, Formicinae, and Poerinae) from the Foulden Maar fossil *Lagerstätte*, New Zealand, and their biogeographic relevance. *J. Paleontol.* 89, 1043–1055.
- Kaulfuss, U., Moulds, M., 2015. A new genus and species of tettigarctid cicada from the early Miocene of New Zealand: *Paratettigarcta zealandica* (Hemiptera, Auchenorrhyncha, Tettigarctidae). *ZooKeys* 484, 83–94.
- 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.
- Kaulfuss, U., Wappler, T., Heiss, E., Larivière, M.-C., 2011. *Aneurys* sp. from the early Miocene Foulden Maar, New Zealand: the first Southern Hemisphere record of fossil Aradidae (Insecta: Hemiptera: Heteroptera). *J. Roy. Soc. N. Z.* 41, 279–285.
- Kerr, I.A., 2016. Phylogeny, fossil history and biogeography of Ripogonaceae. B.Sc. H. thesis. The University of Adelaide, Australia (60 p).
- Kienle, J., Kyle, P.R., Self, S., Motyka, R.J., Lorenz, V., 1980. Ukinrek Maars, Alaska, I. April 1977 eruption sequence, petrology and tectonic setting. *J. Volcanol. Geoth. Res.* 7, 11–37.
- Lee, D.E., Kaulfuss, U., Conran, J.G., Bannister, J.M., Lindqvist, J.K., 2016a. Biodiversity and palaeoecology of Foulden Maar: an early Miocene *Konservat-Lagerstätte* deposit in southern New Zealand. *Alcheringa* 40, 525–541.

- Lee, D.E., Lee, W.G., Jordan, G.J., Barreda, V.D., 2016b. The Cenozoic history of New Zealand temperate rainforests: comparison with southern Australia and South America. *N. Z. J. Bot.* 54, 100–127.
- Lee, D.E., McDowall, R.M., Lindqvist, J.K., 2007. *Galaxias* fossils from Miocene lake deposits, Otago, New Zealand: the earliest records of the Southern Hemisphere family Galaxiidae (Teleostei). *J. Roy. Soc. N. Z.* 37, 109–130.
- Lehmann, T., Schaal, S.K., 2012. “Messel and the terrestrial Eocene” – Proceedings of the 22nd Senckenberg Conference. *Palaeobio. Palaeoenv.* 92, 397–402.
- 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. *Sediment. Geol.* 222, 98–110.
- Lutz, H., Kaulfuss, U., 2006. A dynamic model for the meromictic lake Eckfeld Maar (Middle Eocene, Germany). *Z. Dt. Ges. Geowiss.* 157, 433–450.
- Lutz, H., Kaulfuss, U., Wappler, T., Löhnertz, W., Wilde, V., Mertz, D.F., Mingram, J., Franzen, J.L., Frankenhäuser, H., Koziol, M., 2010 Eckfeld Maar: Window into an Eocene terrestrial habitat in Central Europe. *Acta Geol. Sin.-Engl.* 84, 984–1009.
- 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., Townms, 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. Phylum Arthropoda, Subphylum Hexapoda. Protura, springtails, Diplura, and insects, in: Gordon, D.P. (Ed.), *New Zealand Inventory of Biodiversity, Volume 2*. Canterbury University Press, Christchurch pp. 233–467.
- Matthes, H., Kroner, C., Jahr, T., Kämpf, H., 2010. Geophysical modelling of the Ebersbrunn diatreme, western Saxony, Germany. *Near Surf. Geophys.* 8, 311–319.
- McDowall, R.M., Pole, M., 1997. A large galaxiid fossil (Teleostei) from the Miocene of Central Otago, New Zealand. *J. Roy. Soc. N. Z.* 27, 193–198.
- Micklich, N., 1985. Biologisch-paläontologische Untersuchungen zur Fischfauna der Messeler Ölschiefer (Mittel-Eozän, Lutetium). *Andrias* 4, 1–171.
- Mildenhall, D.C., Pocknall, D.T., 1989. Miocene–Pleistocene spores and pollen from Central Otago, South Island, New Zealand. *N. Z. Geol. Surv. Pal. Bull.* 59, 1–128.

- Mildenhall, D.C., 1980. New Zealand Late Cretaceous and Cenozoic plant biogeography: a contribution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 31, 197–233.
- Mildenhall, D.C., Pocknall, D.T., 1989. Miocene–Pleistocene spores and pollen from Central Otago, South Island, New Zealand. *N. Z. Geol. Surv. Pal. Bull.* 59, 1–128.
- Möller, A.L., Kaulfuss, U., Lee, D.E., Wappler, T., 2017. High richness of insect herbivory from the early Miocene Hindon Maar crater, Otago, New Zealand. *PeerJ* 5: e2985.
- Mrlina, J., Kämpf, H., Kroner, C., Mingram, J., Stebich, M., Brauer, A., Geissler, W.H., Kallmeyer, J., Matthes, H., Seidl, M., 2009. Discovery of the first Quaternary maar in the Bohemian Massif, Central Europe, based on combined geophysical and geological surveys. *J. Volcanol. Geoth. Res.* 182, 97–112.
- Németh, K., White, J.D.L., 2003. Reconstructing eruption processes of a Miocene monogenetic volcanic field from vent remnants: Waipiata Volcanic Field, South Island, New Zealand. *J. Volcanol. Geoth. Res.* 124, 1–21.
- Pirrung, M., Büchel, G., Lorenz, V., Treutler, H.-C., 2008. Post-eruptive development of the Ukinrek East Maar since its eruption in 1977 A.D. in the periglacial area of south-west Alaska. *Sedimentology* 55, 305–334.
- Pirrung, M., Fischer, C., Büchel, G., Gaupp, R., Lutz, H., Neuffer, F. 2003. Lithofacies succession of maar crater deposits in the Eifel area (Germany). *Terra Nova* 15, 125–132.
- Pocknall, D.T., Mildenhall, D.C., 1984. Late Oligocene – early Miocene spores and pollen from Southland, New Zealand. *N. Z. Geol. Surv. Pal. Bull.* 51, 1–66.
- Pole, M.S., 1993. Early Miocene flora of the Manuhirikia Group, New Zealand. 4. Palm remains. *J. Roy. Soc. N. Z.* 23, 283–288.
- Raine, J.I., Mildenhall, D.C., Kennedy, E.M., 2011. New Zealand fossil spores and pollen: an illustrated catalogue, 4<sup>th</sup> edition (GNS Science Miscellaneous Series No. 4). [http://www.gns.cri.nz/what/earthhist/fossils/spore\\_pollen/catalog/index.htm](http://www.gns.cri.nz/what/earthhist/fossils/spore_pollen/catalog/index.htm).
- Raine, J.I., Beu, A.G., Boyes, A.F., Campbell, H.J., Cooper, R.A., Crampton, J.S., Crundwell, M.P., Hollis, C.J., Morgans, H.E.G., Mortimer, N., 2015. New Zealand Geological Timescale NZGT 2015/1. *N. Z. J. Geol. Geophys.* 58, 398–403.
- Rasser, M.W., Bechly, G., Böttcher, R., Ebner, M., Heinzmann, E.P.J., Höltnke, O., Joachim, C., Kern, A.K., Kovar-Eder, J., Nebelsick, J.H., Roth-Nebelsick, A.,

- Schoch, R.R., Schweigert, G., Ziegler, R. 2013. The Randeck Maar: Palaeoenvironment and habitat differentiation of a Miocene lacustrine system. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 392, 426–453.
- Schmidt, A.R., Kaulfuss, U., Bannister, 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., Perrichot, V., Rikkinen, J., Sadowski, E.-M., Seyfullah, L.J., Stebner, F., Szwedo, J., Ulbrich, P., Lee, D.E., 2018. Amber inclusions from New Zealand. *Gondwana Res.* 56, 135–146.
- Schwarzshans, W., Scofield, R.P., Tennyson, A.J.D., Worthy, J.P., Worthy, T.H., 2012. Fish remains, mostly otoliths, from the non-marine early Miocene of Otago, New Zealand. *Acta Palaeontol. Pol.* 57, 319–350.
- Self, S., Kienle, J., Huot, J.P., 1980. Ukinrek Maars, Alaska, II. Deposits and formation of the 1977 craters. *J. Volcanol. Geoth. Res.* 7, 39–65.
- Stinton, F.C., 1975. Fish otoliths from the English Eocene. *Palaeontograph. Soc. M.* 129, 1–56.
- Steiger, R.J., Jäger, E., 1977. Subcommission on geochronology: Convention on the use of decay constants in geo- and cosmochemistry. *Earth Planet. Sc. Lett.* 36, 359–362.
- Wedmann, S., Poschmann, M., Hörnschemeyer, T., 2010. Fossil insects from the Late Oligocene Enspel Lagerstätte and their palaeobiogeographic and palaeoclimatic significance. *Palaeobio. Palaeoenv.* 90, 49–58.
- White, J.D.L., Ross, P.-S., 2011. Maar-diatreme volcanoes: A review. *J. Volcanol. Geoth. Res.* 201, 1–29.
- Worthy, T.H., Worthy, J.P., Archer, M., Hand, S.J., Scofield, R.P., Marshall, B.A., Tennyson, A.J.D., Salisbury, S., 2013 Insights from the St Bathans fauna on the early Miocene land and freshwater animals of Zealandia. Programme and abstracts ,VII Southern Connections Congress 2013, Dunedin, New Zealand, , p. 147.
- Wuttke, M., Schindler, T., Smith, K.T., 2015. The *Fossil-Lagerstätte* Enspel – a crater lake in a volcanic-influenced terrestrial environment of the Westerwald Basin (late Oligocene, Western Germany). *Palaeobio. Palaeoenv.* 95, 1–4.

- Youngson, J.H., 1993. Mineralized vein systems and Miocene maar crater sediments at Hindon, East Otago, New Zealand. M.Sc. thesis. University of Otago, New Zealand (258 p).
- Zolitschka, B., Francus, P., Ojala, A.E.K., Schimmelmann, A., 2015. Varves in lake sediments – a review. *Quaternary Sci. Rev.* 117, 1–41.

## Figure captions

**Fig. 1.** Aerial geomagnetic map of the Hindon Maar Complex in southern New Zealand, showing positive anomalies (red colours) associated with four maar-diatreme structures (1–4) and the lava-capped Fortification Peak. Blue and green colours indicate low magnetic intensities of metamorphic basement rocks (Otago Schist). Outcrops of fossiliferous maar lake sediments and position of fossil localities are shown. Line of seismic profile in Figure 2 and the location of basanite samples dated in this study are indicated.

**Fig. 2.** Surface and sub-surface structure and outcrop setting of partly eroded maar-diatremes of the Hindon Maar Complex exemplified by Maar 1. **A,** The surface expression of the crater is characterized by a shallow, subcircular and c. 1000 m wide topographic depression. The line of sheep in the foreground marks the eastern crater rim; the upper level of the crater and the tephra ring have been removed by erosion. Lava-capped Fortification Peak (see text) is indicated in the distance. **B,** Seismic profile of Maar 1, showing steep contacts to metamorphic Otago Schist (white lines) and laterally continuous reflections interpreted as stratified pyroclastic diatreme fill. Common depth point spacing is 4 m. See section 4.1 for relationship between two-way travel time and depth. **C,** Temporary outcrop of black, fossiliferous maar lake sediments below a thin cover of alluvium and loess (site I44/f0392, March 2014). Numerous fossils described herein were collected from the sediment pile next to the pit.

**Fig. 3.** Lithofacies at the Hindon Maar complex. **A,** Stratigraphy of crater sediments and tuff breccia of the diatreme logged in drill cores from maars 1 and 3. **B,** Enhanced-contrast photograph of laminated, highly fossiliferous gyttja from maar 1. Lamination is caused by an alternation of dark-brown spicule-rich laminae with brown clay-rich laminae. **C,** Enhanced-contrast photograph of wetted diatomite section from maar 1. This 16.5 cm section consists of dark, homogeneous or intra-clast turbidite beds (T) and subordinate finely, dark/light laminated intervals (L; seasonal biogenic varves). Small offsets associated with compressional faultlets are shown.

**Fig. 4. A,**  $^{40}\text{Ar}/^{39}\text{Ar}$  laser step heating age spectra and inverse isochron plots on two basanite groundmass samples (Hindon Maar 3 and Fortification Peak). **B,** Stratigraphic



position of the Hindon Maar fossil *Lagerstätte* (Langhian, New Zealand local stage Lillburnian) and Fortification Peak in the Miocene period. Position of the earliest Miocene Foulden Maar fossil *Lagerstätte* (referred to in the text) is shown for comparison. Miocene benthic foraminiferal delta  $^{18}\text{O}$  data and temperature curve are modified from Hornibrook (1992). Temperature trends are based on warm shallow water invertebrates, mangroves and *Cocos* normalised to Lat. 42° S.

**Fig. 5.** SEM images of common and sediment-building microfossils in the lacustrine sediments of the Hindon Maar Complex. **A** Slender siliceous megascleres of *Spongilla* sp., **B** *Spongilla* gemmule with stout and ornamented gemmuloscleres, **C** Siliceous frustule of pennate diatom, **D** Siliceous frustules of centric diatoms, cf. *Aulacoseira*, **E** Cluster of siliceous Chrysophyceae stomatospores, **F** Colony of the green alga *Botryococcus braunii*.

**Fig. 6.** Examples of plant fossils from the Hindon Maar Complex. **A** Podocarpaceae, aff. *Dacrydium* sp., shoot with male cone (OU35170), **B** Podocarpaceae, *Podocarpus* sp., cuticle (OU35171), **C** Podocarpaceae, aff. *Prumnopitys* sp., shoot (OU35172), **D and E** Monocot, aff. *Typha* sp., leaf and cuticle, (OU35174), **F** Monocot, *Astelias* leaf (OU35176), **G** Ripogonaceae, *Ripogonum*, leaf (OU35175), **H and I** Araliaceae, aff. *Pseudopanax* sp., compound leaf and cuticle (OU35177), **J and K** Araliaceae flower (OU35178) and associated *Rhoipites aralioides* pollen, **L** Myrtaceae, capsular fruits (OU35179), **M and N** Lauraceae, leaf and cuticle (OU35180), **O** Menispermaceae, leaf (OU35181), **P** Nothofagaceae, *Nothofagus* sp., leaf (OU35182), **Q** Sapindaceae, aff. *Alectryon* sp., leaf (OU35183), **R** Fern pinna (OU35173).

**Fig. 7.** Examples of the mid-Miocene fauna from the Hindon Maar complex. **A and B** Hemiptera: Pentatomoidea, partly preserved specimens (OU45472, OU46504), **C** Hemiptera: Psylloidea (jumping plant-lice), wing (OU46559), **D** Thysanoptera: Tubulifera, apterous taxon (OU45478), **E** Coleoptera: Curculionidae (OU45421), **F** Coleoptera: Curculionidae (OU45429), **G** Hymenoptera, Apocrita, possibly Apoidea (OU46558) **H–I** undetermined Diptera, isolated wing (OU46486) and pupa (OU46553), **J** Trichopteran larval case made of mineral grains and woody debris (OU46562) **K** Trichoptera larvae in a case constructed of small sticks, woody debris and leaf litter (OU46480), **L** Hymenoptera: Ichneumoidea (OU45452), **M** Hymenoptera, aff.

Formicidae (OU46500), **N** Aves, undetermined feather (OU22837), **O** Pisces: Teleostei, juvenile *Galaxias* sp. preserved with cranial osteology, eyes and skin pattern (OU22846), **P–R** Variably shaped and sized sandy coprolites from fish or birds. A–D and G–O photographed under ethanol.

**Fig. 8.** Composition of the insect fauna from the Hindon Maar fossil *Lagerstätte*. Insects that were not determinable to order-level are excluded.

**Table 1.** Algae and animal taxa recovered from the Hindon Maar Complex *Lagerstätte*.

<b>Bacillariophyceae (diatoms)</b>	
	<i>Achnanthes</i> cf. <i>hungaria</i> (Grunow) Grunow
	<i>Achnanthes</i> Bory sp.
	<i>Encyonema minutum</i> (Hilse) D.G.Mann (s.l.)
	<i>E.</i> cf. <i>silesciacum</i> (Bleisch) Mann
	<i>Eunotia</i> cf. <i>pectinalis</i> (Kützing) Rabenh.
	<i>Gomphonema</i> cf. <i>intricatum</i> Kützing
	<i>Stauroneis</i> cf. <i>pygmaea</i> Kieger
	<i>Staurosira</i> cf. <i>construens</i> Ehrenb.
	<i>Aulacoseira</i> cf. <i>ambigua</i> (Grunow) Simonsen
	<i>Aulacoseira</i> Thwaites spp.
<b>Chrysophyceae (golden algae)</b>	
	at least two unidentified morphotypes
<b>Trebouxiophyceae (green algae)</b>	
	<i>Botryococcus braunii</i> Kützing
<b>Demospongiae: Spongillidae</b>	
	<i>Spongilla</i> Lamarck sp.
<b>Insecta</b>	
Odonata	
	Argiolestidae
Hemiptera	
	Aleyrodidae
	Aradidae
	Miridae?
	Pentatomidae
	Psyllidae
	Tettigarctidae
Thysanoptera	
	Phlaeothripidae
	Terebrantia indet.
Coleoptera	
	Hydrophilidae
	Buprestidae
	Elateridae
	Curculionidae
	Apioninae
	Cryptorhynchinae

## Curculioninae

---

**Insecta**

---

Chrysomelidae?

Diptera

Bibionidae

Chironomidae

Muscidae?

Hymenoptera

Apidae?

Ichneumonidae

Formicidae?

Trichoptera

Leptoceridae?

Oeconesidae?

---

**Pisces**

---

Anguilliformes

Anguillidae

Osmeriformes

Galaxiidae

---

**Aves**

---

Family indet.

---

Algal nomenclature follows Algaebase (<http://www.algaebase.org/>)

---

**Table 2.** Families and genera of higher plants recovered as macrofossils at the Hindon Maar Complex *Lagerstätte*.

Family and genus	Leave s	Cuticle s	Flower s or cones	In situ polle n	Fruits or seeds	Pollination , dispersal
<b>Ferns</b>						
Family & genus indet.	X					W, W
<b>Conifers and cycads</b>						
Podocarpaceae						
<i>Dacrycarpus</i> (Endl.) de Laub.	X	X	X	X		W, B
<i>Dacrydium</i> Lamb.	X	X	X	X		W, B
<i>Podocarpus</i> L'Hér ex Pers.	X	X	X	X		W, B
<i>Prumnopitys</i> Phil.	X	X				W, B
Zamiaceae						
<i>Pterostoma</i> R.S.Hill	X	X				?I, B
<b>Basal angiosperms</b>						
Atherospermataceae						
<i>Laurelia</i> Juss.	X	X				I, B
Lauraceae						
aff. (?) <i>Beilschmiedia</i> Nees	X	X				I, B
aff. <i>Cryptocarya</i> R.Br.	X	X				I, B
aff. <i>Litsea</i> Lam.	X	X				I, B
Monimiaceae						
<i>Hedycarya</i> J.R.Forst. & G.Forst.	X	X			X	I, B
<b>Monocots</b>						
Ripogonaceae						
<i>Ripogonum</i> J.R.Forst. & G.Forst.	X	X				I, B
Asteliaceae						
<i>Astelia</i> Banks & Sol. ex R.Br.	X	X				I, B
Typhaceae						
<i>Typha</i> L.	X	X				W, W
Arecaceae						
<i>Rhopalostylis</i> H.Wendl. & Drude				X	X	

Family and genus	Leave s	Cuticle s	Flower s or cones	In situ polle n	Fruits or seeds	Pollination , dispersal
<b>Eudicots</b>						
Araliaceae spp.	X	X	X	X	X	I, B
<i>Pseudopanax</i> K.Koch	X	X				I, B
<i>Schefflera</i> J.R.Forst. & G.Forst.	X	X				I, B
Bignoniaceae					X	I/B, W
Cunoniaceae	X	X				I, B
?Elaeocarpaceae						
<i>?Phymatocaryon</i> F.Muell.					X	I, B
Euphorbiaceae sp.	X					I, B
Loranthaceae spp.			X	X		I/B, B
Menispermaceae	X	X				I, B
Myrtaceae spp.	X	X				I/B, I/W
Myrsinaceae	X	X				I, B
Nothofagaceae						
<i>Nothofagus</i> Blume spp.	X	X			cupule s	W, W
Sapindaceae						
<i>Alectryon</i> Gaertn.	X	X				I, B
<i>?Cupaniopsis</i> Radlk.	X	X				I, B

Pollination and dispersal syndrome codes: B = birds, I = insects, T = water, W = wind.

**Highlights**

- Hindon Maar Complex is a new mid-Miocene Fossil-*Lagerstätte* in New Zealand
- Anoxia in maar lakes allowed exquisite preservation of plant and animal fossils
- The biota is from a lake and *Nothofagus*/podocarp/mixed broadleaf forest ecosystem
- Fossils record high diversity at humid, warm Southern Hemisphere mid-latitudes

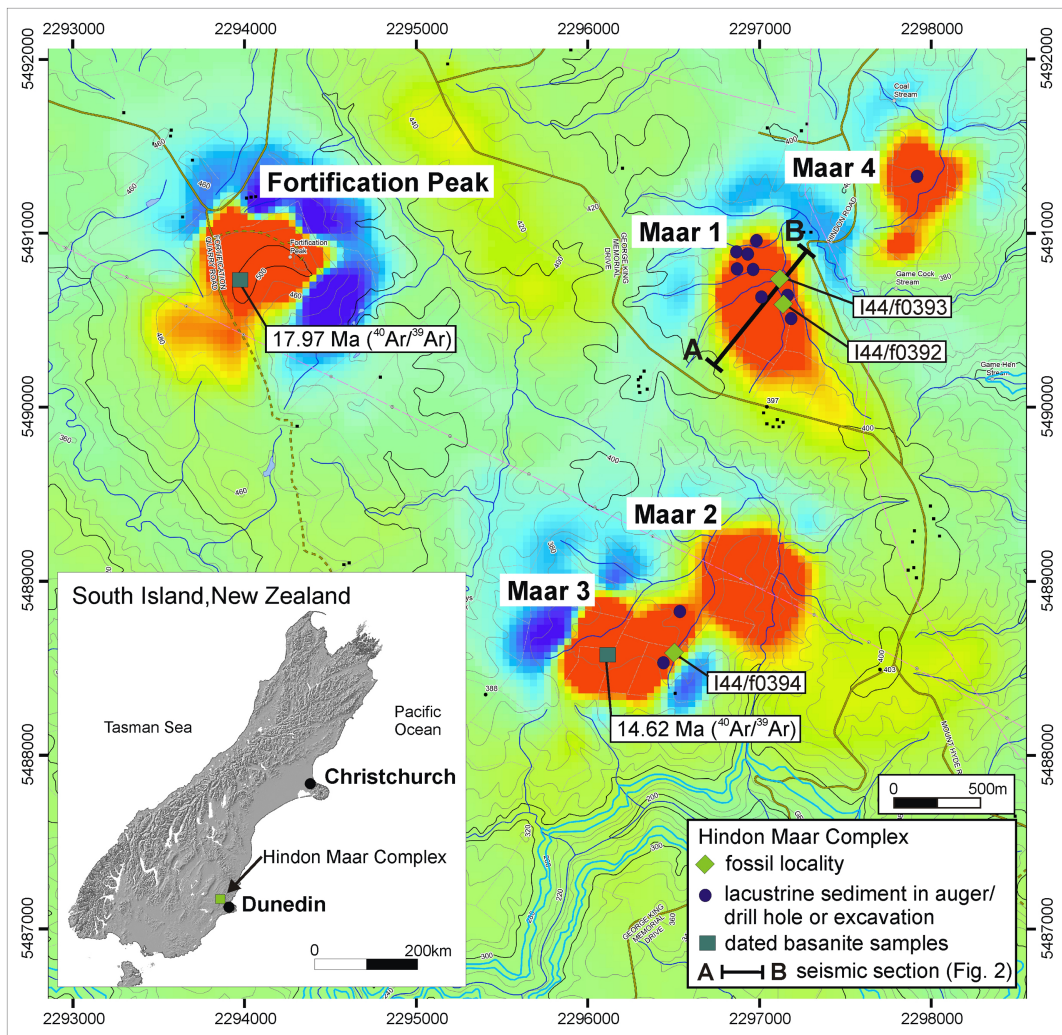


Figure 1



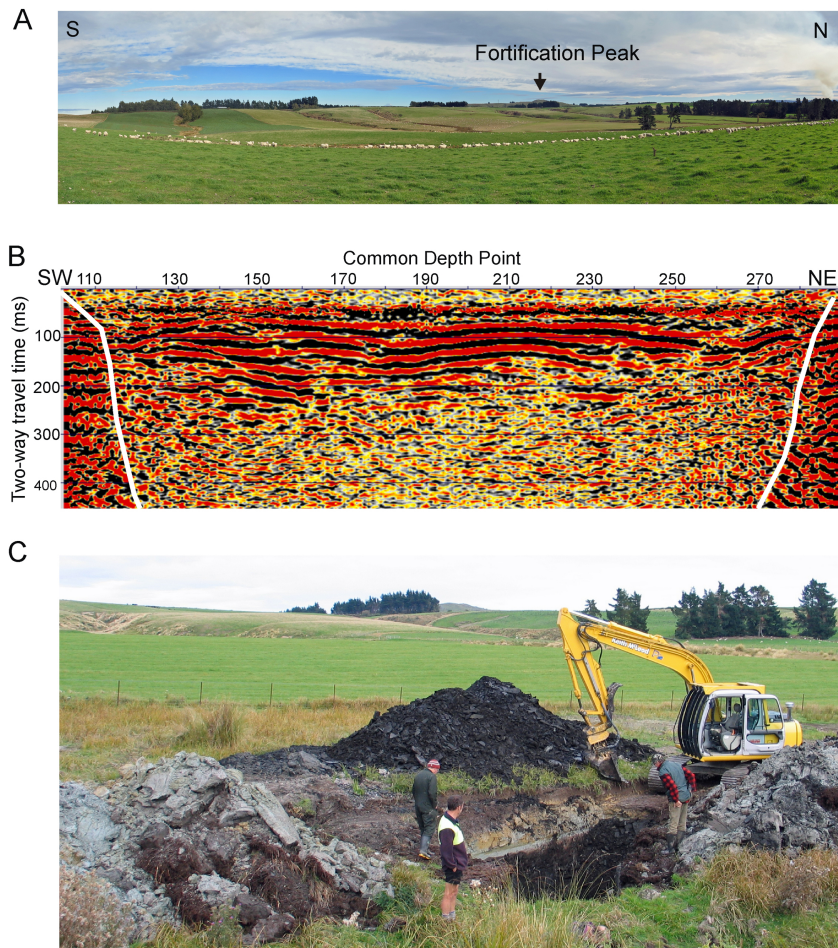
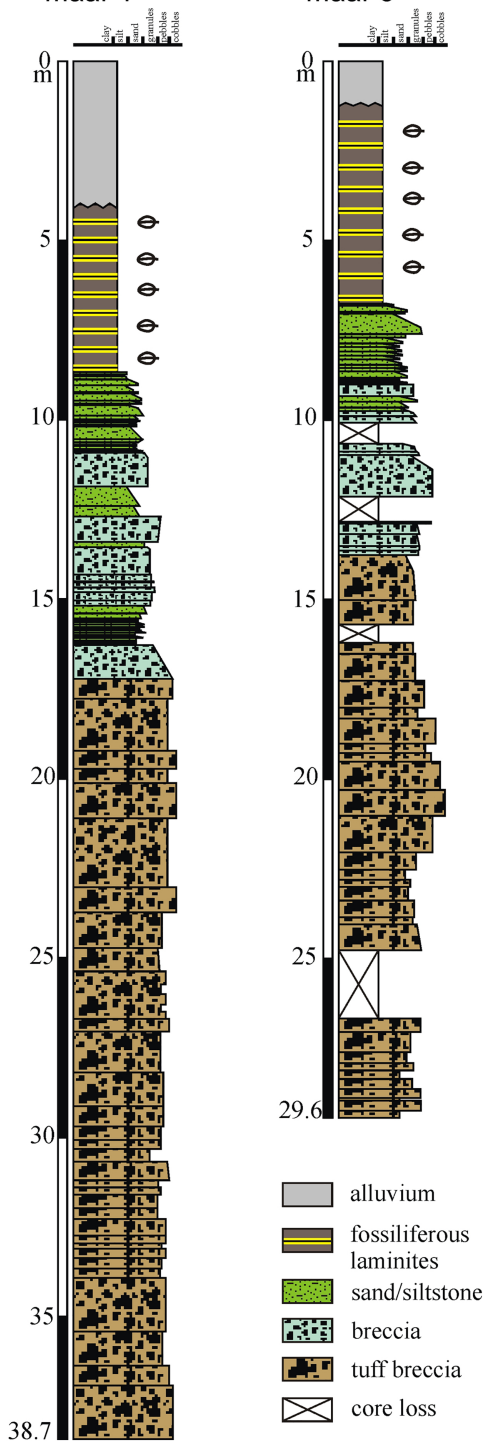


Figure 2

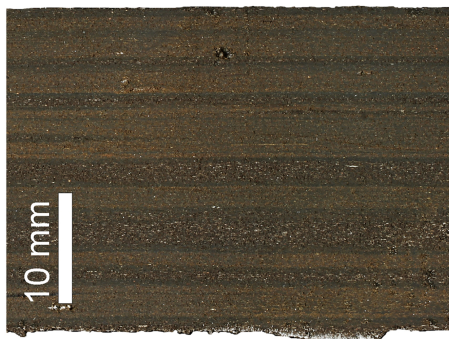
A

maar 1

maar 3



B



C



Figure 3

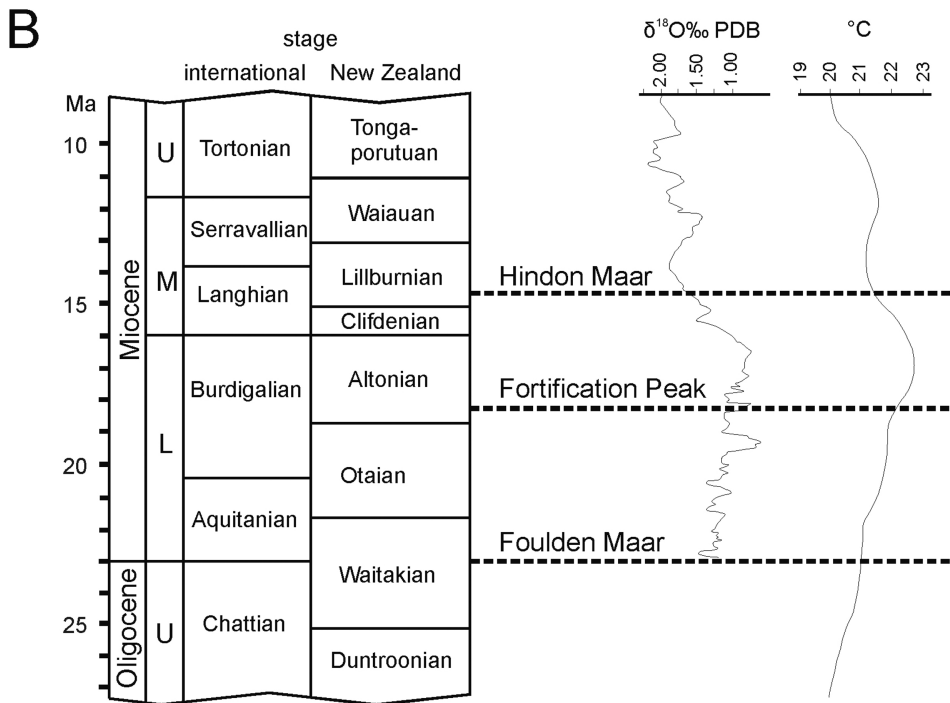
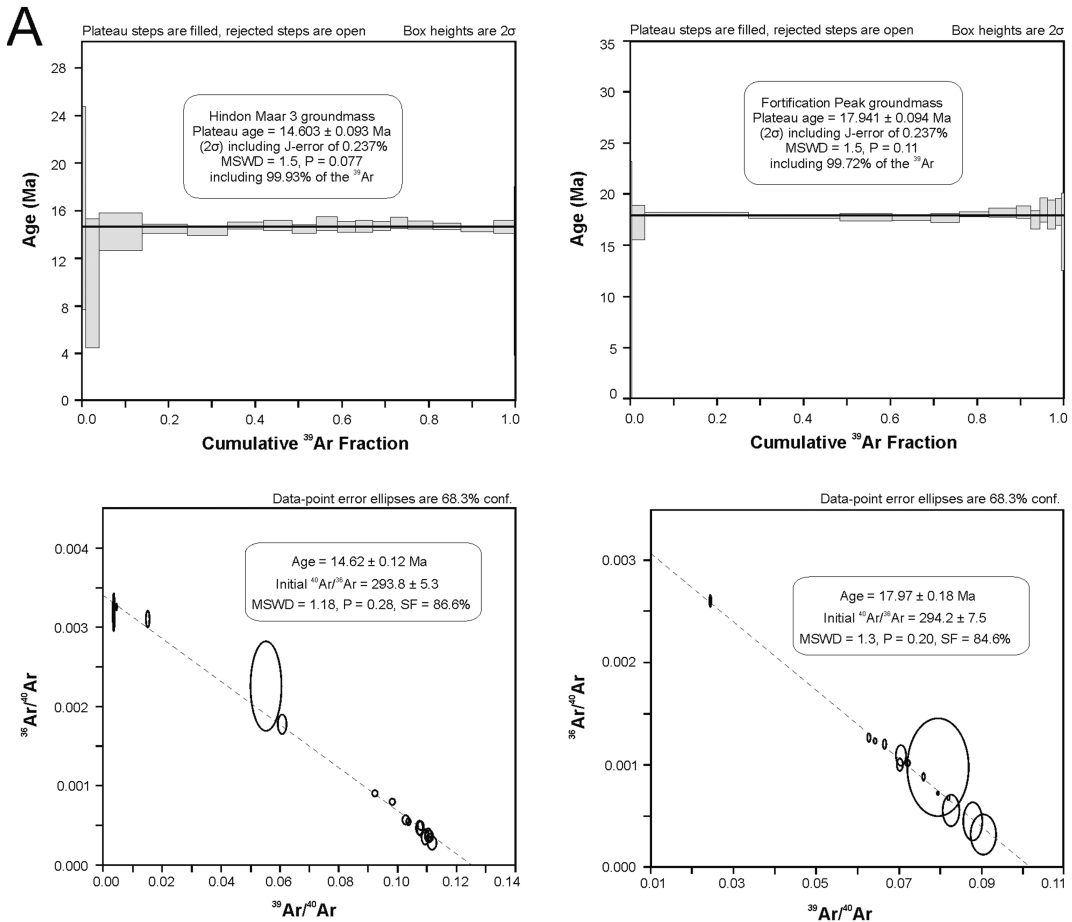


Figure 4

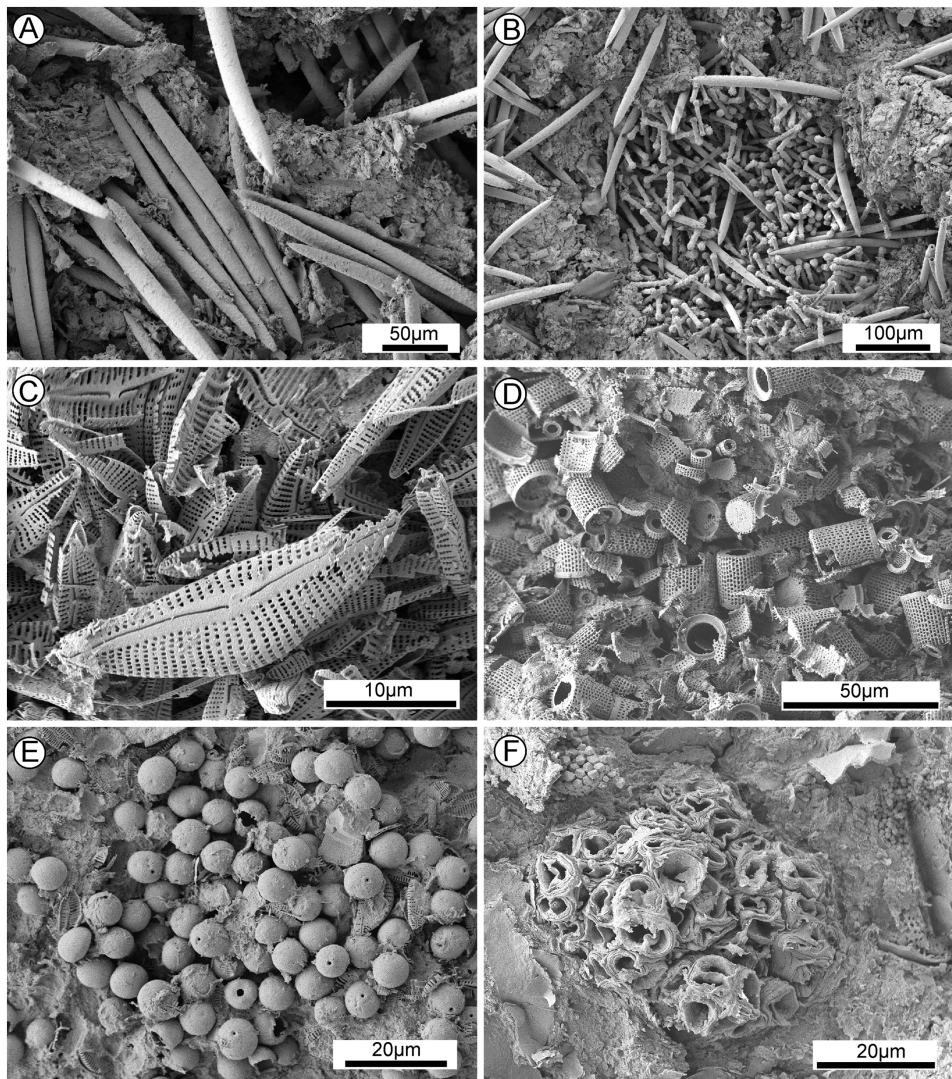


Figure 5



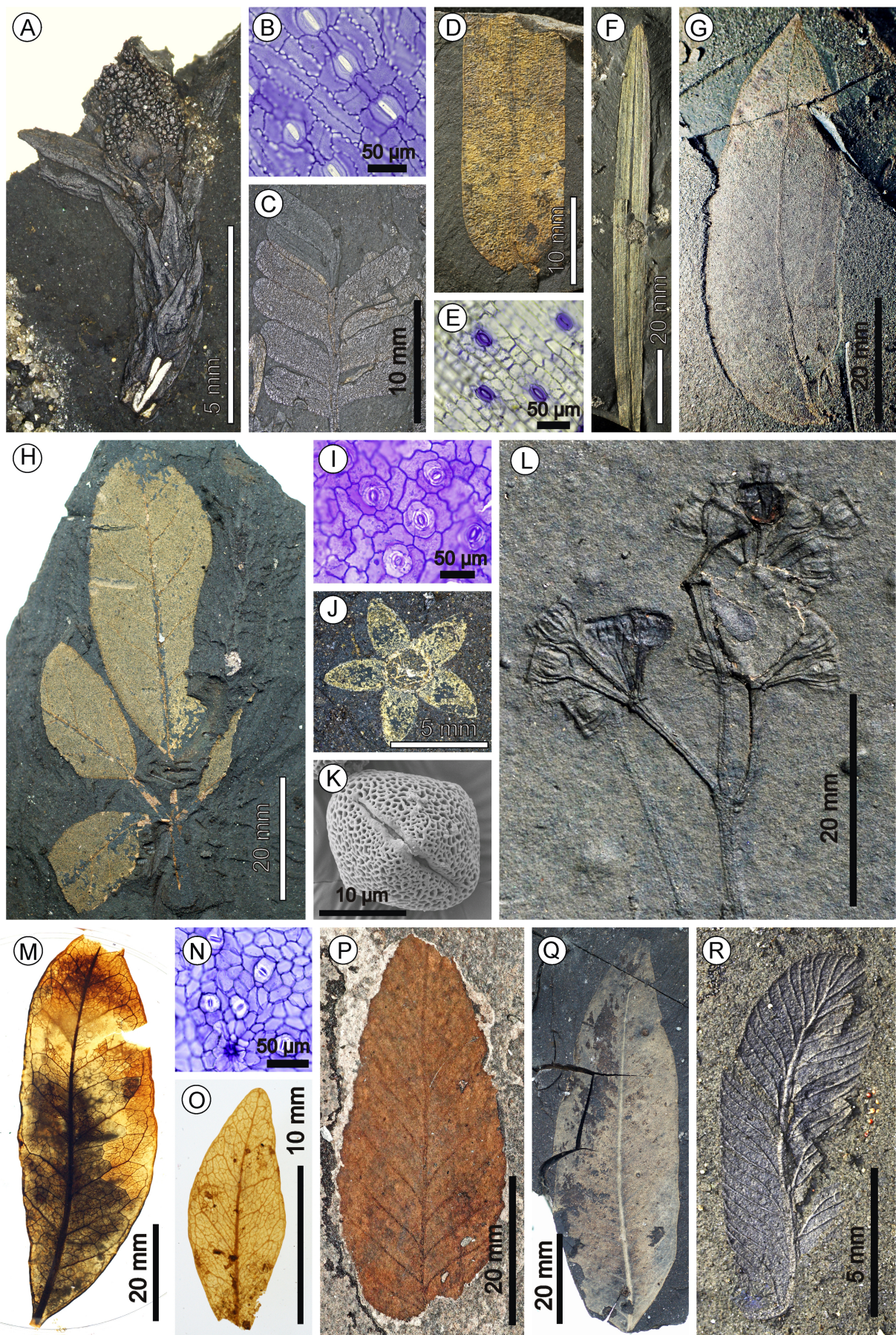


Figure 6



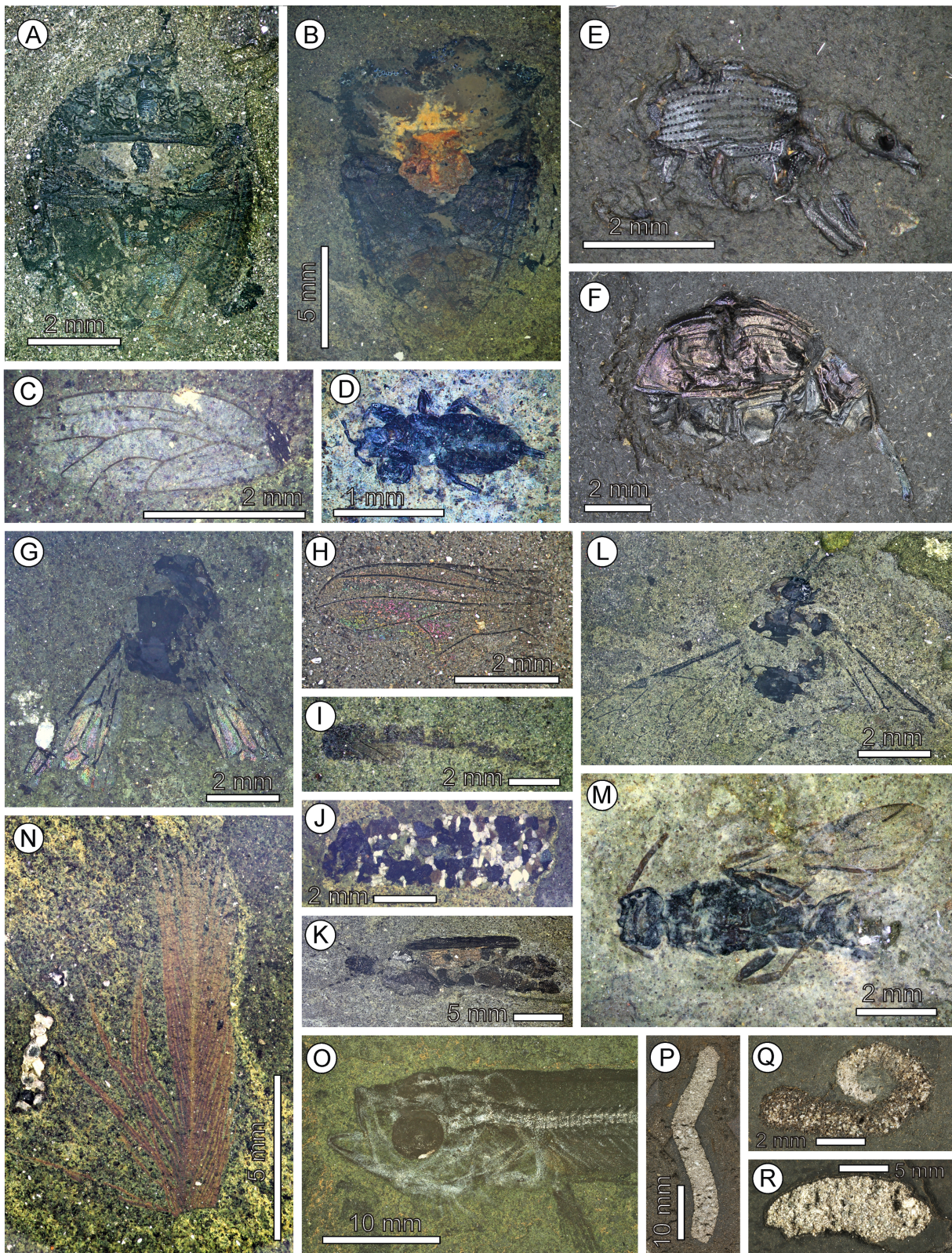


Figure 7



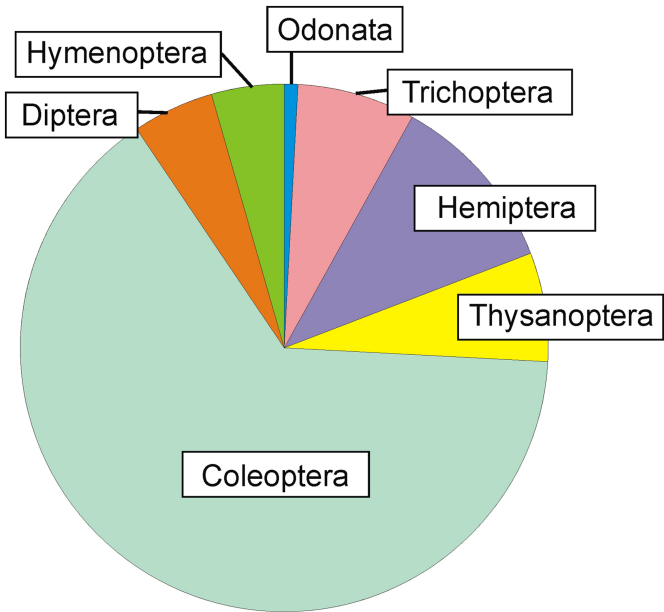


Figure 8