



Contents lists available at ScienceDirect

International Journal of Coal Geology

journal homepage: www.elsevier.com/locate/ijcoalgeo

The taphonomy of a remarkable leaf bed assemblage from the Late Oligocene–Early Miocene Gore Lignite Measures, southern New Zealand

David K. Ferguson^a, Daphne E. Lee^{b,*}, Jennifer M. Bannister^c, Reinhard Zetter^a, Gregory J. Jordan^d, Norbert Vavra^a, Dallas C. Mildenhall^e

^a Department of Paleontology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria

^b Department of Geology, University of Otago, PO Box 56, Dunedin, New Zealand

^c Department of Botany, University of Otago, PO Box 56, Dunedin, New Zealand

^d School of Plant Sciences, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia

^e GNS Science, PO Box 30-368, Lower Hutt, New Zealand

ARTICLE INFO

Article history:

Received 3 February 2009

Received in revised form 19 July 2009

Accepted 22 July 2009

Available online xxx

Keywords:

Cenozoic

Coal

Leaf compressions

Pollen

Resin

Ombrotrophic mire

ABSTRACT

A diverse assemblage of fossil leaves showing cellular detail is reported from the Late Oligocene–Early Miocene Gore Lignite Measures, southern New Zealand. The leaf-remains include at least five conifers, such as the genera *Agathis*, *Dacrycarpus*, *Phyllocladus* and *Dacrydium*, as well as a number of angiosperms including *Gymnostoma*, *Nothofagus* Subgenus *Brassospora*, *Phormium*, Proteaceae, Sapindaceae and Ericaceae. A parallel palynological study has identified a number of the same elements. The leaf layers represent litter horizons laid down in pools on the surface of a subtropical ombrotrophic forest mire that formed on an extensive low-lying coastal plain. Highly acidic water ponded in tree-fall depressions prevented microbial decay of the foliage. Taxa represented by both leaves and pollen are considered to have been components of the autochthonous swamp forest. Some other pollen grains are thought to represent local elements, based on the pollination biology of their nearest living relatives. Other taxa whose extant representatives are wind-pollinated may have grown further away.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

New Zealand with its abundant Late Cretaceous and Tertiary coal measures and unusual and evolutionarily important extant flora (Wardle, 1991) exerts an inherent attraction to paleobotanists. In eastern Southland lignite-bearing sediments extend over 2700 km² (Isaac and Lindqvist, 1990), some of which have been made accessible by opencast mining. In February 2006, the senior author was given permission to visit the Newvale opencast mine, 15 km south-west of Gore (latitude 46.1427°S, longitude 168.7518°E, c. 100 m above sea level (Fig. 1) Here the Gore Lignite Measures consist of 10 major seams or seam groups separated by sandstone and mudstone which are overlain by 60 m or more of quartzose sandy conglomerate (Isaac and Lindqvist, 1990: fig. 63). The coal typically contains large quantities of wood, some *in situ* stumps, and innumerable lumps of resin. However, of particular interest were numerous leaf compressions in blocks of lignite from a horizon about 5 m below the top of the 17 m thick Seam W6 of the middle Gore Lignite Measures (Figs. 2

and 3). A specimen was shown to Daphne Lee (University of Otago), who made a large collection with Jon Lindqvist later the same month. The limited areal extent of the leaf beds became apparent when only a few leaf compressions were found on a further collecting trip in February 2007. This is the first record from New Zealand of such leaf beds within lignite.

The Gore Lignite Measures accumulated on a low-lying coastal plain, at a similar latitude to that of present day southern New Zealand (c. 46°S). There is no evidence for high relief, although there may have been low ridges up to 100–200 m in the hinterland. According to Isaac and Lindqvist (1990, p. 165), the Gore Lignite Measures were mainly deposited “in a range of fluvial channel, overbank splay, floodplain and swamp environments, as indicated by the presence of *in situ* terrestrial plant remains, lateral persistence of the multiple coal seams, common root-penetrated seat earths, large scale upward-fining clastic sequences typical of ... cyclothems, and the paucity of marine fauna. The depositional setting was a prograding deltaic plain, which advanced across a shallow marine shelf during Late Oligocene–Early Miocene time.” The extensive, multiple coal seams such as that exposed in the Newvale Mine are typical of the middle Gore Lignite Measures and probably formed as “blanket peats, in lower to middle delta plain interchannel areas” (Isaac and Lindqvist (1990, p. 165). The huminite-rich lignite in Seam W6 consists largely of degraded woody material. It has a low ash content of between 3 and 5%, and bed

* Corresponding author. Tel.: +64 3 479 7525; fax: +64 3 479 7527.

E-mail addresses: david.kay.ferguson@univie.ac.at (D.K. Ferguson),

daphne.lee@otago.ac.nz (D.E. Lee), jennifer.bannister@xtra.co.nz (J.M. Bannister),

reinhard.zetter@univie.ac.at (R. Zetter), Greg.Jordan@utas.edu.au (G.J. Jordan),

norbert.vavra@univie.ac.at (N. Vavra), D.Mildenhall@gns.cri.nz (D.C. Mildenhall).

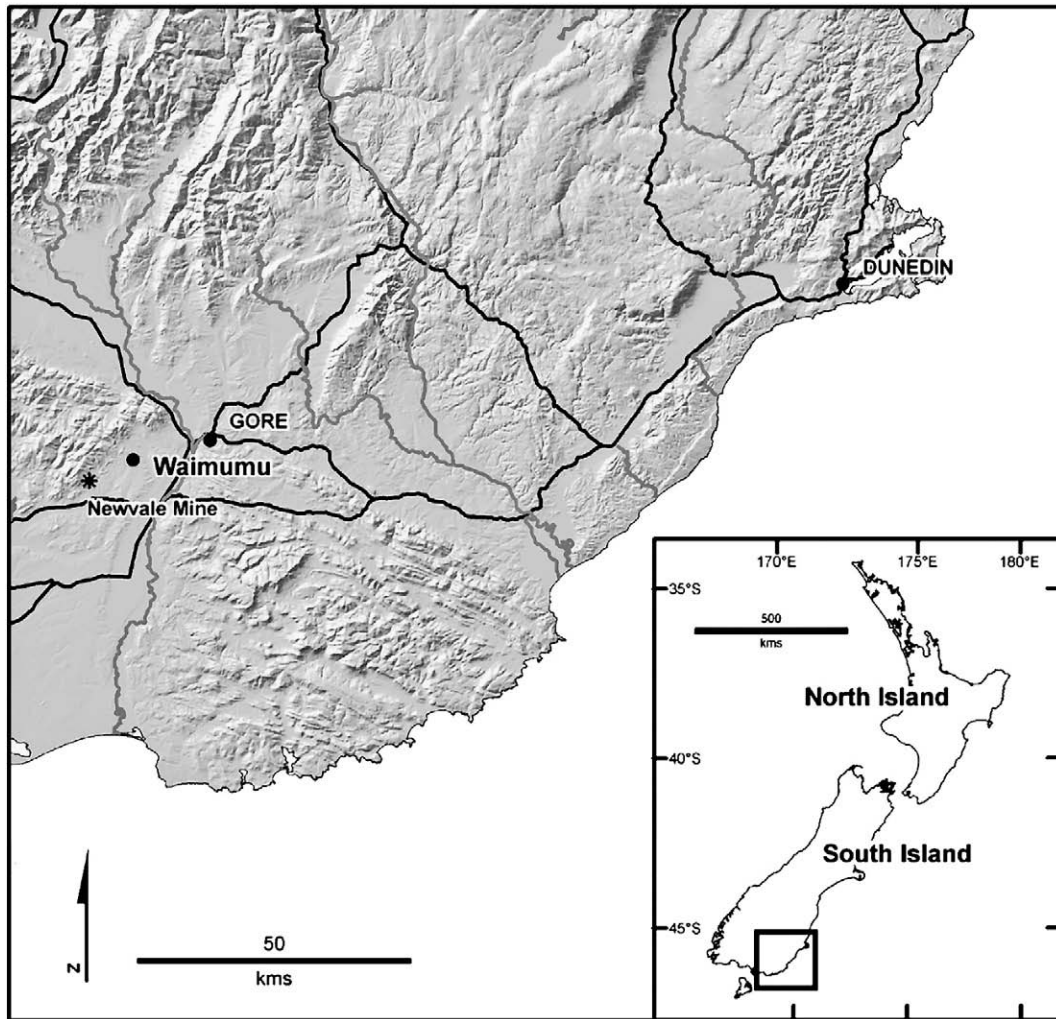


Fig. 1. Location map of Newvale Mine, Waimumu, Southland, New Zealand.



Fig. 2. Mechanically disrupted leaf beds from about 5 m below top of the gently dipping 17 m thick Seam W6, middle Gore Lignite Measures, Newvale Mine, Waimumu, Southland, New Zealand.

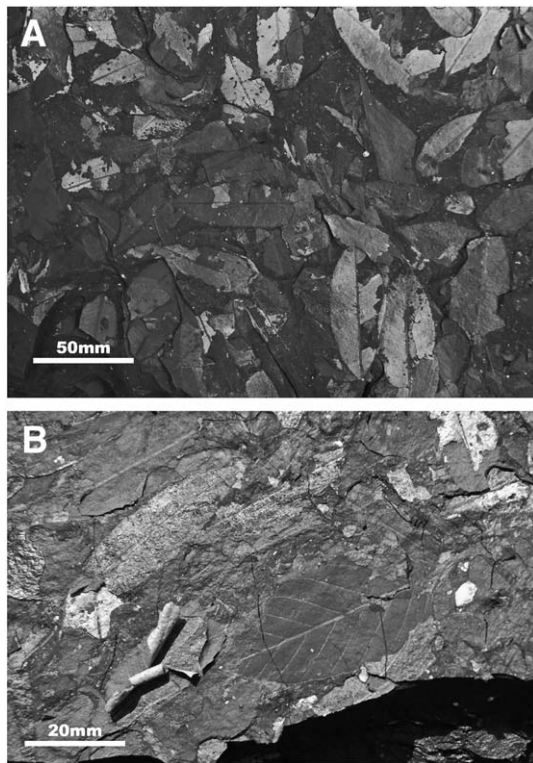


Fig. 3. A, Bedding plane covered with detached, randomly oriented angiosperm leaves. B, Bedding plane showing a variety of gymnosperm and angiosperm leaves with well-preserved cuticle. Light-coloured blebs are resin.

moisture content of 40–42% (Black, 1989; Isaac and Lindqvist, 1990). Partings are very rare within this thick seam, which is likely to have formed as a domed ombrotrophic mire above the level of surrounding rivers (J. K. Lindqvist, Personal Communication, May, 2009).

The fossil site from which the leaves were collected is registered as F45/f0394 in the New Zealand Fossil Record File administered by the Geological Society of New Zealand. The NZ Map Grid reference on Infomap series NZMS 260 is F45/817434 (46.1427°S, 168.7518°E). The age of the middle Gore Lignite Measures is Late Oligocene or Early Miocene (Waitakian to Altonian Stage) based on studies of palynofloras of Oligocene and Miocene strata of Otago and Southland by Pocknall and Mildenhall (1984) and Mildenhall and Pocknall (1989). Palynofloras from Seam W6 in the Newvale Mine were placed in the *Proteacidites isopogiformis* Zone (Pocknall in Isaac and Lindqvist, 1990), which is regarded as equivalent to the lower part of the Otaian Stage (Cooper, 2004, fig. 12.6). However, “the development of finer Neogene pollen zonations has been hampered by problems of precise correlation with the marine stages, and the boundaries are not based on any independently dated events”, as pointed out in Cooper (2004, p. 175). Given the close association between marine strata of Waitakian age and the lower and middle Gore Lignite Measures in the Waimumu area (Isaac and Lindqvist, 1990), we consider that the lignite is probably Waitakian (late Oligocene to early Miocene) in age.

2. Material and methods

The leaves occur on poorly defined bedding planes as single or multiple layers only a few leaves in thickness (Fig. 3A, B). The twenty or so large blocks collected for this study were numbered and photographed before being split into smaller pieces for ease of handling and to expose as many individual leaves as possible. The leaves are held in the Department of Geology, University of Otago. The excellent preservation of the leaves and lignite offered the possibility of using a

multidisciplinary approach (macrofossils, resin, and sporomorphs) to interpret the paleoenvironment.

2.1. Leaf compressions

Most of the leaves are brittle, but with excellent cuticular preservation (Figs. 3B and 4A, and B). Cuticle preparations were made by removing a piece of leaf with a scalpel, soaking it in 30% hydrogen peroxide to which a few crystals of sodium pyrophosphate were added and heating for several hours on a hotplate. The cuticle was then rinsed, cleaned with a fine paintbrush, and either mounted in glycerine jelly for light microscopy or placed on a stub for scanning microscopy (SEM). Cuticle pieces on SEM stubs were sputter-coated with gold and palladium and examined and photographed with a Cambridge S360 Stereoscan electron microscope.

2.2. Sporomorphs

Small pieces of lignite from the leaf-bearing horizon were treated according to the method developed by Zetter (1989) and described in Ferguson et al. (2007). After acetolysis (chlorination plus acetylation), glycerine was added to the organic fraction to form a suspension. A drop of this fluid was transferred to a glass slide with a pipette. Using a

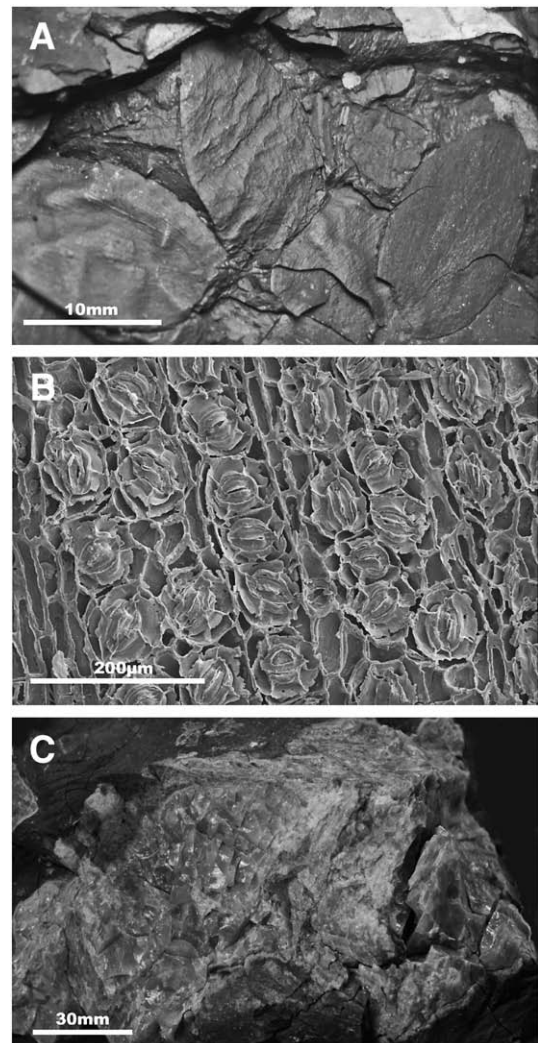


Fig. 4. *Agathis* leaves, cuticle and resin from Newvale Mine leaf beds. A, Several detached *Agathis* leaves in close proximity. B, SEM photograph of inner view, abaxial cuticle, showing discontinuous stomatal rows and predominantly oblique orientation of stomata. C, Large block of resin from Newvale Mine.

dissecting needle to which a nasal hair had been affixed, grains to be examined were flicked to the edge of the glycerine, before being transferred to another glass slide for photography under a light microscope (LM). Since no cover slip was employed, the same grain could be photographed in various orientations. The pollen was then transferred to a SEM stub to which a drop of absolute ethanol had been added in order to disperse the glycerine prior to coating the grains with gold in a BIORAD Sputter Coater. The pollen grains were then examined in a JEOL 6400 at 10 kV. Using this single-grain technique it was possible to examine the same grain under both LM and SEM.

2.3. Resin

Fist-sized lumps and smaller blebs of yellow-brown fossil resins ('amber') are abundant in the Gore Lignite Measures at Newvale Mine and elsewhere (Figs. 3B and 4C). Some preliminary chemical investigations into the botanical origin of this material have been performed, although the araucarian terpenoid fraction of such resins is still largely understudied (Langenheim, 2003).

To test if the material collected included chemically different types of resin, solutions in methanol were analysed by means of HPLC (High Performance Liquid Chromatography). The chromatograms achieved were often practically identical or at least very similar to each other. Remarkable differences could be observed however in comparing with 'ambrite' and a fossil resin from the Neogene of New Zealand. In this respect further studies seem promising.

To identify if single terpenes were useful as 'biomarkers' samples were analysed using combined gas liquid chromatography/mass spectrometry following standard procedures. For this purpose three different samples were prepared: a fraction of the fossil resin soluble in boiling methanol (ca. 70 mg in 2 ml methanol), a solution of the material after refluxing in chloroform (ca. 51 mg in 2 ml chloroform) and finally also a silylated sample (reflux of 101 mg with BSA in pyridine). Using a number of chromatograms the following substances could be identified on the basis of their mass spectra: camphene, isocineole, isopropyltoluene (= p-cymene), p-menth-3-en-1-ole, borneole, 1-methyl-4-(1-methylethyl)-cyclohexene, fenchyl alcohol, α -terpinene, camphor, and abietic acid. A number of other substances could only be tentatively identified: α -terpineole, α -terpinene, 1,8-cineole, and longifolene (possibly: δ -cadinene).

Essential oils of Araucariaceae have been investigated for the past eighty years (Hoskins, 1928) and have more recently been used for chemotaxonomical purposes to compare the terpene patterns for the three genera *Agathis*, *Araucaria*, and *Wollemia* (Brophy et al., 2000). On the basis of detailed data achieved for recent material our few identifications of 'biomarkers' seem to fit rather well. Camphene, 1,8-cineole, p-cymene, and δ -cadinene have been found in the essential oils of all three genera of Araucariaceae by Brophy et al. (2000). Since fenchene is only reported from the genus *Agathis* and we could identify the corresponding fenchyl alcohol in our resin sample, this may point towards an *Agathis* origin of the material under study. This alcohol can also be found in succinite samples, but the lack of any succinic acid in the fossil resins studied excludes such an identification.

The results achieved so far indicate that an araucarian origin – possibly genus *Agathis* – can be proposed for this fossil resin.

3. Results

The Newvale assemblage is still being investigated by a team of paleobotanists and palynologists, so the lists given here are provisional.

The lignite samples contain macrofossils of Araucariaceae (*Agathis*) (Fig. 4) and four conifers belonging to Podocarpaceae *sensu lato* (*Dacrydium*, *Dacrycarpus*, *Phyllocladus* and *Halocarpus*) (Fig. 5). Leaves from at least eight angiosperm families are represented in the leaf

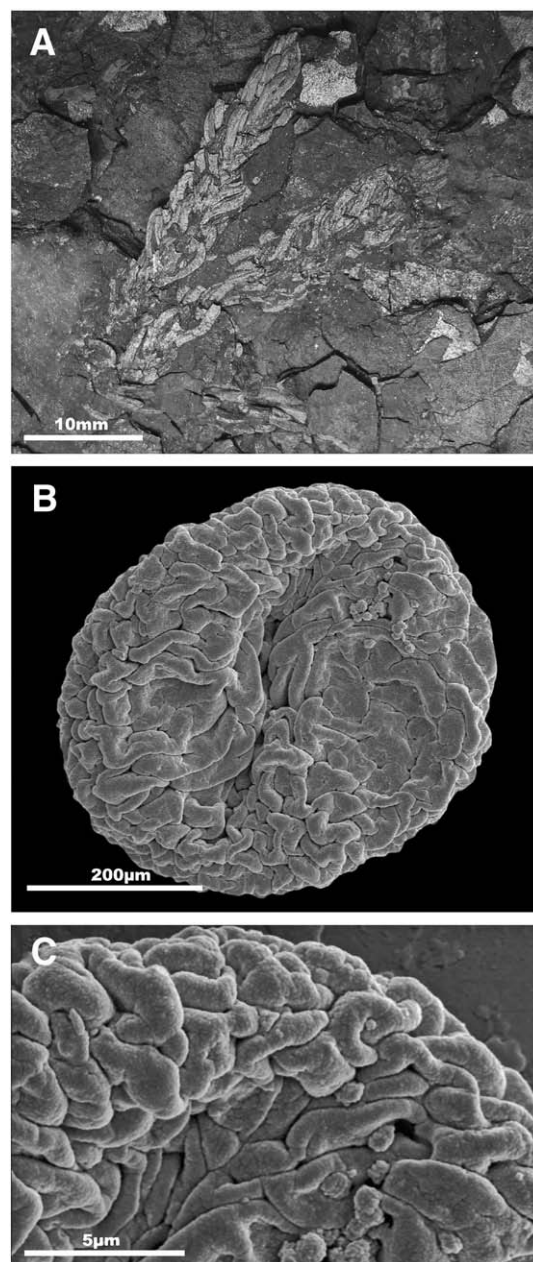


Fig. 5. *Dacrydium* foliage and pollen from Newvale Mine leaf beds. A, Several foliage shoots of *Dacrydium* on a bedding plane. B, View of pollen grain. C, Close-up of sculpture on previous grain.

litter: Araliaceae (cf. *Schefflera*), Casuarinaceae (*Gymnostoma*) (Fig. 6), Cunoniaceae, Nothofagaceae (*Nothofagus* Subgenus *Brassospora*) (Fig. 7), Ericaceae, Sapindaceae (cf. *Alectryon*) (Fig. 8), and one monocot, *Phormium* (Asparagaceae) (Fig. 9). While most of the families are represented by macrofossils of only one or two species, approximately 6 species of Proteaceae are present (R. J. Carpenter, Personal Communication, December, 2008). All of the macrofossils have exceptionally well-preserved cuticle.

The majority of the above-mentioned taxa have been found in the palynological samples. The commonest sporomorph in the coal is *Haloragacidites harrisii* (Casuarinaceae) (Fig. 6C, D). Although the pollens of the four extant genera of Casuarinaceae are quite similar, it would seem reasonable to infer that at least some of the *H. harrisii* pollen represents *Gymnostoma* given the presence of abundant macrofossils of this genus at Newvale (Fig. 6A). Although *Rhoipites aralioides* could represent the pollen of *Schefflera*, the affinities of this

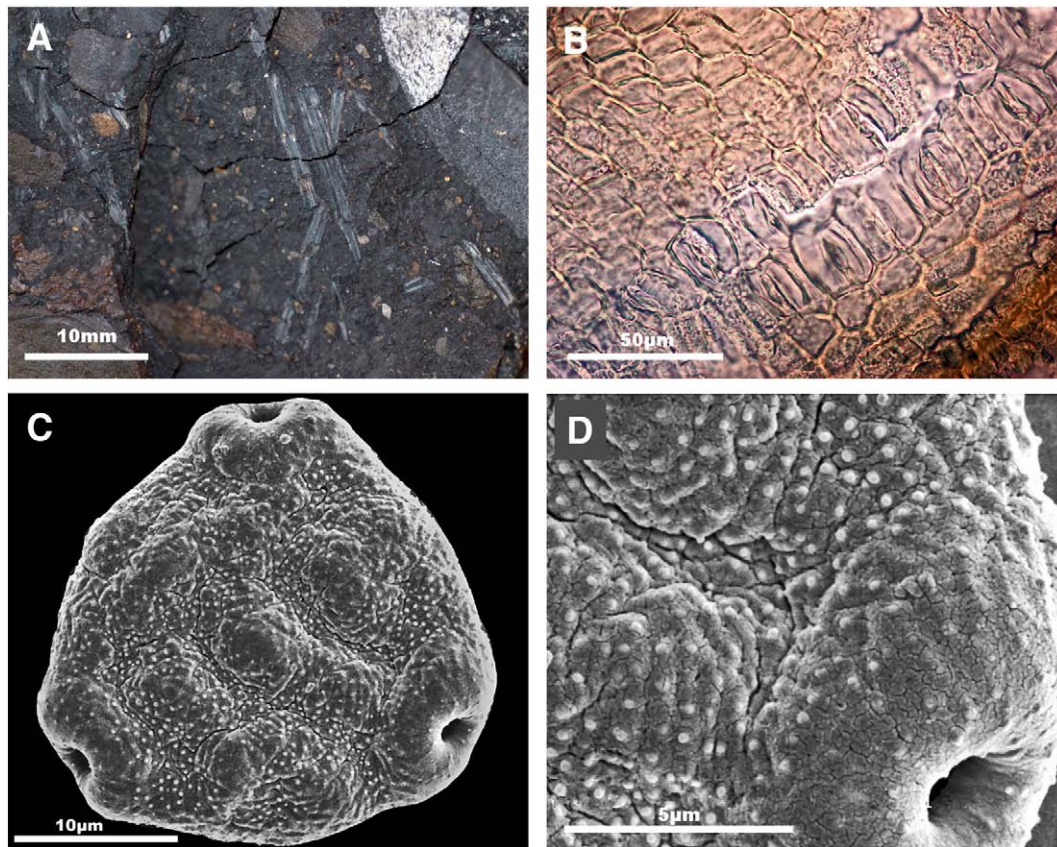


Fig. 6. *Gymnostoma* foliage, cuticle, and Casuarinaceae pollen from Newvale Mine leaf beds. A, Several fragmentary shoots of *Gymnostoma*. B, Cuticle of *Gymnostoma* showing two rows of stomata. C, Pollen grain of *Haloragacidites harrisii* (Casuarinaceae), most abundant pollen type in Newvale leaf beds. D, Close-up of previous pollen grain to show sculpture.

sporomorph are equivocal. So far, it has only been found in clastic sediments immediately overlying Seam W6 at Newvale. The absence of Araucariaceae pollen is surprising considering the large numbers of *Agathis* leaves in the litter (Fig. 4A; Lee et al., 2007), and the fact that all the resin can be attributed to that family. However, *Agathis* pollen is known to have a poor preservational potential (Pocknall, 1982; Mildenhall, 1985, 2001; Ogden et al., 1992; Newnham et al., 1993).

The leaf litter also contains several sporomorph taxa that are not represented as macrofossils e.g. *Dictyophyllidites arcuatus*, a spore which can be ascribed to *Dicranopteris* (Gleicheniaceae), a fern that grows on wet, nutrient-poor soils. In addition to the conifers, two pollen grains of the gymnospermous *Equisetosporites notensis* (*Ephedra*, Ephedraceae) were also encountered in the leaf bed. This shrub grows in open areas, and has a propensity for long-distance transport (Maher, 1964). However, it is found, albeit rarely, throughout New Zealand upper Cretaceous to upper Neogene sediments (Couper, 1960; Raine et al., 2008) and could be locally derived. Some of the pollen, e.g. *Milfordia homeopunctata* (Joinvilleaceae/Restionaceae), *Rhoipites alveolatus* (*Euphorbia* [cf. *E. glauca*, Euphorbiaceae]), *Tricolpites reticulatus* (*Gunnera* [Gunneraceae]) came from herbaceous angiosperms, which would explain their absence in the macroscopic record. Herbs often lack resistant cuticle and fibrous tissues, and are generally under-represented as macrofossils. Other, angiospermous pollen, viz. *Clavatipollenites ascarinoides* (*Ascarina*, Chloranthaceae), *Ericipites* sp. (Ericaceae s.l.), *Myrtacidites* sp. (Myrtaceae), *Nyssapollenites endobalteus* (*Mallotus/Macaranga*, Euphorbiaceae), and *Tetracolporites spectabilis* (*Dysoxylum*, Meliaceae), representing insect- or bird-pollinated shrubs/trees, could not have travelled far from their life position, and might be expected to have a macroscopic record. However, different taxa have considerably different resilience to decay (e.g., Carpenter and Horwitz, 1988), and this characteristic is unknown for these taxa.

The initial identifications indicate that the flora consisted of a number of elements still present in the Southland flora (*Ascarina*, *Dacrydium*, *Dacrycarpus*, *Euphorbia*, *Gunnera*, *Phormium*, *Phyllocladus*). However, a high proportion of the taxa in the fossil flora are now restricted to warmer climates. Within New Zealand *Agathis* now occurs only in the northern half of the North Island, while *Dysoxylum* extends north from the northern part of the South Island (Poole and Adams, 1986). Other taxa now only occur in tropical regions including the wet tropics of Queensland, New Guinea and New Caledonia, e.g. *Beauprea*, *Gymnostoma*, *Nothofagus* Subgenus *Brassospora*). This is strongly suggestive of higher temperatures and a relatively high sea level at the Oligocene–Miocene boundary (Zachos et al., 2001), when the New Zealand land area was increasing after a period of partial or, more controversially, total submergence in the Oligocene (Cooper and Cooper, 1995; Campbell and Landis, 2001; Landis et al., 2008).

4. Paleoenvironmental interpretation

High temperatures and rainfall suggested by the subtropical elements, as well as by the accumulation of a 17 m thick lignite seam, indicate productive environmental conditions supporting high biomass, but such conditions are also likely to favour high microbial degradation rates. In order for plant detritus to accumulate as peat two conditions had to be fulfilled, namely a high water table maintained over an extended period, and a broad area of southern New Zealand that was slowly subsiding (Isaac and Lindqvist, 1990). Because peat/coal is mostly decayed organic matter, it rarely contains any entire macroscopic organically preserved leaves (Gastaldo and Staub, 1999). The only scenario that can satisfactorily explain the presence of leaf beds such as those at Newvale Mine is a low pH, whereby saprophytic fungal activity is curtailed (Gastaldo and Staub, 1999). Indeed, the fossil cuticles display little evidence of fungal

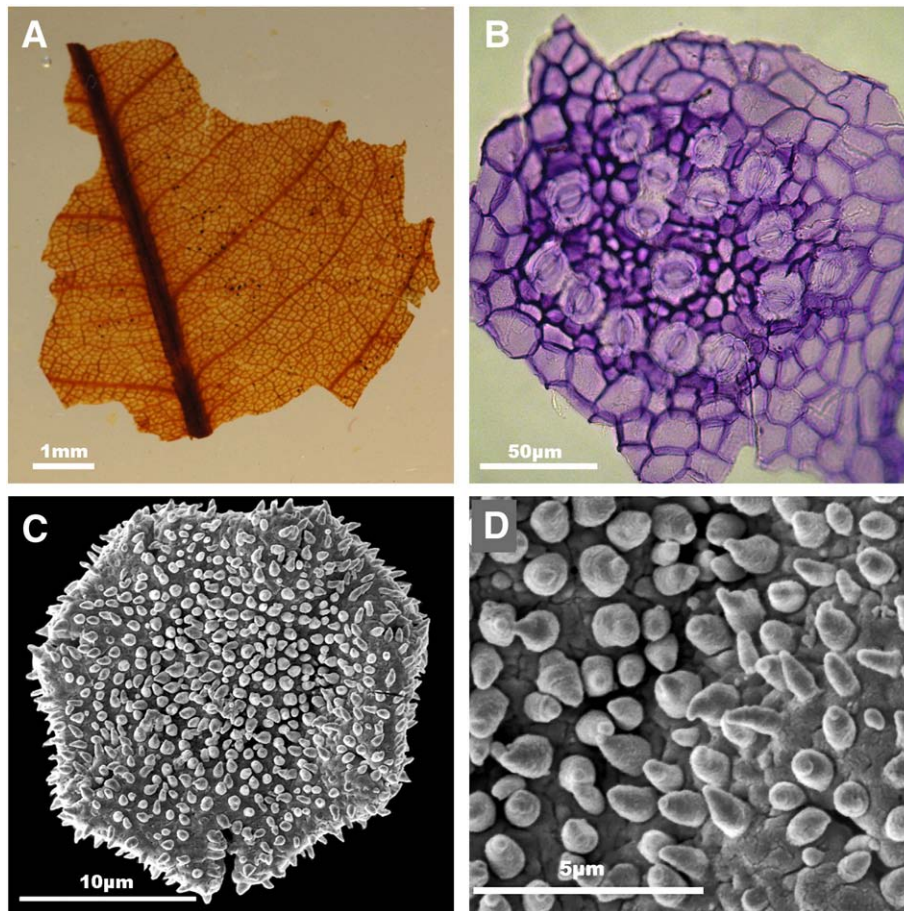


Fig. 7. *Nothofagus* Subgenus *Brassospora* leaf, cuticle, and pollen from Newvale Mine leaf beds. A, Venation of partial *Nothofagus* leaf with cuticle of Subgenus *Brassospora* type. B, Cuticle showing stomata in tight areoles. C, Pollen grain of *Nothofagidites cranwelliae* (Nothofagaceae), Subgenus *Brassospora* type. D, Close-up of previous pollen grain to show sculpture.

hyphae. In order to achieve a low pH the vegetation must have been fed by rainwater rather than ground-water, or rapid accumulation of organic material in still water may have induced rapid development of anoxic conditions. During the mid-Cenozoic the rainwater may have been particularly acidic due to the higher CO₂ levels in the atmosphere (Pearson and Palmer, 2000; Kürschner et al., 2008).

Shallow-rooted trees growing on ombrotrophic mires are likely to be vulnerable to windthrow, creating depressions in the mire. These depressions fill with acidic water from the surrounding peat and can be replenished by subsequent rainfall (cf. Gastaldo and Staub, 1999). Windthrow will result in pool-and-hummock patterning on the surface of the mire, providing a mosaic of somewhat drier hummocks and wet depressions. The former provide a suitable substrate for the plants that in turn will contribute leaves to the peat accumulating in the depressions. Mire systems can support vegetation mosaics reflecting different successional phases associated with moisture and nutrient gradients created by disturbances.

The observed fossil flora is entirely consistent with the Newvale site being the result of an ombrotrophic mire. Many of the woody plants encountered in the leaf beds are from groups well known to be successful in nutrient-poor and often acid environments. Proteaceae, Casuarinaceae, Ericaceae and many of the conifers (e.g., *Phyllocladus*, *Halocarpus*) are very successful in nutrient-poor habitats (Wardle, 1991). The Proteaceae, Casuarinaceae and Ericaceae are highly scleromorphic groups of angiosperms that evolved in nutrient-poor wet climates then radiated into dry climates (e.g. Crayn et al., 1998; Steane et al., 2003; Jordan et al., 2008). A large number of the species have papillose cuticles, a characteristic that is, contrary to anecdotal opinion, more often associated with wet climates than dry (Haworth

and McElwain, 2008; Jordan et al., 2008). Since the substrate of the hummocks would have been more aerated, saprophytic fungi would in time remove all evidence of the forest litter (leaves first, then angiospermous wood and finally coniferous wood).

Restionaceae and New Zealand flax (*Phormium*) would have been amongst the first colonizers after disturbance, as they can grow in marshy conditions. By creating a raised platform and protection for seedlings, *Phormium* acts as a nurse plant for the woody species that replace it (Reay and Norton, 1999; Robertson et al., 1991). Light-demanding taxa such as *Gymnostoma* (Casuarinaceae), Cunoniaceae, Myrtaceae and various Proteaceae were probably the first woody species to colonize the peat. Organic nitrogen and phosphorus locked up in the peat would have been unavailable to the plants. This could explain the relatively small size of the leaves (notophylls) discovered in the leaf beds (Fig. 3).

Many of the woody plants encountered in the leaf beds have developed strategies to overcome the shortage of nutrients. In the Proteaceae, root exudates mobilize mineral nutrients (Duhoux et al., 2001; Watt and Evans, 1999). Other plants have nitrogen-fixing nodules and/or mycorrhizal symbionts, which allow them to grow on nutrient-poor substrates (Duhoux et al., 2001; Kottke et al., 2004). The first generation of woody plants would have been able to persist at the forest margins adjoining the peaty pools as they in turn were replaced by more shade-tolerant taxa like southern beech (*Nothofagus* spp.), representatives of the Podocarpaceae, and kauri (*Agathis*). The abundance of *Agathis* resin and the numerous leaves of *Agathis* found within the leaf bed indicate that this genus was growing in the immediate neighbourhood of the pools (Fig. 10). The heavy leaves accumulate around the bole of the tree, supplying nutrients to the fine

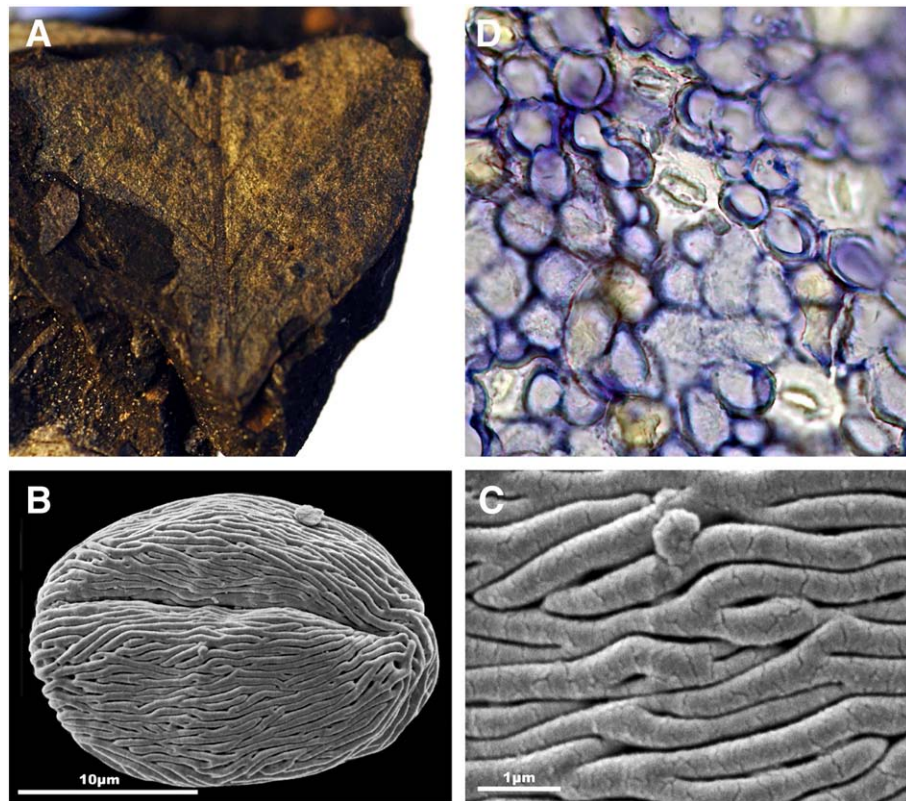


Fig. 8. Sapindaceae leaf, cuticle, and pollen from Newvale Mine leaf beds. A, Incomplete leaf with cuticle resembling that of *Alectryon* (Sapindaceae). B, Cuticle showing stomata and papillae. C, Pollen grain of *Rhoipites striatus* (Sapindaceae). D, Close-up of previous pollen grain to show sculpture.

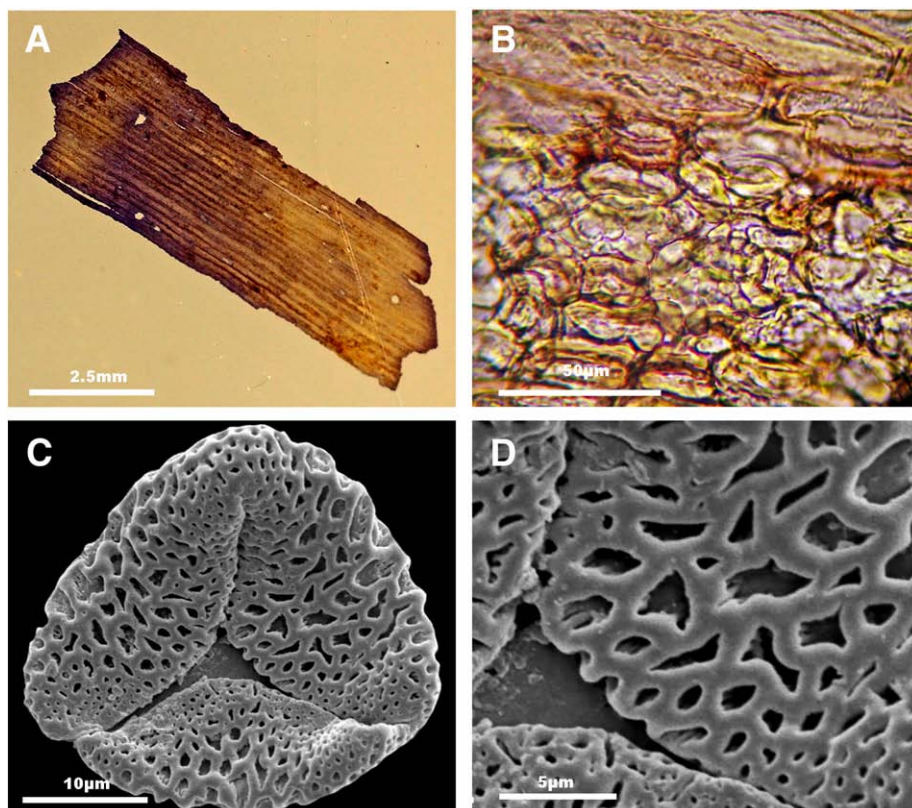


Fig. 9. Partial leaf, cuticle, and pollen of *Phormium* from Newvale Mine leaf beds. A, Fragment of leaf of *Phormium* (Asparagaceae). B, Cuticle from leaf shown in A. C, Pollen grain of *Luminidites reticulatus*, an extinct species of *Phormium*. D, Close-up of previous pollen grain to show sculpture.

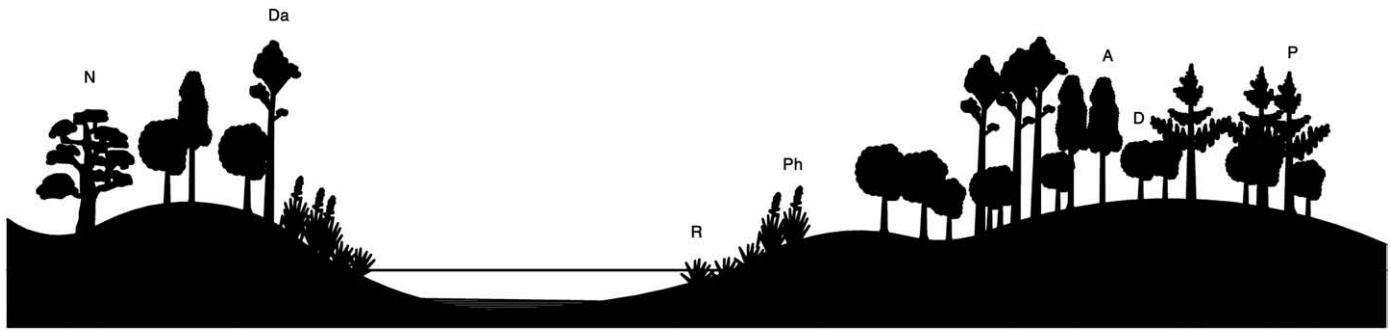


Fig. 10. Schematic reconstruction of vegetation growing on an ombrotrophic mire at Newvale Mine in Late Oligocene times. N = *Nothofagus*; Da = *Dacrydium*; R = *Restionaceae*; Ph = *Phormium*; A = *Agathis*, D = *Dysoxylum*; P = *Phyllocladus*.

feeder roots (vesicular–arbuscular mycorrhizae). Forest rejuvenation caused by windthrow of the canopy trees, was probably an ongoing feature of this ecosystem. The reduced life expectancy could explain the almost complete absence of fruits and seeds in the leaf beds.

Most abscised leaves accumulate under the canopy, although in the absence of long-distance water transport, some leaves can be transported laterally up to a distance equivalent to the height from which they were released (not necessarily the height of the tree) (Ferguson, 1985). In a study of an *in situ* fossil swamp forest, Rowell et al. (2001) showed that the diversity of pollen considerably exceeded that of the leaf macrofossils, which in turn considerably exceeded that of the *in situ* tree stumps. Since the trees on the raised mire were probably stunted, the distance of transport may be no more than 20 m from the bole. Only under exceptional circumstances, such as during a storm, could they have been blown well away from the tree. Since wind was the only transport medium involved, the Newvale assemblage must be considered as parautochthonous (Gastaldo et al., 1996). This is confirmed by other features of the Newvale leaf beds including the absence of any clastic sediment, the lack of any preferential leaf orientation based on inspection, and local concentrations of conspecific leaves, patterns found in undisturbed forest litter (Ferguson, 1985). Lastly, although fern spores are found, their fronds are absent. Fragments of fern fronds (including Gleicheniaceae) are relatively common in Quaternary and Neogene assemblages in Australia (Blackburn and Sluiter, 1994; Jordan, 1997; Macphail et al., 1993). However, most fern fronds are not abscised, but wither *in situ*, and their presence as macrofossils usually indicates some sort of catastrophic event like flooding or fire.

Pollen can, under exceptional circumstances, be transported for thousands of kilometres; however most pollen is dispersed over short distances. As in the case of leaves and seeds, pollen dispersal follows a negative exponential pattern (Ferguson, 1993). The voluminous pollen of wind-pollinated plants is disseminated much further afield than leaves (Ferguson, 1995), whereas pollen from insect- or bird-pollinated plants can be absent from nearby surface samples. The presence of pollen of *Ascarina* and *Dysoxylum* in the leaf bed therefore indicates their local presence. The combination of macrofossils and pollen belonging to the same taxon would tend to suggest that even the pollen from wind-pollinated plants is probably of local origin. The only likely candidates for possible long-distance dispersal are the two grains of *Ephedra* found in the coal.

5. Conclusions

The assemblage of well-preserved fossil leaves and associated pollen and spores from the Late Oligocene–Early Miocene Gore Lignite Measures, southern New Zealand, suggests a subtropical, oligotrophic peat-bog system subject to occasional mass windthrow which created a hump-and-hollow topography with diverse successional phases representing vegetation establishment following disturbances. The material from Newvale has been identified using a combination of

macro- and micro-morphological characters. Detailed SEM analyses have enabled us to correlate some of the dispersed pollen with the leaf-remains which has resulted in a much more reliable reconstruction of the paleovegetation than has been possible previously (e.g., Wolfe and Upchurch, 1987; Gregor, 1990). Many pollen types from Newvale have not yet been identified, reflecting the lack of pollen atlases and comparative material from places like New Guinea and New Caledonia. The pollen of many of the genera has never been looked at with the SEM. By undertaking a joint study of the macro- and microfossils, it has proved possible to expand the total list of plants and thus narrow down the paleoclimatic parameters, and also to suggest which of the pollen grains were parautochthonous and which are more likely to have originated from the regional vegetation. In this way we can attempt to reconstruct vegetation at multiple scales. In any paleoclimatic interpretation of the vegetation it is essential that the ecological backdrop should be considered. In the case of Newvale, sclerophylly would appear to be edaphically rather than climatically controlled.

Acknowledgements

The authors wish to thank Norman and Ross Dickie for organizing the first visit to the Newvale coal mine, and for supplying an additional specimen of the leaf litter. We are grateful to Mr B. Highsted and Mr K. McLaren of Solid Energy for kindly allowing us access to the Newvale Mine on several occasions. Jon Lindqvist provided assistance in the field, Brent Pooley made thin sections of the coal, Lorna Little prepared some cuticles, Nadja Kavcik prepared the palynological samples, and Kay Swann and John Conran prepared the figures. Liz Girvan from the Otago Centre for Electronmicroscopy, University of Otago, is thanked for the SEMs of cuticles. We are also grateful to Bill Lee for helpful comments on earlier drafts of this paper, Ray Carpenter for information on Proteaceae from Newvale, Lena Ohneiser for taking photographs of the leaf blocks, and Elizabeth Lee for drawing Fig. 10. Funding for this research was provided by the Department of Paleontology, University of Vienna and the Department of Geology, University of Otago. The visit of DKF to the University of Otago was assisted by a William Evans Fellowship from the University of Otago. We would also like to thank Mark Scheihing and Christopher Wnuk for the invitation to submit a paper to this volume honouring Hermann Pfefferkorn, and for helpful editorial advice.

References

- Black, P.M., 1989. Petrographic and coalification variations in the Eastern Southland lignites, New Zealand. *International Journal of Coal Geology* 13, 127–141.
- Blackburn, D.T., Sluiter, I.R.K., 1994. The Oligo-Miocene coal floras of southeastern Australia. In: Hill, R.S. (Ed.), *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, U.K., pp. 328–367.
- Brophy, J.J., Goldsack, R.J., Wu, M.Z., Fookes, C.J.R., Forster, P.I., 2000. The steam volatile oil of *Wollemia nobilis* and its comparison with other members of the Araucariaceae (*Agathis* and *Araucaria*). *Biochemical Systematics and Ecology* 28, 563–578.

- Campbell, H.J., Landis, C.A., 2001. New Zealand awash. *New Zealand Geographic* 51, 6–7.
- Carpenter, R.J., Horwitz, P., 1988. Leaf litter in two southern Tasmanian creeks and its relevance to palaeobotany. *Papers & Proceedings, Royal Society of Tasmania* 122, 39–45.
- Cooper, A., Cooper, R.A., 1995. The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proceedings of the Royal Society of London, Series B* 261, 293–302.
- Cooper, R.A. (Ed.), 2004. *The New Zealand Geological Timescale: Institute of Geological and Nuclear Sciences Monograph*, vol. 22, pp. 1–284.
- Couper, R.A., 1960. New Zealand Mesozoic and Cainozoic plant microfossils. *New Zealand Geological Survey Paleontological Bulletin* 32, 1–87.
- Crayn, D.M., Kron, K.A., Gadek, P.A., Quinn, C.J., 1998. Phylogenetics and evolution of epacrids: a molecular analysis using the plastid gene *rbcl* with a reappraisal of the position of *Lebetanthus*. *Australian Journal of Botany* 46, 187–200.
- Duhoux, E., Rinaudo, G., Diem, H.G., Auguy, F., Fernandez, D., Bogusz, D., Franche, C., Dommergues, Y., Huguenin, B., 2001. Angiosperm *Gymnostoma* trees produce root nodules colonized by arbuscular mycorrhizal fungi related to *Glomus*. *New Phytologist* 149, 115–125.
- Ferguson, D.K., 1985. The origin of leaf-assemblages – new light on an old problem. *Review of Palaeobotany and Palynology* 46, 117–188.
- Ferguson, D.K., 1993. Plant taphonomic studies with special reference to Messel. In: Schrenk, F., Ernst, K. (Eds.), *Monument Grube Messel – perspectives and relationships*. *Kaupia* 2, 117–126.
- Ferguson, D.K., 1995. Plant part processing and community reconstruction. *Eclogae Geologicae Helvetiae* 88, 627–641.
- Ferguson, D.K., Zetter, R., Paudyal, K.N., 2007. The need for the SEM in palaeopalynology. *Comptes Rendus Palevol* 6 (6–7), 423–430.
- Gastaldo, R.A., Ferguson, D.K., Walther, H., Rabold, J.M., 1996. Criteria to distinguish parautochthonous leaves in Tertiary alluvial channel-fills. *Review of Palaeobotany and Palynology* 91, 1–21.
- Gastaldo, R.A., Staub, J.R., 1999. A mechanism to explain the preservation of leaf litter lenses in coals derived from raised mires. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149, 1–14.
- Gregor, H.-J., 1990. Contributions to the Late Neogene and Early Quaternary floral history of the Mediterranean. *Review of Palaeobotany and Palynology* 62, 309–338.
- Haworth, M., McElwain, J., 2008. Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf and cuticular micromorphology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 262, 79–90.
- Hoskins, J.R., 1928. Das aetherische oel von *Agathis australis*. *Recueil des Travaux Chimiques des Pays-Bas* 47, 578–584.
- Isaac, M.J., Lindqvist, J.K., 1990. Geology and lignite resources of the East Southland Group, New Zealand. *New Zealand Geological Survey Bulletin* 101, 1–202.
- Jordan, G.J., 1997. Evidence of Pleistocene plant extinction and diversity from Regatta Point, western Tasmania, Australia. *Botanical Journal of the Linnean Society* 123, 45–71.
- Jordan, G.J., Weston, P.H., Carpenter, R.J., Dillon, R.A., Brodribb, T.J., 2008. The evolutionary relations of sunken, covered, and encrypted stomata to dry habitats in Proteaceae. *American Journal of Botany* 95, 521–530.
- Kottke, I., Beck, A., Oberwinkler, F., Homeier, J., Neill, D., 2004. Arbuscular endomycorrhizas are dominant in the organic soil of a neotropical montane cloud forest. *Journal of Tropical Ecology* 20, 125–129.
- Kürschner, W.M., Kvaček, Z., Dilcher, D.L., 2008. The impact of Miocene atmospheric carbon dioxide fluctuations on climate and the evolution of terrestrial ecosystems. *Proceedings of the National Academy of Science* 105, 449–453.
- Landis, C.A., Campbell, H.J., Begg, J.G., Mildenhall, D.C., Paterson, A.M., Trewick, S.A., 2008. The Waipounamu erosion surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geological Magazine* 145, 173–197.
- Langenheim, J.H., 2003. *Plant Resins. Chemistry, Evolution, Ecology, and Ethnobotany*. Timber Press, Portland, Cambridge.
- Lee, D.E., Bannister, J.M., Lindqvist, J.K., 2007. Late Oligocene–Early Miocene leaf macrofossils confirm a long history of *Agathis* in New Zealand. *New Zealand Journal of Botany* 45, 565–578.
- Macphail, M.K., Jordan, G.J., Hill, R.S., 1993. Key periods in the evolution of the flora and vegetation in western Tasmania. I. The Early–Middle Pleistocene. *Australian Journal of Botany* 41, 673–707.
- Maher, L.J., 1964. *Ephedra* pollen in sediments of the Great Lakes Region. *Ecology* 45, 391–395.
- Mildenhall, D.C., 1985. Quaternary palynology: North Kaipara Barrier. Pp. 121–127. In: Richardson, R.J.H. (Ed.), *Quaternary Geology of the North Kaipara Barrier, Northland, New Zealand: New Zealand Journal of Geology and Geophysics*, vol. 28, pp. 111–127.
- Mildenhall, D.C., 2001. Pollen analysis of the Pliocene–Pleistocene Kowai Formation (Kurow Group), Mackenzie Basin, South Canterbury, New Zealand. *New Zealand Journal of Geology and Geophysics* 44, 97–104.
- Mildenhall, D.C., Pocknall, D.T., 1989. Miocene–Pleistocene spores and pollen from Central Otago, South Island, New Zealand. *New Zealand Geological Survey Paleontological Bulletin* 59, 1–128.
- Newnham, R.M., Ogdén, J., Mildenhall, D.C., 1993. Late Pleistocene vegetation history of the Far North of New Zealand. *Quaternary Research* 39, 361–372.
- Ogdén, J., Wilson, A., Hendy, C., Newnham, R.M., Hogg, A.G., 1992. The Late Quaternary history of *Agathis* (*Agathis australis*) in New Zealand and its climatic significance. *Journal of Biogeography* 19, 611–622.
- Pearson, P.N., Palmer, M.R., 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* 406, 695–699.
- Pocknall, D.T., 1982. Early Miocene vegetation at Kapuka, Southland, New Zealand: a study based on pollen analysis of a coal seam. *New Zealand Geological Survey PAL Report* 48, 1–15.
- Pocknall, D.T., Mildenhall, D.C., 1984. Late Oligocene–early Miocene spores and pollen from Southland, New Zealand. *New Zealand Geological Survey Paleontological Bulletin* 51, 1–66.
- Poole, A.L., Adams, N.M., 1986. *Trees and Shrubs of New Zealand*. Government Printing Office, Wellington, New Zealand.
- Raine, J.I., Mildenhall, D.C., Kennedy, E.M., 2008. *New Zealand Fossil Spores and Pollen: an Illustrated Catalogue*, 3rd edition. : GNS Science miscellaneous series, vol. 4. http://www.gns.cri.nz/what/earthhist/fossils/spore_pollen/catalog/index.htm, 844 html pages.
- Reay, S.D., Norton, D.A., 1999. *Phormium tenax*, an unusual nurse plant. *New Zealand Journal of Ecology* 23, 81–85.
- Robertson, A.W., Mark, A.F., Wilson, J.B., 1991. Ecology of a coastal lagoon to dune forest sequence, south Westland, New Zealand. *New Zealand Journal of Botany* 29, 17–30.
- Rowell, M.V., Jordan, G.J., Barnes, R.W., 2001. *An in situ*, late Pleistocene *Melaleuca* fossil forest at Coal Head, western Tasmania, Australia. *Australian Journal of Botany* 49, 235–244.
- Steane, D.A., Wilson, K.L., Hill, R.S., 2003. Using matK sequence data to unravel the phylogeny of Casuarinaceae. *Molecular Phylogenetics and Evolution* 28, 47–59.
- Wardle, P., 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge.
- Watt, M., Evans, J.R., 1999. Proteoid roots. *Physiology and development*. *Plant Physiology* 121, 317–323.
- Wolfe, J.A., Upchurch, G., 1987. Leaf assemblages across the Cretaceous–Tertiary boundary in the Raton Basin, New Mexico and Colorado. *Proceedings of the National Academy of Sciences* 84, 5096–5100.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.
- Zetter, R., 1989. Methodik und Bedeutung einer routinemäßig kombinierten lichtmikroskopischen und rasterelektronenmikroskopischen Untersuchung fossiler Mikroflora. *Courier Forschungsinstitut Senckenberg* 109, 41–50.