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Davallia (Polypodiales: Davalliaceae) macrofossils from Early Miocene Otago (New Zealand) with *in situ* spores

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ABSTRACT

Fossil fern fronds referable to the extant fern genus *Davallia* (Polypodiales: Davalliaceae) bearing sporangia with *in situ* spores are described from the Early Miocene Foulden Maar diatomite deposit, Otago, New Zealand. The fronds are the first published Southern Hemisphere macrofossil record for the family and provide valuable palaeoclimate data supporting warm conditions in Early Miocene New Zealand. The matching of *Davallia* fronds to the form spore taxon *Polypodiisporites radiatus* shows that the genus has had a long, apparently continuous history throughout late Cenozoic New Zealand.

1. Introduction

Ferns (Polypodiopsida) have a long fossil history extending back to the Early Devonian boundary, with extensive records reported from Cretaceous and Cenozoic sites, where they were often dominant understorey components (see Rothwell, 1999; Collinson, 2001; Pigg and Rothwell, 2001), much as they still are in many Southern Hemisphere temperate rainforests (Webb, 1959; Wardle, 1964, 1991). Molecular studies of fern evolution suggest that the leptosporangiate ferns evolved during the Carboniferous, with the more derived, highly diverse polypod ferns diverging during the Permian (Pryer et al., 2004) to Triassic (Schuettpelz, 2007). Epiphytic ferns from a range of lineages appear to have emerged at around the K/T boundary (Schuettpelz, 2007), with epiphytic anatomical adaptations reported from Early Eocene fossils (Poole and Page, 2000) and obligate epiphytes in Davalliaceae and related polygrammoid ferns apparently evolving from terrestrial ancestors via secondary hemi-epiphytes (Tsutsumi and Kato, 2006).

Similarly, ferns and fern allies have a long and diverse history in New Zealand. There are more or less continuous pteridophyte records for at least the last 285 million years (e.g. Mildenhall, 1980; Retallack, 1980; Rees, 1993; Tidwell and Ash, 1994; Skog, 2001), with 24 families reported as fossils from the Cretaceous and Cenozoic (Cieraad, 2003; Cieraad and Lee, 2006). Nevertheless, despite early records for many groups, Brownsey (2001) argued that most of the 194 extant New Zealand pteridophytes are the result of relatively recent dispersal, following the isolation and contraction of Zealandia in the Late Cretaceous and early Cenozoic. This was further supported by molecular evidence of long-distance dispersal, either into or out of New Zealand for many modern fern taxa (Perrie et al., 2003; Perrie and Brownsey, 2005, 2007).

The majority of New Zealand pteridophyte fossils represent either dispersed spores or leaf frond impressions, and anatomically- or organically-preserved fronds with *in situ* spores are very uncommon (Cieraad, 2003; Cieraad and Lee, 2006). The discovery at the lower Miocene Foulden Maar fossil site of a fern frond bearing *in situ* spores within terminal, cup-shaped sporangia and resembling the extant genus *Davallia* Smith (Polypodiales: Davalliaceae) allowed comparison of the specimens with extant genera and species, as well as verification of the taxonomic placement and identity of its spores and their association with dispersed fossil spore records.

The Davalliaceae have been reported from the Middle Miocene to Holocene of New Zealand (Cieraad, 2003; Cieraad and Lee, 2006), generally as spores of *Polypodiisporites inangahuensis* (Couper) Potonié or *Polypodiisporites radiatus* Pocknall & Mildenhall. The family has

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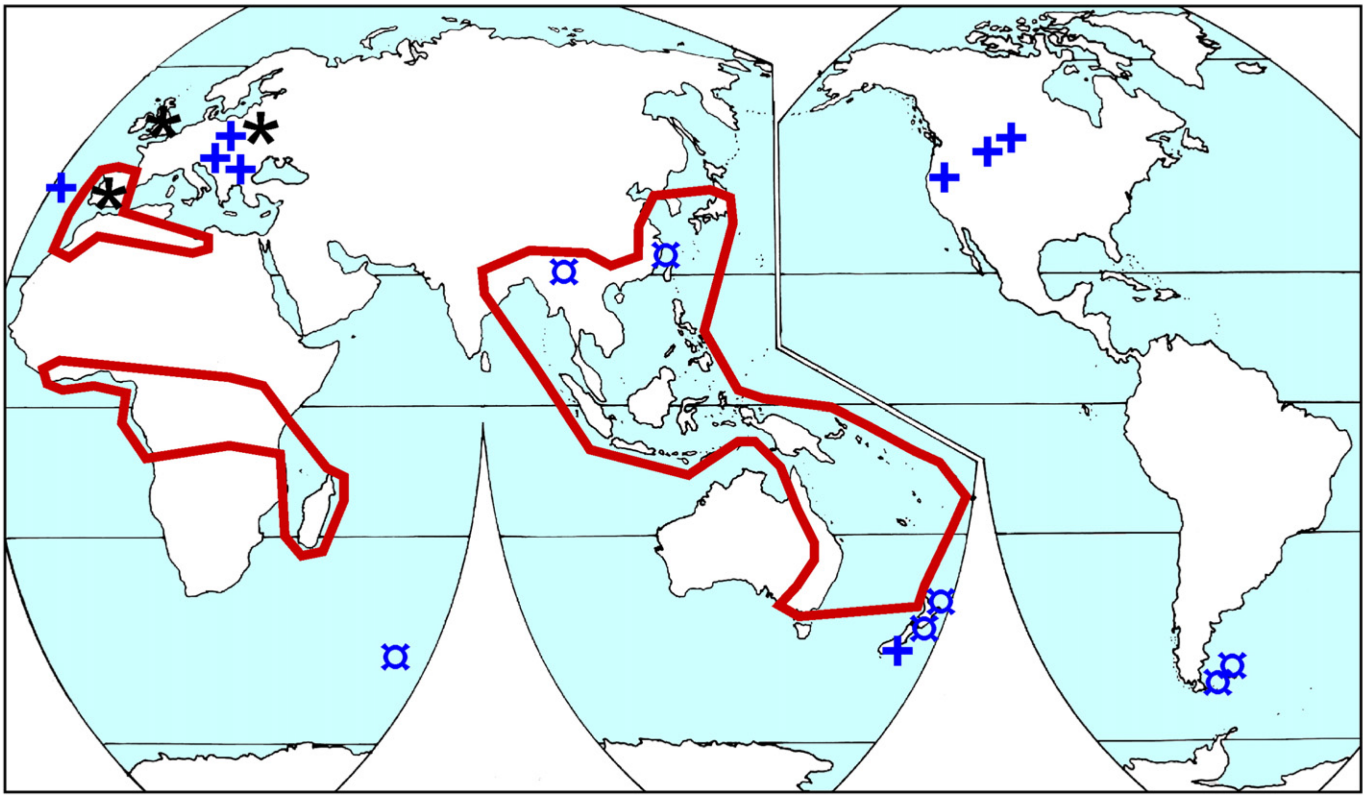

Fig. 1. Map showing distribution of extant Davalliaceae (heavy line), macrofossil *Davallia* (+), dubious *Davallia* macrofossil records (*) and spore-based fossil records (¤).

also been reported from the Upper Cretaceous to Neogene as *P. inangahuensis* (Couper, 1953; Potonié, 1956; Mildenhall, 1980; Pocknall and Mildenhall, 1984), *Polypodiisporites favus* (Potonié) Potonié (Potonié, 1931, 1934; Couper, 1960; Krutzsch, 1967), *P. minimus* (Couper) Khan & Martin (Couper, 1960; Khan and Martin, 1971; Pocknall and Mildenhall, 1984; Raine et al., 2008) or *Polypodiisporites perverrucatus* (Couper) Khan & Martin (Couper, 1953, 1960; Khan and Martin, 1971; Pocknall and Mildenhall, 1984; Raine et al., 2008), but these form species have also been associated with Polypodiaceae. Pocknall and Mildenhall (1984) also noted the similarity of *P. minimus* to the modern genus *Nephrolepis* Schott (Lomariopsidaceae).

At present, *Davallia* is restricted in New Zealand to a single species (*Davallia tasmanii* H.C.Field) with one subspecies from the Three Kings Islands, where it is a common lithophyte, and a second from a single locality in Northland (von Konrat et al., 1999; Brownsey and Smith-Dodsworth, 2000). Although Holden (1983) reported *D. tasmanii* and a second, undescribed species from the Middle Miocene near Murchison, Westland, there are no formally published descriptions of macrofossils for the family in New Zealand.

Because of the previously suggested presence of the extant *Davallia tasmanii* in New Zealand during the Miocene and the claims of extinction and recent fern recolonisation, the identity of our fossil and its relationship to spore form taxa becomes important. Our study aims to determine whether *Davallia* was present in Early Miocene New Zealand, as well as to investigate the palaeoclimatic implications for this largely palaeotropical taxon occurring at mid-southern palaeolatitudes.

2. Materials and methods

2.1. Study site, geological setting and age

The specimen was collected from a mining pit in the middle Foulden Maar Diatomite (I43/f8503: NZ Map Grid Infomap I43 reference 929166: 45.5271° S, 170.2218° E). The sediments were deposited in a deep volcanic maar lake (Lee et al., 2007; Lindqvist and Lee, 2009) and spore and pollen data suggest an Early Miocene age in the *Spinitricolpites latispinosus* Zone (Bannister et al., 2005). This is consistent with the c. 23.2 ± 0.2 Ma radiometric age from basalts associated with the maar crater (Lindqvist and Lee, 2009).

2.2. Botanical analyses

The mummified fronds are preserved on bedding planes in the finely laminated diatomite. They were collected by manual splitting of diatomite blocks with a knife blade and wrapped in cling-film to prevent drying out and flaking. Fine needles and wet paintbrushes were used to free frond edges and tips where they dip into the diatomite and to remove debris from the frond surface. The fronds were photographed using a Nikon D70 SLR digital camera. Specimens are held at the Geology Museum (OU), University of Otago, Dunedin, New Zealand.

The spores were extracted using a fine paint brush into dilute (6%) H_2O_2 and allowed to clear for 3 h. Cleared spores were then mounted in phenol-glycerine jelly for light microscopy (LM). Dried spores extracted directly from the fossil were mounted onto a stub, sputter coated with gold and palladium, and examined and photographed with a Cambridge S360 Stereoscan electron microscope.

The fossil was compared with *Davallia tasmanii* and the undescribed fossil species reported by Holden (1983). In addition, the fossil was compared to *Davallia* specimens at the Otago Regional Herbarium (OTA) and South Australian Herbarium (AD), as well as published descriptions and keys for Davalliaceae from Australasia and Malesia by Morton (1957), Clifford and Constantine (1980), Jones and Clemesha (1981), Tryon and Lugardon (1991), Nooteboom (1998) and Rödl-Linder and Nooteboom (1997). Nomenclature follows von Konrat et al. (1999) and Brownsey and Smith-Dodsworth (2000), with spore terminology from Large and Braggins (1991).