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Epiphyllous fungi and leaf physiognomy indicate an ever-wet humid mesothermal (subtropical) climate in the late Eocene of southern New Zealand

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ABSTRACT

A diverse group of epiphyllous fungi from at least 10 genera as well as numerous germlings were isolated from late Eocene leaf litter, preserved as carbonaceous material associated with the Pikopiko Fossil Forest, near Tuatapere, Southland, New Zealand. These fungi are associated with a variety of angiosperm leaves and, together with CLAMP analyses of the fossil leaf assemblages at the site, suggest that climatic conditions in the southern South Island of New Zealand at a palaeolatitude of ~54°S during the late Eocene (ca. 35 Ma) were mesothermal (subtropical) and had near-permanent high vapour pressure. The mesothermal conditions at mid-latitudes in New Zealand are concurrent with reduced latitudinal temperature gradients during the Eocene. High precipitation rates and humidity are suggestive of high moisture transport from lower latitudes.

1. Introduction

Eocene palaeofloras can provide insights into terrestrial ecosystems during times of higher than modern atmospheric pCO_2 (Beerling and Royer, 2011). Enhanced atmospheric heat transport during the Eocene reduced latitudinal temperature gradients and enhanced moisture availability over the continents (Wing and Greenwood, 1993; Greenwood and Wing, 1995) while moisture availability at mid- to high-latitudes played a major role in reducing heat loss in winter, as cloud cover would minimize radiative heat flux (Wilf et al., 1998; Spicer and Herman, 2010). Such enhanced temperatures and constant high humidity are ideal conditions for high plant and fungal diversity and these climatic parameters concomitantly would increase plant-fungal interactions although these have rarely been examined.

The fossil record for New Zealand fungi is almost non-existent (Cookson, 1947; Truswell, 1996), despite their forming a major component of the modern biota (Landcare Research, 2011). However, over the last decade, a diverse range of epiphyllous fungi, microthyriaceous shields, fungal germlings and an assortment of spores and hyphae have been found at the Pikopiko Fossil Forest site in Southland, southern New Zealand (Fig. 1A), the majority still attached to leaf cuticle fragments (Bannister et al., 2003).

Epiphyllous fungi mainly comprise a diverse guild of generally non-pathogenic, obligate commensals or symbionts (Taylor et al., 2014), though some species are parasitic or saprophytic (Hofmann, 2010 and references therein). Many of these are placed traditionally in the orders Meliolales and Hemisphaeriales sensu Luttrell (1973), Microthyriales and/or the families Asterinaceae and Microthyriaceae (sensu Lumbsch and Huhndorf, 2010). These are often referred to collectively as microthyriaceous fungi, although recent studies show that Microthyriaceae, in particular, represent a diverse assemblage of taxa now belonging to several orders (Wu et al., 2011). Nevertheless, regardless of taxonomy, these phyllobiont fungi often display strong ecological and microhabitat preferences (e.g. Bélanger and Avis, 2002; Zak, 2002; Reynolds and Gilbert, 2005; Gilbert et al., 2007; Du et al., 2012; Ma et al., 2015), allowing them to be used as proxies for past and present site climatic conditions.

Microthyriaceous fungi have an extensive fossil record (Stubblefield and Taylor, 1988; Taylor et al., 2014) and are known from Mesozoic sites on several continents (including Antarctica) as far back as the Early Cretaceous (e.g. Douglas, 1973; Elsik, 1978; Dettmann and Thomson, 1987; Venkatachala et al., 1998; Tripathi, 2001). There are also reports

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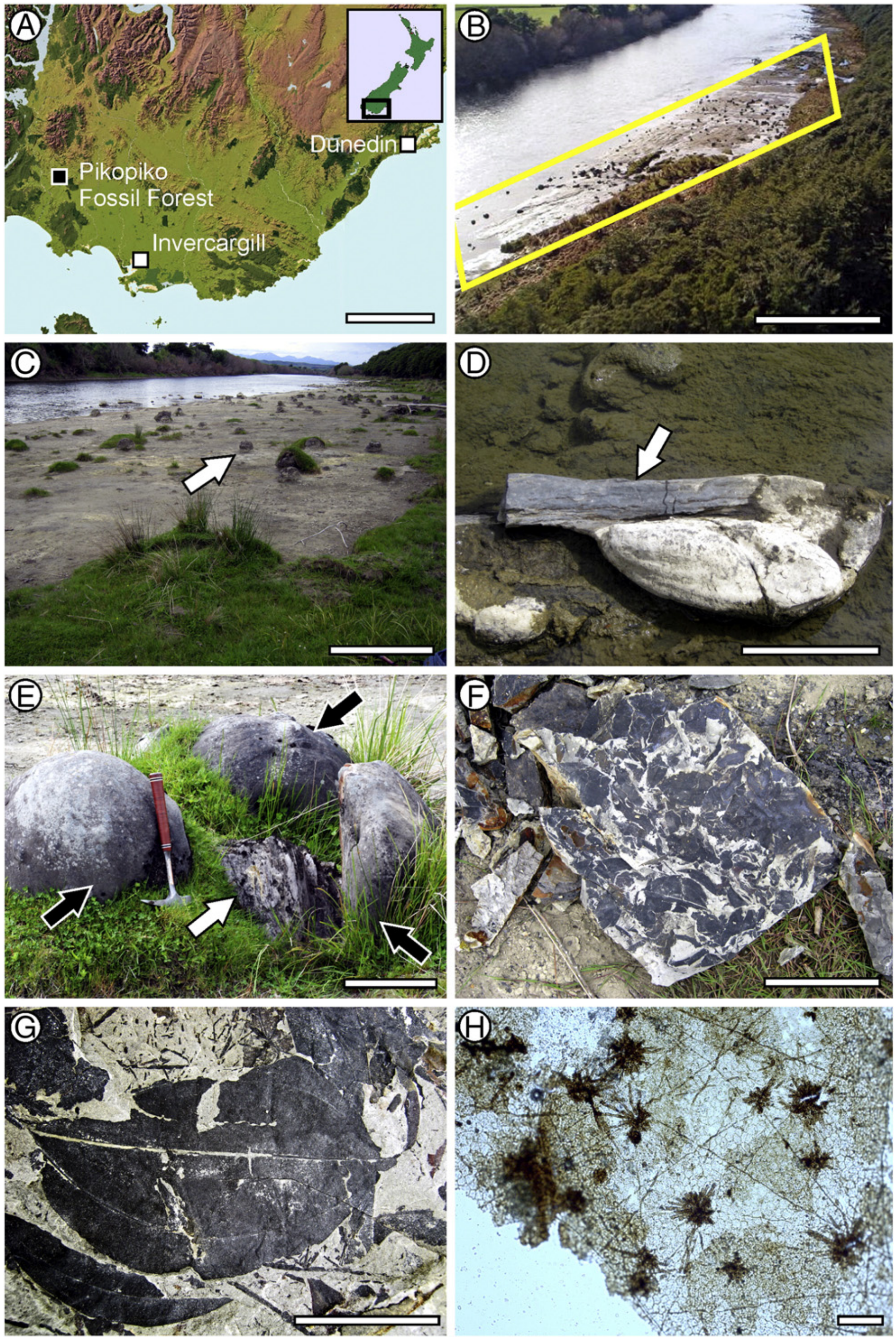

Fig. 1. A. Map of southern New Zealand showing the location of the Pikopiko Fossil Forest; B. Aerial view of the exposed fossil forest on the bank of the Waiau River (inset); C. Scattered fossilised in situ tree trunks encased in calcite-cemented concretions (arrow); D. Fallen fossilised tree trunk (arrow); E. Concretions (black arrows) surrounding a fossilised remnant tree trunk (white arrow); F. Fossil leaf bed; G. Fossil *Cryptocarya*-like Lauraceae leaf; H. Dispersed leaf cuticle fragment showing abundant fungal hyphae, shield and germlings. Scale bars A = 50 km, B = 20 m, C, D = 1 m, E, F = 20 cm, G = 20 mm, H = 100 μm.

of fungal spores and hyphae on *Glossopteris* Raf. leaves from the Permian of India (Srivastava, 1993) and anatomically preserved leaf-surface rosette thalli from the Early Carboniferous (Mississippian) of Germany (Hübers et al., 2011). However, the vast majority of fossil epiphyllous fungi are reported from Cenozoic rainforest deposits (e.g. Elsik, 1978; Smith, 1980; Tripathi, 2001, 2014 and references therein; Phipps and Rember, 2004).

Based on the strong associations of modern epiphyllous communities with warm, humid, generally ever-moist conditions, qualitative modern analogue associations have been made for fossil occurrences (e.g. Phadtare, 1989; Wells and Hill, 1993; Lodge and Cantrell, 1995; Ren et al., 2010; Ding et al., 2011). In particular, the types and complexity of epiphyll germlings are strongly suggestive of high rainfall and humid conditions (Lange, 1978, 1981; Wells and Hill, 1993). Although the fungal diversity of Asian Neogene *Fagus* L. and *Buxus* L. phylloplane communities has been compared to related modern host leaves (Doi, 1983; Doi and Uemura, 1985), most commensal epiphyllous fungi appear to display broad to no host preferences (Reynolds and Gilbert,