



Climatic implications of *Ginkgoites waarrensis* Douglas emend. from the south polar Tupuangi flora, Late Cretaceous (Cenomanian), Chatham Islands☆

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ABSTRACT

The flora of the Cenomanian–Turonian (ca. 96–90 Ma) Tupuangi Formation, Chatham Islands, New Zealand, was inhabiting a region well within the south polar circle (~70–80° S) during the early Late Cretaceous, an interval characterised by extreme global greenhouse conditions. The Tupuangi flora offers a unique perspective into an ecological and environmental setting which has no extant analogue, whilst providing proxies of polar palaeoclimatic conditions during a phase of extreme global warming. *Ginkgoites waarrensis* Douglas, 1965 (emended herein), a species known previously from a single occurrence in Australia, is an abundant element of the Tupuangi flora. Forty-five leaf samples from three localities are reported, and a systematic treatment of this species revealed a wide morphological range. In contrast to the exclusively riparian niche of more recent members of Ginkgoales, associated sedimentological and palaeoecological data suggest that this species had an ecological preference for regularly disturbed, coastal deltaic settings. Herein, we review the geographic and stratigraphic distributions of Cretaceous Gondwanan ginkgoalean leaf taxa. An increasing diversity of this group from the Early Cretaceous to the early Late Cretaceous supports a broader trend of floral provincialisation throughout this interval, most likely driven by concurrent global transgression and active tectonic extension across southern Gondwana. Carbon dioxide has been inferred as a primary proximate cause of the mid-Cretaceous global greenhouse. The leaf cuticles of *Ginkgoites waarrensis* were utilised to approximate atmospheric carbon dioxide ($p\text{CO}_2$) during the Cenomanian. Stomatal index (SI) data were collected from ten specimens, and the stomatal ratio method yielded a semi-quantitative $p\text{CO}_2$ estimate of 1150–1350 ppmv, which is consistent with modelled and proxy estimates of the Cenomanian. The present study explores the inherent limitations of the transfer function method for estimating CO_2 when applied to taxa with very low SI values, such as *G. waarrensis*. In addition to $p\text{CO}_2$, temperature and irradiance are identified as environmental variables which may have systematically promoted the low SI of *G. waarrensis*, but their combined influence is likely mitigated by the relatively high temperature of this region during the mid-Cretaceous and the high summer insolation at polar latitudes.

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1. Introduction

1.1. Climate and Gondwanan flora of the Cretaceous

The global climate of the mid-Cretaceous (Albian–Turonian; ca. 113–89.8 Ma) has often been characterised as an equable “greenhouse”

(e.g. Sloan and Barron, 1990; Fassell and Bralower, 1999; Hay, 2008). Marine fossil proxies consistently support an oceanic warming trend from the Albian to the Turonian (Huber et al., 1995; Huber, 1998; Clarke and Jenkyns, 1999; Bice et al., 2006). Whilst mid-Cretaceous warming is evident from localities at tropical palaeolatitudes (Norris and Wilson, 1998; Huber et al., 2002; Schouten et al., 2003; Forster et al., 2007), warming was primarily expressed at polar latitudes, resulting in a relatively low equator-to-pole thermal gradient (Barron, 1983; Huber et al., 1995; Fluteau et al., 2007). Preliminary palaeoclimatic estimates from fossil flora proxies of the Antarctic Peninsula have supported polar warming during the mid-Cretaceous (Hayes, 1999; Francis and Poole, 2002). Furthermore, palaeotemperature estimates derived from the leaf physiognomy of a New Zealand Cenomanian floral assemblage suggest mean annual temperatures of ~10 °C (Parrish et al., 1998). Several palaeoclimatic studies have suggested that a high concentration of atmospheric carbon

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dioxide (CO₂) was primarily responsible for the long-term greenhouse conditions of the mid-Cretaceous (e.g. Barron and Washington, 1985; Royer et al., 2004; Bice et al., 2006). During the mid-Cretaceous, atmospheric CO₂ concentrations (herein approximated to atmospheric partial pressure of carbon dioxide; $p\text{CO}_2$) have been estimated at ~1000–1650 ppmv from geochemical models (Berner and Kothavala, 2001; Berner, 2006). Broadly consistent with this, stable isotopes from marine microplankton (Bice et al., 2006) and fossil liverworts (Fletcher et al., 2008) have indicated high $p\text{CO}_2$ during the Albian–Cenomanian (~900–2000 ppmv). More recently, $p\text{CO}_2$ estimates for the Albian have been further constrained to ~500–1100 ppmv by a climate model which incorporates a combination of stable carbon isotope and fossil leaf physiology data (Franks et al., 2014). Atmospheric CO₂ concentrations of the Cretaceous have also been estimated by examining the distribution of stomata on fossilised leaf cuticles, including members of the Araucariaceae (Passalia, 2009), Cheirolepidiaceae (Haworth et al., 2005; Aucour et al., 2008; Passalia, 2009), Laurales (Barclay et al., 2010) and Ginkgoales (Chen et al., 2001; Retallack, 2001; Sun et al., 2007; Passalia, 2009; Quan et al., 2009; Wan et al., 2011; see Section 1.3 for a discussion of this technique). When biases resulting from taxonomic variations have been controlled for, these studies have yielded estimates of $p\text{CO}_2$ which are largely congruous with each other, and all are substantially higher than modern global $p\text{CO}_2$ levels (~400 ppmv). Stomatal proxies provide the following early Late Cretaceous $p\text{CO}_2$ estimates: 600–1250 ppmv for the Albian (Haworth et al., 2005; Passalia, 2009); 600–1700 ppmv for the Cenomanian and 500–1900 ppmv for the Turonian (Wan et al., 2011, recalculated from Retallack, 2001; see review by Wang et al., 2014). However, the utility of $p\text{CO}_2$ estimates with such coarse, stage-scale temporal resolutions as those above is severely limited, particularly with regards to patterns of the early Late Cretaceous global warming. Whilst fossil data and models exhibit a cooling trend throughout the Late Cretaceous (Bice et al., 2006; Franks et al., 2014), the relatively warmer early Late Cretaceous (Cenomanian–Turonian) global conditions were interrupted by severe, but transient $p\text{CO}_2$ fluctuations. Upon review of the available geochemical models and fossil data, Bice and Norris (2002) inferred a higher degree of instability in mid-Cretaceous atmospheric $p\text{CO}_2$ than was previously suspected. This instability is best expressed by a series of rapid fluctuations in $p\text{CO}_2$, and associated palaeotemperature changes, concurrent with the Cenomanian/Turonian Oceanic Anoxic Event (OAE 2; ca. 94 Ma; Barclay et al., 2010; Sinninghe Damsté et al., 2010). Because of these fluctuations, a greater resolution of fossil proxies is required to constrain the estimates of $p\text{CO}_2$ throughout the Cenomanian–Turonian.

Throughout mid-Cretaceous global greenhouse conditions, various polar and sub-polar palaeolatitude localities of the Southern Hemisphere were consistently inhabited by highly productive forest ecosystems. These regions feature a high proportion of coniferous gymnosperms, minor seed-ferns, ginkgoaleans and angiosperms, locally abundant ferns and bryophytes, and rare lycopods. Macrofloral evidence for this derives from Albian strata of the Antarctic Peninsula (see review by Cantrill and Poole, 2012) and southeast Australia (e.g. Seward, 1904; Medwell, 1954b; Douglas, 1969; Cantrill and Webb, 1987; Tosolini et al., 2015), Albian/Cenomanian strata of mainland New Zealand (e.g. Arber, 1917; McQueen, 1956; Daniel, 1989), and Cenomanian–Turonian strata of the Chatham Islands (Pole and Philippe, 2010; Mays et al., 2015). A diverse, gymnosperm-dominated floral biota for this region is also reflected in the mid-Cretaceous palynological record of Australia (Dettmann, 1994; Nagalingum et al., 2002; Wagstaff et al., 2013), the Antarctic Peninsula (Dettmann and Thomson, 1987; Cantrill and Poole, 2002) and the Chatham Islands (Mays, 2015). Cantrill and Poole (2012) characterised the Early Cretaceous forests of the high southern latitudes as evergreen, with regions of mixed evergreen-deciduous which became increasingly dominated by evergreen forms into the Late Cretaceous (e.g. New Zealand). Ginkgoaleans represent significant deciduous components in regions of mixed forest biome throughout this interval.

1.2. Mesozoic fossil record of Gondwanan Ginkgoales

By the Triassic, the Ginkgoales were highly diverse and widespread across Gondwana (e.g. Australia: Walkom, 1917; Chapman, 1927; Holmes and Anderson, 2007; New Zealand: Retallack, 1980, 1981; South Africa: Seward, 1903; Baldoni, 1980; Anderson and Anderson, 1989; South America: Menendez, 1951; Troncoso and Herbst, 1999; India: Pal, 1984). Leaf fossils of the this group have been commonly recorded from Lower Cretaceous strata of the Otway and Strzelecki basins, southeast Australia (e.g. Seward, 1904; Medwell, 1954a, 1954b; Douglas, 1969; Drinnan and Chambers, 1986). Cretaceous ginkgoaleans have been reported from northeastern Australia (e.g. Walkom, 1918, 1919; Day, 1964; McLoughlin et al., 1995; Pole and Douglas, 1999). Ginkgoaleans have been recognised from Early to early Late Cretaceous localities of South America (Archangelsky, 1965; Del Fueyo and Archangelsky, 2001; Passalia, 2007) and Early Cretaceous localities of India (e.g. Zeba-Bano et al., 1979). Despite the palaeogeographic distances of these disparate localities, specimens from India, Argentina and Australia reveal remarkable morphological similarities throughout the Mesozoic. Presently, the Cretaceous record of Ginkgoales from Antarctica is restricted to undescribed leaves recovered from Alexander Island, Antarctic Peninsula (Cantrill and Nichols, 1996; Howe and Cantrill, 2001); however, pollen of possible ginkgoalean affinity (*Cycadopites* [Wodehouse 1933] Wilson and Webster 1946; junior synonym: *Ginkgocycadophytus* Samoilovitch 1953) has been found from upper Lower Cretaceous and throughout Upper Cretaceous strata of the Antarctic Peninsula (Dettmann and Thomson, 1987). The Cretaceous record of ginkgoalean fossils in Zealandia (which includes New Zealand, New Caledonia, Lord Howe Island and the Chatham Islands) is limited, with isolated leaves from Middle Clarence Valley, South Island (Daniel, 1989), and cuticle fragments from the Chatham Islands (Pole and Philippe, 2010). An impression fossil, *Ginkgocladus novae-zeelandiae* von Ettingshausen, 1890, from Cenozoic (Eocene) sediments of Nelson, New Zealand, was first ascribed to Ginkgoales (von Ettingshausen, 1890), from which the author derived the generic name. However, the leaf appears to possess a midrib, rather than the two primary halves of the lamina being innervated by a pair of veins at the leaf base, as is common for late Mesozoic and Cenozoic ginkgoaleans. Even at the time (von Ettingshausen, 1890), and in subsequent publications (Seward, 1919; Florin, 1940; Hill, 1989), the venation of this fossil has been compared to the conifer *Phyllocladus* Rich. ex Mirb. Due to the low preservation quality of this fossil, Seward (1919) criticised it as being not “...of value as (a) botanical record...” (p. 33). Whilst ginkgoalean leaves have been reported from Palaeogene (Eocene) strata of South America (Berry, 1935), Douglas (1969) reviewed the available literature and concluded that this group had gone extinct in Australia by the early Cenozoic. More recently however, a Palaeogene occurrence of *Ginkgo* L. has been recorded from Tasmania, Australia (Hill and Carpenter, 1999). These Palaeogene specimens represent the last stratigraphic occurrences of Ginkgoales in Gondwana; however, this group is well-reported throughout Cenozoic strata of Eurasia (see review by Zhou (2009) and references therein), particularly in eastern Asia (see review by Uemura (1997)) where *Ginkgo biloba* L. resides today, the sole extant species of this group.

1.3. Stomatal index proxy for ancient atmospheric CO₂ concentrations

Stomata are pores on plant leaf surfaces, through which gas exchange takes place: carbon is acquired for photosynthesis from CO₂, whilst water vapour and oxygen are lost by diffusion. Stomatal density, or the related and more commonly used stomatal index (the number of stomata relative to epidermal cells per given leaf area, expressed in %; Salisbury, 1927), of fossil plants is widely used in reconstructing past $p\text{CO}_2$ values. This is possible because stomatal index (SI) is primarily controlled by the atmospheric $p\text{CO}_2$ in which the plants grow, displaying an inverse relationship. This was initially reported by

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