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Original article

The first Cenozoic *Equisetum* from New Zealand[☆]Mike Pole ^a, Stephen McLoughlin ^{b,*}^aQueensland Herbarium, Brisbane Botanic Gardens Mt Coot-tha, Mt Coot-tha Rd, Toowong QLD 4066, Australia^bDepartment of Palaeobiology, Swedish Museum of Natural History, Box 50007, 104 05 Stockholm, Sweden

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ABSTRACT

Equisetum is described for the first time from Cenozoic deposits of New Zealand. The fossils derive from two early to earliest middle Miocene assemblages in South Island, New Zealand. The fossils are ascribed tentatively to subgenus *Equisetum* based on their possession of whorled branch scars, but they cannot be assigned with confidence to a formal species. The decline of equisetaleans, otherwise unknown from the Cenozoic of the New Zealand-Australian-Antarctic domain, was possibly a consequence of severe environmental changes – particularly, abrupt shifts in the temperature and soil moisture regime – experienced by this region in the Neogene, coupled with competition from opportunistic angiosperms.

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1. Introduction

Equisetum is an almost cosmopolitan genus of about 15 extant species and several extinct species (Hauke, 1963, 1978). It includes the only extant representatives of Equisetopsida – traditionally placed in Division Equisetophyta Scott, 1900, Calamophyta Smith, 1955, Sphenophyta Benson, 1957, or Arthropphyta Bold et al., 1987, and more recently considered a basal member of, or sister group to the ferns based on both morphological and molecular studies (Kenrick and Crane, 1997; Pryer et al., 2001, 2004; Des Marais et al., 2003; Guillot, 2004, 2007; Smith et al., 2006). New Zealand, Australia and Antarctica have a natural absence of extant *Equisetum* (commonly known as ‘horsetails’ or ‘scouring rushes’). The absence of indigenous *Equisetum* from New Zealand and Australia is curious, because these regions host a rich Paleozoic and Mesozoic fossil record of equisetaleans, and representatives of the extant genus thrive in these regions today as exotic weeds (Clifford and Constantine, 1980; Brownsie and Perrie, 2015).

Today *Equisetum* is the sole surviving genus of a once diverse plant group (generally called sphenopsids or equeisetsids) that appeared in the Devonian (Taylor et al., 2009). Equeisetsid fossils are known from all the major Southern Hemisphere landmasses with a record extending back to at least the Carboniferous (Morris, 1985; Gutiérrez, 1995). The group maintained a high diversity,

including some arborescent forms (Rössler and Noll, 2002, 2006) through the late Paleozoic (Boureau, 1964), was represented by a reduced diversity of mainly herbaceous forms through the early and middle Mesozoic, then declined through the Cretaceous, apparently concomitant with the diversification of angiosperms (Coiffard et al., 2007). Late Mesozoic and Cenozoic fossil *Equisetum* are assigned to *Equisetites* by some authors, although typically this is an expression of philosophy – there are essentially no morphological differences between these genera (Harris, 1961; Gould, 1968) and we presume that they belong to the same monophyletic group. In this paper, we use *Equisetum* for fossils.

Based on molecular dating, Des Marais et al. (2003) proposed that the crown group of *Equisetum* diverged about 64.8 ± 12.7 million years ago (early Paleocene). However, the stem lineage is much older; several mid-Mesozoic taxa including the Early Jurassic *Equisetum dimorphum* Elgorriaga et al. (2015) from Patagonia, the Middle Jurassic *Equisetum laterale* Gould (1968) from Australia, and the Late Jurassic *Equisetum thermale* Channing et al. (2011) from Patagonia are among the oldest confirmed records of the genus.

In New Zealand, equeisetsids have been reported from the Permian (*Equisetites*; McQueen, 1954), Triassic (*Neocalamites*; Retallack, 1980, 1985), Jurassic (*Equisetites*; Arber, 1917; Edwards, 1934), and Cretaceous (*Equisetum*; Daniel, 1989; Daniel et al., 1990; Parrish et al., 1998). It is probable that von Ettingshausen's (1891) slender jointed stems assigned to *Casuarina deleta* Ett. from Shag Point (Campanian), and *Bambusites australis* Ett. and *Casuarinites cretaceus* Ett. from Pakawau (late Campanian–Maastrichtian) constitute the youngest known *Equisetum* fossils from

☆ Corresponding editor: Marc Philippe.

* Corresponding author.

E-mail address: steve.mcloughlin@nrm.se (S. McLoughlin).

New Zealand thus far, since at least some of those specimens represent segmented axes that are too broad for typical photosynthetic twigs of *Casuarina*; dispersed pollen of Casuarinaceae first appears in New Zealand only in the Paleocene (Mildenhall, 1980; Macphail et al., 1994).

The Australian equisetopsid record extends back further, at least to the Carboniferous (Retallack, 1999) and is more diverse, with many genera known from Permian and Triassic deposits (e.g., Rigby, 1966; McLoughlin, 1992a, 1992b; Holmes, 2001). The group persisted through the Jurassic and Early Cretaceous in Australia with moderate representation of herbaceous forms (Gould, 1968; Douglas, 1973; McLoughlin and Drinnan, 1995; McLoughlin et al., 2000, 2002; Turner et al., 2009) but declined to just a single known occurrence in the Cenomanian (McLoughlin et al., 2010). No records are known from the Cenozoic. In Antarctica, diverse equisetopsids are known from Permian–Jurassic strata (Rigby, 1969; Gee, 1989; Osborn et al., 2000; Rees and Cleal, 2004; Bomfleur et al., 2013) and persisted until at least the late Albian in the Alexander Island region (Falcon-Lang et al., 2001). Thus, the previous youngest records of equisetopsids from Australia, Antarctica and New Zealand are all of mid- to Late Cretaceous age.

Here we describe *Equisetum* remains from two early to earliest middle Miocene fossil assemblages of New Zealand. We also assess the potential causes of equisetalean decline in southeastern Gondwana during the Late Cretaceous and Cenozoic.

2. Geological setting

Fossil *Equisetum* specimens were recovered from two localities in New Zealand. One is near the village of Bannockburn, central Otago, South Island. The material was collected in 1990, and derives from a layer at about 25 m on the 'Bannockburn Section' figured by Pole (1993a: fig. 9; coordinates: New Zealand Transverse Mercator 1298664, 5000792; Fig. 1(1, 3)). The specimens form a monospecific assemblage preserved in massive,

soft, pale, clay-rich mudstone that forms part of the fluvial Dunstan Formation of the Manuherikia Group (Douglas, 1986). The Bannockburn Section broadly correlates with the Kawarau Section (Douglas, 1986) about 4 km away. Based on palynological content (Mildenhall and Pocknall, 1989), the Kawarau Section is regarded as Altonian at the base (lower to lowermost middle Miocene; Cooper, 2004), but upper levels may range higher into the middle Miocene. Given that they are from relatively low in the Bannockburn Section, the *Equisetum* fossils described here are likely to be Altonian (upper Burdigalian to lowermost Langhian).

The second locality is from the banks of the Buller River, about 200 m north of Nuggety Creek, and nearly 10 km northeast of the town of Murchison in northwestern South Island (coordinates: New Zealand Transverse Mercator 1550440, 5379230; Fig. 1(1, 2)). Leaf macrofossils from this locality have been described previously by Holden (1982a, 1982b). The fossiliferous mudrock is darker, more fissile and more lithified relative to that at Bannockburn. These strata are included in the Longford Formation, which was deposited in the Murchison Basin (Fyfe, 1968; Lihou, 1993). Fossil spore-pollen recovery has been unsuccessful so far but, as the fluvial Longford Formation overlies the estuarine early Miocene (Altonian) Mangles Formation, the age of the former unit is inferred to be middle Miocene (Nathan et al., 1986). In the year 2000, fossil *Equisetum* and ferns were exposed on the bedding surfaces of large fallen blocks of mudstone on the edge of the Buller River. These are some 20–30 m topographically below a leaf bed that was probably the source of Holden's *Nothofagus* fossils. As the strata dip steeply, the *Equisetum*-bearing layer is stratigraphically close (within 10 m) to the *Nothofagus* bed, but the exact relationship is not clear.

3. Material and methods

Numerous fossil *Equisetum* specimens are available from Bannockburn, consisting of external axis impressions and flattened

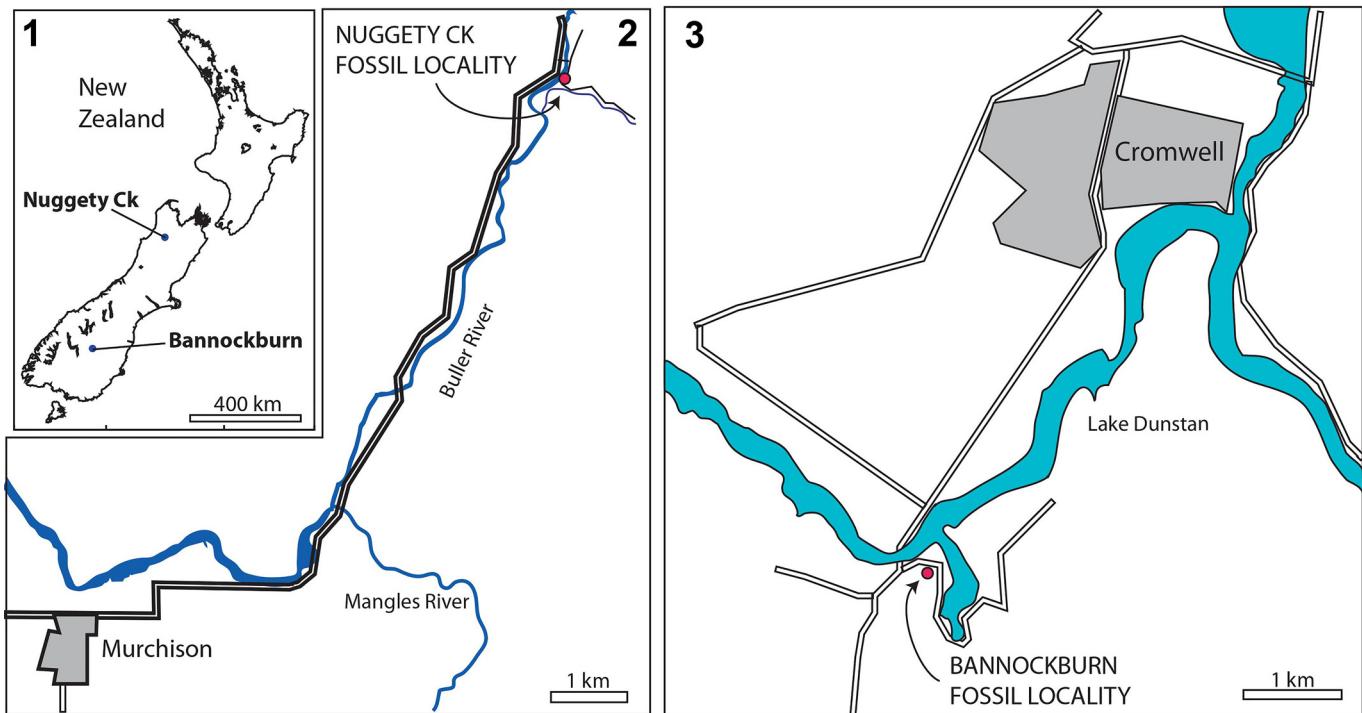


Fig. 1. Fossil locality maps. 1. New Zealand showing the two Miocene fossiliferous localities sampled in this study. 2. Details of the Nuggety Creek locality. 3. Details of the Bannockburn locality.

pith casts in pale grey shale (of which five have been registered). Several specimens (three registered) were recovered from Nuggety Creek near Murchison, comprising coalified compressions and associated impressions in pale grey shale. Specimens were uncovered using a vibrating chisel and photographed in reflected light. Illustrated material is deposited in the collections of the Department of Geology, University of Auckland under the prefix 'LX'.

4. Systematic paleobotany

Division Pteridophyta Schimp. in K.A. Zittel, 1879–1890

Class Equisetopsida C. Agardh, 1825

Order Equisetales de Candolle. ex von Berchtold and Presl, 1820

Family Esuidetaceae Michx. ex de Candolle, 1804

Genus *Equisetum* von Linnaeus, 1753

Subgenus ?*Equisetum* von Linnaeus, 1753

Type species: *Equisetum fluviatile* von Linnaeus, 1753 (extant).

Equisetum sp.

Fig. 2

Material: Bannockburn: LX0833–LX0837; Murchison: LX0881, LX0882, LX2065.

Localities and stratigraphic units: Specimens from Bannockburn (central Otago, South Island, New Zealand) derive from the Dunstan Formation (early to earliest middle Miocene), Manuherikia Group. Specimens listed under the locality 'Murchison' derive from the Longford Formation (middle Miocene), Murchison Basin, at Buller River, about 200 m north of Nuggety Creek, ca. 10 km northeast of Murchison (northwestern South Island, New Zealand).

Description: Parallel-sided, jointed axes ca. 9–19 mm wide, preserved as pith casts (Fig. 2(1)), external impressions (Fig. 2(2, 3, 7–9)), and carbonaceous compressions (Fig. 2(4–6)). Both pith casts and stem surfaces bear longitudinal ridges and nodes ca. 130 mm apart. Ridges are slightly more pronounced on pith casts than stem exteriors, in both cases bearing fine longitudinal striae. Nodes are marked by a ring of elliptical to ovate branch scars (5–15 evident across the exposed half of the axis), which are ca. 0.5–2 mm wide and 0.5–3.5 mm long. Remnants of a leaf sheath are evident on one specimen (Fig. 2(7)) as linear to narrowly triangular, apically pointed, longitudinally striate, basally fused lamina segments.

Remarks: In the context of Cenozoic floras, these axes are best referred to *Equisetum* based on their ribbed and jointed stems with leaf sheaths and branch scars located at the nodes. Of the two extant subgenera of *Equisetum*, subgenus *Hippochaete* tends to lack lateral branches and is distributed in both the Northern and Southern hemispheres, whereas representatives of subgenus *Equisetum* tend to be branched but are restricted mostly to the Northern Hemisphere (Hauke, 1990, 1993). Despite its Southern Hemisphere location, we tentatively assign the New Zealand fossils to subgenus *Equisetum* on the basis of their numerous branch scars preserved at the nodes, but confident assignment to subgenus or species must await the discovery of strobilar or stomatal characters.

Several of the stem impressions and pith cast surfaces bear roughly elliptical to circular stains or dimples (Fig. 2(1, 2, 7, 8)). Although similar-sized features on fossil equisetalean stems have been interpreted as insect oviposition scars in other studies (e.g., Beattie, 2007; Labandeira, 2013), the features on the New Zealand axes lack reaction tissue and are too inconsistent in shape, arrangement and position to represent arthropod damage scars. They probably represent diagenetic features.

The previous youngest (Late Cretaceous) examples of equisetaleans from Australasia are somewhat variable in size, quality and style of preservation but, collectively, they appear to encompass

the dimensions and architectures of the New Zealand Miocene fossils. Daniel's (1989) *Equisetum* sp. from the Cenomanian Warder Formation of the middle Clarence Valley, South Island, New Zealand, is a branched rhizome with short, coarsely ribbed internodes. The specimens attributed by von Ettingshausen (1891) to *Bambusites australis*, *Casuarinites cretaceus* and *Casuarina deleta* from Shag Point (Campanian) and Pakawau (late Campanian–Maastrichtian), South Island, New Zealand, represent jointed and more finely ribbed rhizomes and subaerial axes (some with whorls of scale-like leaves) that range from ca. 1 to 35 mm wide. *Equisetites* sp. of McLoughlin et al. (2010) from the Winton Formation (latest Albian–earliest Turonian; Tucker et al., 2013) of eastern Australia is represented by probable rhizome pith casts 12–22 mm wide with variable-length internodes, coarse longitudinal ridges, rings of small circular (?root) scars at the nodes, and associated nodal diaphragms with up to 28 tubercles around the rim.

All of the Australasian Cretaceous specimens lack sufficient characters for confident attribution to a formal species. Given the absence of diagnostic reproductive organs or cuticular features, and the limited macromorphological details available from the segmented axes, we also refrain from assigning the New Zealand Miocene specimens to a new or established species. Nevertheless, these new fossil records are important for deciphering the vegetation history of the landmasses that formerly constituted southeastern Gondwana.

5. Discussion

5.1. Australasian refugium for Mesozoic plants

Despite the rich paleobotanical heritage of the region, the new fossils are the only record of equisetaleans in New Zealand (and Australasia) from the past 70 million years. The 500 km separating the two Miocene localities suggests that *Equisetum* was widely distributed in the South Island at that time. The fossils also suggest that the current absence from New Zealand (as well as from Australia and the Pacific islands) is a relatively recent phenomenon. The *Equisetum* fossils add to a large group of plants that were present in New Zealand in the early–middle Miocene, became extinct there, but continued to exist on other landmasses. For example, various genera of conifers, *Eucalyptus*, *Acacia* and *Casuarina* are known from Miocene fossils of New Zealand but are absent from the extant flora (Mildenhall, 1980; Campbell and Holden, 1984; Pole, 1993b, 2007, 2012; Macphail et al., 1994). *Equisetum* also adds to a list of typical Mesozoic plant groups (e.g., cheirolepid conifers, *Ginkgo*, corystosperms and bennettitaleans) that survived the moderate rates of extinction at southern high-latitudes at the end of the Cretaceous (Pole and Vajda, 2009; Vajda and Bercovici, 2014) but disappeared from these regions some time during the Cenozoic (Carpenter and Hill, 1999; McLoughlin et al., 2008, 2011; Barreda et al., 2012).

The landmass that became New Zealand broke away from the Australian–Antarctic margin of Gondwana in the mid-Cretaceous. The notion of the Tasman Sea (or even the Pacific) as being an insurmountable barrier for plants has begun to change (Pole, 1994; Winkworth et al., 2002). Long-distance dispersal to New Zealand of plants that do not appear to have any long-distance dispersal ability appears to be a reality. Like ferns, *Equisetum* reproduces by spores. It is conceivable that the Miocene examples in New Zealand were a short-lived lineage of *Equisetum* that had dispersed to the South Island from outside the region in the mid-Cenozoic. However, given its earlier Mesozoic record, but current absence in the Australasian-Pacific region, it is perhaps most likely that the Miocene occurrences of this genus were relictual – and that New

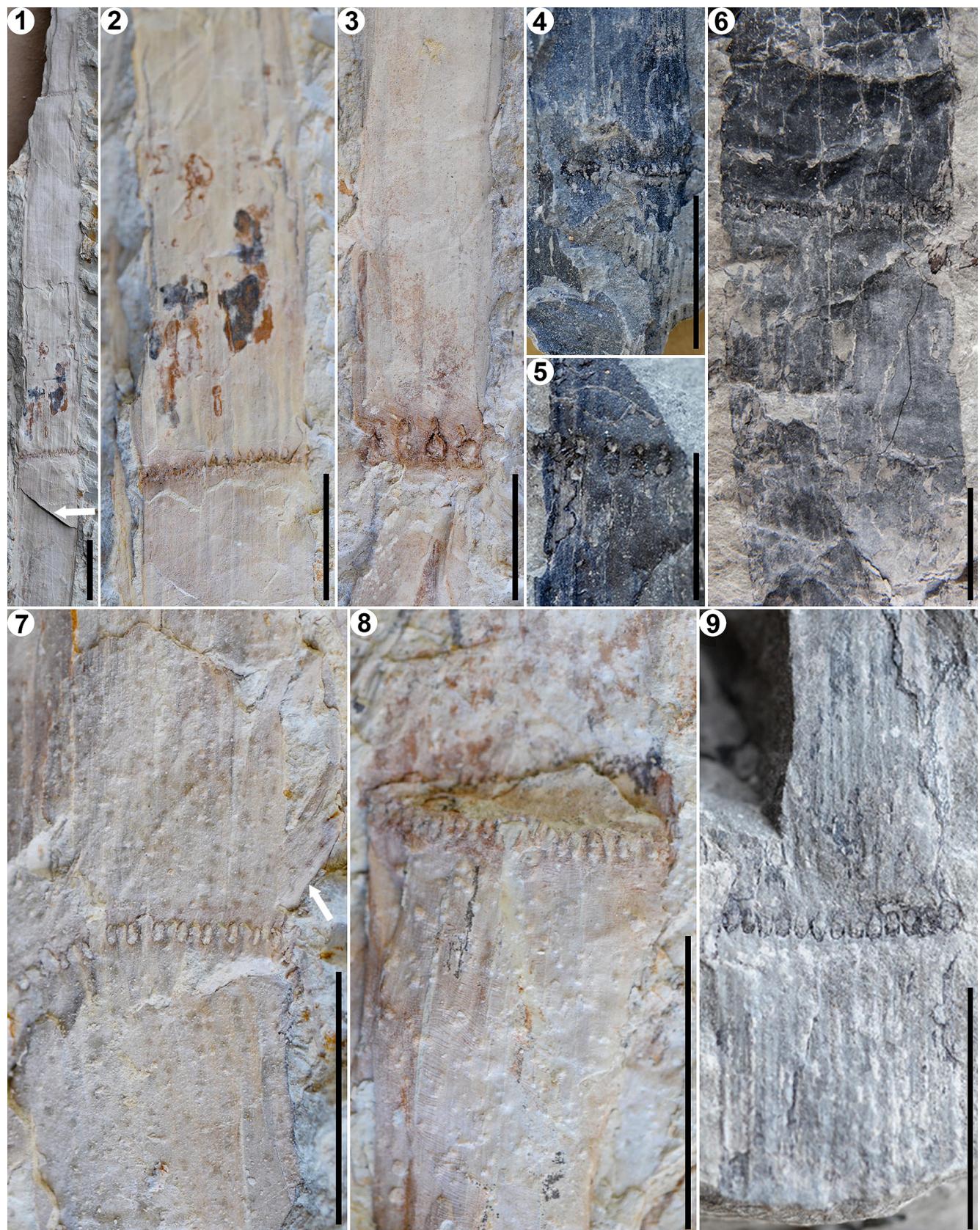


Fig. 2. *Equisetum* sp. fossils from Bannockburn (1–3, 7, 8) and Nuggety Creek near Murchison (4–6, 9), New Zealand. 1. LX837, slender axis consisting of pith cast (above arrow) and external impression (below arrow). 2. LX836, jointed axis external impression. 3. LX833, slender axis impression with ovate branch scars at node. 4. LX882, carbonaceous compression of jointed axis. 5. LX881, carbonaceous compression of jointed axis. 6. LX2065, carbonaceous compression of large jointed axis. 7. LX834, impression of exterior of axis with whorl of fused leaves (arrowed) above node. 8. LX834, impression of exterior of axis with numerous tightly spaced branch scars at node. 9. LX880, impression of exterior of jointed axis with well-defined ribbing. Scale bars: 10 mm (1–4, 6–9), 5 mm (5).

Zealand carried a compliment of *Equisetum* with it as it rafted into the Pacific in the Cretaceous. A closer look at the fossil record is likely to extend its record in New Zealand, and may well do so in Australia as well.

5.2. Equisetalean extinction in Australasia

A single cause for the demise of *Equisetum* in the New Zealand–Australian–Antarctic region is difficult to resolve. The rapid development of an extensive ice sheet over Antarctica around the Eocene–Oligocene transition (Coxall et al., 2005) may account for the loss of *Equisetum* on that continent, but New Zealand and Australia did not experience continental-scale glaciation. Australia, characterized by subdued topography and low-nutrient soils over much of its area, experienced stepwise warming and aridification, together with a dramatic change in its photoperiod regime as the continent shifted rapidly from high to middle and low southern latitudes through the mid-Cenozoic (Wilford and Brown, 1994). Concomitant vegetation changes saw the dramatic contraction of *Nothofagus*-dominated closed-forests and Proteaceae/Casuarinaceae-rich moist heathlands, and the expansion of *Eucalyptus*- and *Acacia*-dominated open sclerophyll forests and savanna (Hill et al., 1999). New Zealand has a complex Cenozoic history. By the early Paleocene, New Zealand had broken away from Australia via the south-to-north opening of the Tasman Sea. By the Eocene, New Zealand had moved to middle latitudes (40–50°S; Veevers et al., 1991), i.e., at equivalent latitudes to northern Australia at that time. New Zealand supported a broadly similar flora to that of southern mainland Australia at that time in terms of taxonomic composition, leaf size and low proportion of conifers (Pole, 1993c). New Zealand remained at middle latitudes during Australia's rapid northward drift through the Miocene, but still experienced significant shifts in vegetation composition.

Pole (1993c, 2003) concluded that the current absence of *Eucalyptus* in New Zealand was the result of a wet phase following a middle Miocene relatively dry and fire-prone period – a scenario adopted by Hill et al. (2017). Low fire frequencies in the landscape, and the ensuing effects of an increase in closed-forest communities and changes in soil moisture and microbe/fungal associations later in the Neogene, may have all contributed to the decline of *Eucalyptus* in New Zealand. Modern *Equisetum* species thrive under a very broad range of conditions, being tolerant to disturbance, soil anoxia, high levels of metals, high salinity (Husby, 2013), at least low-intensity fire regimes (Ivanova et al., 2014), and they also have moderate levels of shade tolerance (Humbert et al., 2007). We cannot test directly whether a shift in the fire regime and the extent of closed-forest vegetation was relevant to the decline of *Equisetum*, but we note that, at least until the Miocene, New Zealand's vegetation ranged from various ?pure? rainforest types to some communities with a fire-induced sclerophyll component (Mildenhall and Pocknall, 1989; Pole, 1993c).

Through the late Neogene and Quaternary, the combined influences of New Zealand falling directly within the tracks of the mid-latitude westerly cyclones, rain shadow effects and sedimentation changes associated with the uplift of the Southern Alps, and cooling, drying and alpine glaciation associated with expansion of the polar ice sheets, wrought significant changes to the New Zealand flora (McGlone et al., 2001; Pole, 2003). In addition, extant *Equisetum* species appear to be vulnerable to competition from ruderal angiosperms, especially in areas with low soil moisture and/or high nitrogen (Husby, 2013). This combination of substantial environmental change (particularly drying and abrupt warming/cooling) and competition from diversifying angiosperm groups probably contributed to the demise of equisetaleans across the New Zealand–Australian–Antarctic region through the Cenozoic.

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