Polar wildfires and conifer serotiny during the Cretaceous global hothouse

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ABSTRACT

Several highly effective fire-adaptive traits first evolved among modern plants during the mid-Cretaceous, in response to the widespread wildfires promoted by anomalously high atmospheric oxygen (O₂) and extreme temperatures. Serotiny, or long-term canopy seed storage, is a fire-adaptive strategy common among plants living in fire-prone areas today, but evidence of this strategy has been lacking from the fossil record. Deposits of abundant fossil charcoal from sedimentary successions of the Chatham Islands, New Zealand, record wildfires in the south polar regions (75°–80°S) during the mid-Cretaceous (ca. 99–90 Ma). Newly discovered fossil conifer reproductive structures were consistently associated with these charcoal-rich deposits. The morphology and internal anatomy as revealed by neutron tomography exhibit a range of serotiny-associated characters. Numerous related fossils from similar, contemporaneous deposits of the Northern Hemisphere suggest that serotiny was a key adaptive strategy during the high-fire world of the Cretaceous.

INTRODUCTION

The mid-Cretaceous (Albian–Turonian; 112–90 Ma) was one of the warmest intervals in geological history. Paleoclimate records indicate some of the highest oceanic temperatures known in the marine realm (Friedrich et al., 2012), and warming was primarily at high latitudes, leading to a relatively low temperature difference between the tropics and the poles (Huber et al., 1995). These conditions were promoted by high CO₂ levels, estimated from fossil plant proxies as ~2–5 times preindustrial levels (Barclay et al., 2010; Mays et al., 2015). High CO₂ levels and polar temperatures promoted productivity in mid-Cretaceous polar forests (Beerling and Osborne, 2002). Evidence from sedimentary inertinite (fossil charcoal) indicates that the atmospheric oxygen concentration (*p*O₂) was as high as 29% during the mid-Cretaceous (modern ~21%), the highest levels of the past 250 m.y. (Bergman et al., 2004; Glasspool and Scott, 2010), making wildfires far more likely to occur (Brown et al., 2012).

The Tupuangi Formation was deposited in a vast riverine-deltaic system within the south polar circle (75°–80°S; Mays, 2015) and crops out on Pitt Island in the Chatham Islands, eastern Zealandia (Fig. 1). A fossil conifer seed cone scale (ovuliferous complex, OC, herein; sensu Escapa et al., 2016; Fig. 2) and associated sedimentary record from these strata indicate the presence of fire-adapted floras at south-polar latitudes during the mid-Cretaceous, an interval of high O₂, CO₂, and some of the highest average global temperatures in Earth history.

METHODS

Sample Details

Specimens were collected from Cenomanian (99–94 Ma) Tupuangi Formation outcrops of Pitt Island. Photographs were taken using a Canon EOS 700D digital SLR camera. Maceral data were collected by soaking >40 g of sedimentary rock from each target horizon in 1% HCl (diluted with deionized water) for 7–14 days, and gently sieving with water. Macerals 0.5–10 mm in diameter were sorted, dried at 60 °C for 24 h, then weighed. Charcoalified (fusinized) and noncharcoalified (coalified) wood categories follow those in Scott (2010). Collection and curation details, a discussion on taxonomic nomenclature, and comments on statistical analyses are in the GSA Data Repository¹. Locality, lithofacies, and maceral data are in Table DR1; fossil specimen details are in Table DR2.

Neutron Tomography: Experimental Setup

Computed tomography methods involve the collection of images, or radiographs, by capturing radiation that has penetrated a target sample; in the case of neutron tomography, neutrons are transmitted for this purpose. The neutron source for this study was the Open-Pool Australian Lightwater (OPAL) reactor housed at the Australian Nuclear Science and Technology

¹GSA Data Repository item 2017382, supplementary images, tables and videos, are available online at <http://www.geosociety.org/datarepository/2017/> or on request from editing@geosociety.org.

Figure 1. Fossil locality maps. A: Eastern Zealandia; gray areas—emergent; gray line—2000 m isobath. B: Northern Pitt Island, Chatham Islands, with fossil localities recorded in this study. All locality numbers have the locality prefix CH/f, as outlined in the text. Modified from Mays et al. (2015, with permission).

Organisation (ANSTO), Lucas Heights, New South Wales, Australia. Except for the primary scan parameters, which are included in Table DR3, all experimental setup details follow those in Mays et al. (2017).

RESULTS

Charcoal, Resin, and Plant Fossil Records

Sediment samples from fossiliferous horizons of the mid-Cretaceous Tupuangi Formation revealed high abundances of fossil charcoal (Fig. 3), indicative of intermittent wildfires. All sediment samples yielded fossil resin (amber), with one exception (B1476); fossil resin pieces are as large as 1 cm in diameter. Bulk sediment samples showed a statistically significant positive correlation between the following two variables: (1) resin mass/total bulk sample mass and (2) charcoal mass/total bulk sample mass (Pearson's *r* = 0.463; *p* = 0.035; *N* = 21); this suggests a temporal association between wildfires and resin production and/or excretion.

One conifer fossil, Tupuangi *Protodammara* herein (Fig. 2; additional details on specimen nomenclature in the GSA Data Repository), was particularly common on horizons with high charcoal and resin content. These fossils have features common to both Araucariaceae

Figure 2. Tupuangi *Protodammara*. **A:** Abaxial fossil impression with apical cusp and in situ resin delineating abaxial resin canals; arrow—abaxial ridge, PL1255B. **B:** Adaxial fossil impression. Black arrow shows adaxial ridge, white arrow shows arcuate crest, PL1228. **C:** Neutron tomographic reconstruction of compression fossil, volume rendering, abaxial view. RNA—relative neutron attenuation, in situ resin represented by highest neutron attenuation; grid width on RNA spectrum indicates relative transparency, PL1231A. **D:** Morphology and resin canal paths; colored canals can be traced from pedicellate region to distal margin. Canals: red—apical, blue—medial, orange—lateral, PL1231A. **E:** Seed cones of the serotinous species, *Pinus banksiana*, for comparison (Britton and Brown, 1913). **F–H:** Schematic reconstruction of two specimens of Tupuangi *Protodammara* on a partial mature seed cone. **F:** Distal view (form based on PL1244); vertical line indicates cross section in G. **G:** Syn-fire cross section; fire destroys the resin adhesion between the subtending ovuliferous complexes (OCs), promoted by the large subsurface resin reservoirs on the distal surface. Note that the adaxial reservoirs are laterally offset from the section. **H:** Post-fire cross section; the cone opens hygroscopically for seed release (analogous to *Pinus*; Dawson et al., 1997), which would likely facilitate OC detachment, but the timing and mechanism are uncertain (i.e., question mark).

and Cupressaceae, but the following support a stronger affinity with the latter family: (1) three seed scars (cf. one seed/ovule per OC for Araucariaceae; Farjon, 2010); (2) no discrete ovuliferous scale (cf. *Araucaria*, *Wollemia*); and (3) an elongated pedicellate base. The combination of preserved characters indicates that these fossils represent a Cupressaceae stem group within the taxodioid Cupressaceae (sensu Rothwell et al., 2011), with close alliance to *Taiwania*, *Athrotaxis*, and several extinct taxa (see the Data Repository). There was a statistically significant abundance in relative charcoal in samples with this species ($N = 7$) compared to other examined bulk sediment samples ($N = 14$; Student's $t = 4.109$; $p = 0.0006$). The cooccurrence of this species with environmental fire was reinforced by two charcoalified specimens of Tupuangi *Protodammara*.

Neutron Tomography

Neutron tomography provides a nondestructive approach to virtually extract three-dimensional fossil material. The technique has been particularly applicable to organically preserved fossils too delicate to extract from sediment using traditional methods (Mays et al., 2017). By employing high-resolution neutron tomography, the resin canals of these fossils were digitally isolated due to the anomalously high neutron attenuation of in situ resin compared to the surrounding organic fossil remains and matrix. In this way, a three-dimensional compositional map of each specimen was constructed (Figs. 2C, 2D). Resin canal paths were corroborated

in part by several dissected compression fossils. Several of these anatomically preserved fossil specimens had no surface expression and were only revealed and analyzed by neutron penetration of their enclosing silicate matrix.

DISCUSSION

Fossil Evidence for Fire-Adaptive Traits

Fire-adaptive traits among plants are those that promote survival and/or reproductive success in the presence of fire. Serotiny is a fire-adaptive reproductive strategy whereby seeds are stored in the plant canopy for prolonged intervals (Lamont et al., 1991). Fire triggers serotinous seed cone opening and, during the post-fire interval, the mature seeds are released into an environment with minimal soil surface litter, a severe reduction in predation and adult competition, and increased light, nutrient, and/or water availability; these factors ensure relatively rapid renewal of the cohort (Lamont et al., 1991, and references therein). A suite of seed cone characters is consistently associated with this strategy among modern conifers: (1) a lignified rachis promoting long-term seed support and storage (Moya et al., 2008; He et al., 2016); (2) thick, interlocking protective seed-bearing structures (e.g., OCs) to insulate seeds for long durations against environmental factors such as granivores, pathogens, heat, or changes in aridity or humidity (Lamont et al., 1991; He et al., 2016); (3) buoyant seeds for wind dispersal, because animal vectors will generally be absent immediately after a fire (He et al., 2016); and (4)

the use of resin as a binding agent to hold the cones closed during dormancy (Ahlgren, 1974; Lamont et al., 1991).

The morphological features of the fossils are consistent with the requirements for serotinous cones (He et al., 2016). The distal thickenings on both abaxial and adaxial surfaces would have provided an interlocking cone structure, serving to seal the cone margins until the seed release stage. While these thickenings are likely homologous to the thickened peltate forms of other cupressaceous taxa like *Athrotaxis* or Sequoioidae (e.g., *Sequoia*), they are analogous in form and function to the imbricated cone scales of serotinous *Pinus* L. species (e.g., *P. banksiana* Lamb; Farjon, 2010). Furthermore, neutron

Figure 3. Scatterplot of relative abundances of fossil resin and charcoal for bulk sediment samples of the Tupuangi Formation. The line of best fit was estimated using the least squares method.

tomography revealed a very high resin volume within this species with increasing resin canal width distally, and the primary resin reservoirs beneath the abaxial and adaxial ridges (Figs. 2G, 2H); as such, thickening of this region would be promoted during development by the engorgement of the canals. This robust interlocking cone structure is common to all serotinous species, and provides a protected internal environment for the seeds over extended intervals (Lamont et al., 1991; He et al., 2016).

Protodammara likely had a wind seed-dispersal mechanism. All specimens of Tupuangi *Protodammara* were isolated with no attachment to a cone axis; numerous specimens were found on individual, near-monotypic beds, and they were generally densely packed within the sediment, e.g., eight dispersed specimens within a neutron tomography–reconstructed hand sample 70.9 cm³ in volume (PL1231). These accumulations support the interpretation of synchronous shedding, analogous to deposits of deciduous leaves (Mays et al., 2015). All specimens exhibited regular, straight, or gently tapering bases, which are typical of cone scale abscission zones in some members of extant Araucariaceae (*Araucaria*, *Wollemia*; Farjon, 2010). This suggests that the OCs were shed from their cones during normal life cycles, rather than via mechanical damage. The thin, broad distal wings would have promoted buoyancy and wind dispersal, as expressed in some extant Araucariaceae (e.g., *Agathis*, *Araucaria* sect. *Eutacta*; Farjon, 2010). The seeds were not found attached to the OCs; not only did the seed cones disintegrate when mature, but the seeds themselves detached from their OCs. These characters are present within *Agathis* and serve to increase seed dispersal range; it is likely that the morphology of *Protodammara*, and the comparable *Protodammara*-like OCs of the Northern Hemisphere (Hollick and Jeffrey, 1906, and references therein), provided a similar function. Although the buoyant OCs of Araucariaceae are not fire adapted, the abiotic dispersal they facilitate is a necessary component of serotiny (He et al., 2016). This necessitates a slight broadening of the He et al. (2016) requirements for serotiny to include the shedding of airborne OCs, rather than only seeds, as a method of post-fire seed dispersal. The occurrence of Tupuangi *Protodammara* among samples with exceptionally high charcoal (Fig. 3) suggests that these OCs were dispersed in response to fire, rather than some other environmental trigger (e.g., drying conditions; Nathan et al., 1999).

The anatomy indicates the probable application of resin both as a binding agent to promote serotiny and to increase flammability. In several extant serotinous *Pinus* (Pinaceae) and *Cupressus* L. (Cupressaceae) species, resin is distributed near the distal margins of the OCs, the adhesion of the resin holding the cones closed

during dormancy (Ahlgren, 1974). Upon heating, the resin bonds are destroyed and the cones are free to open and disperse their winged seeds (Lamont et al., 1991). This function is likely responsible for the relatively large resin canals of the serotinous *Pinus halepensis* Mill. (Moya et al., 2008). The OCs of the Early Cretaceous *Sphenolepis kurriana* are morphologically similar to the fossils reported here, and resin has been shown to excrete from the adaxial crest and bond to the subtending OCs, thus providing a resin-mediated seal for the cone (Harris, 1953). This mechanism is analogous to extant serotinous *Pinus* cones (e.g., *P. banksiana*; Ahlgren, 1974) and suggests a serotinous reproductive strategy for *S. kurriana*, which provides a closely related fossil precedent for this function of resin among Cretaceous taxodioid Cupressaceae. Anatomically, the OCs of *S. kurriana* feature distinct abaxial and adaxial resin canal series and an arcuate crest enervated by large adaxial canals (Harris, 1953); the newly reported fossils exhibit all of these features, and the largest resin reservoirs are directly beneath the adaxial crest (Figs. 2G, 2H). This supports an adhesive function of the resin by sealing the cone until heated or desiccated. Furthermore, the abaxial canals terminate close to the distal margins of the OCs, resulting in prominent resin reservoirs near the surface in these regions, including the apical cusp. All known conifer resins consist of terpenoids, a group of highly flammable unsaturated hydrocarbons, and their abundance in coniferous biomass has been associated with hotter fires and faster combustion rates (Ormeño et al., 2009). Excretion of resin onto the outer surfaces of the cones would promote the flammability of these cones and thus increase the chances of melting the resin adhesive during a fire.

A proposed mechanism of fire-triggered cone opening is illustrated in Figures 2F–2H.

Widespread Emergence of Fire-Adaptive Strategies during the Mid-Cretaceous

While there is indirect evidence of serotiny evolving among a range of extinct conifer groups nearly 350 m.y. ago (He et al., 2016), Pinaceae and Cupressaceae are the only two extant conifer families that express serotiny (Lamont et al., 1991). Molecular studies of Pinaceae indicate that this reproductive strategy emerged among *Pinus*, the conifer genus with the highest number of extant serotinous species, during the mid-Cretaceous (ca. 89 Ma; He et al., 2012; Fig. 4). While fire-adapted Cupressaceae are present in the Northern Hemisphere (Cupressoideae; Lamont et al., 1991), this group is a major component of fire-prone regions in Australia and southern Africa (Callitroideae). Among Cupressaceae, the oldest fossils of an extant genus with serotinous cones, *Widdringtonia* Endl. (Callitroideae), are approximately coeval with the Tupuangi

Protodammara fossils (Cenomanian; McIver, 2001). All extant members of *Widdringtonia* are serotinous (Farjon, 2010), suggesting that the relevant fire-adapted cone features may be synapomorphic for this genus. If this can be demonstrated from the fossil record, this would lend greater support to the emergence of fire-adaptive traits across disparate plant taxa during the oxygen-rich climate of the mid-Cretaceous (He et al., 2012). Regardless, *Protodammara*, and the closely allied *S. kurriana* and several OC fossil taxa ascribed to *Dammara* (Hollick and Jeffrey, 1906), provide evidence of synchronous serotiny among taxodioid Cupressaceae. Such features are lacking in taxodioid Cupressaceae groups that likely diverged after these stem groups (e.g.,

Figure 4. Paleoclimate and fossil charcoal records, and evidence of fire adaptations in extant conifer families over the past 350 m.y. **A:** Fossil evidence of serotiny in Cupressaceae (stratigraphic ranges in Data Repository; see footnote 1). 1—*Sphenolepis kurriana*, 2—first occurrence of *Widdringtonia*, 3—*Protodammara*, 4—Tupuangi *Protodammara* (this study). **B:** Molecular clock divergence estimates of fire-adapted traits among Pinaceae (He et al., 2012). **C:** Charcoal (inertinite) abundance as a proportion of total maceral content (Glasspool and Scott, 2010). **D:** Temperature expressed as deviation to modern global mean, estimated from CO₂ proxies (bold; Royer et al., 2004) and biogeochemical modeling (dashed; Berner and Kothavala, 2001); SST—sea-surface temperature. **E:** Atmospheric oxygen (O₂) estimated from charcoal proxy (purple; Glasspool and Scott, 2010) and biogeochemical modeling (green; Bergman et al., 2004, COPSE, baseline run). **F:** Simulated biomass burn probability (Belcher et al., 2010; He et al., 2012) as a function of modeled O₂ (Bergman et al., 2004); bold—median, dashed—95% quantile (lower limit). Adapted from He et al. (2012, with permission).

Sequoioideae and Taxodiaceae; Mao et al., 2012). As such, these fire-adaptive traits most likely emerged independently in the taxodioid Cupressaceae, and the serotinous taxa of the more derived Callitroideae and Cupressoideae.

This study records the oldest Cretaceous fire-adapted conifers in the Southern Hemisphere; it also demonstrates the influence of fire on shaping the south polar ecosystem and reinforces the emerging consensus that fire played a key role in the evolution of plants during the Cretaceous (Brown et al., 2012). Exceptionally high mid-Cretaceous O₂ levels were the likely catalyst of common wildfires around the world during that time (Belcher et al., 2010; Brown et al., 2012; He et al., 2012; Fig. 4). Because of this global climatic phenomenon, it is likely that a similar suite of fire-adaptive traits should be expressed in mid-Cretaceous conifers the world over. There are numerous dispersed resinous OCs reported from the Cretaceous, especially from mid-Cretaceous localities of Europe, Greenland, and North America (*Protodammara* and *Dammara*; Hollick and Jeffrey, 1906). For example, most of the fire-adaptive anatomical (voluminous adaxial and abaxial resin canals including an apical canal, and large distal resin reservoirs) and morphological (distally thickened with broad wings, and basal abscission zone) traits of the Tupuangi *Protodammara* specimens are also seen in *Protodammara speciosa*, which has been recorded from the fossil charcoal- and resin-rich mid-Cretaceous Raritan Formation, northeastern United States (Hollick and Jeffrey, 1906). The disparate distribution of these fire-adapted conifer fossils lends support for a high-fire mid-Cretaceous world (Brown et al., 2012).

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