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Past diversity of Proteaceae on subantarctic Campbell Island, a remote outpost of Gondwana

Livia Wanntorp[a,b,*], Vivi Vajda[a], J. Ian Raine[c]

[a] Department of Earth and Ecosystem Sciences, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden
[b] Department of Phanerogamic Botany, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden
[c] GNS Science, Post Office Box 30-368, Lower Hutt, New Zealand

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ABSTRACT

Twelve fossil species of Proteaceous pollen, predominantly attributable to *Proteacidites* and *Beaupreaidites*, were recovered from the Maastrichtian–Paleocene sedimentary succession of the Garden Cove Formation on Campbell Island, the southernmost landmass of the Zealandia continent. Among these are two new species, *Proteacidites campbellensis* and *Proteacidites hortisinus*. The high diversity of Proteaceae pollen in the sediments encompassing the Cretaceous–Paleogene boundary on Campbell Island is consistent with the fossil record from neighbouring landmasses but strongly contrasts with the impoverished record of the family in the extant New Zealand flora. Examples of *Beauprea*- and *Knightia*-like pollen in the Campbell Island assemblages confirm the presence of these lineages on Zealandia by the end of the Cretaceous and suggest that their present endemism in New Caledonia and New Zealand can be explained in terms of relictual vicariant distributions, perhaps modified by northward tracking of warmer climates on Zealandia through the Cenozoic.

1. Introduction

Although a Gondwanan origin for New Zealand and adjacent islands is now undisputed in geological terms, there is still no consensus about the origins of the biotas occupying New Zealand and its neighbouring islands (Trewick et al., 2007). During the late Palaeozoic and Mesozoic, the New Zealand region amalgamated as part of the southeastern margin of Gondwana from a series of isolated tectonic terranes (Mortimer, 2004). Within this region, the Campbell Plateau constitutes an area of continental crust now largely covered by a cool-water shallow sea. At various times since the late Mesozoic, parts of this plateau have been emergent and, thus, may have played an important role in the distribution and exchange of land plants between the New Zealand, Antarctic and Australian sectors of Gondwana (McLoughlin, 2001). Terrestrial fossil floras, particularly the abundantly preserved remains of spores and pollen, can provide a useful tool for assessing the palaeogeographic affinities of ancient terranes whose geological structure and origin are not yet resolved, and may also contribute useful data pertaining to the antiquity, distribution, and evolution of modern plant groups.

The angiosperm family Proteaceae includes about 80 genera and 1700 extant species of mainly woody perennial shrubs or trees with compound inflorescences of tetramerous flowers that produce achenes, follicles or drupaceous fruits. Pollination is mainly by insects although vertebrate and wind pollination syndromes are also present in the family (Weston, 2007). Proteaceae pollen is generally isopolar and triporate with a few exceptions as in *Beauprea* from New Caledonia, which has pollen with colpoidate apertures, and in the tribe Banksieae, which has biporate pollen (Dettmann and Jarzen, 1998).

The Proteaceae are generally regarded as an iconic Gondwanan group occurring in South America Africa, Madagascar, India, Southeast Asia, New Guinea, Australia, New Zealand, and New Caledonia but with two main centres of modern diversity in Australia and Africa (Barker et al., 2002). The family has an extensive fossil record that indicates a much greater past diversity in New Zealand and Australia (e.g., Cookson, 1950; Couper, 1953, 1960; Jordan et al., 1975; Mildenhall, 1980; Mildenhall and Pocknall, 1989; Pocknall, 1990; Pocknall and Mildenhall, 1984; Raine, 2004; Vajda and Raine, 2003; Weston, 2007; Pole and Vajda, 2009). The

* Corresponding author. Department of Phanerogamic Botany, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden.
E-mail address: livia.wanntorp@nrm.se (L. Wanntorp).

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evolution and diversity of proteaceous pollen have only recently been investigated in a phylogenetic context (Sauquet and Cantrill, 2007; Sauquet et al., 2009). Also recently, fossil pollen has been used for calibrating molecular phylogenies and the diversification rates of Proteaceae in southwestern Australia and the Cape Floristic Region biodiversity hotspots. Such analyses have invoked a minimum age of c. 119 Ma for the crown group of Proteaceae (Anderson et al., 2005; Barker et al., 2007). However, the oldest Proteaceae fossils yet reported are pollen grains of *Triorites africaensis* from the Cenomanian–Turonian (c. 93 Ma) of northern Africa and Peru (Ward and Doyle, 1994). During the subsequent 10 million years, the Proteaceae steadily diversified, making their first appearance in the Australian succession by the Santonian (Dettmann, 1994) and reaching an apparent peak on that continent during the Eocene (Pole, 1998).

In New Zealand, Proteaceae pollen first appear during the Late Cretaceous but they are claimed to have been less diverse there than in Australia at that time (Specht et al., 1992). Species diversity increased until its acme in the early to middle Eocene, when several clades of Proteaceae were represented in New Zealand (Pole, 1998). Proteaceae remained an important floristic element there until the Neogene. Species diversity subsequently decreased and only two species of the family survive in New Zealand: *Knightia excelsa* R. Br., fossil pollen of which has been recorded from the Paleogene of New Zealand (Mildenhall and Suggate, 1981), and *Toronia toru* (A. Cunn.) L.A.S. Johnson & B.G. Briggs, first known from the Pliocene of New Zealand (Nelson et al., 1988). Neither of these species currently inhabits the islands of the Campbell Plateau.

To date, little information is available on the Cenozoic fossil floras from islands surrounding New Zealand (New Caledonia, the Chatham Islands, and the Campbell Plateau islands). This study surveys the past diversity of Proteaceae in nearshore marine sediments of the Garden Cove Formation (Maastrichtian–Danian) on Campbell Island in the extreme south of this region. We discuss affiliations of the fossil taxa with forms from neighbouring landmasses and we discuss the role that the fossil pollen may play in understanding the biotic history of southeastern Gondwana and the patterns of diversification within the Proteaceae.

2. Geological setting

Zealandia is a continental fragment representing the easternmost part of Gondwana and includes the New Zealand mainland, Campbell Plateau, Chatham Rise, Lord Howe Rise, Challenger Plateau, and New Caledonia (Adams, 2008). The subantarctic Campbell Island, located approximately 700 km south of mainland New Zealand close to the southern margin of the Campbell Plateau at 52° S 169° E, is the southernmost emergent part of Zealandia (McGlone et al., 1997; Given et al., 2004). The Campbell Plateau connected New Zealand to Marie Byrd Land in West Antarctica before Gondwanan breakup (McLoughlin, 2001).

Campbell Island is the remnant of a Miocene shield volcano emplaced on Mesozoic and Paleogene rocks and has a land area of 114 km^2. This study investigates the Garden Cove Formation, which constitutes the only Upper Cretaceous and Paleocene succession exposed between the New Zealand mainland and Antarctica (Hollis et al., 1997). The Garden Cove Formation consists of c.30 m of mudstones and sandy mudstones exposed around the head of Perseverance Harbour and in Northwest and Cattle Bays on the west coast of the island. These strata were deposited in a nearshore coastal situation after the late Mesozoic peneplanation of the area but before deposition of the overlying marine Eocene–Oligocene Tucker Cove Limestone and intrusion by basaltic dykes of the Miocene volcanic episode (Beggs, 1978).

3. Material and methodology

Samples were collected from a continuous exposure along the shore of Camp Cove, Perseverance Harbour (Fig. 1) by VV and JIR during an expedition led by Ian Turnbull in March 2004. This section incorporates the topmost part of the Garden Cove Formation and the sediments have previously been dated by dinoflagellates to span the Maastrichtian–Danian boundary (Wilson, 1972; Hollis et al., 1997). Studies to more closely locate the boundary are under way. Some palynological specimens from Garden Cove and Camp Cove localities encountered during the biostratigraphic study by Hollis et al. (1997) and held in the collections of GNS Science were also examined. Sample localities (e.g. CA/f189) are recorded in the New Zealand Fossil Record File, a public repository of fossil locality information: further collection details including precise geographic coordinates are available online at http://fred.org.nz. A stratigraphic column showing lithologies and sampling localities is shown in Fig. 1B.

Palynological processing was carried out at GNS Science, Lower Hutt, New Zealand, using standard procedures including treatment with hydrochloric acid, followed by hydrofluoric acid, Schulze reagent oxidation, ammonium hydroxide, and heavy liquid flotation using sodium polytungstate solution (s.g. 2.0) to concentrate the organic material. The processed residues were subsequently sieved with a 10 μm mesh and the organic residue was mounted on glass slides in glycerine jelly. Subsequently, additional samples were processed at Global Geolab Limited, Canada, using the same procedures outlined above but excluding the heavy liquid separation. Slides prepared by Global Geolab ltd are labelled starting with R- Twenty-seven slides were examined using an Olympus BX51 light microscope and 613 proteaceous pollen grains were identified and photographed using an Olympus DP71 camera at the Swedish Museum of Natural History, Stockholm. Light microscopy was used in this study since this is the methodology employed for routine palynostratigraphic analysis. Species descriptions are typically based on a minimum of ten specimens but in a few cases fewer than 10 specimens were recovered, as noted in the species description. The microscopy slides and processed residues are stored at GNS Science, Lower Hutt, New Zealand.

The taxonomy of fossil Proteaceae pollen is complex and taxon recognition varies depending on the morphological characters used for segregation and on the methodologies employed to investigate the specimens (e.g., Srivastava, 1969; Martin, 1973; Mildenhall, 1978; Milne, 1998). A comprehensive revision of the many Proteaceae pollen grains described over the past six decades is currently lacking, resulting in a plethora of synonyms currently in use for some taxa and poor delimitation of some groups. Since it is beyond the scope of this paper to provide a general revision of fossil Proteaceae pollen, we use a traditional nomenclatural approach. For example, we use *Proteacidites* Cookson ex Couper for all the species traditionally included in the genus rather than employing various subdivisions, such as *Propylipollis, Lewalanipollis, Cranwellipollis* (Martin and Harris, 1974; Dettmann and Jarzen, 1996). We also retrieved species of *Triorites* and *Gambierina,* whose taxonomic affiliation with Proteaceae remains less certain.

4. Results

We recovered 11 fossil pollen species of *Proteacidites* (Fig. 2A-P; Fig. 3A–C; Fig. 4A–H) and one species of *Beaupreaidites* (Fig. 3D) in the Maastrichtian–Danian sediments of the Garden Cove Formation of Campbell Islands. Two of these 12 fossil species are new and described below. We also recorded specimens of *Gambierina edwardsii* (Fig. 3E) and of *G. rudata* (Fig. 3F), as well as two fossil species of *Triorites* (Fig. 3G–H). The names of all fossil pollen species with descriptions and details of their stratigraphic occurrences and ranges are summarised below.