

Pre-Gondwanan-breakup origin of *Beauprea* (Proteaceae) explains its historical presence in New Caledonia and New Zealand

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New Caledonia and New Zealand belong to the now largely submerged continent Zealandia. Their high levels of endemism and species richness are usually considered the result of transoceanic dispersal events followed by diversification after they re-emerged from the Pacific Ocean in the mid-Cenozoic. We explore the origin and evolutionary history of *Beauprea* (Proteaceae), which is now endemic to New Caledonia but was once spread throughout eastern Gondwana, including New Zealand. We review the extensive *Beauprea*-type pollen data in the fossil records and analyze the relationship of these fossil taxa to extant genera within Proteaceae. We further reconstruct the phylogenetic relations among nine extant species of *Beauprea* and estimate the age of the *Beauprea* clade. By incorporating extinct taxa into the *Beauprea* phylogenetic tree, we reconstruct the ancient distribution of this genus. Our analysis shows that *Beauprea* originated c. 88 Ma (million years ago) in Antarctica–Southeastern Australia and spread throughout Gondwana before its complete breakup. We propose that *Beauprea*, already existing as two lineages, was carried with Zealandia when it separated from the rest of Gondwana c. 82 Ma, thus supporting an autochthonous origin for *Beauprea* species now in New Caledonia and historically in New Zealand up to 1 Ma. We show that the presence of *Beauprea* through transoceanic dispersal is implausible. This means that neither New Caledonia nor New Zealand has been entirely submerged since the Upper Cretaceous; thus, possible vicariance and allopatry must be taken into account when considering the high levels of endemism and species richness of these island groups.

INTRODUCTION

Phylogenetic analyses, divergence-time estimation, and ancient distribution reconstruction of extant taxa are increasingly used to test biogeographical hypotheses (1). Extinction has long been acknowledged as a key component of observable diversity and biogeographical patterns, and it is essential to include extinct taxa, wherever possible, when identifying regional diversification patterns (2), particularly when the ranges of fossil species do not overlap those of extant species. Fossil records are crucial in explaining extant biodiversity because phylogenetic analyses of extant organisms cannot replace paleontology as a way of reconstructing the past and cannot reveal the existence of extinct taxa or lineages (3).

The Antarctic continent is the most inhospitable place on Earth because of its freezing climate, blizzards, and ice caps, with 99.7% of the current terrain covered by permanent 4-km-thick ice. Yet as far back as two-and-a-half centuries ago, both Charles Darwin and Joseph Hooker speculated that the Antarctic continent must have supported a flora containing elements now restricted to southern forests. One of the most important breakthroughs in Antarctic geological research over the last three decades has been the elucidation of the continent's fossil records. A surprising diversity of fossil plants and animals has now been recorded in Antarctica, mainly in the Antarctic Peninsula (nearest South America), supporting the idea that dense vegetation was once able to survive close to the South Pole (4). Francis *et al.* (5) reconstructed the vegetation of Antarctica over the past 100 My (million years) and suggested that flowering plants thrived under subtropical climates in Antarctica 85 Ma (million years ago; mid–Late Cretaceous). Analysis of leaf and flower

fossils indicates that summer temperatures averaged 20°C during this global thermal maximum (5). Our knowledge of the paleontological and paleobotanical history of Antarctica has increased greatly over the last few decades, with detailed studies of many key groups (5–7) that have been important in developing our understanding of the broad patterns of the history of life on Earth. It has become apparent that Antarctica has had a much more significant role than simply acting as a convenient stepping stone for taxa that originated elsewhere (8) and may in fact be the center of the origin and early diversification of some important plant taxa.

New Caledonia is a fragment of the continental crust Zealandia—which also includes New Zealand, Lord Howe Rise, Norfolk Ridge, Campbell Plateau, and Chatham Rise—that rafted away from Antarctica on its southwest side about 82 Ma and reached its present position 50 Ma (9, 10). It had already separated from Australia on its northwest side by 89 to 85 Ma (11). New Caledonia is a global biodiversity hot spot, harboring extraordinary levels of species richness and endemism (77%) among the angiosperms (12). There has been a debate over the origin of New Caledonia's unique biota, which can be traced to Gondwanan times owing to its long geological history and the presence of phylogenetic relicts (13). However, some geological evidence indicates that New Caledonia may have been submerged for long periods in the Paleocene and Eocene (9, 14), with the main island only becoming available for terrestrial colonization 38 to 33 Ma (15). The origin of New Caledonian biodiversity has therefore been explained by two incompatible hypotheses. Espeland and Muriene (16) studied the evolutionary history of *Angustonicus* (a neocaledonian cockroach genus) as a general model for the New Caledonian biota and concluded that the high New Caledonian biodiversity is a result of recent dispersal events followed by diversification. Buckley *et al.* (17) analyzed the diversification patterns of nine New Caledonian groups and found a significant variation in the diversification

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rates. As a consequence, Espeland and Murienne (16) argued that the original New Caledonian biota was wiped out during an episode of submersion. Other groups have similarly demonstrated diversification in New Caledonia subsequent to recent dispersal (18–20). However, the generalization of this hypothesis to the entire New Caledonian biota seems implausible, as there are unambiguous counterarguments. These center on the existence of many taxa endemic to New Caledonia with poor dispersal ability and the existence of clades that can be traced beyond the time when New Caledonia supposedly re-emerged in the Late Eocene. These include the world's most ancient extant flowering plant *Amborella*, the arachnid Trogloniridae (21), Gondwanan moss bugs (22), the beetle family Passalidae (23), and the saw moth *Sabatinka* (24). Many of these New Caledonian endemics are traditionally viewed as an inheritance from Gondwana (11), which points to a hypothesis of vicariance where New Caledonia is perceived as a Gondwanan refuge for these relictual taxa.

Similarly, New Zealand has a rich, highly endemic flora at the species level [82% (25)], with interpretations of its history varying from emphasizing continuous links to its Gondwanan past, especially among its temperate rainforest species (26), to proposing that the entire flora has a transoceanic origin (27). The latter is supported by geological evidence indicating that the entire subcontinent was submerged in the Late Oligocene to the Early Miocene (28). More recent work indicates that continuous uplift among basement blocks ensured that some land persisted above sea level even then (29). The topic is so controversial that an entire issue of the *New Zealand Journal of Geology and Geophysics* was devoted to it in 2014 (30).

The proteaceous genus *Beauprea* now contains 13 species, all endemic to New Caledonia (31). *Beauprea* species usually occur in mountainous regions bearing diverse rainforests in the interior region of the main island Grande Terre (32). Ten species, except for *Beauprea spathulifolia*, *Beauprea montana*, and *Beauprea neglecta*, have strictly local distributions known only from a few records. For example, the upland *Beauprea penariensis* was last collected in 1876 as the only known specimen. (Note that T.H. and B.B.L. failed to locate this species at the recorded location during a collecting trip in 2013.) There are no *Beauprea*-type pollen fossils recorded in New Caledonia. However, *Beauprea*-like pollen in the fossil records has been described from New Zealand (33, 34), Australia (35, 36), Antarctica (37–39), and southern South America (40) over a continuous 85-My period from the mid–Upper Cretaceous to the mid-Pleistocene. *Beauprea* mostly became extinct in mainland Australia from the Early Miocene, with final records in the mid-Pleistocene (41), probably initially from the onset of aridity and fire (32) followed by the cold associated with glaciation (41). The genus existed in New Zealand until recently, with extinction in the area undoubtedly resulting from increasing climatic cooling as the Cenozoic progressed (42), supported by the youngest recorded *Beauprea* fossils (1 Ma) located at the northernmost tip of the North Island (34).

Sauquet *et al.* (42) estimated that *Beauprea* originated 69 Ma in the Late Cretaceous, although they did not make use of fossil records known to be older than that. Despite questioning the provenance and identification of the Early Cenozoic, *Beauprea*-like pollen (*Peninsulapollis*) in Antarctica (38), Pocknall and Crosbie (32) accepted that the genus arose in the Late Cretaceous and speculated that its center of origin lay where Antarctica, Australia, and New Zealand retained possible connections. However, a phenetic analysis by Sauquet *et al.* (42) confirmed that both *Beaupreaidites* and *Peninsulapollis* are uniquely linked to *Beauprea*, whereas both have since been recorded even earlier in the

Campanian–Maastrichtian sediments of the Antarctic Peninsula (32–48), alluding to a possibly more significant role for Antarctica in the origin of *Beauprea*. Although not specifically mentioning *Beauprea* and (mistakenly) treating New Zealand as separating from Australia, Barker *et al.* (49) invoked “island hopping” to explain the distribution of other proteaceous genera in Zealandia. Also neglecting a possible role for Antarctica, Sauquet *et al.* (42) were uncertain of *Beauprea*'s immediate origins but, once linked with the African genus *Protea*, they posited an Australian origin for its clade.

Here, we aimed to trace the origin and reconstruct the evolutionary history of *Beauprea*. Because *Beauprea*-like pollen was widespread in eastern Gondwana before the severance of Zealandia from Antarctica/Australia in the Upper Cretaceous, our intention was to explore its pathway to New Caledonia and New Zealand. Our working hypothesis was that *Beauprea* was already present throughout Zealandia at the time of separation, making (recent) transoceanic dispersal, say from Australia, redundant. We first reviewed the presence of *Beauprea*-type pollen in the fossil records and analyzed the relationship of a selection of fossil taxa with extant genera within the Proteaceae. We further reconstructed the phylogenetic relationships among extant species of *Beauprea* and estimated the age of the *Beauprea* clade and its species. Lastly, by incorporating extinct taxa into the *Beauprea* phylogenetic tree, we were able to reconstruct the ancient geographical distribution of this genus. Together with an understanding of its dispersal biology, we were also able to use the history of *Beauprea* in New Caledonia and New Zealand to comment on the likelihood that both landforms were completely submerged at some point during the last 82 My.

RESULTS

Our literature search revealed 129 records for *Beaupreaidites*/*Peninsulapollis* fossil pollen, which Sauquet *et al.* (42) assigned with confidence to *Beauprea*, and these records were spread over much of Australia, New Zealand, Antarctica, and South America for an extended period (83.8 to 1 Ma; Fig. 1 and Table 1). The oldest record was for *Beaupreaidites orbiculatus* in the Otway Basin, Southeastern Australia (SE Australia), at 83.8 Ma, whereas the youngest record was for the *B. orbiculatus* “type” in the Antarctic at 51.5 Ma. *Peninsulapollis gillii* was the second oldest pollen and was recorded in the Antarctic Peninsula at 81.4 Ma. *P. gillii* was also recorded at 80.3 Ma in the Gippsland Basin, Victoria. The *Beaupreaidites elegansiformis* type has the longest time span, ranging from 77.6 Ma in the Antarctic Peninsula to 1 Ma in Auckland, New Zealand. *B. elegansiformis* was recorded from the Campbell Plateau (between Antarctica and New Zealand) in the period 83.5 to 70.6 Ma, and from the Sydney and Gippsland Basins continuously from 55.8 to 9.7 Ma. Pocknall and Crosbie (32) compared *B. elegansiformis* favorably with extant *Beauprea gracilis* (in particular), *Beauprea filipes*, and *B. spathulifolia*. *Beaupreaidites verrucosa* (often co-occurring with, but distinct from, *B. elegansiformis*) was recorded from the Antarctic Peninsula 67.5 Ma, and from the Sydney and Gippsland Basins 57.4 to 30 Ma. For 38 records of *Beaupreaidites*/*Peninsulapollis* in the Cretaceous, 92% co-occurred with *Nothofagites*; for 40 records in the Cenozoic, 98% co-occurred with *Nothofagites*.

Beauprea-type pollen (*Beaupreaidites* and *Peninsulapollis*) was first recorded in the Santonian to Campanian of the Upper Cretaceous in the Antarctic Peninsula and the Otway Basin, when Australia and Antarctica were still joined (Fig. 1A). Antarctica–SE Australia accounted for 80% of records in the period 85 to 70 Ma, dropping to 40% in the period 70

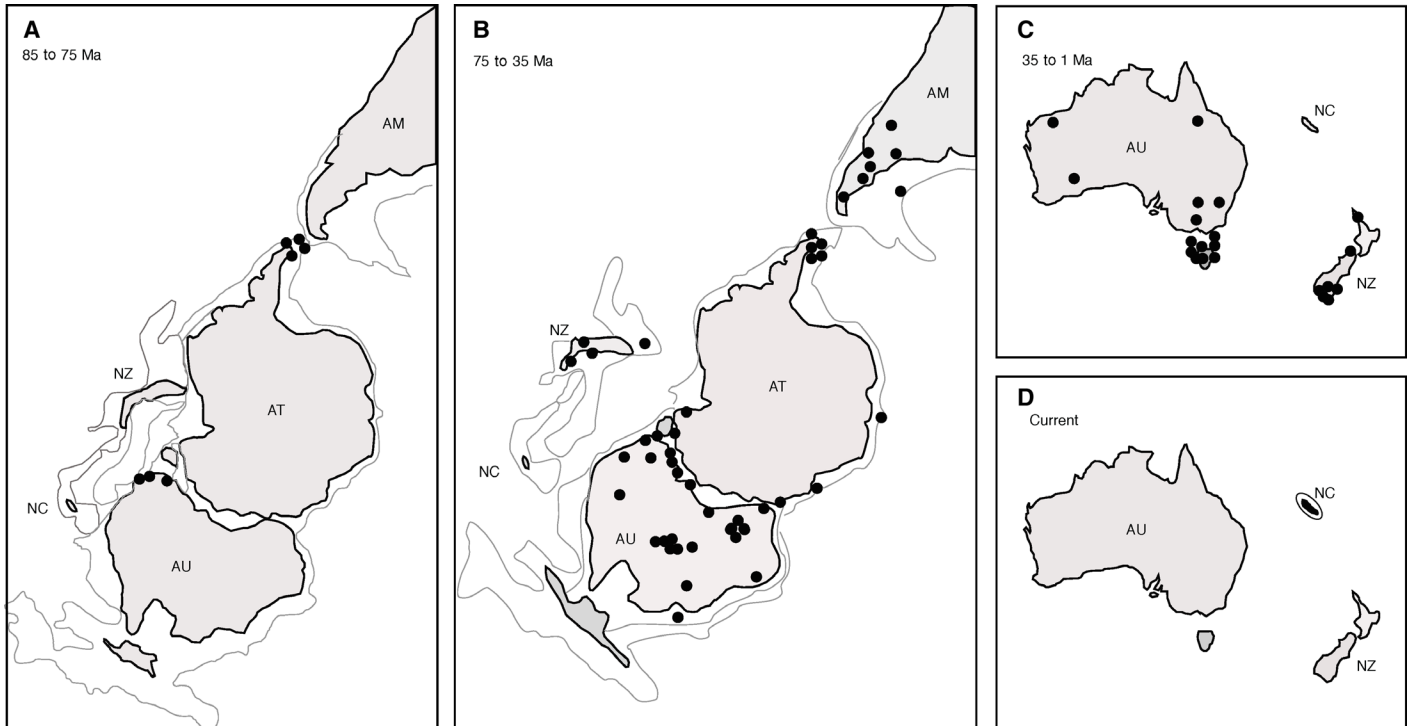


Fig. 1. Occurrences of *Beauprea*-type pollen and their geographical location at 85 to 75 Ma (A), 75 to 35 Ma (B), 35 to 1 Ma (C), and present time (D). AT, Antarctica; NZ, New Zealand; NC, New Caledonia; AU, Australia; AM, America. The light gray line indicates the boundary of landmass at that time.

Table 1. Records for the five regions where *Beauprea*-like fossils have been identified at 15-My intervals through the geological record. Mean age was used to assign each species observed in a given study, although multiple entries are given if species occurred in successive 15-My intervals.

		Antarctica	SE Australia	Rest of Australia	Zealandia	South America
Oldest pollen recorded (Ma)		81.4	83.8	74.5	*	68.0
Period (Ma)	Approximate epoch					
84–70	Upper Cretaceous	6	8	3	1*	0
69–55	Paleocene	9	3	9	4	5
54–35	Eocene	12	11	13	4	3
34–20	Oligocene	2	8	4	6	1
19–5	Miocene	0	2	3	3	0
<5	Pliocene/Quaternary	0	3	0	6	0
Total records		29	34	32	24	9
<i>P</i> (Fisher’s exact probability test, two-tailed) for the last three periods combined		—	0.0099	0.3327	0.0001	0.3739
<i>P</i> (Fisher’s exact probability test, two-tailed) for the last three periods omitted		—	0.2651	0.7046	0.8839	0.2778

*Upper Cretaceous” Couper (67).

to 55 Ma as *Beauprea* spread more widely (Table 1). *Beauprea* fossils peaked in Antarctica and Australia and, overall, during the Eocene (Figs. 1B and 2, and Table 1). The occurrence of *Beauprea* fossils fell markedly in the Oligocene-Neogene-Quaternary overall, especially in Antarctica and South America, although it peaked in New Zealand (Figs. 1C and

2, and Table 1), eventually becoming extinct everywhere except in New Caledonia (Fig. 1D). The Antarctic Peninsula recorded the highest richness of any region, with seven *Beauprea*-type species in the Late Cretaceous/Paleocene, finally falling to one species in the Pleistocene at Stony Creek, Victoria [(41); Fig. 2].

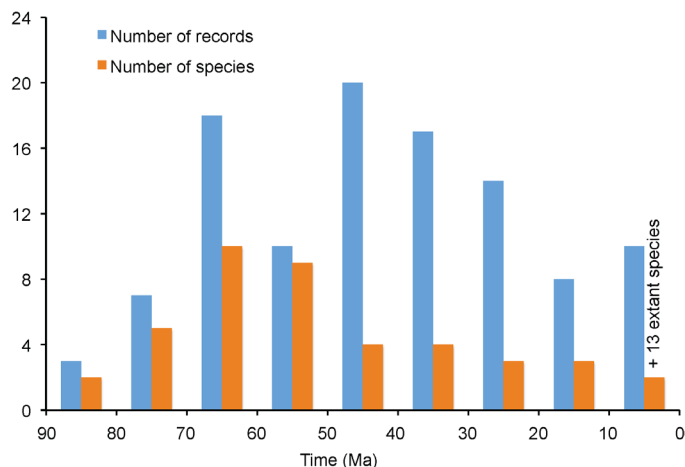


Fig. 2. Number of records and number of species with *Beuprea*-type pollen.

Our phenetic analysis of 11 pollen characters for eight extant *Beuprea* species and four fossil species with *Beuprea*-type pollen showed close relationships among all *Beuprea*, *Beupreaidites*, and *Peninsulapollis* species, but not with other extant genera in the same subfamily such as *Protea*, *Faurea*, *Franklandia*, and *Eidothea* (Fig. 3). *Beupreaidites* is clearly embedded among *Beuprea*, whereas *Peninsulapollis* is also well within *Beuprea*. Maximum likelihood analysis indicated that *B. orbiculatus* and *Beuprea montisfontium* have very similar pollen, followed by *Beuprea balansae*, as Dettermann and Jarzen (33) suggested (Fig. 3). The eight extant *Beuprea* species and four *Beuprea*-type fossil species were clustered into two groups. All four fossil species and five extant species formed a group, whereas *Beuprea asplenoides* and another two extant species formed another group (Fig. 3). *Cranwellipollis* pollen was grouped with *Franklandia* (both having almost identical morphology).

Our molecular phylogenetic reconstruction of extant *Beuprea* species revealed two major lineages within the genus. Age estimates using Monte Carlo Markov chain (MCMC) procedures suggested that the two lineages diverged at 82.5 Ma [79.5 to 84.7 Ma; 95% highest posterior density (HPD)], a few million years after the genus originated 88.4 Ma (83.7 to 92.1 Ma; 95% HPD). This early divergence was strongly supported in the phylogenetic reconstruction with a posterior probability of 1.0. Both lineages have a typical “broom-and-handle” shape, with a number of lineages arising in a relatively short period at the end of a long stem. *Beupreopsis*, another New Caledonian endemic proteaceous genus, was dated at 64.2 Ma (50.1 to 74.8 Ma; 95% HPD) from an immediate ancestor at 93.4 Ma.

All four fossil species incorporated into the phylogeny were grouped with the lineage containing *B. montisfontium* and *B. spathulifolia*, which have a pollen structure similar to that of *B. orbiculatus* and *B. elegansiformis*, respectively. *Beupreaidites diversiformis* and *P. gillii* were positioned at 80.6 Ma, and the two species share a similar pollen structure, as revealed by the neighbor-joining tree (Fig. 3). Because the actual age of *B. orbiculatus* (83.5 Ma) exceeded the median crown age, as estimated from MCMC (82.5 Ma), the age of the lineage was pulled back to 83.5 Ma, which was still within the 95% HPD of the MCMC age estimate of the lineage (Fig. 4). In the supertree incorporating known fossil and extant species of *Beuprea* (Fig. 4), taxa in the earliest branches were first recorded in Antarctica and/or SE Australia, suggesting a possible Antarctica–SE Australian origin for the genus.

DISCUSSION

A central Gondwanan origin for *Beuprea*

Beuprea-type pollen (*Beupreaidites* and *Peninsulapollis*) were first recorded in the Santonian to Campanian of the Upper Cretaceous in the Antarctic Peninsula and the Otway Basin—the rift valley that developed between Antarctica and Australia before they finally separated 45 Ma. Time-based molecular phylogenetic analysis, in conjunction with the fossil records, indicates that *Beuprea* diverged from the rest of Proteaceae 88.4 Ma (92.1 to 83.7 Ma; 95% HPD), well before the post-African/Indian landmasses of Gondwana (Antarctica, Australia, Zealandia, and South America) began to separate 82 Ma (50). This means that, despite the unavailability of most of Antarctica for fossil sampling, the origins of *Beuprea* can be traced to the central core of Gondwana in the Early Upper Cretaceous. Initiation of the two extant lineages occurred 82.5 to 83.5 Ma, when Zealandia was still connected to Antarctica. Although direct records for Zealandia are limited (earliest *Beuprea* fossils for New Zealand and the Campbell Plateau are described vaguely as “Upper Cretaceous”; Table 1), it is thus likely that *Beuprea*, including its two basal lineages, was already widespread across Antarctica and Zealandia before they separated 82 Ma.

The idea of Antarctica being the center of origin of certain taxa is not new. Charles Darwin and Joseph Hooker were the first to recognize the possible importance of the Antarctic region in the origins of southern floras. Furthermore, Wardle (51) proposed that preglacial Antarctica must have been a major source of New Zealand’s mountain plants. Truswell (43) summarized the available fossil records and proposed an Antarctic origin for the fern *Lophosia*, for the podocarp gymnosperms *Lagarostrobus* and *Dacrydium*, and for *Nothofagus*, *Ilex*, and several lineages of Proteaceae, including *Beuprea*. Recently, Barreda *et al.* (52) proposed that Asteraceae, the most diverse angiosperm family, might have originated in Antarctica during the Cretaceous. To date, our analysis provides the best evidence to support a pivotal role for Antarctica in the possible origin and early diversification of a Southern Hemisphere genus.

An autochthonous origin for *Beuprea* in New Caledonia and New Zealand

Our analysis supports an autochthonous origin for *Beuprea* in New Caledonia and New Zealand: (i) by the time Zealandia split from Antarctica, *Beuprea* had been present in Antarctica–SE Australia for >6 My, giving it ample time to spread overland to, or even diversify in, Zealandia, and (ii) the fossil/extant record indicates continuous occupation of Zealandia from the Upper Cretaceous to present (Table 1). An alternative explanation would require early transoceanic dispersal from Antarctica/Australia (and/or islands associated with the Lord Howe Rise, Campbell Plateau, or Chatham Rise) to New Zealand/New Caledonia and/or later dispersal from New Zealand (and/or islands associated with the Challenger Plateau or Norfolk Ridge) to New Caledonia. Furthermore, were New Caledonia and New Zealand to have had periods of complete submergence in the Cenozoic, as proposed by some (9, 14, 28, 30), then not only would transoceanic transport be required but suitable sources/pathways would need to be demonstrated. Finally, since *Beuprea* bifurcated c. 83 Ma, two independent migration events to New Caledonia would be required. We show below that these alternative scenarios are both implausible and redundant.

Low supply of propagules for dispersal. Records show that both *Beupreaidites* and *Peninsulapollis* are of low abundance throughout

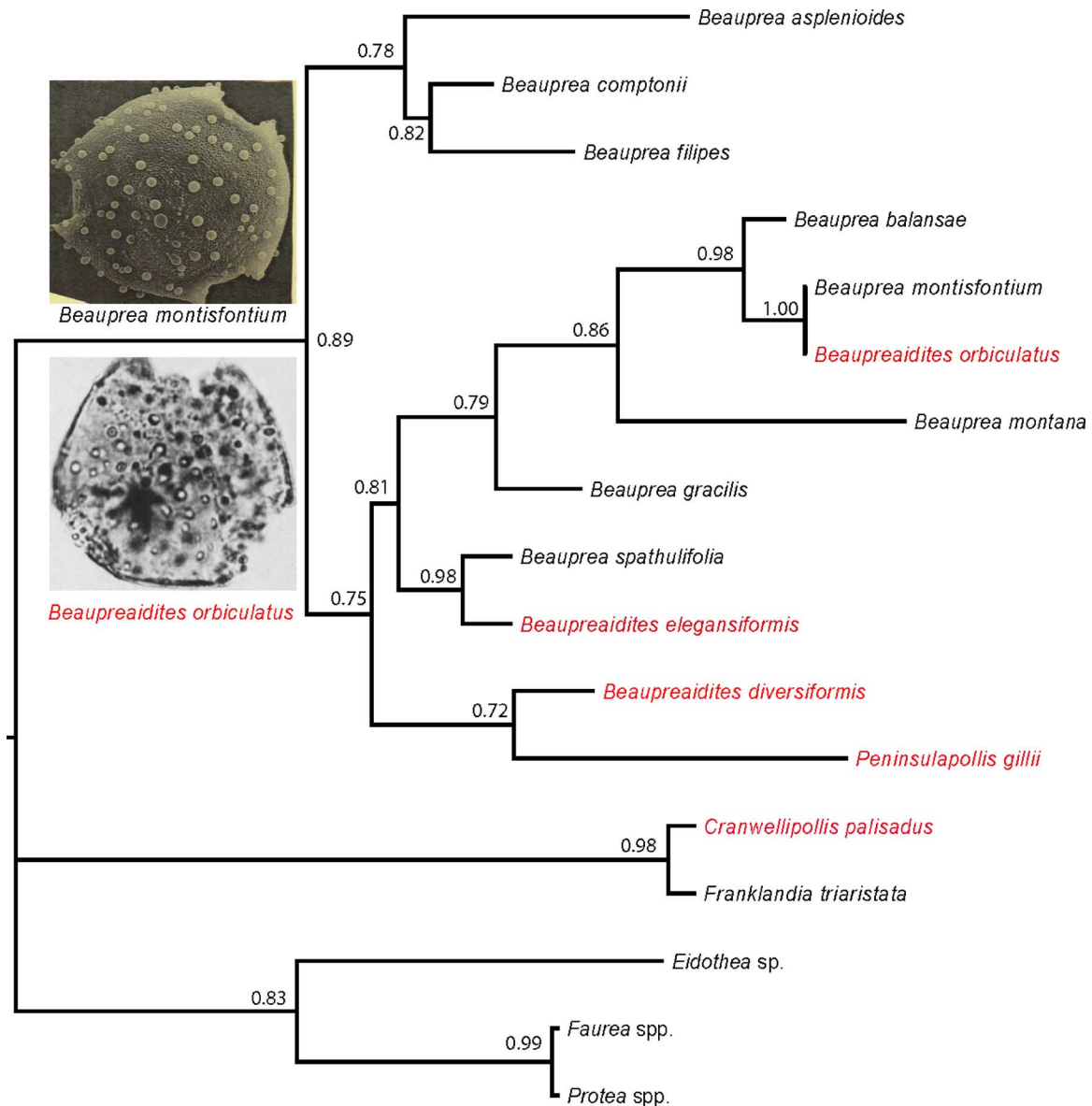


Fig. 3. Neighbor-joining tree of fossil species (in red) and extant species. Bootstrapping values are shown on the node. The tree was rooted using *Franklandia*, *Eidothea*, *Faurea*, and *Protea* as outgroup.

their entire geological history (32), suggesting that *Beuprea* was never a prominent element in its plant communities. We have observed that this is true even today in New Caledonia. Such rarity would become even more extreme following its peak abundance in the Eocene (Fig. 1). Indeed, our literature survey showed a decline in fossil records in mainland Australia since 35 Ma (Table 1). Even if New Zealand was not totally drowned in the Oligocene, it is accepted that its land area was greatly reduced at that time (29). The diversification of *Beuprea* began 28.5 Ma (36.3 to 22 Ma; 95% HPD), at about the time New Caledonia supposedly re-emerged (14). *Beuprea* would then have had to (re)colonize New Caledonia between 33 Ma (when the island became re-inhabitable) and 28.5 Ma (when *Beuprea* began diversifying). However, populations of *Beuprea* in either Australia or New Zealand may not have been large enough

or may not have existed long enough to produce a propagule source pool sufficient to colonize a new landmass in that small “window of opportunity,” as high propagule pressure is one of the key mechanisms facilitating successful invasion (53). Similarly, if New Zealand was also submerged in the Oligocene but supposedly had re-emerged c. 22 Ma (28), both New Caledonia (itself just recovering from inundation) and distant Australia (with *Beuprea* on a rapid decline) would be poor propagule sources.

Low dispersibility. Transoceanic dispersal of *Beuprea* via ocean currents is unlikely for four reasons. First, the distributions of modern *Beuprea* species are mostly in the mountainous regions of New Caledonia, away from watercourses and coastal environments where water dispersal would be possible. *Beuprea*-type pollen fossils are rarely found in coastal environments, which led Pocknall and Crosbie (32) to suggest that *Beuprea*

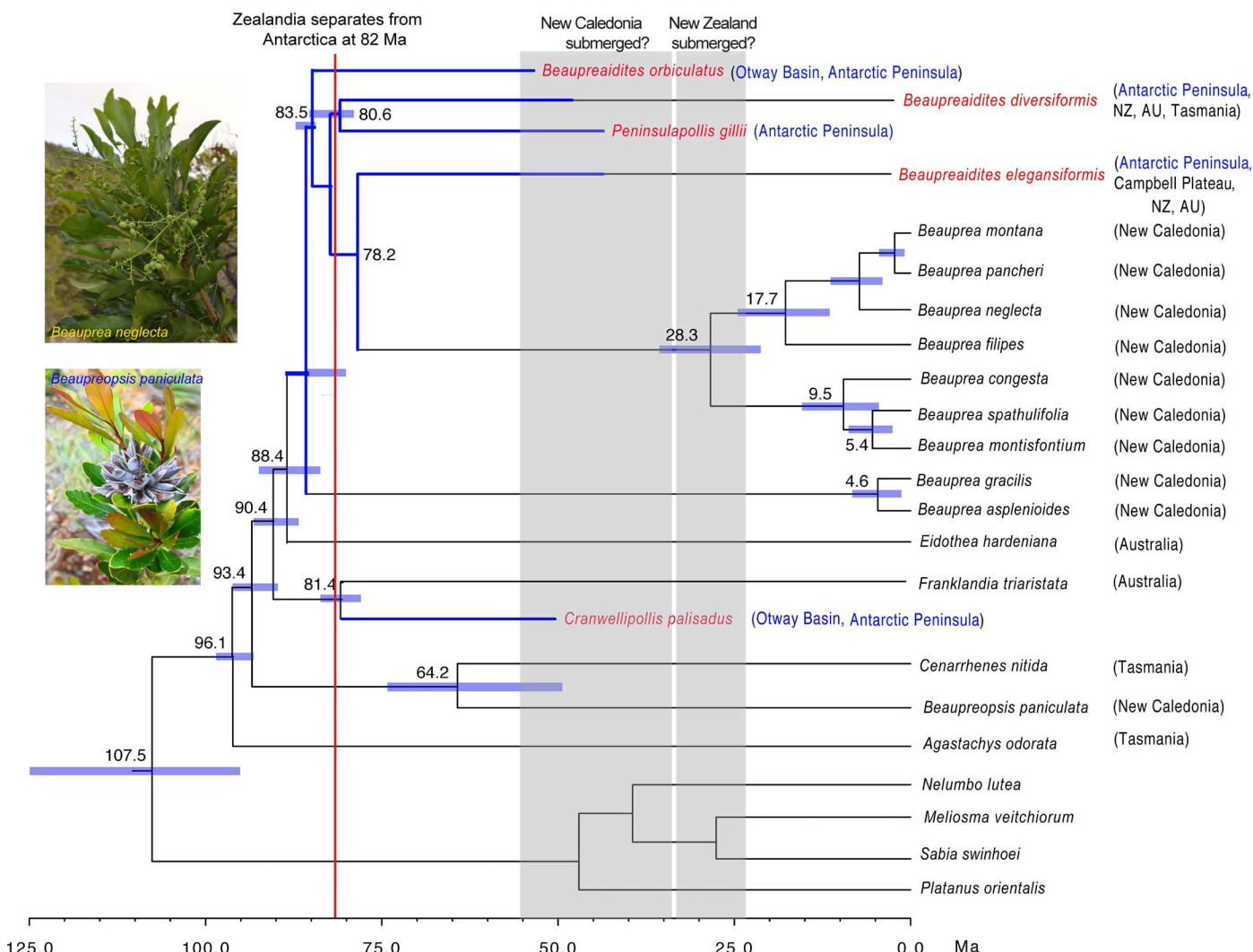


Fig. 4. Supertree of *Beuprea* with fossil (in red) and extant taxa, and the closest phylogenetically related outgroup species. Blue lines indicate the known or estimated duration of fossil species in Antarctica and SE Australia (AU); blue bars are 95% HPD of the divergence age. Note that *Beuprea* arose at a mean age of 88.4 Ma. Gray areas indicate the hypothesized time period when New Caledonia and New Zealand (NZ) were submerged according to some studies (but shown here to be unlikely).

in the past only occupied habitats similar to where it now occurs in New Caledonia, that is, highlands some distance from the sea. Second, ocean currents run in the “wrong” direction—the South Equatorial Current travels east to west, bypassing New Caledonia, runs north to south along the east Australian coast, and then moves west to east as the South Pacific Current passing north and south over New Zealand toward South America (54). Thus, Australia could be a source of propagules to New Zealand, but exchanges between New Caledonia and New Zealand are not possible. Third, *Beuprea* fruits do not float in seawater. In a simple experiment, we (B.B.L. and T.H.) collected 50 mature fruits from *B. neglecta* in Kone, New Caledonia, in 2013, placed them in a bowl of seawater, and found that 37 fruits sank immediately, whereas the remaining 13 sank within 24 hours. Fourth, any attraction of the slightly fleshy fruits to birds is unknown, but this would be confined to forest dwellers and not seabirds that might on occasion be swept vast distances over the ocean (again, in the wrong direction).

Biological evidence for a lack of complete submergence in the Cenozoic

Although evidence from molecular systematics has pointed to the need for transoceanic dispersals in understanding the evolution of the New Caledonian biota (14, 15, 55), *Beuprea* is an important anomaly whose evolutionary history does not support the hypothesis that New Caledonia and/or New Zealand was completely submerged during the Eocene-Oligocene or Oligocene-Miocene, respectively. The fossil records indicate continuous occupation of New Zealand by *Beuprea*, most notably at the Oligocene-Miocene boundary (Table 1), including the pollen species *B. elegansiformis* that can be traced from the Upper Cretaceous to the Late Pleistocene. The final extinction of *Beuprea*, with its subtropical affinities, in New Zealand was attributable to climaxing climate deterioration (14), not submergence. Similarly, New Caledonia could never have been completely submerged, because it is not possible for *Beuprea* to have reached its shores from elsewhere subsequent to emergence, as

we have shown above. Instead, our analysis indicates that *Beauprea*, which arose in Antarctica–SE Australia 88 Ma, must have already been present in Zealandia when it separated from Antarctica 82 Ma.

Hopper (56) predicts that organisms in very old, climatically buffered, infertile landscapes—of which New Caledonia is an example—should exhibit reduced dispersibility, high numbers of localized rare endemics, and strongly differentiated population systems, with elevated persistence of old lineages. *Beauprea* and a number of other relict taxa in New Caledonia, such as *Nothofagus*, *Beaupreopsis* (which we show here as having a history similar to that of *Beauprea*), and *Amborella*, fit this description well. Although it is unlikely that New Caledonia and New Zealand have existed intact over 82 My, we provide biological support for the idea that some emergent land has existed continuously in each island complex—sufficient for the survival and moderate speciation of an ancient genus—during that time. This complements the fluctuating, but increasing, geological support for a continuous terrestrial presence there (29, 57).

Relationship with *Nothofagus* and other ancient lineages

From the fossil records, *Beaupreaidites* and *Peninsulapollis* are invariably (95%) associated with *Nothofagidites* rainforests. *Nothofagus* has been considered a key group for understanding Southern Hemisphere biogeography because it has a low dispersal capacity (58) and its fossil pollen record dates back to 84 Ma (59). Dettmann (44) suggested that *Nothofagus* likely originated in Antarctica. There are five endemic species of *Nothofagus* in New Caledonia. Swenson *et al.* (60) speculated that the presence of *Nothofagus* in New Caledonia was the result of a single migration from New Zealand along a possible past land link. It is likely that several species of *Beauprea* and *Nothofagus*, plus many other species, spread from Antarctica into, or arose within, Zealandia while they remained connected up to 82 Ma, eventually reaching New Caledonia overland. The details of how *Beauprea* moved within Zealandia remain unknown, but it may have involved land bridges associated with the Campbell Plateau and Chatham Rise (from Antarctica to New Zealand) and the Challenger Plateau and Norfolk Ridge (from New Zealand to New Caledonia). Much of Gondwana, including New Caledonia and the Lord Howe Rise, was above sea level at 90 Ma (11), that is, at about the time *Beauprea* originated. Because there are no fossil records for *Beauprea* in New Caledonia, it is not clear when the ancient stock of extant *Beauprea* reached New Caledonia from Antarctica, but it cannot be later than the severance of the land connection between New Caledonia and New Zealand that occurred 50 Ma.

For the Late Cretaceous vegetation in the narrow rift valley separating Antarctica from southern Australia, Hill and Scriven (61) recorded pollen of *Beauprea*, diverse conifers (*Podocarpus*, *Dacrydium*, *Dacrycarpus*, and *Araucariaceae*), *Nothofagus*, *Ilex*, *Gunnera*, *Ascarina*, Winteraceae, and Trimeniaceae. Most of these groups have extant members endemic to New Caledonia and New Zealand. Given the recognition of historical connections between New Zealand and New Caledonia via Antarctica, it is now redundant to invoke hypotheses of dispersal across essentially insurmountable oceans as the origin of some of the floras of these island complexes. Instead, vicariance and allopatry must be considered when interpreting the high levels of endemism and diversity of their floras. Refuge spots must have existed in the mountainous uplands from which these relicts would have spread and speciated as the full islands re-emerged, and this can explain the spurt in speciation of *Beauprea* from 28 Ma. Complete submergence would not have allowed recovery because we have shown that the likelihood of the transoceanic dispersal of *Beauprea* from another region is negligible.

MATERIALS AND METHODS

Fossil *Beauprea*-type pollen records

The key words *Beauprea*, *Beaupreaidites*, and *Peninsulapollis* were fed into Google Scholar for the period 2013–2015, and all scholarly papers where they were mentioned were obtained. These were supplemented with records in volume 11 (Proteaceae issue) of *Australian Systematic Botany*. The identity of each *Beauprea*-type pollen species—rarely leaves—as assigned was noted (“aff.” was treated as a separate species and “cf.” was treated as the same species), as well as its geographical location, estimated geological age, and whether it co-occurred (same sample) with *Nothofagidites* pollen. The age of the pollen was taken as the oldest recorded in actual stratigraphy diagrams (including multiple records in the same paper) or the exact midpoint if only part of a geological stage was noted; for example, if given as Late Santonian (that is, 85.9 to 83.5 Ma), late was taken as the youngest quarter (that is, 84.1 to 83.5 Ma), and the midpoint of this is 83.8 Ma [for *Beaupreaidites* (syn. *Proteacidites*) *orbiculatus*]. Records with a range of ≥ 20 My were ignored as too vague. Records were plotted onto recreated maps for the periods 85 to 70, 70 to 35, and ≤ 35 Ma, and collated at the level of records and species for all 10-My intervals. Records were also collated at 15-My intervals by region (Antarctica, SE Australia and the rest of Australia, Zealandia, and South America), although records for the same site were repeated if they spanned >15 My and also added to the next interval.

Fossil pollen structure and phenetic analysis

We assembled a matrix of pollen characters for four fossil species with *Beauprea*-type pollen, *Cranwellipollis palisadus*, eight extant *Beauprea* species, and species from apparently close genera (*Franklandia*, *Eidothea*, *Faurea*, and *Protea*) based on the study of Sauquet *et al.* (42) (table S1). This included *Beaupreaidites* (syn. *Proteacidites*) *orbiculatus*, which Sauquet *et al.* (42) were unable to link to *Beauprea*. However, Dettmann and Jarzen (33) considered that “*Beauprea montisfontium* shows a remarkable similarity to the fossil specimens [of *Beaupreaidites orbiculatus*] in size, aperture structure, exine stratification, and surface details” and justified our inclusion of this fossil in our analysis. Carpenter *et al.* (62) have recently accepted *B. orbiculatus* as being synonymous with *Beauprea*. We independently assessed all characters for *Beauprea*, *Beaupreaidites*, and *Peninsulapollis* but only supplemented characters for the other taxa from those listed by Sauquet *et al.* (42) to ensure that all characters used were in common. Data or pollen photos were obtained from the studies of Pocknall and Crosbie (32), Dettmann and Jarzen (33), and Sauquet *et al.* (42) and from other relevant papers. Characters that were unchanged among all species or for which complete data were unavailable were omitted. The consequent pollen morphological matrix comprised 11 binary and multistate characters (ordered for analysis). A neighbor-joining tree was constructed using PAUP software (63). Estimates of the statistical significance of phylogenies were calculated by performing 1000 neighbor-joining bootstrap replicates.

Divergence-time estimates

We collected fresh leaf material from nine extant *Beauprea* species, and the single species of *Beaupreopsis paniculata*, from the wild in New Caledonia. For each species, we sequenced eight DNA fragments: nuclear ribosomal internal transcribed spacers, the chloroplast *matK*, *rbcl*, a *trnL* intron, a *trnL-trnF* intergenic spacer, *atpB*, an *atpB-rbcl* intergenic spacer, and an *rpl16* intron, following the protocols in Sauquet *et al.* (42). Outgroup species included species from closely related genera in the

Proteaceae, *Eidothea*, *Cenarrhenes*, *Franklandia*, and *Agastachys*, as well as species from families close to Proteaceae. Their sequences were either generated with the same protocol as for *Beauprea* or extracted from the National Center for Biotechnology Information (NCBI). Species and voucher specimens and NCBI sequence numbers are given in table S2. The sequences were edited and aligned, and the alignments were joined using the computer software CLC Bio Genomics Workbench (CLC Bio-Qiagen). We used BEAST v2.1.0 to estimate phylogeny and divergence times under a relaxed clock model (64). The data set partition for chloroplast DNA was unlinked and set to a general time-reversible model with γ -distributed rate heterogeneity. We used a Yule prior for rates of cladogenesis and ran 10,000,000 analyses with a 10% burn-in and sampling every 2000 generations.

Two fossil species were used to calibrate the tree. A minimum age for crown *Beauprea* was based on *B. orbiculatus* (38), the oldest pollen with *Beauprea* affinities according to our literature search, set at 83.8 Ma (exact midpoint of the Upper Santonian, 84.1 to 83.5 Ma, in which the fossil was located). The crown of Proteaceae was set at 95.1 Ma, the midpoint of the Upper Cenomanian (96.6 to 93.6 Ma) in which the oldest pollen (*Triorites africaensis*) with Proteaceae affinities is recorded (48), as also supported by Sauquet *et al.* (42). We used the lognormal distribution prior for age reconstruction in BEAST. The Bayesian framework, as implemented in BEAST, allows modeling of calibration uncertainties (65), and 95% HPD intervals of age estimates are given as output data. Five separate runs were implemented, and results were viewed in Tracer and then combined using the LogCombiner package in BEAST. TreeAnnotator v2.0.3 was used to generate a maximum credibility tree based on this analysis (66).

Constructing a supertree incorporating fossil and extant species

Combining the species relationship from pollen morphology analysis and molecular phylogenetic reconstruction, we created a “supertree” recognizing both extant *Beauprea* species and fossil species with *Beauprea*-type pollen. Because there was a small discrepancy between fossil age and molecular estimates of the age of the extinct species that resembles the fossil species (see Results), we assigned the fossil species to a clade containing the closest extant species, and pulled the age of that clade to that of the fossil species but within the 95% HPD of the age estimate for that node. Fossil species were assigned to a region where they were first recorded.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/2/4/e1501648/DC1>

table S1. Numerical states for 11 pollen characters assessed on eight *Beauprea* species, five fossil pollen types, and four other extant genera in the same subfamily (Proteoideae) as *Beauprea*.

table S2. Species, voucher information, and GenBank accession for all sequences included in this study.

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