Fossil Ericaceae from New Zealand: Deconstructing the Use of Fossil Evidence in Historical Biogeography

Gregory J. Jordan, Jennifer M. Bannister, Dallas C. Mildenhall, Reinhard Zetter, and Daphne E. Lee

The Australasian Ericaceae epitomize many problems in understanding the biogeography of the southern hemisphere, especially the relative contributions of Gondwanan vicariance and dispersal. Late Cretaceous fossil pollen of the family suggests extreme antiquity of the group in Australasia, but recent phylogenetic evidence suggests much younger histories for most of the groups in that region. This paper documents two new species of latest Oligocene-Early Miocene macrofossils of Ericaceae from New Zealand. Cyathodophyllum novae-zelandiae G.Jord. & Bannister gen. et sp. nov. is the oldest record of the tribe Styphelieae, but is of a clade now extinct in New Zealand, possibly related to the Tasmanian genus Cyathodes. Richeaphyllum waimuensis G.Jord. & Bannister sp. nov. is a member of Richeeae, but it is ambiguous as to whether it is a member of the impressive modern New Zealand radiation in Dracophyllum. These fossils emphasize the fact that at least some of the fossil pollen of Ericaceae may have been derived from extinct lineages and therefore should not be used as evidence for the antiquity of any modern New Zealand clade of Ericaceae. New fossils and/or detailed analysis of fossil and extant pollen may help resolve such uncertainty.

Key words: Cyathodes; Dracophyllum; Epacridaceae; Ericaceae; extinction; fossil; historical biogeography; long-distance dispersal; palynology; vicariance.

The Ericaceae, and particularly the epacrids (subfamily Styphelioideae; formerly known as Epacridaceae), epitomize many of the controversies in the historical biogeography of Australasia. In particular, they are relevant to the current, often highly polarized discussions about the relative contributions of long-distance dispersal vs. Gondwanan vicariance in the New Zealand biota (e.g., Pole, 1994; Macphail, 1997; Winkworth et al., 2002; Sanmartín and Ronquist, 2004; McGlone, 2005; Wagstaff et al., 2006; Crisp and Cook, 2007; Lee et al., 2007; McDowall, 2008). The epacrids have all of the characteristics that, in the recent past, were used to infer a Gondwanan history. This group of plants is almost exclusively restricted to Gondwanan fragments—being centered on Australia, but also occurring in New Zealand, New Caledonia, and South America, with only a handful of species occurring naturally on non-Gondwanan landmasses (some Pacific islands and Malesia) (Fig. 1). The greatest phyletic diversity of the epacrids is within two vegetation types with compelling evidence for antiquity: montane rainforest and its close relative, wet, undisturbed alpine heath. Many of the dominant groups in these vegetation types have fossil records extending to times prior to the breakup of Gondwana. For example, the four subgenera of Nothofagus, Eucryphia, and most of the relevant conifer genera all have fossil records extending at least as far back as the Early Eocene (Carpenter et al., 1994; Hill, 1994; Hill and Brodribb, 1999). Similarly, the record of Ericaceae in Australasia extends back to the Late Cretaceous, and Dettmann (1994) used this evidence to infer a Gondwanan presence for the epacrids. Even though epacrid macrofossils are extremely rare, fossil leaves show the presence of two clades of epacrids (tribe Richeeae and another clade of more ambiguous affinity) as far back as the Early Oligocene (Jordan and Hill, 1995).

However, recent evidence has suggested that, in spite of fossil evidence for the presence in Gondwana of the relevant genera or families, many of the New Zealand rainforest taxa are relatively recently arrivals. In particular, molecular dating methods have been used to argue that the New Zealand clades of Nothofagus, Atherospermataceae, and Phyllocladus are too young to be explained by Gondwanan vicariance (Renner et al., 2000; Wagstaff, 2004; Cook and Crisp, 2005; Knapp et al., 2005). In the case of epacrids, Wagstaff et al. (in press) argued that the New Zealand Dracophyllum were an order of magnitude too young to have a Gondwanan vicariant origin.

Beyond the ecological and geographic considerations described, the probability of long-distance dispersal within Australasian Ericaceae is not clear because some of their traits increase this probability, whereas others decrease it. Australasian Ericaceae are woody, mostly grow in forest or sclerophyllous woodlands and heaths, and have small seeds enclosed in capsules or small fleshy fruit (tribe Styphelieae and Monotoca tamariscina F.Muell. of tribe Oligarrheneae). Woody plants of forests, woodlands, and heaths have a lower probability of transoceanic dispersal compared to herbaceous, aquatic, and coastal plants (Jordan, 2001), whereas this probability increases...
strongly with having small seeds. The general effect of fleshy fruit on effective long-distance dispersal remains ambiguous (Jordan, 2001; Howarth et al., 2003).

Overall, to describe the historical biogeography of Ericaceae in New Zealand at least 16 and possibly as many as 18 disjunctions need to be explained (Table 1). Many of these disjunctions
are between apparently closely related taxa (either populations of the same species or between sister species in quite derived genera) (Table 1, Fig. 1), which suggests that the disjunctions are relatively recent and the consequence of long-distance dispersal.

This work records the presence of two well-preserved Late Oligocene-Early Miocene epacrid macrofossil types from Southland, New Zealand. To give as precise phylogenetic placements as possible for these taxa, we have reassessed the diagnostic characters of epacrid leaf fossils (Jordan and Hill, 1996) in light of significant increases in phylogenetic evidence (Crayn et al., 1998; Crayn and Quinn, 1998; Taaffe et al., 2001; Quinn et al., 2003, 2005; Manaaki Whenua—Landcare Research, 2000 onward; Bush et al., 2009a, b; C. J. Quinn personal communication; Wagstaff et al. in press; C. J. Quinn, National Herbarium of New South Wales, personal communication). The number of species in New Zealand (NZ) is given for each clade. Note there are only 9 New Zealand species of Gaultheria, but the other disjunctions are nested within the New Zealand/American disjunction.

### MATERIALS AND METHODS

**Survey of extant species**—Prepared cuticles of 138 species of epacrids, including representatives of 34 of the 36 genera, were available for this study (Appendix S2, see Supplemental Data with the online version of this article). This collection is held in the School of Plant Science, University of Tasmania.

The distribution of character states observed in the living species was related to published phylogenetic evidence summarized in Fig. 1. Ancestral state analysis using Fitch optimization (as implemented in the program Mesquite 2.5) within this phylogeny was used to determine the association of derived states with clades. Where Acctran and Deltran optimizations differed, nodes were treated as ambiguous. Reconstructions assumed hard polytomies, although analyses assuming soft polytomies were also investigated. Large polytomies and different coverage of taxa in published molecular phylogenies of epacrids make it difficult to make precise phylogenetic placements of most fossils, although allocation to tribes, and sometimes groups within tribes appears to be possible based on the characters described later.

### RESULTS

**The site and fossils**—The fossils are from the Newvale Mine lignite (Seam W6) in the Gore Lignite Measures (Lee et al., 2007). The fossil site is registered as F45/f0394 in the New Zealand Fossil Record File administered by the Geological Society of New Zealand. The site is at 46.143°S, 168.752°E, 100 m above sea level (NZ Map Grid reference NZMS 26 F45/817434). The fossils are best interpreted as being of Late Oligocene to Early Miocene age based on palynostratigraphy (Pocknall and Mildenhall, 1984; Lee et al., 2007).

The fossils were observed on pieces of lignite, split by hand. Cuticles were isolated for light microscopy by removing small fragments, soaking them in 30% hydrogen peroxide with a few grains of tetrasodium pyrophosphate until clear. The resulting cuticles were rinsed, stained with either crystal violet or 2% aqueous aniline blue solution, then mounted on microscope slides in phenol glycerine jelly. For scanning electron microscopy, small fragments were mounted on double-sided tape on aluminum stubs, sputter coated with platinum, then observed with a Qanta 600 environmental scanning electron microscope (FEI Co., Hillsboro, Oregon, USA) under high vacuum at 15 kV and a working distance of 1 mm. All fossil leaf material is held in the Department of Geology, University of Otago.

**Key identifying features of leaf fossils of Styphelioideae**—In the following discussion, features are only described as being useful for identifying epacrid leaf fossils if ancestral state reconstructions imply that they are derived states. Most of the features show some degree of homoplasy within Styphelioideae, so the presence of several derived features is necessary to make confident identifications. Descriptions from our data are supplemented when possible with published data (Taaffe et al., 2001; Quinn et al., 2005). The characters are summarized in Table 2, which also includes the character numbers in the following description. Data and ancestral state analyses are given in online Appendices S1 and S2. Appendix S1 includes taxonomic authorities.
### Table 2. Summary of characters useful in identifying epacrid leaf fossils. Ancestral and derived states are inferred.

<table>
<thead>
<tr>
<th>Character</th>
<th>Ancestral state</th>
<th>Derived states</th>
<th>Clades with derived state</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Sinuosity of adaxial epidermal cells</td>
<td>Straight or weakly sinuous</td>
<td>1a. Highly sinuous (sinuosity &gt; 1.8)</td>
<td>Styphelioideae</td>
<td>No homoplasy except as described next</td>
</tr>
<tr>
<td>2. Sinuosity of abaxial epidermal cells</td>
<td>Straight or weakly sinuous</td>
<td>2a. Highly sinuous (sinuosity &gt; 1.7)</td>
<td>Styphelioideae</td>
<td>No homoplasy except as described next</td>
</tr>
<tr>
<td>3. Epidermal cell arrangement</td>
<td>Irregular shape, not in ranks</td>
<td>3a. ± Rectangular and in ranks parallel to the main veins</td>
<td>Styphelioideae</td>
<td>Reversion to the ancestral state</td>
</tr>
<tr>
<td>4. Mean length of adaxial epidermal cells</td>
<td>&lt; 70 μm long</td>
<td>4a. &gt; 70 μm long</td>
<td>Sphenotoma, Epacreae, most Styphelioideae</td>
<td>Increased regularity of cells</td>
</tr>
<tr>
<td>5. Length : width of abaxial epidermal cells</td>
<td>&lt; 3</td>
<td>5a. &gt; 3</td>
<td>Many Styphelioideae clades, occasional in other tribes</td>
<td>Quite homoplasious in Epacreeae</td>
</tr>
<tr>
<td>6. Main veins</td>
<td>Only one major vein arising in the petiole</td>
<td>6a. Three or more major longitudinal veins arising in the petiole</td>
<td>Styphelioideae</td>
<td>No homoplasy except in some very narrow leaves</td>
</tr>
<tr>
<td>7. Main vein equality</td>
<td>Middle vein more prominent</td>
<td>7a. Main veins approximately equal</td>
<td>Styphelioideae except Prionoteae, Archerieae, Epacreae</td>
<td>Some homoplasy within Epacreae</td>
</tr>
<tr>
<td>8. Vein branching</td>
<td>Reticulate</td>
<td>8a. Occasionally branched</td>
<td>Archerieae, Epacreae, many Styphelioideae</td>
<td>Oligorrheneae is not known</td>
</tr>
<tr>
<td>9. Main vein prominence</td>
<td>Flat, or slightly raised</td>
<td>9a. Abaxial lamina with veins raised</td>
<td>Many Styphelioideae, especially Leucopogon</td>
<td>Homoplasious</td>
</tr>
<tr>
<td>10. Leaf teeth</td>
<td>Teeth present, ending secondary veins</td>
<td>10a. Leaves without true teeth</td>
<td>Styphelioideae except Prionoteae</td>
<td>No homoplasy within Styphelioideae</td>
</tr>
<tr>
<td>11. Leaf base sheathing</td>
<td>Leaf bases narrowed, often shortly petiolate</td>
<td>11a. Sheathing leaf bases</td>
<td>Richeeae, Cosmelieae</td>
<td>One or two origins, no other homoplasy</td>
</tr>
<tr>
<td>12. Proximity of vascular bundles to the abaxial epidermis</td>
<td>Separated by mesophyll cells</td>
<td>12a. Proximal or separated by a single layer of lignified cells</td>
<td>Styphelioideae except Trochocarpa, Cyathopsis and Pentachondra dehiscens</td>
<td>Little homoplasy</td>
</tr>
<tr>
<td>13. Attachment of abaxial mesophyll to epidermis</td>
<td>Attached</td>
<td>13a. Epidermis + uniseriate hypodermis detached from the mesophyll</td>
<td>Archerieae</td>
<td>No homoplasy (but see text re A. comberi)</td>
</tr>
<tr>
<td>14. Leaf size</td>
<td>Medium-sized leaves</td>
<td>14a. Erioid leaves (scleromorphic leaves? Styphelioideae &lt; 5 mm wide)</td>
<td>Some Styphelioideae</td>
<td>Quite homoplasious within Styphelioideae</td>
</tr>
<tr>
<td>15. Specialized trichomes over the stomatal regions of the abaxial surface</td>
<td>Absent</td>
<td>15a. Short conical trichomes (&quot;papillae&quot;)</td>
<td>Styphelioideae, some Leucopogon</td>
<td>Present in many other Ericaceae</td>
</tr>
<tr>
<td>16. Micropapillae on abaxial epidermal cells</td>
<td>Absent</td>
<td>15b. Long trichomes</td>
<td>Several clades of Styphelioideae</td>
<td>Little homoplasy</td>
</tr>
<tr>
<td>17. Guard cell arrangement</td>
<td>Anomocytic</td>
<td>17a. Brachyphyacetic</td>
<td>Some Styphelioideae</td>
<td>Homoplasious (see text)</td>
</tr>
<tr>
<td>18. Stomatal arrangement</td>
<td>Irregularly arranged</td>
<td>17b. Aligned parallel to leaf axis</td>
<td>Leucopogon sensu stricto, Styphelia clade</td>
<td>Quite homoplasious</td>
</tr>
<tr>
<td>19. Stomatal distribution</td>
<td>Hyperstomatous</td>
<td>18a. Unevenly amphistomatic</td>
<td>Styphelioideae</td>
<td>Absent from some species within these clades</td>
</tr>
<tr>
<td>20. Length:width of guard cell pair</td>
<td>More or less circular (length : width &lt; 1.2)</td>
<td>20a. Elongate (length : width &gt; 1.2)</td>
<td>Most Styphelioideae</td>
<td>No homoplasy apparent</td>
</tr>
</tbody>
</table>

**Sinuosity of epidermal cell walls**—The sinuosity of the anticlinal walls of epidermal cells provides important and distinctive characters for identifying epacrid fossils (Jordan and Hill, 1995). In the present study, we have developed a quantitative measure of this trait. Because the epidermal cells in Styphelioideae are more or less rectangular and aligned parallel to the main veins, sinuosity can be measured from prepared cuticles. It is calculated as the ratio of the length of a traced outline of
longitudinal cell wall to the linear distance between the ends of
the measured section of wall. A straight wall has a sinuosity of
1, and higher numbers indicate increasing sinuosity. For this
study, abaxial sinuosity was measured on the epidermal cells
along the main veins, adaxial sinuosity was measured mid lam-
ina. Measurements were made on digital light micrographs us-
ing the image analysis software ImageJ (National Institutes of
Health, Bethesda, Maryland, USA). Means of several measure-
ments per specimen were used. Phase contrast microscopy was
used to highlight the cell walls of some taxa with thin cuticles.

High sinuosities (Fig. 2A) of both abaxial and adaxial epider-
mal cells appear to be synapomorphies for the epacrids. Except
for derived forms described later, all measured Styphelioideae
have adaxial sinuosities greater than 1.8 (character 1) and abax-
ial sinuosities greater than 1.7 (character 2). Low abaxial and
adaxial sinuosities appear to be apomorphic in some Styph-
elieae. All members of this tribe except Melichrus and Tro-
chocarpa species (excluding T. thymifolia) have abaxial
sinuosities less than 1.4 and, in almost all cases, less than 1.25
(Fig. 2B, 2C). While low adaxial sinuosities are widespread in
Styphelieae, moderately to highly sinuous (sinuosity > 1.6)
walls (Fig. 2E) occur in Acrothamnus, Acrotiche, Croninia,
Cytadhes, Cyathopsis violaceaepicata, Gen. nov. (Cytadhes
dealbata/C. pumila), Leptecophylla, Leucopogon fasciculatiis,
L. appressis, Melichrus, many Monotoca species, Pentachon-
dra, and Trochocarpa.

Epidermal cell shape and dimensions—The shape of the
epidermal cells provides distinctive characters in Styph-
elioideae. Both adaxial and abaxial epidermal cells of the sub-
family have the apomorphy of being more or less rectangular
and arranged in longitudinal rows (character 3; Fig. 2A–E),
whereas other tribes of Ericaceae sampled had irregularly
shaped and arranged cells. Richeeae and Cosmelieae have an
apomorphy of this character, in that the longitudinal walls
are more clearly parallel than in other epacrids, resulting in a
greater regularity than in the other tribes (Fig. 2A).

The mean size of the adaxial epidermal cells appears to be
useful in identifying groups within Styphelioideae (character
4), although the reconstructions are complicated by the con-
tinuous nature of the characters. The ancestral state within the
subfamily is reconstructed as having small or intermediate-
sized cells (in the range ~30–70 μm). Prionotaeae, Archerieae,
Cosmelieae, and Oligarrheneae all have mean cell lengths less
than 70 μm (less than 55 μm in the latter two groups), which
is interpreted as plesiomorphic. Longer cells are derived in
three clades, Sphenotoma (Richeaeae), Epacreeae, and Styph-
elieae (excluding the exceptions listed below) species (Fig.
2B). Most clades within tribe Styphelieae have long cells
(mean > 90 μm and up to 320 μm); however, many have short
cells (mean < 70 μm). The ancestral state analyses suggest that
the latter state is secondarily derived, though there is consid-
erable uncertainty in this due to the phylogenetic uncertainty
about relations among major clades within this tribe. An ad-
ditional feature of possible significance is that several clades
within Styphelieae (Croninia, Cyathopsis, Planocarpa, Pen-
tachandra pumila, and Trochocarpa) have very short cells
(mean lengths < 55 μm).

A length to width ratio of the interveinal regions of the abax-
ial epidermal cells of 3 :1 appears to be phylogenetically useful
(character 5; Fig. 2A–E). The ancestral state within Styph-
elioideae is clearly of short cells (length to width < 3). Groups
with longer cells include Prionotes; Dracophyllum sayeri and
most Sphenotoma species within Richeaeae; isolated species of
Cosmelieae; most Epacreeae except the possibly basal taxon
Lysinema; many clades of Styphelieae.

Venation, leaf size—Venation provides several good charac-
ters (although very narrow-leaved species may possess only
one or two main veins and are excluded from this discussion).
The presence of several main veins arising in the petiole and
extending up the leaf (character 6; Fig. 2F–l) provides a clear
synapomorphy for the family, although this may be associated
with parallel, subparallel, palmate, or even pinnaate (exclud-
ing the major veins) venation.

Many species of Prionotaeae, Archerieae, and Epacreeae have
a more prominent central vein (a midrib), but the longitudinal
veins of most species of the other tribes are approximately equal
(character 7; Fig. 2I).

Reticulate venation occurs in the other subfamilies of Eric-
ceae and, except for the three main veins, in Prionotaeae (char-
acter 8; Fig. 2I). In Archerieae, Epacreeae and some Styphelieae
the longitudinal veins are occasionally branched (character state
8a). The longitudinal veins of Richeaeae (Fig. 2H), Cosmelieae,
Oligarrheneae, and some Styphelieae (notably Leptecophylla,
Lissanthe, and Planocarpa; e.g., Quinn et al., 2005) are strongly
parallel and almost never branched (character state 8b). In some
Styphelieae groups (e.g., many Leucopogon) minor veins often
connect the main veins (character state 8c; Fig. 2F).

In some members of Styphelieae (Androstoma, Croninia,
Lissanthe, Melichrus, some Acrotiche, some Leptecophylla,
some Leucopogon, Agiortia cicatricata, Astrolooma pinfoli
nium, and Cyathopsis albicans), the major veins are distinctly raised
(character 9).

Prionotaeae, and many members of the sister group of Styph-
elioideae, Vaccinioideae, have true leaf teeth terminating sec-
ondary veins (character 10). The epacrids excluding Prionotaeae
have the derived state of lacking true teeth, although some
of these species are serrulate with single-celled “teeth” not associ-
ated with veins.

All Richeaeae and Cosmelieae have sessile leaves with broad
bases that form a sheath around the stem (character 11). All
other epacrids retain the plesiomorphic state of leaves narrowed
either to a sessile base or to a short petiole.

Several features of leaf cross sectional anatomy can be useful
in identifying fossils with three-dimensional preservation (see
Jordan et al., 2007 for a description of these). The main vascu-
lar bundles of Styphelieae (except Cyathopsis, Trochocarpa,
and Pentachandra dehiscent) are adjacent to the abaxial epi-
dermis or separated from it by a single layer of lignified cells
(Watson, 1967; Quinn et al., 2005; Jordan et al., 2007), whereas
other Styphelioideae have the more typical structure of angio-
sperms — the abaxial epidermis and a hypodermis of pho-
tosynthetic cells or fibers (in the form of bund-
le sheath extensions) between the veins and the epidermis
(character 12). Richeaeae have the derived state of bundle sheath
extensions comprising stacks of longitudinal fibres or sclereids
connecting each main vein with both upper and lower epidermides
(character state 12b). There has been secondary loss of adaxial
and/or abaxial bundle sheath extensions in some Dracophyllum
species.

Archerieae has a feature apparently unknown in any other
angiosperms—the abaxial epidermis and a hypodermis of pho-
tosynthetic cells is not directly connected to the rest of the mes-
ophyll (character 13). In one species (A. comberi), unpitted,
arm-shaped tubes connect the mesophyll and the epidermis +
hypodermis.
Leaf dimensions are very homoplasious, although there does appear to be some phylogenetic signal. Most species have small to very small, scleromorphic leaves, typically less than 5 mm wide (character state 14a). However, the other tribes of Ericaceae are very variable for this trait, so the ancestral state is ambiguous. Large to very large leaves (more than 15 cm and, in some species, up to 1.5 m long) occur in many Richeeae and are absent from all other tribes except for a few species of Leucopogon.

**Papillae and trichomes**—Trichomes occur widely within the epacrids, but two types of trichome associated with the stomatal bands appear to be important in identifying epacrid leaf fossils. Short, conical trichomes (often described as papillae; e.g., Quinn et al., 2005) obscure the stomata in most or all species of Acrothamnus, Acrotiche, Cyathodes, Cyathopsis, Leptecophylla, Lissanthe, Monotoca, and Planocarpa (character 15; Fig. 2C, 2D). This list includes members of all major clades of Styphelieae except Pentachondra (Quinn et al., 2003, 2005), and well-supported clades (Agioritia and Acrotriche) and even species (e.g., Planocarpa species) show both presence and absence of these trichomes. In the taxa with stomatal regions sunken below the veins listed earlier (except Astroloma pinifolium), the
Stomatal regions are densely hairy with conical trichomes that are longer than the short trichomes mentioned above (character state 15b). The relationship between these two trichome types is not clear, but both traits are very distinctive and unknown in any other tribes of Styphelioidae.

The abaxial epidermal cells of most species of _Leucopogon_ sensu stricto and the _Styphelia_ clade have papillae formed from small thickening of the outer (periclinal) walls of the epidermal cells (character 16; Fig. 2B). Most cells have a longitudinal line of papillae, which are sometimes fused into an uneven ridge, whereas the conical trichomes described earlier are complete cells and occur singly. An unrelated species (_Brachyloma daphnoides_) has a single domed papilla on each cell.

**Stomatal characters**—The apparently ancestral state for guard cell arrangement in Styphelioidae is anomocytic (character 17; Fig. 2B), whereas Richeeae have brachyparacytic stomata (Fig. 2A). Watson (1967) proposed that Cosmelieae have cyclocytic stomata, but in the present study, we could not reliably distinguish this state from the anomocytic state. However, some Vaccinioideae have brachyparacytic stomata. In those species in which short conical trichomes obscure the stomata, the stomata can be seen by mounting well-prepared cuticles with the inner surface up and observing at high magnification (1000×).

The Styphelioidae share a synapomorphy of having stomata aligned more or less parallel to the main veins, whereas other Ericaceae have more or less randomly aligned stomata (character 18). Rare exceptions include some species of _Lysinema_ in which a high proportion of the stomata occur at angles from the main veins.

Most Styphelioidae and the other subfamilies of Ericaceae have hypostomatic leaves (character 19), but most Cosmelieae, a few Richeeae ( _Richea pandanifolia, Dracophyllum minimum, D. sayeri_ ), several New Caledonian _Dracophyllum_ species, and most species of _Dracophyllum_ subgenus _Oreothamnus_ ), and a few Stypheliaceae ( _Cyathodes glauca, Lissanthe sapida, some Leucopogon_ from Western Australia (Fig. 2E) also have some stomata on the adaxial surface.

The general state within Ericaceae, including all Styphelioidae except tribe Stypheliaceae, is of more or less circular stomata (character 20). Virtually all Stypheliaceae have elongated stomata (length to width of guard cell complex > 1.2) (Fig. 2B), the exceptions being _Androstoma, Planocarpa_, some species of the genera _Acrotiche, Leucopogon, Brachyloma, Trochocarpa_, and _Cyathopsis_. This state is virtually unknown among other the other tribes (the exception being some Richeeae).

**Macrosilos**—Two distinct types of leaf macrofossils were identified as likely eparids in the lignites. The first type consisted of quite common leaf fragments in blocks of lignite. These were leaves with broad, very short petioles, parallel venation with branches leading to the margins, and occasional branches in inner veins. Cuticle preparations revealed sinuous epidermal cell walls and the characteristic short conical trichomes characteristic of some Stypheliaceae (compare Figs. 2 and 3). The second type was identified from macerated material alone and consisted of fragments lacking base or apex (Fig. 4A–C). However, the specimens had apparently unbranched parallel venation, very highly sinuous epidermal cell walls and brachyparacytic stomata, which is entirely consistent in morphology with Richeeae, which includes _Dracophyllum_, by far the most diverse genus of Ericaceae in New Zealand. These two types are described as new species, and their affinities discussed later.

**Fossil pollen**—Most Ericaceae, excluding the two earliest-diverging subfamilies, Enkianthoideae and Monotropoideae (Golam Sarwar and Takahashi, 2006), produce scabrate, oblicate tetrads pollen with equal-sized, tricolporate monads. Fossil pollen conforming to this description have mostly been described as _Ericipites_ species, although they may also be described as species of _Dicotetradites_ or _Bismapollis_. Such pollen is produced by all Styphelioidae except some Stypheliaceae that produce tetrads in which three of the four grains are aborted and highly reduced. Fossil pollen with this form is described as _Monotocidites galeatus_ Macphail, Partridge & Truswell or _Monotoca_-type. Although _Ericipites_ includes a range of morphotypes (sometimes described as separate species and sometimes described informally), these pollen are morphologically conservative. As a result, there are few characters on which to base identifications. Furthermore, most pollen types that have been assigned to living groups have been identified only on the basis of general similarity to extant taxa, without recognition of apomorphic features. In general, these morphotypes are difficult to assign to living or extinct groups within Ericaceae.

The relative lack of taxonomic precision in identifying _Ericipites_ and related forms can be illustrated by the fact that _E. longisulcatus_ was first described from Colorado and matches pollen of disparate Ericaceae, including _Andromeda_, a member of Vaccinioideae (Wodehouse, 1933) and several groups of Styphelioidae. Another example is the fossil tetrad _Paripollis ochesis_ Partridge, which Macphail et al. (1994) described as _Eparis virgata_-type but was considered by Raine et al. (2008) to be from an unknown dicotyledon. This taxon has been recorded from both Australia and New Zealand since the Middle Eocene (Macphail et al., 1994). Also, members of other families (e.g., _Carpodetus_; Rousseaeae) have pollen that could be placed in _Ericipites_ if found as fossils.

One fossil pollen type of particular pertinence to the current study is _Ericipites longisulcatus_ Wodehouse. This pollen species contains a range of morphotypes that have been variously ascribed to _Dracophyllum, Leptocypella_ (as _Cyathodes_), and _Eparis_ (Raine et al., 2008). The _Dracophyllum_-type tetrads are similar to those of _Extant Dracophyllum_, but there is insufficient data on pollen at present to determine whether they belong to the New Zealand clades of this genus. Also, given that some of the genera within tribe Richeae are paraphyletic (Wagstaff et al., in press; see Fig. 1), it is not even possible to ascribe the pollen to the crown group of the tribe.

_Ericipites_ species first appear in the fossil records of New Zealand and Australia/Antarctica in the Late Cretaceous (e.g., Mildenhall, 1980; Dettmann, 1994, Macphail et al., 1994) and have been present apparently continuously since then. _Dracophyllum_-type pollen (though usually less well preserved and therefore less confidently identified) has occurred since the Middle Eocene. Another type, _Bismapollis emaciatus_ Partridge in Stover and Partridge (1973) was identified in New Zealand Late Eocene by Pocknall and Turnbull (1989), and compared with the Eparidaceae (cf. _Eparis_?) by Macphail (1999). Well-preserved grains of _Ericipites_ occur in the same leaf beds as the macrofossils at Newvale (Ferguson et al., in press). These grains include rare specimens of _Dracophyllum_-type (Fig. 4D, 4E).
SYSTEMATICS

Family—Ericaceae

Subfamily—Styphelioideae

Tribe—Styphelieae

Cyathodophyllum G. J. Jord. & Bannister, gen. nov. (Fig. 3)—
Diagnosis—Leaves simple, entire, or finely serrate, shortly petiolate or sessile, bifacial; scleromorphic; stomata restricted to the abaxial surface or nearly so. Leaves with many major veins arising separately from the base of the lamina and extending down the lamina, outermost veins branching occasionally, inner veins rarely branching. Anticlinal cell walls of adaxial epidermal cells highly sinuous. Abaxial leaf surface with short, conical trichomes covering the stomatal region and obscuring the stomata. Stomatal axes approximately parallel to long axis of leaf. Subsidiary cells obscured by guard cells. Guard cells forming an elliptical torus in surface view.

Type species—Cyathodophyllum novae-zelandiae

Etymology—
Referring to the possible affinity with extant Cyathodes.

Cyathodophyllum novae-zelandiae G. J. Jord. & Bannister sp. nov. (Fig. 3)—Diagnosis—Leaves ovate, apex acuminate, adaxial epidermal cells about 40–100 µm by 20–30 µm, abaxial epidermal cells over the veins with straight anticlinal walls.

Description—Leaves ovate, slightly convex, obovate, or elliptical, maximum estimated length 25 mm, maximum width 6 mm, subsessile, petiole broad and flattened, apex unknown. Leaves with numerous closely spaced veins arising in the petiole.
and running more or less parallel up the leaf, outer veins occasionally branched with the outer branch diverging at an angle of ~75° from the long axis of the leaf, inner branch continuing more or less parallel to the long axis of the leaf; inner main veins occasionally branched, with both branches running more or less parallel. Adaxial cuticle with epidermal cells 40–100 μm by 11–15 μm, elongate, aligned in incomplete ranks up the leaf, anticlinal walls strongly sinuous (sinuosity ~2.4), side walls parallel with the veins, end walls often oblique, periclinal walls lacking papillae or other thickenings, trichomes or stomata apparently absent. Abaxial cuticle with stomata restricted to interveinal areas, obscured by a dense covering of short conical trichomes, ~15 μm long by 8 μm wide, located at the junctions of epidermal cells; stomata elliptical, anomocytic, more-or-less uniform in size and shape, 21–25 μm long by 18–20 μm wide; stomatal pores ~9 μm long. Epidermal cells in stomatal bands isodiametric or slightly elongated parallel to the long axis of the leaf, rectangular, rhomboidal, pentangular or hexangular. Epidermal cells over veins rectangular 25–40 μm by 9–13 μm wide, end walls sometimes oblique, arranged in long, but incomplete ranks parallel to the veins, anticlinal walls straight, periclinal walls uniform.

Holotype—OU32743 held in the collections of the Department of Geology, University of Otago.

Etyology—Named for the occurrence of this species in New Zealand.

Type locality—Newvale Mine Seam W6, Gore Lignite Measures, Southland, New Zealand

Specimens examined—OU32167, OU32734–OU32744

Remarks—This species has a series of apomorphic features by which it can be confidently identified as an epacrid—the small, scleromorphic, entire leaves with parallel but occasionally branched veins, the rectangular adaxial epidermal cells aligned with the veins and with strongly sinuous anticlinal walls, the short conical trichomes obscuring the stomata, and the stomatal arrangement. Furthermore, this species has apomorphic features that are only known in Styphelieae—short, conical trichomes obscuring the stomata and nonsinuous abaxial epidermal cell walls. Also, the venation and elongate stomata are typical of many Styphelieae and unlike almost all other epacrids.

Cyathodophyllum novae-zelandiae is similar to the Tasmanian endemic genus Cyathodes sensu stricto. It is consistent with Cyathodes, especially C. glauca and C. platystoma C.M. Weiller, in all features except that the adaxial sinuosity is higher (2.4 for the fossils vs. ~1.3–1.9 for extant Cyathodes) and having slightly higher frequency of vein branching. Given that high adaxial sinuosity is clearly the plesiomorphic state, there is nothing to preclude this fossil from being sister to extant Cyathodes.

An alternative, but less convincing placement of the fossil could be as sister to the New Caledonian genus Cyathopsis. The fossils differ from the three extant species of Cyathopsis, in some cuticular features—notably the adaxial sinuosity of the fossils (2.4) is considerably greater than any Cyathopsis (all < 1.8), and the adaxial epidermal cells of the fossils (mean of ~65 μm) are longer than those of Cyathopsis (means < 55 μm). However, the fossils are similar to Cyathopsis species, especially C. violaceospicata, in all other features. Overall, affinity with Cyathopsis cannot be excluded.

Although the evidence placing these fossils as sister to Cyathodes is not compelling, one can infer that Cyathodophyllum novae-zelandiae is not ancestral to, or sister of, any extant New Zealand epacrids. This inference can be made because the extant New Zealand clades of Styphelieae are each nested within small clades also present in Australia, and these clades have characteristic features. The fossils lack the narrow, mucronate leaves of Lep-tecophylla. Androstoma can be excluded because this clade has tiny, closely revolute-margined leaves, long conical trichomes, and adaxial epidermal cells with moderate sinuosity epidermal cell walls (sinuosity ~1.6 compared to 2.4 in the fossils). The Cyathodes dealbata/pumila clade can be excluded because this clade has tiny leaves, only moderately sinuous epidermal cell
walls (sinuosity ~1.7) and small, narrow stomata (~19 × 9 μm compared to ~23 × 19 μm). Pentachondra pumila can be excluded because the fossil leaves are large, with abaxial short conical trichomes. The fossils are unlikely to be close to any of the extant New Zealand Leucopogon species: these latter all lack the short conical trichomes and have elongate stomata, adaxial epidermal cells that are elongated with nonsinusuous walls, and micropapillae on the abaxial epidermal cells. It is unlikely that the fossil is a sister or direct ancestor of Acrothamnus colensoi because that species is nested within a well-supported clade (Acrothamnus species except A. spathaceus; Quinn et al., 2005) that has very long adaxial epidermal cells (~150 μm vs. ~65 μm for the fossils) and small leaves (~15 mm long).

Cyathodes sensu stricto is largely restricted to forests and heaths in relatively well-watered regions (Curtis, 1963) and, like most epacrids, are associated with nutrient-poor soils (Stevens et al., 2004).

**Tribe**—Richeeae

*Richeaphyllum G. J. Jord. & R. S. Hill—Richeaphyllum waimumuensis* G. J. Jord. & Bannister sp. nov. (Fig. 4A–C)

*Etymology*—Named for the occurrence of this species in the Waimumu Coalfield.

*Holotype*—OU32214 held in the collections of the Department of Geology, University of Otago.

*Type locality*—Newvale Mine Seam W6, Gore Lignite Measures, Southland, New Zealand

*Other specimens examined*—OU32213, OU32194

*Diagnosis*—Leaves more than 4 mm wide, epidermal cells of adaxial surface ~30 μm long, epidermal cells of the abaxial surface ~25 μm long.

*Description*—Leaves at least 10 mm long, at least 5 mm wide, but plausibly considerably larger. Veins parallel, apparently unbranched, closely spaced. Leaves hypostomatic or nearly so. Stomata in bands 2–3 rows wide, brachyparacytic, aligned with long axis of the leaves, guard cell pairs broadly elliptical ~21–24 μm by 18–20 μm, pores ~11 μm long. Epidermal cells of the abaxial surface between stomatal bands shortly rectangular, strongly aligned parallel to the veins, with approximately 4 rows between adjacent stomatal bands, cells 18–25 μm by 10–14 μm, with strongly sinusuous antical walls (sinuosity ~2.5). Epidermal cells of the abaxial surface rectangular to rhomboidal, aligned parallel to the veins, cells 18–50 μm by 13–18 μm, with strongly sinusuous antical walls (sinuosity ~2.5).

*Remarks*—This fossil is clearly a member of Richeeae because of the combination of parallel venation, brachyparacytic stomata, stomata aligned with the long axis of the leaf, and very strongly sinusuous, rectangular epidermal cell walls. It therefore should be assigned to *Richeaphyllum*, the fossil genus described by Jordan and Hill (1995) for members of this tribe. This species is distinct from the other described species of *Richeaphyllum*, *R. jonesii* G.J.Jord. & R.S.Hill from the Early Oligocene in Tasmania (Jordan and Hill, 1995) in having larger leaves (*R. jonesii* has leaves less than 4 mm wide), and much smaller epidermal cells (*R. jonesii* has epidermal cells ~75 × 25 μm).

On the basis of the observed features in these fossils, *Richeaphyllum waimumuensis* could be placed equally parsimoniously in virtually any place within Richeeae except nested within *Sphenotoma*. The adaxial and abaxial epidermal cells are unusually small for Richeeae, but relatively small cells of similar shape occur in all clades within Richeeae except *Sphenotoma*, which has much larger cells (mean lengths of adaxial and abaxial cells > 90 μm and > 60 μm for all species sampled). The large cells of *Sphenotoma* appear to represent a derived state.

As with *Cyathodophyllum*, these fossils are entirely consistent with wet climates and nutrient-poor soils. Most Richeeae (except some members of the New Zealand subgenus, *Oreothamnus*) occur in such habitats.

**DISCUSSION**

The fossils described here show that by the Early Miocene, and possibly as early as the Late Oligocene, New Zealand hosted at least two lineages of epacrids. Prior to the present work, there have been no clear Pre-Pliocene fossil records of epacrids from New Zealand. An Early Miocene cuticle described by Pole (2008) as being epacrid may represent an extinct epacrid lineage or some unknown group. Although that fossil cuticle shows several representative features of the subfamily (strongly sinusuous cell walls, longitudinally aligned stomata consistent in general form with epacrid stomata), it is inconsistent with any extant group of the subfamily. The stomata are brachyparacytic (a characteristic of Richeeae), but the cuticle lacks the distinctive, strongly parallel-sided epidermal cells and regularly arrayed stomata found in all known Richeeae. The stomata and epidermal cell shapes of some *Gaultheria* (*Vaccinioideae*) are similar to those of the fossil cuticle, but we are unaware of extant Vaccinioideae with strongly sinusuous walls.

*Cyathodophyllum novae-zelandiae* is the first unambiguous pre-Pleistocene macrofossil of Stylphelieae anywhere (Jordan and Hill, 1996; Jordan et al., 2007). The previous record was the Mid Miocene occurrence in Australia of the distinctive and derived pollen type, *Monotocidites galeatus* (*Monotoca*-type) (Martin, 1993), although Jordan and Hill (1996) illustrated Late Oligocene-Early Miocene leaves from Tasmania that may be from this tribe. The Newvale fossils therefore provide a calibration point for molecular dating of southern hemisphere Ericaceae. The fossils are of a clade (possibly *Cyathodes sensu stricto*) now extinct in New Zealand.

The fossils also document the Late Oligocene-Early Miocene fossil presence in New Zealand of tribe Richeeae, now represented by two taxonomically and ecologically diverse clades of the genus *Dracophyllum* (Wagstaff et al., in press). However, the features present in *Richeaphyllum waimumuensis* appear to be plesiomorphic within Richeeae, so that, while the fossils are consistent with the extant New Zealand clades they could also belong to some clade extinct in New Zealand. The species that produced these leaf fragments may have contributed some or all of the well-preserved *Dracophyllum*-type pollen that occur within the sediments, particularly considering that another study of leaves and pollen from the Newvale leaf bed (Ferguson et al., in press) has shown a relatively close match between the overall assemblages of leaf macrofossils and pollen. However, like the macrofossils, the pollen tetrads show plesiomorphic features of the whole tribe and therefore do not provide clear evidence for continuous presence of *Dracophyllum* in New Zealand.

Unpublished molecular dates for the extant New Zealand Richeeae are much younger (~7 million years old; Wagstaff et al., in press) than the New Zealand fossils attributed to Richeeae (25–20 million years for the leaves and 47–40 million for *Dracophyllum*-type pollen). Thus, either the molecular dates substantially underestimated the ages of New Zealand Richeeae or
the older records of Dracophyllum-type pollen and the Newvale macrofossils were produced by plants belonging to lineages no longer in the archipelago. There are relatively large uncertainties in these molecular age estimates (Wagstaff et al., in press), but constraining the stem of the New Zealand clades to be at least 20 million years old (i.e., consistent with the fossils) generates unrealistically old estimates of other clades within Ericaceae (e.g., an estimate of 1.33 billion years for the crown of Ericaceae). This would suggest that Richeaphyllum waimumuensis and the Dracophyllum-type pollen were produced by extinct lineages, although the uncertainty in molecular dating methods leaves some ambiguity in this inference.

**Biogeographic implications**—As noted by Jordan and Hill (1996), the early (pre-Miocene) fossil pollen record of Ericaceae in Australasia is of Ericipites grains that cannot be confidently assigned to any living group. The presence of an extinct lineage of Styphelieae reinforces this inference that some or all of the Late Cretaceous and Paleogene Ericipites pollen in New Zealand (Couper and McQueen, 1954; Couper, 1960; Mildenhall, 1980; Raine, 1984) may be derived from lineages of epacrids now extinct in New Zealand. The cuticle described by Pole (2008) is also consistent with these inferences—either this species is an extinct lineage of epacrid not closely related to any extant New Zealand epacrid, or it is not an epacrid at all.

Thus, even though the fossil record suggests that Ericaceae has been present in New Zealand since the Late Cretaceous, this should not be taken as evidence that any group within the family has been present since this time. The fossil evidence therefore provides no compelling evidence for great antiquity of any of the 16–18 disjunctions between New Zealand and other continents apparent within the family (Table 1). However, discovery of new macrofossils, and/or critical reanalysis of living and fossil pollen, using for example scanning and/or transmission electron microscopy, and analyzing this evidence phylogenetically—as done for Proteaceae pollen by Sauquet et al. (2009)—may overcome these limitations.

The biogeographic implications of the macrofossils presented here, as well as the potential for better taxonomic resolution for pollen also illustrate how careful analysis and critical appraisal of the fossils should help avoid misleading inferences. In one case presented here, detailed evaluation of both fossils and living plants was needed to demonstrate that Cyathodophyllum was an extinct lineage in New Zealand. In the second case, it would be easy and incorrect to argue that the presence of Dracophyllum-like pollen sporadically through the fossil record, combined with an isolated incidence of Dracophyllum-type macrofossils is evidence for continuous presence of Dracophyllum in New Zealand. While, of course not disproving continuity of presence, careful treatment of the fossil data reveals that positive evidence is lacking.

**Conclusions**—The Australasian Ericaceae provide an interesting illustration of the value of fossils in explaining disjunctions. Although the fossil pollen record suggests continuous presence of the family in both Australia and New Zealand, the pollen rarely provide diagnostic characters for clades within the family, and the large number of geographic disjunctions deeply nested within this relatively derived group would suggest relatively recent origins for the living New Zealand clades. The fact that the pre-Pliocene New Zealand fossils are lineages that can be shown to be extinct from New Zealand (Cyathodophyllum) or may be regionally extinct (Richeaphyllum waimumuensis and the Ericaceae-type cuticle of Pole [2008]) indicates that the pollen record could well be a product of extinct taxa and therefore sheds no light on the extant New Zealand Ericaceae. This example is by no means unusual—many taxa, such as ferns, Cyperaceae, Poaceae, and Asteraceae show many more major disjunctions than do fossil types. The results also highlight the importance of extinction in biogeography. In a comparable case, Jordan and Macphail (2003) argued that even though fossil pollen of Caryophyllaceae have been present in Australia since the Mesozoic, macrofossils showed that at least some of this pollen type was carried by an extinct lineage apparently unrelated to any modern Australian Caryophyllaceae, and all the extant disjunctions in Australian Caryophyllaceae appear to be much younger. The key criterion is that, to provide evidence for the antiquity of a group of organisms within a region, fossils need to shown to be a member of, or sister to, the extant clade within that region. Even then, the possibility of repeated immigration and extinction (as argued by Graham, 2006, for Rhizophoraceae in the Caribbean region) should also be considered.

**LITERATURE CITED**


