

Origins and biogeographic patterns in Ericaceae: New insights from recent phylogenetic analyses

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Ericaceae are a diverse group of woody plants that span the temperate and tropical regions of the world. Previous workers have suggested that Ericaceae originated in Gondwana, but recent phylogenetic studies do not support this idea. The theory of a Gondwanan origin for the group was based on the concentration of species richness in the Andes, southern Africa, and the southwest Pacific islands (most of which are thought to be of Gondwanan origin). The Andean diversity is comprised primarily of Vaccinieae with more than 800 species occurring in northern South America, Central America, and the Antilles. In the Cape Region of South Africa the genus *Erica* is highly diverse with over 600 species currently recognized. In the southwest Pacific islands, Vaccinieae and Rhodoreae are very diverse with over 290 species of *Rhododendron* (sect. *Vireya*) and approximately 500 species of Vaccinieae (*Dimorphanthera*, *Paphia*, *Vaccinium*). Recent phylogenetic studies have also shown that the Styphelioideae (formerly Epacridaceae) are included within Ericaceae, thus adding a fourth extremely diverse group (approximately 520 species) in areas considered Gondwanan in origin. Phylogenetic studies of the family on a global scale, however, have indicated that these highly diverse "Gondwanan" groups are actually derived from within Ericaceae. Both Fitch parsimony character optimization (using MacClade 4.0) and dispersal-vicariance analysis (DIVA) indicate that Ericaceae is Laurasian in origin. Thus, previous suggestions that Ericaceae are Gondwanan in origin are not supported. Separate analysis of geographic areas and phylogenetic relationships among the diverse South American Vaccinieae using dispersal-vicariance analysis (DIVA) indicate that dispersal has likely played a major role in the diversification of the Andean clade of Vaccinieae into Central America and the lower elevations in northern South America. Results of the analysis indicate an Andean origin for this group, which comprises most of the ericaceous species diversity described from South America. This analysis also indicates that in taxa such as *Cavendishia* and *Satyria* s.s., the Central American species are the result of relatively recent dispersal from a South American (*i.e.*, Andean) ancestor.

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Introduction

Ecologically and economically important, the Ericaceae are a diverse group of woody plants that can be found in a variety of habitats throughout much of the temperate and tropical regions of the world (Appendix 1). They are usually found in acid soils and are associated with mycorrhizal fungi. In the tropics, Ericaceae are most diverse in mid- to high-elevation montane cloud forests (Luteyn 2002), which are also some of the most threatened ecosystems in the world (Knapp 2002). The most recent classification of the family (Kron *et al.* 2002a) recognizes eight subfamilies and 20 tribes. The distribution of these groups is generally cosmopolitan in scale, with concentrations of species diversity in the tropics, Himalayas, Australia, and the Cape Region of South Africa (Fig. 1, Appendix 1).

The most recent global treatment of Ericaceae biogeography is by Raven and Axelrod (1974) who presented a general overview of the biogeography of angiosperms and suggested that Ericaceae (not including Styphelioideae, then a separate family, Epacridaceae) likely originated in Gondwana with direct migration from Africa to South America. They considered that long distance dispersal from North America in the late Miocene had added to the diversity of Ericaceae in South America, which was already established there via the earlier African-South American land connection. The Styphelioideae (Epacridaceae) were considered to be of relatively ancient descent resulting from long distance dispersal between west Gondwana and Australasia (Raven & Axelrod 1974). Heads (2003) postulated a globally widespread complex as ancestral to Ericaceae, but his supporting argument was confined to descriptions of Malesian ericad distributions.

The most species-rich groups within the Ericaceae do indeed appear to be concentrated in what are now considered to be Gondwanan

regions of the world. These concentrations of diversity occur in four major clades within Ericaceae: Vaccinieae, Rhodoreae, Ericaceae, and Styphelioideae (Appendix 1). Vaccinieae are most diverse in the montane tropics of South America and Asia. Although generic limits within Vaccinieae are poorly understood, phylogenetic studies have shown that of the five major clades identified in a molecular systematic study of the group (Kron *et al.* 2002b), those with the largest number of species are tropical and occur in Gondwanan regions (*e.g.*, South America, New Guinea). In the Rhodoreae, *Rhododendron* section *Vireya* is the most species rich group within *Rhododendron*. *Vireyas* are tropical and most diverse in New Guinea. Africa, another Gondwanan region, also has the large and morphologically diverse *Erica* (Ericaceae) and one of the highest concentrations of species in a single genus in the world in the Cape Region. Lastly, Styphelioideae, which contain approximately 450 species are most diverse in Australia. This group was formerly thought to be distinct from Ericaceae, but recent phylogenetic studies using molecular and morphological data have shown that the group is sister to the Vaccinioideae (Kron *et al.* 2002a) and therefore derived from within Ericaceae.

Recent phylogenetic analyses in Ericaceae have provided good resolution with strong statistical support of major clades within the family based on both molecular and morphological data. With this phylogenetic framework, biogeographic patterns may be analyzed with the goal of shedding some light on the origins of the group. Here we investigate the origin and biogeographic patterns of Ericaceae using dispersal-vicariance analysis (DIVA; Ronquist 1997) and Fitch parsimony character optimization using MacClade 4.0 (Maddison & Maddison 2000). In addition, the biogeographic areas of the Andean clade within the Vaccinieae are analyzed using DIVA.

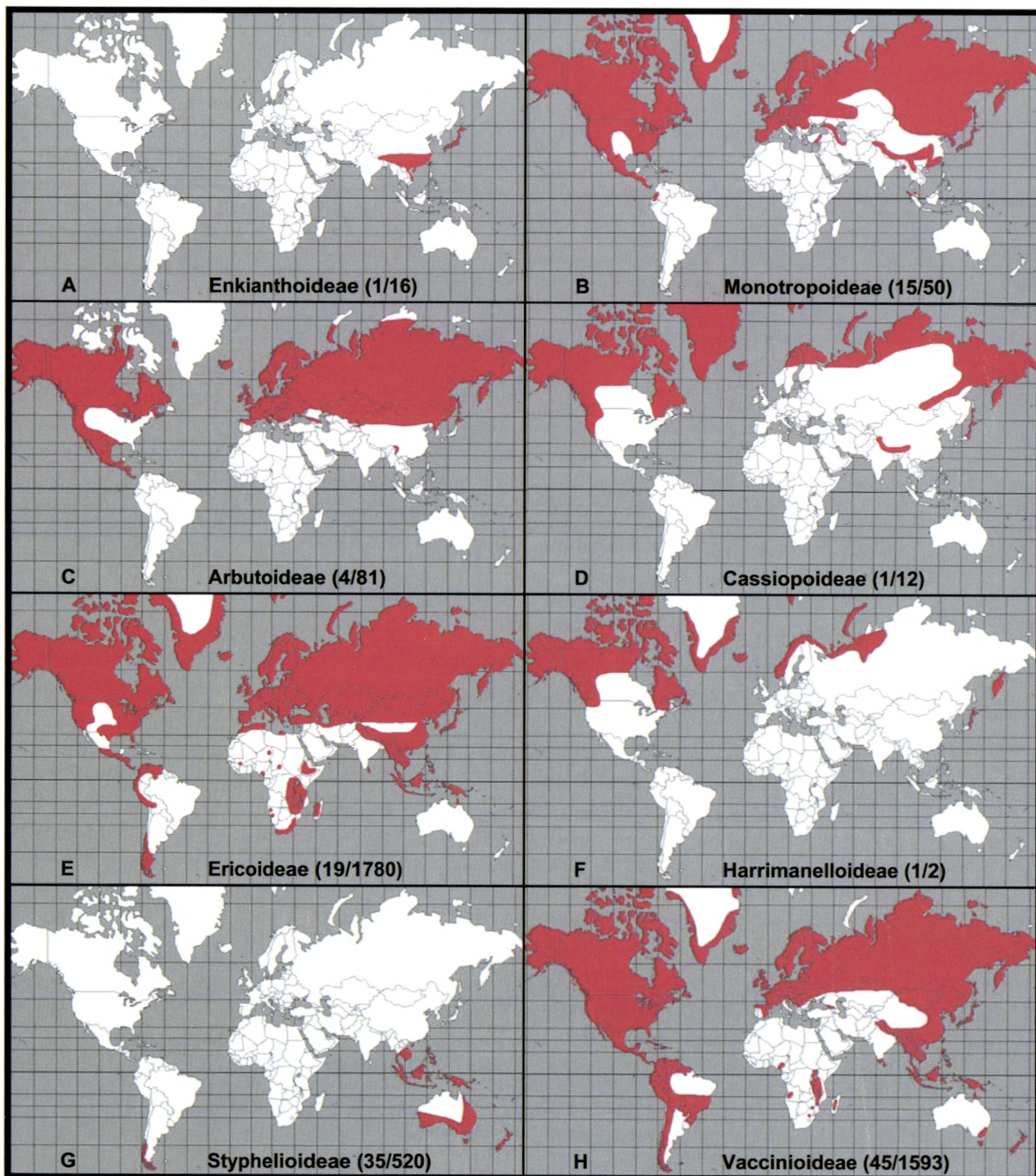


Fig. 1. World-wide distribution maps for the eight subfamilies of Ericaceae. A, Enkianthoideae. B, Monotropeoideae. C, Arbutoideae. D, Cassiopoideae. E, Ericoideae. F, Harrimanelloideae. G, Styphelioideae. H, Vaccinioideae.

Methods

In addition to DIVA and Fitch parsimony character optimization, there are several other approaches to biogeographic analysis (*e.g.*, COMPONENT; Page 1993,). We chose DIVA because it can be used with a single phylogenetic tree, rather than requiring trees from several different groups in order to construct area cladograms. DIVA does not require any a priori knowledge of geologic history and does not assume areas have a strictly divergent history (Ronquist 1997). DIVA treats areas as characters (in a presence/absence format), but minimizes dispersal and extinction events relative to vicariance (no cost) events in ancestral state (*i.e.*, area) reconstruction. Therefore, DIVA offers the possibility of identifying potential vicariance events at deep branches in the tree. However, the deepest nodes within the tree are also prone to more error (Ronquist 1997), so it is important to evaluate the group of interest at more than one taxonomic scale.

Fitch parsimony character optimization uses areas as character states and these are mapped onto the tree using MacClade 4.0 (Maddison & Maddison 2000). This provides a simple way of viewing the distribution of current taxa relative to the branching patterns in the tree. However, Fitch parsimony optimization allows fewer possible ancestral area reconstructions than DIVA because only terminals can have more than one state (*i.e.*, area).

We investigated the origin of Ericaceae using two trees. One tree included Ericaceae and several other members of the Ericales (APG 1998) and the other tree included more taxa within Ericaceae, but was rooted with *Enkianthus*. Phylogenetic trees for Ericaceae, and for the subset of the Ericales were obtained from published results in Kron *et al.* (2002a). These trees were obtained using molecular data (*matK*, *rbcL*, *nr18s*) for the Ericales tree, and combined analysis of molecular (*matK*, *rbcL*) and

morphological (91 characters) data for the Ericaceae tree. The sampling of ericalean taxa is relatively small, but relationships in the tree are in general agreement with the recent study by Anderberg *et al.* (2002) that used more genes and many more taxa. For the Andean clade analysis we used the most recent molecular tree based on three chloroplast genes/regions (*matK*, *ndhF*, *rps4*) and the nuclear internal transcribed spacer region, ITS (Powell & Kron 2003). All of the trees used for biogeographic analysis exhibited moderate to strong bootstrap support for most clades. Few polytomies were present in the Ericales and Andean trees, and the Ericaceae tree was fully resolved. Because DIVA requires fully resolved trees, the Ericales tree of Kron *et al.* (2002a) was resolved according to the results of more detailed analyses (Kron *et al.* 2002a; Kron 1997) and the Andean tree was resolved arbitrarily. The Ericales tree was modified to include an additional taxon (*i.e.*, *Clethra arborea*, authors of species names are given in Appendices 2-4) in order to better represent the geographic distribution of the Clethraceae. The placement of *C. arborea* sister to *C. alnifolia* was based on the analysis of Anderberg *et al.* (2002) which provided better statistical support and resolution for nodes basal to the Ericaceae. Two widespread species were removed from the Andean clade to facilitate the DIVA analysis.

In the biogeographic analysis of Ericaceae (both the Ericales tree and the Ericaceae tree) different scorings of areas for DIVA and Fitch parsimony character optimization were used. The broadest scoring (largest scale) used geologic information and present day distribution to define a Laurasian area and a Gondwanan area. The designation of a present day location as Laurasian or Gondwanan was determined by geologic reconstructions that place current regions in previously existing supercontinents (*e.g.*, Hallam 1994;

Scotese 2000). A smaller scale designation of areas used present day distributions on existing continents as areas. In the Andean clade analysis, five areas were recognized: Central America, Chocó (NW Colombian lowlands), Andean highland arc, an eastern lowland arc, and the Antilles.

Terminals in the biogeographic analyses are species, the same terminals as those in the molecular and molecular plus morphological phylogenetic analyses used to obtain the trees (Kron *et al.* 2002a; Powell & Kron in press). Although using species as terminals may not include the entire geographic range of the clade of interest, it avoids the same problems encountered when using higher taxa as terminals in cladistic analyses, such as polymorphisms and potential lack of monophyly (Kron & Judd 1997; Ronquist 1997; Wiens 1998).

For each analysis a matrix was constructed in MacClade 4.0. Matrices constructed for the DIVA analyses used areas as characters and scored taxa as present or absent for each area (Appendices 2-4). These matrices were then converted to batch files and analyzed using the DIVA software instructions outlined in Ronquist (1997). The "printrecs" command was used to find all of the equally optimal reconstructions. Fitch parsimony character optimization was performed in MacClade 4.0 using the trees obtained from Kron *et al.* (2002a) and Powell and Kron (2003). Matrices constructed for these analyses (Appendices 2 and 3) designated areas as alternate states of a single character (*i.e.*, geographic distribution).

Results

Both Fitch parsimony character optimization and DIVA analyses indicate a Laurasian origin for Ericaceae (Figs. 2, 3). DIVA analysis of the Ericalean matrix using smaller scale areas (Fig. 4) indicated either a North American, or

North American + Eurasian origin for Ericaceae. In the Ericales tree, both Fitch character optimization and DIVA failed to result in definitive ancestral areas for some of the deeper branches within Ericaceae. DIVA identified several equally optimal reconstructions at the *Arbutus canariensis* to *Vaccinium macrocarpon* node, as well as the next two nodes leading to the rest of the Ericaceae. Fitch analysis using more taxa within Ericaceae (Fig. 5) indicated North America as an ancestral area for many clades within the family, but was equivocal in its assessment of ancestral areas at the base of the tree. DIVA assigned North America and Asia or North America, Asia, and Europe as the Most Recent Common Area (MRCA) in two of the three equally optimal reconstructions of ancestral areas at the base of the Ericaceae tree (Fig. 6). A third equally optimal ancestral reconstruction is Africa + North America, Asia, and Europe. However, in DIVA the reliability of ancestral assignments decreases deeper in the tree (Ronquist 1997). Taking this into consideration along with the fact that the first two optimized areas in the Ericaceae tree correspond to the results of the DIVA analysis of Ericales, these results clearly indicate a Laurasian origin for Ericaceae. Within the Ericaceae, Fitch parsimony character optimization (Fig. 5) indicates North America as the ancestral area for much of the group. DIVA analysis (Fig. 6) indicates North America as a key ancestral area for the origin of Vaccinioideae and Ericoideae. Within Vaccinioideae DIVA analysis indicates that there have been at least two dispersals into South America leading to the Vaccinieae and portions of Gaultherieae (Fig. 6). Ancestral area reconstruction within Gaultherieae is not clear, with DIVA recognizing several equally optimal ancestral areas at the *Gaultheria-Diplycosia-Tepuia* node (Fig. 6). Within the Stypelioideae the occurrence of *Lebetanthus myrsinites*, endemic to southern Chile, is indi-

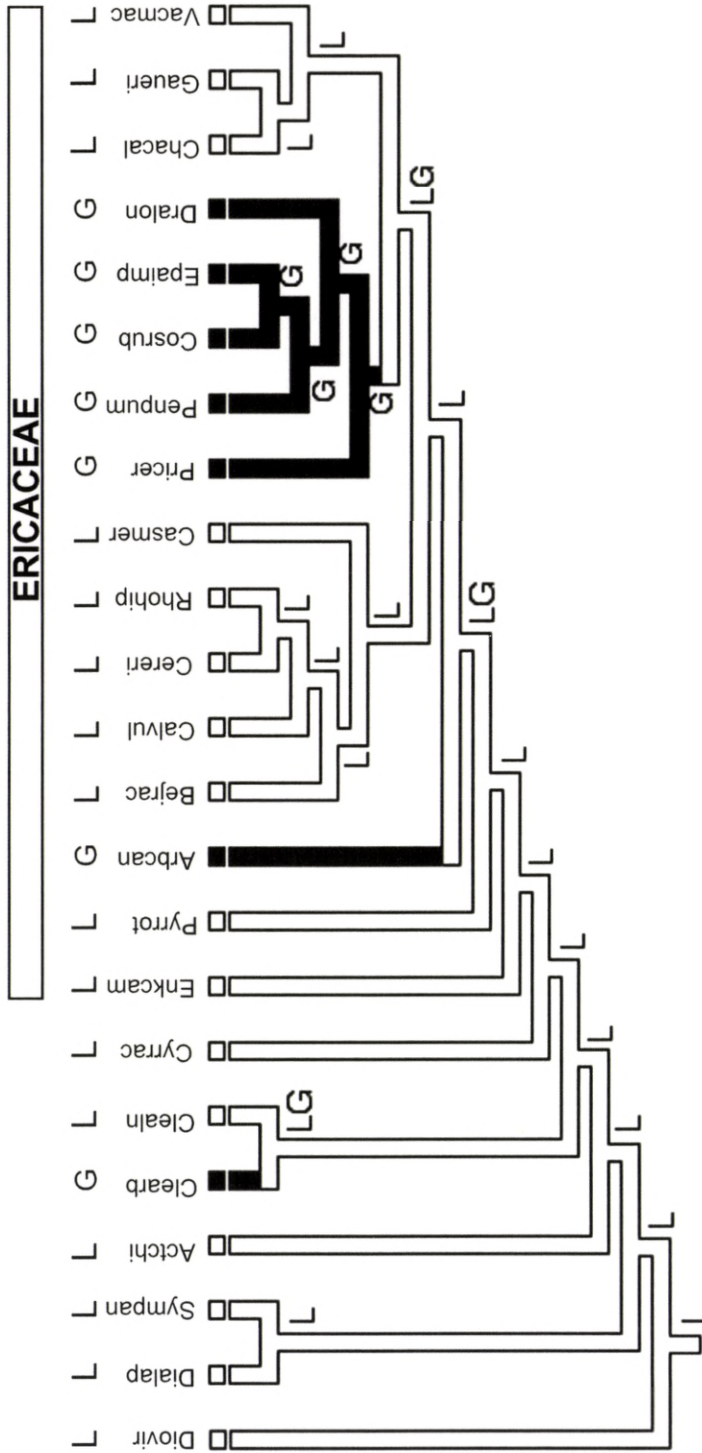


Fig. 2. Results of Fitch parsimony character optimization and DIVA analysis of Ericales using two areas; Laurasia (L, white branches) and Gondwana (G, black branches). Present day areas of occurrence are indicated above terminal branches. DIVA reconstruction of most recent common area (MRCa) is indicated at the nodes. One optimal reconstruction of ancestral areas was found in DIVA. Species are listed in Appendix 2.

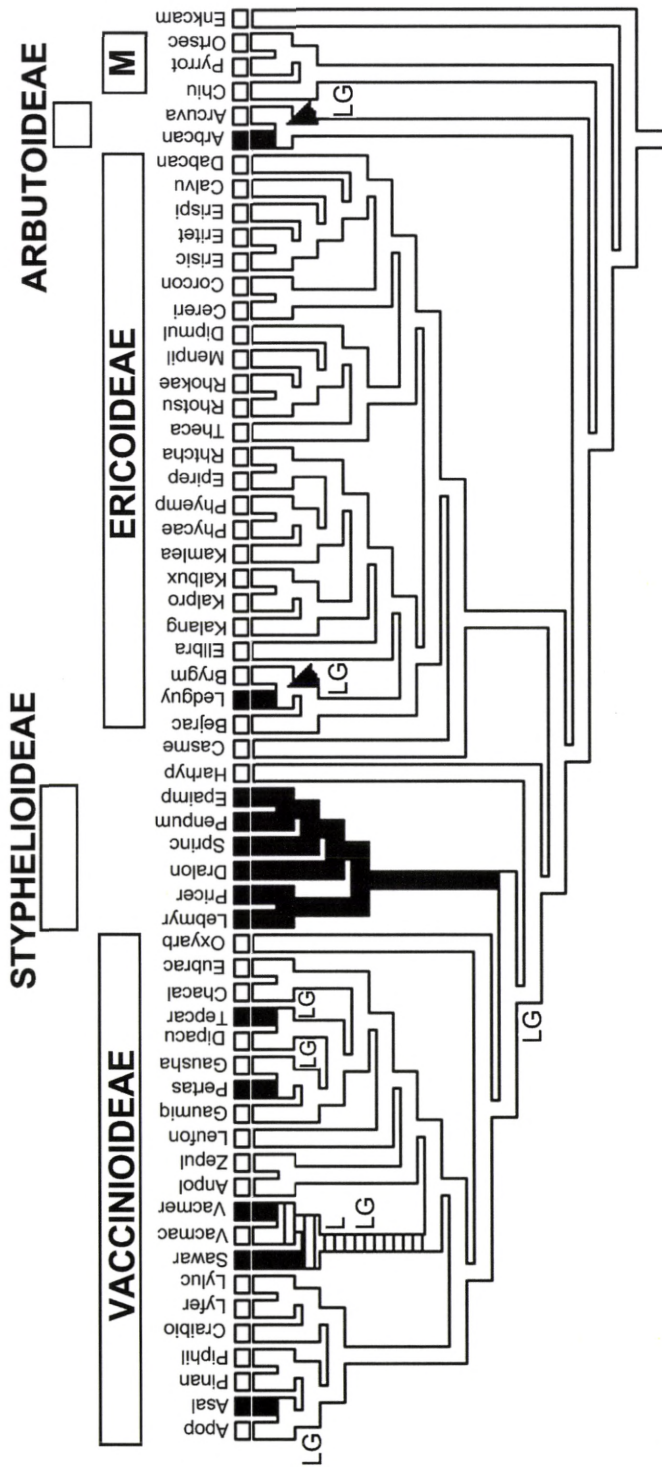


Fig. 3. Results of Fitch parsimony character optimization and DIVA analysis of Ericaceae using two areas: Laurasia (L, white branches) and Gondwana (G, black branches). Present day areas of occurrence are indicated above terminal branches. DIVA reconstruction of MRCA is indicated at the nodes. Nodes with more than one optimal reconstruction are indicated by additional MRCA notations. Two equally optimal reconstructions were found in DIVA. All nodes are Laurasian unless otherwise indicated. M indicates Monotropoideae. Species are listed in Appendix 3.

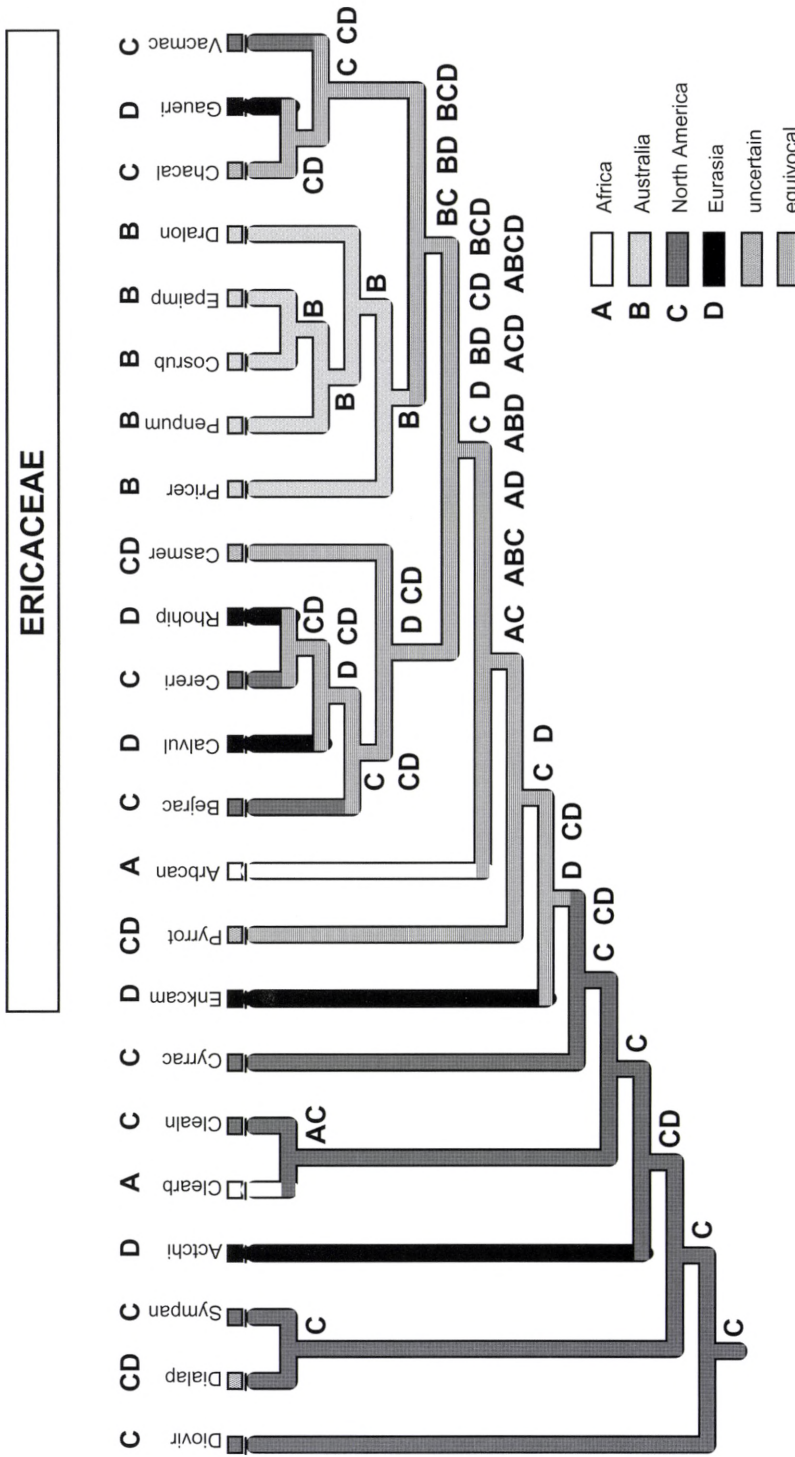


Fig. 4. Fitch parsimony character optimization and DIVA analysis of Ericales using four regions. Notation for MRCAs is the same as for Figs. 2-3. Multiple, equally optimal reconstructions are indicated at the nodes (18 reconstructions total).

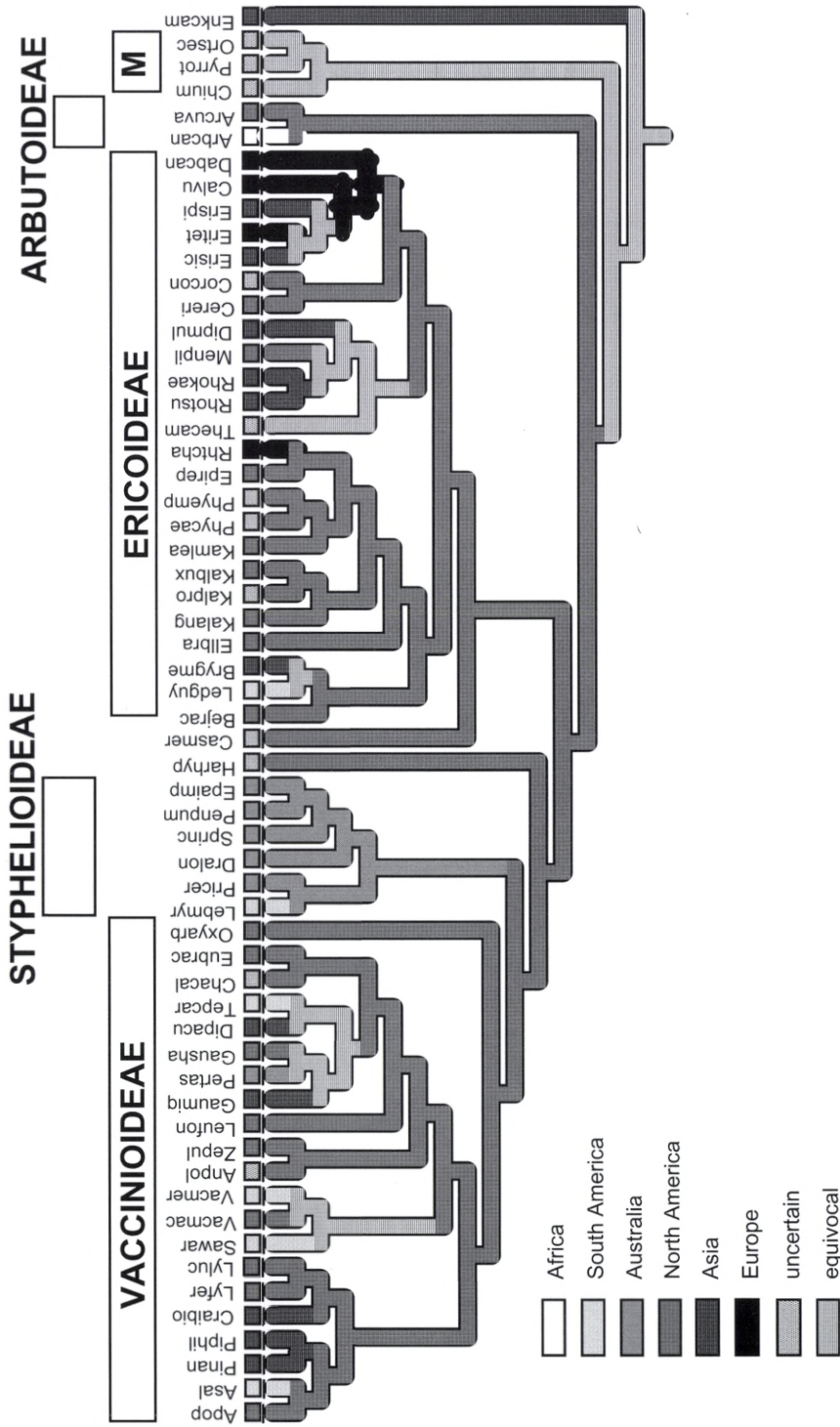


Fig. 5. Results of Fitch parsimony character optimization of Ericaceae using 6 regions. M represents Monotropoideae.

cated as a dispersal event. North America is also indicated as the MRCA of Ericoideae (Fig. 6). The presence of *Bejaria* and *Ledothamnus* in South America is indicated as the result of one or more dispersal events. Within the Rhodoreae, several equally optimal reconstructions are indicated, but all of these suggest a Laurasian origin. Nevertheless, the Asian diversification of *Rhododendron* (here represented by *R. tsusiophyllum* and *R. kaempferi*) appears to be relatively recent. The Ericaceae + Empetreae clade has a MRCA of North America + Europe with a vicariance event indicated in the divergence between Ericaceae (Europe + Asia) and Empetreae (North America). However, these results are likely a simplification of more complex biogeographic relationships because no representative of *Empetrum* (widespread in boreal latitudes, with disjunct *E. rubrum* in southern South America) was included in the analysis. The presence of Arbutoideae (represented by *Arbutus canariensis* and *Arctostaphylos uva-ursi*) in Africa is indicated as a result of vicariance. The Monotropeoideae are generally widespread and DIVA indicates the MRCA of this clade as North America + Europe.

Analysis of biogeographic areas in the Andean clade of the blueberry tribe (Vaccinieae) resulted in eight equally parsimonious reconstructions (Fig. 7). DIVA indicates that much of the diversification in Vaccinieae occurred in the Andean highland arc. More recent speciation may have been the result of subsequent dispersal to lower elevations which could explain the distribution of *Anthopterus wardii* and *Satyria grandifolia* in the Chocó, and *Satyria cerander* in French Guiana. The *Thibaudia* clade is Andean in origin, as is the *Ceratostema-Macleania* clade. The results also indicate dispersal as the primary event responsible for the presence of Andean clade species in Central America. However, the sampling of Vaccinieae must be much more complete

before any detailed conclusions can be made about the role of dispersal in tropical blueberry speciation.

Discussion

The earliest published fossil evidence for likely existence of Ericaceae based on flowers is *Paleoenkianthus* (Nixon & Crepet 1993). This fossil was found in Turonian deposits in North America (New Jersey) and, if correctly identified, indicates the existence of Ericaceae in the Late Cretaceous (~90 mya). At that time, paleogeographic plate reconstructions (Cox 1974; Scotese 2000) place eastern North America connected to Europe (either directly or through a series of islands) and northwestern North America proximate, or possibly connected, to Asia. The DIVA analyses (Figs. 3, 4, 6) that indicate a Laurasian origin (either North America, or North America + Eurasia) for Ericaceae are therefore at least not in conflict with the geological/tectonic information presently available. Based on at least some of the equally optimal reconstructions of ancestral areas by DIVA, a widespread common ancestor to the majority of Ericaceae (all Ericaceae but *Enkianthus* and Monotropeoideae; Fig. 3) may have occurred along the coastline of the developing Tethyan seaway and subsequent vicariance may have been a major factor in the initial divergence of the ancestors of Arbutoideae, Ericoideae, and Vaccinioideae due to the continued drifting apart of Africa, Europe, and North America. Arbutoideae have been postulated as a group that diversified along the Tethys seaway (Hileman *et al.* 2001) which makes their occurrence in what is now North America, Mediterranean Europe, Asia, and Africa comprehensible. However, due to the lack of detailed phylogenetic studies of Arbutoideae, Ericoideae, and Vaccinioideae these hypotheses remain to be tested.

The occurrence of large groups such as *Erica*

spp. and Styphelioideae in regions formerly part of Gondwana is explained by dispersal events according to DIVA. However, widespread occurrence and subsequent extinction is an alternative that DIVA does not readily indicate (Ronquist 1997). In the case of Styphelioideae there is fossil evidence of the occurrence of this group in southern Africa in the Paleocene (Scholtz 1985) and in several sites in northern Europe from the early Eocene (~57 mya) to the late Miocene (~6.7 mya: data from The Paleobiology Database, <http://www.pbdb.org>). DIVA analysis indicates a widespread ancestor across Australia and North America at the Vaccinioideae-Styphelioideae node (Fig. 6), but these two areas were never in direct contact. It seems more likely, given the fossil evidence, that the ancestor to Vaccinioideae and Styphelioideae was widespread and that vicariance and subsequent extinction of Styphelioideae in Europe and Africa are the causes of the present day distribution of Styphelioideae. Although the African species of heather (*Erica*) were not included in the analyses presented here, the addition of these taxa to the tree and subsequent DIVA analysis did not alter the hypothesis of dispersal from Eurasia to Africa (results not shown). This is because the African species of *Erica* are monophyletic and derived from within the European/W. Asian species of *Erica* (McGuire 2003). Other African members of Ericaceae include species of *Agarista* and *Vaccinium* and, based on the results presented here, are likely to be attributed to long distance dispersal. However, phylogenetic studies of these African members of otherwise North American, European, or Asian clades are necessary before details of the biogeography of African Ericaceae can satisfactorily be addressed. In addition, other methods of biogeographic analysis may provide more insight into the history of Ericaceae.

An alternative to the general view that

groups most diverse in the tropics likely originated there may be found in the boreotropics hypothesis. First put into a phylogenetic framework by Lavin and Luckow (1993), the hypothesis originally referred specifically to diversity in tropical North America (Tiffney 1985a, b; Wolfe 1975). The general pattern obtained from DIVA analysis of the Ericaceae is one that supports a boreotropical origin for the group with subsequently more recent diversification in tropical Asia, southern Africa, and tropical South America. In addition, the results presented here support a North American origin for some of the major groups within Ericaceae such as Vaccinioideae and Ericoideae. Within the Vaccinioideae, the MRCA of Gaultherieae (Kron *et al.* 2002b) is difficult to establish, as DIVA found seven equally optimal reconstructions for this node (see double asterisk in Fig. 6). The clarification of phylogenetic relationships within Gaultherieae is obviously a prerequisite for understanding the biogeographic history of this clade. *Gaultheria* (including at least *Pernettya* and possibly *Diplycosia*, see Powell & Kron 2001) is a complex group with the diversity of species concentrated in tropical Asia and around the Pacific rim. This is in contrast to most of the rest of the groups within Ericaceae which tend to have a Laurasian pattern of distribution. A more detailed knowledge of the relationships among Gaultherieae would be helpful in the analysis of its biogeographic history, but the present study would indicate that dispersal is likely a major factor in the history of diversification of the clade, at least in the case of species occurring in Tasmania and South America. Within the Ericoideae the common ancestral area for both the Rhodoreae and Ericaceae is North America. Ericaceae is indicated as European in origin and the African species by extension a more recent diversification.

The Andean clade represents a group of taxa that contain many genera whose greatest

species diversity occurs at higher elevations in the Andes of northern South America. Interestingly, this clade does not include any sampled species of *Vaccinium* (Kron *et al.* 2002b) and some genera such as *Orthaea* and *Notopora* also fall outside of the Andean clade. DIVA analysis of the Andean clade indicates that the ancestor to the Andean + Mesoamerican-Caribbean clades may have been widespread in the Andes and the mountains of Central America and the Antilles (Fig. 7). If this is the case, then the diversification within the Andean clade is very recent (since the late Miocene) and the taxa that are currently found in Central America (*e.g.*, some species of *Cavendishia* and *Satyria*) are recent introductions via dispersal from the northern Andes.

The biogeographic pattern (*i.e.*, recent diversification in areas of Gondwanan origin) found in our analysis of the Andean clade of Vaccinieae is representative of a more general pattern found within Ericaceae. Based on current phylogenetic studies (Kron *et al.* 2002a) the occurrence in Gondwanan regions of groups such as *Rhododendron* and *Erica* that exhibit a wide range of morphological diversity and large numbers of closely related species are recent evolutionary phenomena rather than the result of ancient diversification. This is supported by the results of this study that indicate a Laurasian origin for the Ericaceae.

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Appendix 1. Classification of Ericaceae. Taxonomy of subfamilies, tribes, and genera follow Kron *et al.* (2002a); genera and species numbers follow Stevens *et al.* (in press) and E. Brown (pers. comm.).

ERICACEAE (incl. Empetraceae, Epacridaceae, Monotropaceae, Pyrolaceae, Vacciniaceae) 121/4084
Subfam. Enkianthoideae 1/16
<i>Enkianthus</i> 16, E Asia, (Japan, Taiwan), Himalayas, N Indochina
Subfam. Monotropoideae 15/50
Tribe Pyroleae 4/38 (<i>Chimaphila</i> 5, Boreal-N temperate, North America south to Panama and Hispaniola, Europe, Asia; <i>Moneses</i> 2, N temperate North America, N Europe; <i>Orthilia</i> 1, Circumboreal, south to Mexico, Guatemala; <i>Pyrola</i> 30, Circumboreal-N temperate, south to Guatemala, Himalayas to E China, N Sumatra)
Tribe Monotropae 9/10 (<i>Allotropa</i> 1, Pacific United States and Canada (California to S British Columbia); <i>Cheilothea</i> 2 NE India (Assam), W Malaysia (Malay Peninsula, Perak and Sumatra); <i>Hemitomes</i> 1, Pacific United States and Canada (California to S British Columbia); <i>Hypopitys</i> 1, North America south to Guatemala, Europe to Asia (Japan, Korea, C China), Himalayas; <i>Monotropa</i> 1, N temperate North America south to Colombia, E Asia (Japan, Korea, E China), Himalayas; <i>Monotropastrum</i> 1, E Asia (Japan, Korea, C-SW China), Himalayas, Sumatra; <i>Monotropsis</i> 1, SE United States; <i>Pityopus</i> 1, Pacific United States (California and Oregon); <i>Pleuricospora</i> 1, Pacific United States and Canada (S British Columbia))
Tribe Pterosporeae 2/2 (<i>Pterospora</i> 1, W North America south to N Mexico, Great Lakes region; <i>Sarcodes</i> 1, Pacific United States (California and Oregon) south to N Mexico (Baja California))
Subfam. Arbutoideae 4/81
<i>Arbutus</i> 10, Pacific North America to Mexico, Europe, N Africa, Middle East, Canary Isl.; <i>Arctostaphylos</i> (incl. <i>Arctous</i> , <i>Xylococcus</i>) 60, Circumboreal, esp. W North America, Mexico to Guatemala; <i>Comarostaphylis</i> 10, W United States (California) to W Panama; <i>Ornithostaphylos</i> 1, United States (S California) to Mexico (N Baja California)
Subfam. Cassiopoideae 1/12
<i>Cassiope</i> 12, Circumboreal, Pacific North America, Japan, Himalayas (Kasmir to Yunnan)
Subfam. Ericoideae 19/1780
Tribe Ericae 3/863 (<i>Calluna</i> 1, Europe, Asia Minor; <i>Daboecia</i> 2, Ireland to Spain and Azores; <i>Erica</i> (incl. 32 "minor genera") 860 Europe, scattered N Africa and Middle East, esp. southern Africa, Madagascar)
Tribe Empetreae 3/5 (<i>Ceratiola</i> 1, SE United States; <i>Corema</i> 2, E North America, SE Europe, Azores; <i>Empetrum</i> 2, N temperate and arctic, S Andes, Falkland Isl., Tristan da Cunha)
Tribe Bejarieae 3/23 (<i>Bejaria</i> 15, SE United States, Cuba, Mexico to Bolivia, east to Guyana; <i>Bryanthus</i> 1, E Siberia, Kamchatka, Japan; <i>Ledothamnus</i> 7, Guayana Highland (Venezuela))
Tribe Phyllodoceae 6/28 (<i>Elliottia</i> (incl. <i>Cladothamnus</i> , <i>Tripetaleia</i>) 4 SE United States, Pacific North America (Oregon to Alaska), Japan; <i>Epigaea</i> 3, E North America, E Asia (Japan to Taiwan), Asia Minor, Caucasus; <i>Kalmia</i> (incl. <i>Leiophyllum</i> , <i>Loiseleuria</i>) 11, Circumboreal, North America, Cuba; <i>Kalmiopsis</i> 1, W United States (Oregon); <i>Phyllodoce</i> 7, Circumpolar, N temperate (esp. W United States); <i>Rhodothamnus</i> 2, European Alps, E Turkey)
Tribe Rhodoreae 4/861 (<i>Diplarche</i> 2, E Himalayas, SW China; <i>Menziesia</i> 7, Japan and Sakhalin, W North America, E United States; <i>Rhododendron</i> (incl. <i>Azalea</i> , <i>Ledum</i> , <i>Tsusiophyllum</i>) 850, Temperate Northern Hemisphere, E-SE Asia, esp. Himalayas and Malesia, Philippines, south to Australia (Queensland), E North America, mts. Europe, few spp. Circumboreal; <i>Therorhodon</i> 2, NE Asia, NW North America (W Alaska))
Subfam. Harrimanelloideae 1/2
<i>Harrimanella</i> 2, Circumboreal (interruptedly), North America, Greenland, N Scandinavia to W Russia, Kamchatka, N Japan
Subfam. Styphelioideae 35/520

Tribe Prionoteae 2/2 (<i>Lebetanthus</i> 1, Patagonia, Tierra del Fuego; <i>Prionotes</i> 1, Australia (Tasmania))
Tribe Archerieae 1/6 (<i>Archeria</i> 6, Australia (Tasmania), New Zealand)
Tribe Oligarrheneae 2/2 (<i>Needhamiella</i> (incl. <i>Needhamia</i>) 1 SW Australia; <i>Oligarrhena</i> 1, SW Australia)
Tribe Richeeae 3/65 (<i>Dracophyllum</i> 48, E Australia, Lord Howe Isl., New Caledonia, New Zealand; <i>Richea</i> 11, SE Australia; <i>Sphenotoma</i> 6, W Australia; <i>Epacris</i> 50, Australia, New Zealand, New Caledonia; <i>Lysinema</i> 5, SW Australia; <i>Rupicola</i> 4, Australia (New South Wales); <i>Woolisia</i> 1, Australia (Queensland and New South Wales))
Tribe Cosmelieae 3/27 (<i>Andersonia</i> 22, SW Australia; <i>Cosmelia</i> 1, SW Western Australia; <i>Sprengelia</i> 4, Australia, New Zealand)
Tribe Styphelieae 19/357 (<i>Acrotiche</i> 14, Australia; <i>Androstoma</i> 1, New Zealand; <i>Astroloma</i> 28, Australia; <i>Brachyloma</i> 7, Australia; <i>Coleanthera</i> 3, SW Australia; <i>Conostephium</i> (incl. <i>Conostephiopsis</i>) 7, SW Australia; <i>Croninia</i> 1, SW Western Australia; <i>Cyathodes</i> 19, Australia (Tasmania); <i>Cyathopsis</i> 1, New Caledonia; <i>Decatoca</i> 1, Papua New Guinea; <i>Leptecophylla</i> 13, Australia, New Zealand, Papua New Guinea, W Pacifica; <i>Leucopogon</i> 215, Australia, New Zealand, New Caledonia, SE Asia, W Pacifica; <i>Lissanthe</i> 6, Australia; <i>Melichrus</i> 4, Australia; <i>Monotoca</i> 11, Australia; <i>Pentachondra</i> 5, Australia, New Zealand; <i>Planocarpa</i> 3, Australia (Tasmania); <i>Styphelia</i> , 11 southern Australia; <i>Trochocarpa</i> 6, Malesia (Papua New Guinea, Borneo, Celebes), Australia)
Subfam. Vaccinioideae 45/1593
Tribe Oxydendreae 1/1 (<i>Oxydendrum</i> 1 E United States)
Tribe Lyonieae 4/77 (<i>Agarista</i> (incl. <i>Agauria</i>) 30, SE United States, SE Brazil, scattered Africa and Madagascar; <i>Craibiodendron</i> (incl. <i>Nuihonia</i>) 5, S China (Yunnan), NE India, Indochina; <i>Lyonia</i> 35, E United States, West Indies, Mexico, E Asia (Japan to Pakistan, S to Malay Peninsula); <i>Pieris</i> (incl. <i>Arcterica</i>) 7, E-SE United States, Cuba, E Asia (arc from S Kamchatka to Nepal))
Tribe Andromedeae 2/2 (<i>Andromeda</i> 1, Boreal-N temperate in Northern Hemisphere, N Japan; <i>Zenobia</i> 1, SE United States)
Tribe Gaultherieae 6/246 (<i>Chamaedaphne</i> 1, Circumboreal-N temperate, E Asia south to N Japan, E North America south along Atlantic Coast to South Carolina; <i>Diphycosia</i> (incl. <i>Pernettyopsis</i>) 100, Malesia; <i>Eubotrys</i> 2, E United States; <i>Gaultheria</i> (incl. <i>Chiogenes</i> , <i>Pernettya</i>) 130, Circum-Pacific in North and South Hemispheres, E North America, SE Brazil, Himalayas, New Zealand and Tasmania; <i>Leucothoe</i> 6, Japan, Indochina (Burma, N Vietnam), SW China (Yunnan and SE Tibet), Pacific NW United States (California and Oregon); <i>Tepuia</i> 7, Guayana Highland (Venezuela))
Tribe Vaccinieae 32/1267 (<i>Anthopteropsis</i> 1, C Panama; <i>Anthopterus</i> 11, Costa Rica to NE Peru; <i>Cavendishia</i> 130, S Mexico to Bolivia, east to NW Brazil; <i>Ceratostema</i> (incl. <i>Periclesia</i>) 35, S Colombia to N Peru, Guyana; <i>Costera</i> 9, W Malesia; <i>Demosthenesia</i> 11, C Peru to N Bolivia; <i>Didonica</i> 4, E Costa Rica to C Panama; <i>Dimorphanthera</i> 87, Malesia, mostly New Guinea, Philippines, W Pacifica; <i>Diogenesia</i> 13, W Venezuela to N Bolivia; <i>Disterigma</i> (incl. <i>Killipiella</i>) 35, Guatemala to Bolivia, east to Guyana; <i>Gaylussacia</i> 50, E North America, Colombia to Paraguay, SE Brazil; <i>Gonocalyx</i> 10, West Indies, Costa Rica to N Colombia; <i>Lateropora</i> 3, E Costa Rica to W Panama; <i>Macleania</i> 40, S Mexico to Peru; <i>Mycerinus</i> 3, Guayana Highland (Venezuela); <i>Notopora</i> 5, Guayana Highland (Venezuela); <i>Oreanthes</i> 7, Ecuador to N Peru; <i>Orthaea</i> (incl. <i>Empedoclesia</i> , <i>Lysiclesia</i>) 53, C Mexico to Bolivia, east to Guyana, Trinidad; <i>Paphia</i> (incl. <i>Agapetes</i> p.p.) 16, Malesia, esp. Papua New Guinea, W Pacifica, Australia (Queensland); <i>Pellegrinia</i> 5, C Peru; <i>Plutarchia</i> 11, Colombia to N Ecuador; <i>Polyclita</i> 1, C Bolivia; <i>Psammisia</i> 80, Costa Rica to Bolivia, east to Guianas and Trinidad; <i>Rusbya</i> 1, N Bolivia; <i>Satyria</i> 25, S Mexico to N Bolivia, Guianas to NW Brazil; <i>Semiramisia</i> 5, Venezuela to N Peru; <i>Siphonandra</i> 3, C Peru to N Bolivia; <i>Sphynspermum</i> 25, S Mexico to N Bolivia, Guianas, West Indies; <i>Themistoclesia</i> 30, Costa Rica to N Bolivia; <i>Thibaudia</i> (incl. <i>Calopteryx</i>) 70; Costa Rica to N Bolivia, Guianas, NW Brazil; <i>Utleya</i> 1, Costa Rica; <i>Vaccinium</i> (incl. <i>Agapetes</i> p.p., <i>Oxycoccus</i> , <i>Symphysia</i>) ca. 500, Circumpolar-N temperate, Europe, North America, Japan, Himalayas to E-SE Asia, Malesia)

Appendix 2. List of species (for more details see Kron *et al.* 2002a) used in the DIVA and Fitch parsimony character optimization of biogeographic areas in the Ericales. DIVA characters are 1 = Africa, 2 = Australia, 3 = N America, 4 = Asia, 5 = Europe; Fitch scoring for 4 areas is 0 = Africa, 1 = Australia, 2 = N America, 3 = Eurasia; Fitch scoring for 2 areas is 0 = Laurasia, 1 = Gondwana.

<i>Species</i>	DIVA	Fitch (4 areas)	Fitch (2 areas)
	12345		
<i>Actinidia chinensis</i> Planchon	01030	3	0
<i>Arbutus canariensis</i> Duhamel	10000	0	1
<i>Bejaria racemosa</i> Mutis ex L. f.	00100	2	0
<i>Calluna vulgaris</i> (L.) Hull	00001	3	0
<i>Cassiope mertensiana</i> (Bong.) G. Don	00011	2/3	0
<i>Ceratiola ericoides</i> Michaux	00100	2	0
<i>Chamaedaphne calyculata</i> (L.) Moench	00100	2/3	0
<i>Clethra alnifolia</i> L.	00100	2	0
<i>Clethra arborea</i> Vent.	10000	0	1
<i>Cosmelia rubra</i> R. Br.	01000	1	1
<i>Cyrilla racemiflora</i> L.	00100	2	0
<i>Diapensia lapponica</i> L.	00101	2/3	0
<i>Diospyros virginiana</i> L.	00100	2	0
<i>Dracophyllum longifolium</i> (J. R. Forster) Roem. and Schultes	01000	1	1
<i>Enkianthus campanulatus</i> G. Nicholson	00010	3	0
<i>Epacris impressa</i> Labill.	01000	1	1
<i>Gaultheria eriophylla</i> (Pers.) Sleumer	00010	3	0
<i>Pentachondra pumila</i> (Forster and G. Forster) R. Br.	01000	1	1
<i>Prionotes cerinthoides</i> (Labill.) R. Br.	01000	1	1
<i>Pyrola rotundifolia</i> L.	00111	2/3	0
<i>Rhododendron hippophaeoides</i> Balf. f. and Forrest	00010	3	0
<i>Symplocos paniculata</i> Miq.	00100	2	0
<i>Vaccinium macrocarpon</i> Aiton	00100	2	0

Appendix 3. List of species (for more details see Kron *et al.* 2002a) used in the DIVA and Fitch parsimony character optimization of biogeographic areas in Ericaceae. DIVA characters are 1 = Africa, 2 = South America, 3 = Australia, 4 = North America, 5 = Asia, 6 = Europe; Fitch scorings for 6 areas are: 0 = Africa, 1 = South America, 2 = Australia, 3 = North America, 4 = Asia, 5 = Europe; Fitch scorings for 2 areas are: 0 = Laurasia, 1 = Gondwana.

Species	Subfamily	123456	6 areas	2 areas
<i>Agarista populifolia</i> (Lam.) Judd	Vaccinioideae	000100	3	0
<i>Agarista salicifolia</i> (Comm. ex Lam.) G. Don	Vaccinioideae	100000	1	1
<i>Andromeda polifolia</i> L.	Vaccinioideae	000101	3/5	0
<i>Arbutus canariensis</i> Duhamel	Arbutoideae	100000	0	1
<i>Arctostaphylos uva-ursi</i> (L.) Sprengel	Arbutoideae	000100	3	0
<i>Bejaria racemosa</i> Vent.	Ericoideae	000100	3	0
<i>Bryanthus gmelini</i> D. Don	Ericoideae	000010	4	0
<i>Calluna vulgaris</i> (L.) Hull	Ericoideae	000001	5	0
<i>Cassiope mertensiana</i> (Bong.) G. Don	Cassiopeoideae	000111	3/4/5	0
<i>Ceratiola ericoides</i> Michaux	Ericoideae	000100	3	0
<i>Chamaedaphne calyculata</i> (L.) Moench	Vaccinioideae	000111	3/4/5	0
<i>Chimaphila umbellata</i> (L.) Barton	Pyroloideae	000111	3/4/5	0
<i>Corema conradi</i> Torrey ex Loud.	Ericoideae	000101	3/5	0
<i>Craibiodendron yunnanense</i> W. Smith	Vaccinioideae	000010	4	0
<i>Daboecia cantabrica</i> (Hudson) K. Koch	Ericoideae	000001	5	0
<i>Diplarche multiflora</i> Hook. f. and Thomson	Ericoideae	000010	4	0
<i>Diplycosia acuminata</i> Becc.	Vaccinioideae	000010	4	0
<i>Dracophyllum longifolium</i> (J. R. Forster) Roem. and Schultes	Styphelioideae	001000	2	1
<i>Elliottia bracteata</i> (Maxim.) Hook. F.	Ericoideae	000100	3	0
<i>Enkianthus campanulatus</i> G. Nicholson	Enkianthioideae	000010	4	0
<i>Epacris impressa</i> Labill.	Styphelioideae	001000	2	1
<i>Epigaea repens</i> L.	Ericoideae	000100	3	0
<i>Erica sicula</i> Guss.	Ericoideae	000010	4	0
<i>Erica spiculifolia</i> Salisb.	Ericoideae	000010	4	0
<i>Erica tetralix</i> L.	Ericoideae	000001	4	0
<i>Eubotrys racemosa</i> L.	Vaccinioideae	000100	3	0
<i>Gaultheria miqueliana</i> Takeda	Vaccinioideae	000010	4	0
<i>Gaultheria shallon</i> Pursh	Vaccinioideae	000100	3	0
<i>Harrimanella hypnoides</i> Cov.	Harrimanelloideae	000111	3/4/5	0
<i>Kalmia angustifolia</i> L.	Ericoideae	000100	3	0
<i>Kalmia buxifolia</i> (Berg) Gift, Kron and Stevens	Ericoideae	000100	3	0
<i>Kalmia procumbens</i> (L.) Gift, Kron and Stevens	Ericoideae	000111	3/4/5	0

Species	Subfamily	123456	6 areas	2 areas
<i>Kalmiopsis leachiana</i> (Henderson) Rehder	Ericoideae	000100	3	0
<i>Lebetanthus myrsinites</i> Macl.	Styphelioideae	010000	1	1
<i>Ledothamnus guyanensis</i> Meissner	Ericoideae	010000	1	1
<i>Leucothoe fontanesiana</i> (Steudel) Sleumer	Vaccinioideae	000100	3	0
<i>Lyonia ferruginea</i> (Walter) Nutt.	Vaccinioideae	000100	3	0
<i>Lyonia lucida</i> (Lam.) K. Koch	Vaccinioideae	000100	3	0
<i>Menziesia pilosa</i> Pers.	Ericoideae	000100	3	0
<i>Orthilia secunda</i> (L.) House	Monotropoideae	000111	3/4/5	0
<i>Oxydendrum arboreum</i> (L.) DC.	Vaccinioideae	000100	3	0
<i>Pentachondra pumila</i> (Forster and G. Forster) R. Br.	Styphelioideae	001000	2	1
<i>Pernettya tasmanica</i> Hook. f.	Vaccinioideae	001000	2	1
<i>Phyllodoce caerulea</i> Bab.	Ericoideae	000111	3/4/5	0
<i>Phyllodoce empetriformis</i> D. Don	Ericoideae	000110	3/4	0
<i>Pieris nana</i> (Maxim.) Makino	Vaccinioideae	000010	4	0
<i>Pieris phillyraeifolia</i> (Hook.) DC.	Vaccinioideae	000010	3	0
<i>Prionotes cerinthoides</i> (Labill.) R. Br.	Styphelioideae	001000	2	1
<i>Pyrola rotundifolia</i> L.	Monotropoideae	000111	3/4/5	0
<i>Rhododendron kaempferi</i> Planchon	Ericoideae	000010	4	0
<i>Rhododendron tsusiophyllum</i> Sugim.	Ericoideae	000010	4	0
<i>Rhodothamnus chamaecistus</i> Rchb.	Ericoideae	000001	5	0
<i>Satyria warszewiczii</i> Klotzsch	Vaccinioideae	010000	1	1
<i>Sprengelia incarnata</i> W. Smith	Styphelioideae	001000	2	1
<i>Tepuia cardonae</i> A. C. Smith	Vaccinioideae	010000	1	1
<i>Therorhodium camtschaticum</i> (Pallas) Small	Ericoideae	000110	3/4	0
<i>Vaccinium macrocarpon</i> Aiton	Vaccinioideae	000100	3	0
<i>Vaccinium meridionale</i> Sw.	Vaccinioideae	010000	1	1
<i>Zenobia pulverulenta</i> (Bartram) Pollard	Vaccinioideae	000100	3	0

Appendix 4. List of species used in the DIVA analysis of the Andean clade of the Vaccinieae (see Powell and Kron in press). DIVA characters are: 1 = Central America, 2 = Chocó, 3 = Andean Highlands Arc, 4 = eastern Lowland Arc, 5 = Antilles.

Species	1	2	3	4	5
<i>Anthopterus wardii</i> Ball	1	1	0	0	0
<i>Cavendishia bracteata</i> (Ruiz and Pav. Ex J. St.-Hil.) Hoer.	1	0	1	0	0
<i>Cavendishia capitulata</i> J. D. Smith	1	0	1	0	0
<i>Cavendishia complectens</i> Hemsl.	1	0	1	0	0
<i>Cavendishia grandifolia</i> Hoer.	0	0	1	0	0
<i>Cavendishia martii</i> (Meissner) A. C. Smith	0	0	1	0	0
<i>Ceratostema lanigerum</i> (Sleumer) Luteyn	0	0	1	0	0
<i>Ceratostema rauhii</i> Luteyn	0	0	1	0	0
<i>Ceratostema reginaldii</i> (Sleumer) A. C. Smith	0	0	1	0	0
<i>Ceratostema silvicola</i> A. C. Smith	0	0	1	0	0
<i>Demosthenesia pearcii</i> (Britton) A. C. Smith	0	0	1	0	0
<i>Diogenesia racemosa</i> (Britton) Sleumer	1	0	1	0	0
<i>Disterigma alaternoides</i> (Kunth in H.B.K.) Niedenzu	0	0	1	0	0
<i>Disterigma ovatum</i> (Rusby) S. F. Blake	0	0	1	0	0
<i>Disterigma pernettyoides</i> (Wedd.) Niedenzu	0	0	1	0	0
<i>Disterigma rimbachii</i> (A. C. Smith) Luteyn	1	0	0	0	0
<i>Disterigma trimerum</i> Wilbur and Luteyn	0	0	1	0	0
<i>Macleania bullata</i> Yeo	0	0	1	0	0
<i>Macleania coccoloboides</i> A. C. Smith	0	0	1	0	0
<i>Macleania cordifolia</i> Benth.	0	0	1	0	0
<i>Macleania insignis</i> M. Martens and Galeotti	1	0	0	0	0
<i>Polyclita turbinata</i> A. C. Smith	0	0	1	0	0
<i>Psammisia dolichopoda</i> A. C. Smith	1	1	1	0	0
<i>Psammisia ecuadorensis</i> Hoer.	0	0	1	0	0
<i>Psammisia sodiroi</i> Hoer.	0	0	1	0	0
<i>Psammisia ulbrichiana</i> Hoer.	1	0	1	0	0
<i>Satyria vargasii</i> A. C. Smith	0	0	1	0	0
<i>Satyria allenii</i> A. C. Smith	1	0	0	0	0
<i>Satyria boliviana</i> Luteyn	0	0	1	0	0
<i>Satyria cerander</i> (Dunal) A. C. Smith	0	0	0	1	0
<i>Satyria grandifolia</i> Hoer.	0	1	1	0	0
<i>Satyria leucostoma</i> Sleumer	0	0	1	0	0
<i>Satyria meiantha</i> J. D. Smith	1	0	0	0	0
<i>Satyria polyantha</i> A. C. Smith	0	0	1	0	0
<i>Satyria</i> sp. nov.	1	0	0	0	0

Species	1	2	3	4	5
<i>Satyria ventricosa</i> Luteyn	1	0	0	0	0
<i>Satyria warszewiczii</i> Klotzsch	1	0	0	0	0
<i>Semiramisia speciosa</i> (Benth.) Klotzsch	0	0	1	0	0
<i>Spherospermum ellipticum</i> Sleumer	1	0	1	0	0
<i>Symphysia racemosa</i> (Vahl) Stearn	0	0	0	0	1
<i>Themistoclesia costaricensis</i> Luteyn and Wilbur	0	0	1	0	0
<i>Themistoclesia epiphytica</i> A. C. Smith	0	0	1	0	0
<i>Thibaudia costaricensis</i> Hoer.	1	0	0	0	0
<i>Thibaudia densiflora</i> (Herzog) A. C. Smith	0	0	1	0	0
<i>Thibaudia diphylla</i> Dunal	0	0	1	0	0
<i>Thibaudia floribunda</i> Kunth in H. B. K.	0	0	1	0	0
<i>Thibaudia inflata</i> Luteyn	0	0	1	0	0
<i>Thibaudia litensis</i> Luteyn	0	0	1	0	0
<i>Thibaudia macrocalyx</i> Remy	0	0	1	0	0
<i>Thibaudia martiniana</i> A. C. Smith	0	0	1	0	0
<i>Thibaudia pachyantha</i> A. C. Smith	0	0	1	0	0
<i>Thibaudia parvifolia</i> (Benth.) Hoer.	0	0	1	0	0
<i>Thibaudia tomentosa</i> Hoer.	0	0	1	0	0
<i>Vaccinium poasanum</i> J. D. Smith	1	0	0	0	0