Dragons in the mist

An interview with Steve Wagstaff, evolutionary biologist at Landcare Research

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Introduction

Dr Steve Wagstaff came to New Zealand in 1994 from the USA as the first botanist in New Zealand to have both classical taxonomic training and expertise in the then relatively new technique of DNA sequencing. Steve has used DNA sequencing to solve many of the long-standing problems in the taxonomy of the New Zealand flowering plant and conifer flora. He has now published work on *Hebe* and several groups of daisies including *Brachyglottis*, *Celmisia*, and *Olearia*. His results often tell stories about the biogeography of New Zealand plants: where they came from, how long they have been in New Zealand, how often and when they dispersed from New Zealand to neighbouring islands or continents. Steve's work, along with that of others in the same field, has changed our understanding of the origins of the New Zealand flora. As the interview below illustrates, it seems the majority of our flowering plants evolved from ancestors that arrived in New Zealand about the late Pliocene (less than 5 million years ago) to early Pleistocene (about 1.6 mya), often from Australia. The phrase 'Goodbye Gondwana' (McGlone, 2005) sums up this rejection of the view of New Zealand as being an 'ark' carrying the remnants of an ancient flora. This new view is mainly due to the results of DNA sequencing studies.

A recent project, now complete and soon to be published, was a study of the genus *Dracophyllum*, a tree and shrub genus best known to New Zealanders as turpentine scrub, pineapple scrub, or Dr Seuss trees. The name *Dracophyllum* means dragon-leaves and comes from the resemblance of the leaves to those of the dragon-tree (*Dracaena draco*), a monocot tree of central America that is like our cabbage trees (*Cordyline* species).

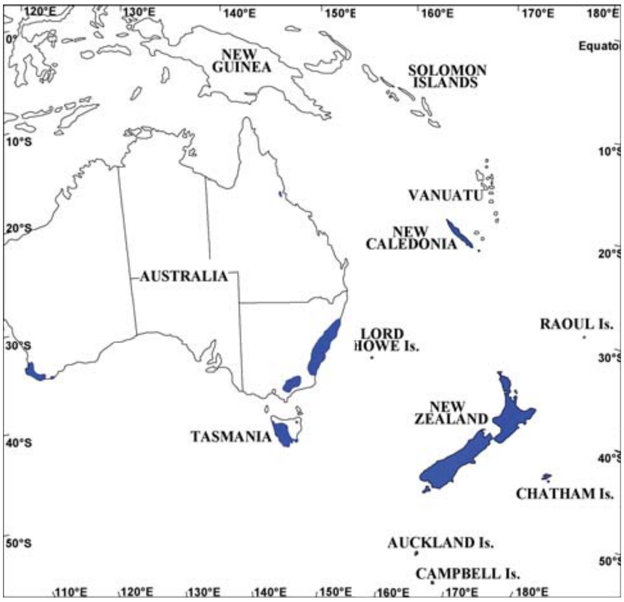

Fig. 1 The world distribution of *Dracophyllum* and its near relatives, *Richea* and *Sphenotoma*.

Steve's field work was supported by the National Geographic Committee for Research and Exploration to study *Dracophyllum* throughout its entire range. This involved field work in New Zealand, Australia including Tasmania, Lord Howe Island, and New Caledonia to collect specimens of most of the *Dracophyllum* species and many species of related genera (Fig. 1).

Interview

Q: You have just completed this project on *Dracophyllum*. What was the topic of this and why did National Geographic fund you to do the field work?

Steve: The aims of the project were to define the underlying reasons for the differences in species richness between New Zealand, Australia, and New Caledonia (see Box 1, p. 18).

Q: Which countries have the most species?

Steve: New Zealand has by far the most species of *Dracophyllum* (35 spp.), followed by New Caledonia (9 spp.), and Tasmania to a lesser degree (2 spp.). We compared islands that are species rich with the Australian continent (4 spp.). We wanted to determine the phylogeny, to find the direction of evolution.

Q: What do you mean by direction of evolution?

Steve: The direction of dispersal – where the genus *Dracophyllum* originated and where it dispersed to. Also, we wanted to find out why there are so many species in New Zealand relative to Australia. *Dracophyllum* is paraphyletic[3] and could include the genus *Richea*, and if you do this, then the number of species of *Dracophyllum* is not so imbalanced in Australia and New Zealand. So the imbalance might be an artefact of the taxonomy. We wanted to find out how old the lineages are in each country. New Zealand species might have had longer to speciate, or the Australian lineage might be older

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[2] See the next article by Dawson and Winkworth (pp. 18–23).
[3] A paraphyletic group is one that is incomplete, i.e., it contains only some of the species that are descendants of the root ancestor species. See the previous article by Glenny and Dawson (pp. 10–12).

but extinction there might have been greater. Rates of speciation and extinction were issues to address. To get at these issues we had to study the larger group that *Dracophyllum* belongs to outside New Zealand. It was critical to include all species from the wider regional perspective. That's partly why we were funded by National Geographic – they saw the importance of doing field work outside of New Zealand.

Q: How much did you know about the group when you started and what put the idea in your head to do this project?

Steve: We already knew quite a bit about the genus. One major reason we got the National Geographic fund is that we had a strong team in all the countries we worked in. International collaboration produces the best science, and besides, it's more fun that way.

Fig. 2 *Dracophyllum elegantissimum* in the Brunner Range, New Zealand. Fanie Venter discovered this new tree species in Nelson province while working on his PhD (Venter, 2004a).

Fanie Venter was working on a revision of the genus for his PhD at Victoria University, Wellington, and had samples from his work of most of the New Zealand species (Fig. 2, 3). He had studied specimens from overseas but had done no field work there. Darren Crayn in Canberra had completed a DNA sequencing survey of the Epacridoideae and contributed sequences from this earlier study. Kristina Lemson of Perth was preparing a flora treatment of a closely related genus, *Sphenotoma*. Dorothy Steane I had known before I came to New Zealand, and she is an expert on the Tasmanian flora. Jérôme Munzinger is writing treatments for the New Caledonian flora; he helped make field work in New Caledonia possible. Murray Dawson assisted with field work in New Zealand, and in the laboratory did all the DNA extraction and sequencing work.

Fig. 3 *Dracophyllum traversii*, a New Zealand species in flower (Photo: ©Paul Ashford, www.NZplantpics.com).

Q: You did some interesting field work. Where was this? Who did you do the field work with?

Steve: I organised two trips to Western Australia with Kristina Lemson of Perth to collect *Sphenotoma* throughout its range. It only occurs in the forests of South West Australia south of Perth, like in the Stirling Range National Park north-east of Albany. *Sphenotoma* is a genus of 7 or 8 species, and Kristina showed me what she believes to be an undescribed species on the summit of the Stirling Range (Fig. 4).

Fig. 4 A beautiful undescribed *Sphenotoma* species on the summit ridge of the Stirling Range, Western Australia.

There were two trips to Tasmania, the first trip with Dorothy Steane in autumn when the *Dracophyllum* and *Richea* species were in flower or fruit, to a number of sites like Mt Field National Park and Cradle Mountain National Park. The second trip was a conference field trip led by Greg Jordan, a paleobotanist in Tasmania. He's studied fossils of *Richea* and took us to three fossil sites and also showed us sites with living *Richea* (Fig. 5) and *Dracophyllum*.

Fig. 5 *Richea pandanifolia* on Mt Field, Tasmania.

And finally I organised two trips to eastern Australia. The first started at Sydney where we collected a *Dracophyllum* species on coastal cliffs, then went up to the New South Wales – Queensland border, and then south to Melbourne. A lot of road travelling.

Q: Who did you do that trip with?

Steve: I hired a research fellow at Sydney Botanic Gardens, Andrew Perkins, who had just finished his PhD and was doing various pieces of contract work—he'd just published a book on orchids.

Then Fanie Venter and I travelled to northern Queensland, and to Lord Howe Island. *Dracophyllum sayeri* is found only on a few peaks in the Bellenden Ker Range south of Cairns where it's a forest gap species on the peaks of the range. *Dracophyllum fitzgeraldii* is only on the summit of Lord Howe Island (Fig. 6).

Fig. 6 Steve Wagstaff on Lord Howe Island. The summit of the island, the sole habitat of *Dracophyllum fitzgeraldii*, is in the distance.

Q: How did you get onto those peaks?

Steve: Well, as it happened, only a week before we went, Cyclone Larry went through Queensland and the national parks and many roads were closed. When we got there, we were told there was a cable car that went to the TV transmitter tower on Mt Bellenden Ker. We contacted the studio executives, and said we were visiting scientists. They rolled out the red carpet for us, much to the annoyance of the cable car operators who had just got it working again and wanted to get supplies up to the transmitter. We had half a day on the summit. The forest around the summit was completely devastated, torn tree trunks, jagged branch ends, the forest was shredded.

Q: You also went to New Caledonia?

Fig. 7 Fanie Venter in *Araucaria humboldtii* forest near the summit of Mont Humboldt, New Caledonia. This is as tall as the trees get.

Fig. 8 *Dracophyllum thiebautii* in cloud, near the summit of Mont Humboldt, New Caledonia.

Fig. 9 *Dracophyllum mackeeanum*, on the ultramafic maquis of New Caledonia, a species described recently by Fanie Venter (Venter, 2004b).

Steve: Yes, with Fanie Venter. For me, New Caledonia was the highlight of all the field work. I have a traditional training in recognition of plant families, but the New Caledonian flora was so exotic I was right out of my depth trying to identify what families the plants were in. After the New Zealand flora with mostly small white flowers it was amazing to see these huge, red, bird-pollinated flowers. Fanie and I climbed Mt Humboldt, the highest point on the main island. We traversed through *Araucaria* forests, very eerie in fog that was coming and going (Fig. 7). At one point below the summit we walked through a 10 m high *Dracophyllum* forest with a tree fern understorey. That particular *Dracophyllum* has been regarded as a variety of *Dracophyllum ramosum*, but Fanie considers it a distinct species called *Dracophyllum thiebautii* (Fig. 8). At the summit, the fog cleared and we got phenomenal views of the island in every direction.

The maquis, sparse shrublands on ultramafic rock (igneous rocks that are very poor in silica but rich in iron and magnesium), was some of the hardest walking I've ever done because of the slippery clay soil – it's like standing on ice. Fanie had already described *Dracophyllum mackeeanum* as a new species from herbarium specimens but had never seen it in the wild, and we found it on the maquis, in a distinct habitat that confirmed it as being a distinct species (Fig. 9). It turned out to be more widespread than the herbarium specimens indicated.

Q: Did you manage to sample all species in the genus?

Steve: We sampled most species, but the experimental design only required single representatives of each species. Our aim was to do a broad survey, to allow calibration of the tree with distantly related genera for which there are fossils with dates. We used gene regions called *rbc*L and *mat*K – these are fairly conservative regions that allowed sampling across the entire subfamily that *Dracophyllum* belongs to.

The trade off in using conservative gene regions was that many of the sequences were identical, especially in the New Zealand species belonging to subgenus *Oreothamnus*. Once we saw identical sequences we could see that we had sampled enough of the New Zealand subgenus. Sequencing is expensive and time-consuming so there was no point continuing to sequence very similar New Zealand species.

We included all Australian species, all New Caledonian species, and 60% of the New Zealand species.

Q: Did the results give you the information you needed to solve the questions you'd asked?

Steve: The results were not completely resolved, not as much as we'd have liked. We were able to answer the questions we had, but not with as much certainty as we'd have liked. And we found out some other things along the way (Box 2, p.18).

Q: What did the results say about the questions you were interested in?

Steve: The results told us how old the *Dracophyllum* lineage is. It separated from other genera of Epacridoideae 20 million years ago (mya), about early Miocene (Fig. 10).

They told us that *Dracophyllum* in New Zealand is younger than in Australia, and that there was one, possibly two, dispersals to New Zealand; the results are ambiguous on that, but my hunch is that there was a single dispersal event. This occurred about 2.2 mya, at the beginning of the Pleistocene era. This corresponds to the time when the mountains in New Zealand began to uplift, and the Pleistocene glaciations started. We didn't know before the study if *Dracophyllum* in New Caledonia had its origin from New Zealand or Australia. The results showed that there was a single dispersal to New Caledonia from Australia, about 7 mya.

Subgenus *Oreothamnus* contains the small-leaved *Dracophyllum* species and is very morphologically diverse in New Zealand with 28 species ranging from tall shrubs to cushion plants. However, within this subgenus there is very little genetic diversity and species with quite different forms are able to hybridise. Its greatest species diversity is in the eastern Southern Alps (Fig. 11). It came as a surprise to discover that DNA sequence evidence suggests that the diminutive Tasmanian species, *D. minimum*, is misplaced in subgenus *Oreothamnus* meaning that the subgenus may now be confined to New Zealand and its offshore islands. However, this result

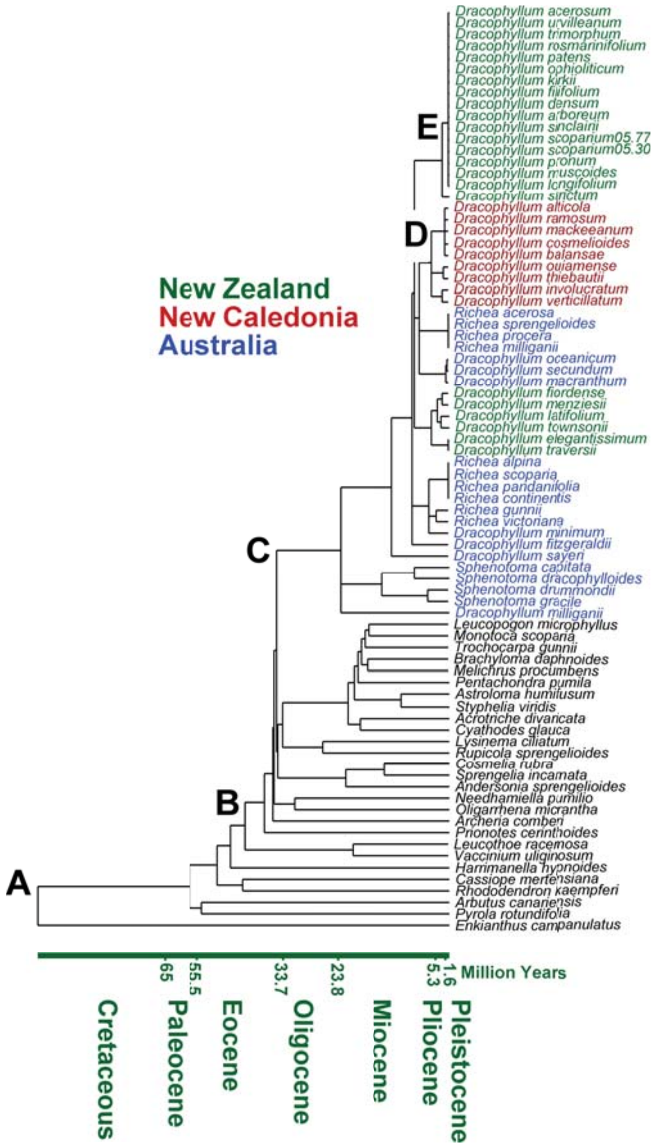

Fig. 10 Chronogram showing the inferred evolutionary history of *Dracophyllum* and its relatives. **A** = the calibration point using the dated *Enkianthus* fossil 90 mya; **B** = the point at which Southern and Northern Hemisphere Ericaceae diverged, 40.5 mya; **C** = the point at which the tribe containing *Dracophyllum* diverged, 37.8 mya; **D** = New Zealand and New Caledonian species of Dracophyllum diverged from eastern Australian species 7.5 mya; **E** = the start of the species radiation of *Dracophyllum* subg. *Oreothamnus* in New Zealand, 1.2 mya. Geographic regions are highlighted in colour and an evolutionary time-scale is shown at the bottom.

Fig. 11 *Dracophyllum rosmarinifolium* on Porters Pass, Canterbury. The dry eastern South Island ranges are habitat for most of the shrubby *Dracophyllum* species that make up the New Zealand *Dracophyllum* subgenus *Oreothamnus*. *Dracophyllum rosmarinifolium* has been known as *D. uniflorum*, but Fanie Venter found these names refer to the same species and *D. rosmarinifolium* is the older of the two names (and thus takes priority).

appears to contradict Fanie Vener's PhD work based on morphology.

Subgenus *Oreothamnus* diverged from the rest of *Dracophyllum* (subgenus *Dracophyllum*) in New Zealand, 1.2 mya.

Dispersal of *Dracophyllum* to Lord Howe Island, from eastern Australia occurred just after the emergence of the island 6.9 mya.

Q: How do you arrive at the dates you mentioned?

Steve: We detected differences in the DNA isolated from the species in our study. DNA mutations are passed on from one generation to the next. When we study a species' DNA profile, a mutation shared by two or more species suggests they are related to one another by descent.

We assume most of these changes are 'silent', not expressed in the morphology of the plants, and that they are also evolving in a clock-like manner (i.e., the rate at which those point mutations occur is uniform over time). To calibrate the DNA molecular clock, we use the fossil record (or the known date of emergence of a volcanic island), and determine the rate at which mutations are occurring in the group under study.

Q: How did you calibrate the *Dracophyllum* phylogeny?

Steve: Using the fossil record. Ninety million year-old fossils of Australian *Enkianthus* flowers were used. Dated fossils of *Rhododendron* and *Richea* leaves were also available and the time of emergence of Lord Howe Island was known. Fossil seeds of *Rhododendron* are known from 60 mya and fossil pollen from 50 mya. The first appearance of *Richea* leaves in the fossil record was from 35–30 mya. Lord Howe Island is the remnant of a large volcano that erupted 6.9 mya. Each gives a different perspective: fossils set a lower age limit, while the emergence of an island sets an upper age limit. We used the single calibration point of *Enkianthus* and checked that the other fossils and the emergence of Lord Howe Island were consistent with that, and got that consistency pretty well.

Q: What do your results say about the imbalance of species between the islands and continent of Australia?

Steve: Most of the species diversity is in New Zealand and New Caledonia. But interestingly, most of the genetic diversity is in Australia. There are a smaller number of species in Australia, but they are the oldest lineages and so we suggest that there have been more extinctions in Australia.

There was dispersal to New Zealand in much more recent times and this was followed by a large species radiation that happened mainly in the New Zealand mountains.

Q: These extinctions in Australia – why would that have happened?

Steve: The three related genera, *Dracophyllum*, *Richea*, and *Sphenotoma*, may have been widespread in Australia in the Miocene at which time temperate forests were prevalent in Australia. Then as a result of climate change at the end of the Tertiary, Australia became a lot drier and the great inland desert formed. The temperate forests shrank to a few localities on the eastern and western edges of the continent. The genus *Sphenotoma* became confined to a small area of mountains at the southern tip of Western Australia. *Dracophyllum* for the most part became confined to the mountains of eastern Australia and Tasmania. *Dracophyllum* likes damp cloud forest. Most Australian species are now confined to small areas on the summits of mountain ranges like the Blue Mountains in New South Wales, also in protected valleys in the area where the famous Wollemi pine was discovered. *Dracophyllum sayeri* is only on a few peaks in tropical Queensland. The Lord Howe Island species, *Dracophyllum fitzgeraldii*, is only on the summit of the island.

Getting back to the question of the imbalance in the species numbers, the DNA results don't convincingly separate *Richea* from *Dracophyllum*. If you include *Richea* in *Dracophyllum*, then the imbalance in species numbers is less marked.

Q: So there are two explanations of the imbalance: one that it's an artefact of the taxonomy, and the other is that it results from climate change at the beginning of the Pleistocene with extinctions due to increasing aridity in Australia, at the same time as new cold-climate and high altitude environments appeared in New Zealand.

What about New Caledonia? Isn't the flora of New Caledonia said to be an ancient piece of Gondwana? How did a species radiation happen there?

Steve: People are now challenging that perception of New Caledonia, and take the view that while some of the flora is very old other elements have arrived by long distance dispersal in geologically recent times.

Q: How does this work fit with other work done on the evolution of the New Zealand flora? Is this the sort of distribution pattern seen in other groups? Is the age of this group similar to others in New Zealand?

Steve: They are good questions. I think we've generated enough independent studies on the New Zealand flowering plant flora to show a common theme on the origin and time of its arrival. There are two clear patterns:

1. A large proportion of the New Zealand flora arrived by long distance dispersal at the beginning of the Pleistocene and radiated after those dispersal events into the flora we see now.
2. There is a disparity between the diversity in morphological forms seen in New Zealand flowering plants and the low level of genetic difference between the species. Many groups are morphologically diverse: *Dracophyllum* for example varies from trees down to small cushion plants with nearly identical sequences for the gene regions we've looked at.

Q: What about the disparity in species richness between Australia and New Zealand? Do you see that in other groups?

Steve: I'm not sure about that, results in other groups vary quite a bit. The most diverse elements in Australia are absent or rare in New Zealand and vice versa. For instance, *Eucalyptus* is very diverse in Australia but is absent from the current New Zealand native flora (but fossil evidence shows that it was here once). In the other direction, hebes and related genera are very diverse in New Zealand but Australia has very few species.

The Australian flora is highly adapted to the arid climate and to fire, while the New Zealand flora has almost none of those adaptations – features like microphyllous leaves and the ability for burnt plants to resprout.

Q: Does this explain why the onset of the Pleistocene glaciations seems to have been the time when much of our current flora had its beginnings in New Zealand?

Steve: The aridification of Australia could be an explanation for groups with higher morphological species diversity in New Zealand than Australia. But also there was rapid speciation in New Zealand throughout the Pleistocene, and that can be seen in a number of groups of plants, particularly in the alpine zone. That shift in climate has been New Zealand's gain and Australia's loss.

Q: It seems that to understand the New Zealand flora we need to relate it to the climate history of the region?

Steve: Yes, something that was apparent in doing this work is that it's vital that we study the New Zealand flora in a wider regional context. We can make incorrect interpretations of the New Zealand flora if we study it in isolation. The wider context allows us to appreciate how unique our flora is, but also how its history is strongly tied to the floras of nearby countries.

References

McGlone, M.S. (2005). Goodbye Gondwana. *Journal of Biogeography 32*: 739–740.

Venter, S. (2004a). *Dracophyllum elegantissimum* (Ericaceae), a new species from north-west Nelson, New Zealand. *New Zealand Journal of Botany 42*: 37–43.

Venter, S. (2004b). *Dracophyllum mackeeanum* (Ericaceae: Richeeae), a new species from New Caledonia. *New Zealand Journal of Botany 42*: 747–752.

Further reading

Steve Wagstaff maintains a website called 'Phylogeny of New Zealand plants' which has evolutionary trees and links to phylogeny literature (see http://plantphylogeny.landcareresearch.co.nz/). Major papers that Steve has coauthored are listed below:

Wagstaff, S.J. and Garnock-Jones, P.J. (1998). Evolution and biogeography of the *Hebe* complex (Scrophulariaceae) inferred from ITS sequences. *New Zealand Journal of Botany 36*: 425–437.

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Box 1 Species diversity in *Dracophyllum* and related genera

Family Ericaceae
- Subfamily Epacridoideae (the Southern Hemisphere part of the family)
  - **Tribe Richeeae**
    - *Dracophyllum*
      - subgenus *Dracophyllum*
        - New Caledonia: 8 species
        - New Zealand: 7 species
        - eastern Australia: 4 species
        - Lord Howe Island: 1 species
        - Tasmania: 1 species
      - subgenus *Oreothamnus*
        - New Zealand: 28 species
        - Tasmania: 1 species (but probably misplaced in this subgenus)
      - subgenus *Cordophyllum*
        - New Caledonia: 1 species
    - *Richea*
      - Tasmania: 9 species
      - Eastern Australia: 2 species
    - *Sphenotoma*
      - Western Australia: 8 species

Box 2 Summary of the findings

- **Tribe Richeeae** (*Dracophyllum, Richea, Sphenotoma*) is monophyletic.
- **Sections & subgenera**
  - New Zealand *Dracophyllum* subg. *Oreothamnus* is monophyletic.
  - Tasmanian *D. minimum* may be misplaced.
  - *Dracophyllum strictum* is sister to *D.* subg. *Oreothamnus.*
  - *Dracophyllum* subg. *Dracophyllum* is polyphyletic.
  - *Dracophyllum* subg. *Cordophyllum* is nested among New Caledonian spp. of *D.* subg. *Dracophyllum.*
  - The two *Richea* clades correspond with *R.* sect. *Cystanthe* and *R.* sect. *Dracophylloides.*
- **Genera**
  - *Dracophyllum* is paraphyletic.
  - *Richea* is polyphyletic.
  - *Sphenotoma* is monophyletic.
- **Biogeography**
  - While most of the morphological species diversity is found in New Zealand and New Caledonia, the phylogenetic diversity is greatest in Australia.
  - Australian species of *Dracophyllum* are remnants of older lineages; their present distributions are fragmented and disjunct.
  - In contrast, New Zealand (esp. subg. *Oreothamnus*) and New Caledonian species have recently radiated following long-distance dispersal from Australia.
- Evolution in the group was spurred by geological and climatic changes during the late Tertiary.