

Correspondence

The importance of dispersal and recent speciation in the flora of New Zealand

Comments on M. Poole (1994) The New Zealand flora – entirely long-distance dispersal? *J. Biogeogr.* 21, 625–635 and letter from M. K. Macphail (1997) *J. Biogeogr.* 24, 113–114.

The origins of the New Zealand flora have been the subject of considerable debate, particularly amongst botanists discussing the relative importance of plant dispersal in the Southern Hemisphere. Wardle (1963, 1968, 1978), although explaining some plant distributions by dispersal, has suggested that New Zealand's flora arose largely through diversification of taxa present on southern ocean lands following the break-up of the Gondwanan supercontinent. In contrast, Raven (1973) has proposed a main route of dispersal from the Northern Hemisphere via Australia for the (sub)alpine flora of New Zealand. Pole (1994) and Macphail (1997) have also argued for the general importance of Australia as a source for the New Zealand flora. However, their view is more extreme. They assume that New Zealand was completely submerged during the Oligocene and that all extant plant lineages in New Zealand (both alpine and lowland) have arrived from Australia by long distance dispersal since the Miocene. Their conclusion follows from observations that in New Zealand there is a poor match between extant species and those from the palynological and/or macrofossil record of the Tertiary period. Pole (1994) and Macphail (1997) argue that, if the current flora is truly of ancient origin, one must expect to find extant or morphologically similar forms in the Tertiary fossil record of New Zealand.

It is generally agreed that from the late Pliocene onward, New Zealand has undergone periods of great change, both geologically and climatically. Increased interactions between the Pacific and Australian tectonic plates led to the rapid uplift of the axial mountain ranges, possibly as early as 5 million years ago (Raven, 1973; Cooper & Millener, 1993). Profound climatic changes were initiated by a pronounced drop in the average temperature during the Late Pliocene, followed by marked temperature

fluctuations during the Pleistocene resulting in the glacial and interglacial cycles of that period. Such changes were unlike the more stable conditions of the preceding 60 MY (Cooper & Millener, 1993). Emerging molecular studies on the New Zealand flora indicate that these phases of climatic and geological change were also times of intensified speciation in the New Zealand flora, and periods when long-distance dispersal had an increased importance in establishing trans-Tasman distributions between Australia and New Zealand. This is well illustrated by our recent studies on *Myosotis* L. (Boraginaceae).

Myosotis is a genus with approximately 100 species and a worldwide distribution (Al-Shehbaz, 1991). Centres of diversity have developed in Western Eurasia & New Zealand. Grau & Schwab (1982) recognized three morphologically defined groups within the genus, two occurring in the northern hemisphere and Africa (section *Myosotis* and section *Exarrhena*, *discolor* group), the third being restricted to Australasia and South America (section *Exarrhena*, austral group). We report here a morphometric analysis (Fig. 1) which supports earlier observations

that the austral taxa display greater variation than the other two groups (Grau & Leins, 1968; Grau & Schwab, 1982). Members of the austral group of section *Exarrhena* exhibit growth forms, floral and pollen characteristics not apparent in the remaining subgeneric groups. This greater morphological diversity has led to the suggestion that the austral group of *Myosotis* holds an ancestral position within the genus (Grau & Leins, 1968). However, we also report comparative DNA sequences from several chloroplast loci and a nuclear locus (Fig. 2). Analysis of these data show that, in comparison to the situation in representative northern hemisphere taxa, little genetic diversity exists within and between members of the austral group. Further, these molecular data, taken together with ITS and *matK* sequences from more widely sampled taxa and outgroups (Winkworth *et al.* in prep) suggest that the *Myosotis* species studied from Australia, New Zealand, and South America are closely related and of northern origin, that their morphological diversification is recent and not of great antiquity, and that they have reached their widely disjunct distribution by long-distance dispersal.

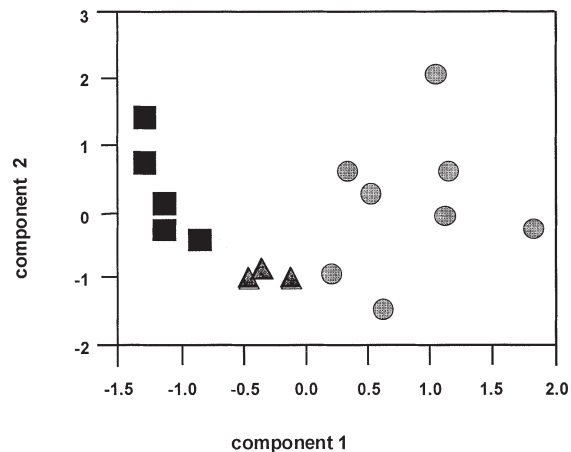


Figure 1 Scattergraph for a Principal Components Analysis (PCA) involving seventeen morphological characters which could be scored for sixteen representative taxa. Data points are coded according to the subgeneric groupings of Grau & Schwab, 1982. Section *Myosotis* (species are from Eurasia, North America and Africa) is indicated by black circles, Section *Exarrhena* *discolor* group (species are from Eurasia and Africa) are open and grey circles denote Section *Exarrhena* Austral group (species are from Australasia and South America). Data taken from Grau & Leins, 1968; Grau & Schwab, 1982, various regional floras not cited and from the authors' personal observations.

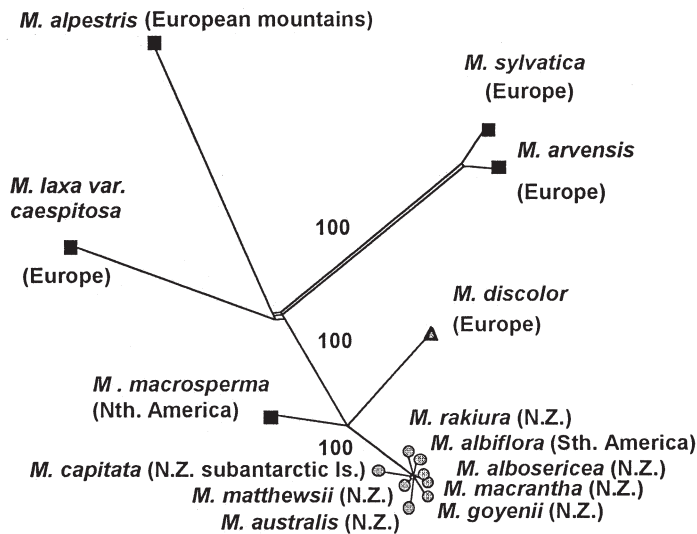


Figure 2 Splitsgraph (using Huson, 1998: SplitsTree2.1) made from a combined dataset of 2548 base pairs. Sequence data include the internally transcribed spacer region (ITS1, ITS2 and 5S gene) of the nuclear ribosomal DNA, the 3' region of the *matK* gene, the 5' region of the *ndhF* gene and the *trnK-psbA* intergenic spacer of the chloroplast genome. Taxa are a selection from a more widely sampled set (Winkworth *et al.* in prep.); subgeneric groups are denoted as for Figure 1 and bootstrap values (250 replicates) for internal edges are given.

Our observations on *Myosotis*, indicating rapid morphological diversification, parallel those for other plant groups in New Zealand (*Hebe*, Wagstaff & Garnock-Jones, 1998; *Gingidia*, Mitchell *et al.*, 1998; *Carmichaelia*, Wagstaff *et al.*, 1999; *Sophora*, Hurr *et al.*, 1999; *Ranunculus*, Lockhart *et al.* submitted; *Anisotome* and *Aciphylla*, Winkworth *et al.* in prep) and from other island archipelagos (the Hawaiian Islands *Bidens*, Carr, 1987, and Silversword alliance Baldwin, Kyhos & Dvorak, 1990; the Juan Fernandez Islands *Robinsonia*, Sang *et al.*, 1994, and *Dendroseris* Sang *et al.*, 1995; and the Macaronesian Islands *Echium*, Böhle *et al.*, 1996 and *Sonchus* Kim *et al.*, 1996). Such diversification, i.e. in the situation of fast changing environments and newly opened island habitats, may be explained from recent observations made in plant developmental genetics (e.g. *Mimulus*, Bradshaw *et al.* (1995) and teosinte, Doebley *et al.* (1997)). These suggest that small amounts of genetic change at relatively few gene loci can underlie dramatic morphological differences in recently evolved plant species. Thus, it may not be surprising to find that little genetic change in neutral DNA markers has accompanied dramatic morphological evolution in island species.

Recent comparative DNA sequencing in several plant groups strongly support the palaeobotanical arguments of Pole (1994)

and Macphail (1997) for the extraordinary evolutionary importance of recent long-distance dispersal in the origin of the extant New Zealand flora. Such an interpretation is clearly evident from molecular data for the (sub)alpine flora which has been strongly affected by climatic changes and the upheaval of the high mountains during the Pliocene and Pleistocene. Presumably, long-distance dispersal also influenced the lower elevation flora of New Zealand during the earlier Tertiary when the distances between Australia, Tasmania, the Antarctic, and South America were smaller than today.

Nevertheless, despite the obvious importance of long distance dispersal, the unexpected rapid and profound morphological differentiation observed in all the genera studied should caution against overinterpreting the palaeobotanical evidence. Are apparent discontinuities always an indicator for the interruption of *in situ* lineages and new long-distance introduction? Many extinctions undoubtedly have occurred, but the complete disappearance of the terrestrial New Zealand biota during the Oligocene transgression and its *de novo* formation by long-distance arrivals in the Miocene as proposed by Pole (1994) certainly appears questionable. This is suggested, not only because of the uninterrupted fossil record of certain taxa given by Macphail (1997: Table 1), but also because of the occurrence of ancient

austral groups at lower elevations in modern New Zealand. Examples include woody seed plants like certain members of Araucariaceae, Podocarpaceae, Proteaceae (Hoot & Douglas, 1998), Winteraceae (Suh *et al.*, 1993; Karol *et al.*, 1999) and *Nothofagus* (Manos, 1997), or animals (Cooper & Millener, 1993) such as *Leiopelma* (frogs), *Sphenodon* (tuatara), *Peripatus*, and some terrestrial gastropods. It is clearly more parsimonious on current information to interpret their presence as continuous lineages in the New Zealand region rather than as examples of long-distance dispersal (Linder & Crisp, 1995). Consequently, one has to assume the existence of at least a limited amount of terrestrial biota throughout the Tertiary in the general New Zealand area.

ACKNOWLEDGMENTS

We thank the New Zealand Marsden Fund, the Alexander Von Humboldt Foundation and the FRG/ISAT linkages program for supporting our studies on the New Zealand flora.

R. C. WINKWORTH^{1,2},
A. W. ROBERTSON²,
F. EHRENDORFER³ and
P. J. LOCKHART¹

Institute of Molecular BioSciences, Massey University, Private Bag 11222, Palmerston North, New Zealand,

²*Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North, New Zealand, and*

³*Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria*

REFERENCES

- Al-Shehbaz, I.A. (1991) The genera of Boraginaceae in the Southeastern United States. *J. Arnold Arbor. (Suppl.) Ser.*, **1**, 1–169.
- Baldwin, B.G., Kyhos, D.W. & Dvorak, J. (1990) Chloroplast DNA evolution and adaptive radiation in the Hawaiian Silversword alliance (Asteraceae-Madiinae). *Ann. Mo. Bot. Gdns*, **77**, 96–109.
- Bradshaw, H.D., Wilbert, S.M., Otto, K.G. & Schemske, D.W. (1995) Genetic mapping of floral traits associated with reproductive isolation in monkeyflowers (*Mimulus*). *Nature*, **376**, 762–765.
- Böhle, U.-R., Hilger, H.H. & Martin, W.F. (1996) Island colonisation and evolution of the insular woody habit in *Echium* L. (Boraginaceae). *Proc. Nat. Acad. Sci.* **93**, 11740–11745.

- Carr, G.D. (1987) Beggars Ticks and Tarweeds: masters of adaptive radiation. *Trends Ecol. Evol.* **2**, 192–195.
- Cooper, R.A. & Millener, P.R. (1993) The New Zealand Biota: Historical Background and New Research. *Trends Ecol. Evol.* **8**, 429–433.
- Doebley, J., Stec, A. & Hubbard, L. (1997) The evolution of apical dominance in maize. *Nature*, **386**, 485–488.
- Grau, J. & Leins, P. (1968) Pollenkorntypen und Sektionsgliederung der Gattung *Myosotis* L. *Ber. Dt. Bot. Gesell.* **81**, 107–117.
- Grau, J. & Schwab, A. (1982) Mikromerkmale der blüte zur gliederung der Gattung *Myosotis*. *Mitt. Bot. München*, **18**, 9–58.
- Hoot, S.B. & Douglas, A.W. (1998) Phylogeny of the Proteaceae based on *atpB* and *atp B-rbcL* intergenic spacer region sequences. *Austr. Syst. Bot.* **11**, 320–339.
- Huson, D.H. (1998) SplitsTree: analysing and visualising evolutionary data. *Bioinformatics*, **14**, 68–73.
- Hurr, K.E., Lockhart, P.J., Heenan, P.B. & Penny, D. (1999) Dispersal of *Edwardsia* section of *Sophora* (Leguminosae) around the Southern Oceans: molecular evidence. *J. Biogeogr.* **26**, 565–577.
- Karol, K.G., Zimmer, E.A., Suh, Y. & Schatz, G. (1999) Molecular evidence for the phylogenetic position of *Takhtajania* in the Winteraceae. *XVI International Botanical Congress, St Louis, USA, August, 1–7, 1999 (Abstracts)*.
- Kim, S.-C., Crawford, D.J., Francisco-Ortega, J. & Santos-Guerra, A. (1996) A common origin for woody *Sonchus* and five related genera in the Macaronesian islands: molecular evidence for extensive radiation. *Proceedings of the National Academy of Science*, **93**, 7743–7748.
- Linder, H.P. & Crisp, M.D. (1995) *Nothofagus* and Pacific biogeography. *Cladistics*, **11**, 5–32.
- Macphail, M.K. (1997) Comment on M. Pole (1994): The New Zealand flora – entirely long-distance dispersal? *J. Biogeogr.* **21**, 625–635. *J. Biogeogr.* **24**, 113–114.
- Manos, P.S. (1997) Systematics of *Nothofagus* (Nothofagaceae) based on rDNA spacer sequences (ITS): taxonomic congruence with morphology and plastid sequences. *Am. J. Bot.* **84**, 1137–1155.
- Mitchell, A.D., Webb, C.J. & Wagstaff, S.J. (1998) Phylogenetic relationships of species of *Gingidia* and related genera (Apiaceae, subfamily Apioideae). *N. Z. J. Bot.* **36**, 417–424.
- Pole, M. (1994) The New Zealand flora – entirely long-distance dispersal? *J. Biogeogr.* **21**, 625–635.
- Raven, P.H. (1973) Evolution of the subalpine and alpine plant groups in New Zealand. *N.Z. J. Bot.* **11**, 177–200.
- Sang, T., Crawford, D.J., Stuessy, T.F. & Silva, O.M. (1994) ITS sequences and the phylogeny of the genus *Robinsonia* (Asteraceae). *Syst. Bot.* **20**, 55–64.
- Sang, T., Crawford, D.J., Kim, S.-C. & Stuessy, T.F. (1995) Radiation of the endemic genus *Dendroseris* (Asteraceae) on the Juan Fernandez Islands: evidence from sequences of the ITS region of the nuclear ribosomal DNA. *Am. J. Bot.* **81**, 1494–1501.
- Suh, Y., Thien, L.B., Reeve, H.E. & Zimmer, E.A. (1993) Molecular evolution and phylogenetic implications of internal transcribed spacer sequences of ribosomal DNA in Winteraceae. *Am. J. Bot.* **80**, 1042–1055.
- Wagstaff, S.J. & Garnock-Jones, P.J. (1998) Evolution and biogeography of the *Hebe* complex (Scrophulariaceae) inferred from ITS sequences. *N.Z. J. Bot.* **36**, 425–437.
- Wagstaff, S.J., Heenan, P.B. & Sanderson, M.J. (1999) Classification, origins, and patterns of diversification in New Zealand Carmichaeliaceae (Fabaceae). *Am. J. Bot.* **86**, 1346–1356.
- Wardle, P. (1963) Evolution and distribution of the New Zealand flora, as affected by Quarternary climates. *N.Z. J. Bot.* **1**, 3–17.
- Wardle, P. (1968) Evidence for an indigenous pre-quaternary element in the mountain flora of New Zealand. *N.Z. J. Bot.* **6**, 120–125.
- Wardle, P. (1978) Origins of the New Zealand mountain flora, with special reference to trans-Tasman relationships. *N.Z. J. Bot.* **16**, 535–550.