

**EVOLUTION AND BIOGEOGRAPHY OF *ABROTANELLA*  
(ASTERACEAE): SMALL DENIZENS OF THE SOUTHERN  
HEMISPHERE<sup>1</sup>**

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**INTRODUCTION**

Nineteenth century botanists exploring the southern hemisphere returned with plants that closely resembled one another but were collected from lands widely separated by the southern oceans. These posed a conundrum for Darwin who postulated descent from a common ancestor rather than multiple centres of creation. In 1859 he wrote "I am inclined to look in the southern, as in the northern hemisphere, to a former and warmer period, before the commencement of the glacial period, when the Antarctic lands, now covered with ice, supported a highly peculiar and isolated flora. I suspect that before this flora was exterminated by the glacial epoch, a few forms were widely dispersed to various points of the southern hemisphere by occasional means of transport, and by the aid, as halting places, of existing and now sunken islands, and perhaps at the commencement of the glacial period, by icebergs. By these means, as I believe, the southern shores of America, Australia, New Zealand have become slightly tinted by the same peculiar forms of vegetable life."

The taxonomic history of *Abrotanella*, a small genus in the Asteraceae or composite family, was largely influenced by these early botanical explorers. It was first discovered by Charles Gaudichaud in the Falkland Islands and described as *Oligosporus emarginatus* (Gaudichaud 1825). However, in the same year Cassini (1825) transferred it to the new genus *Abrotanella*. Hooker (1844, 1846) also collected specimens from the subantarctic islands,

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but placed them in two additional genera (*Trineuron*, *Ceratella*) and from Tasmania he described a third genus, *Scleroleima*. Gray (1862) described two new species of *Abrotanella* from southern South America. Gray's treatment may have influenced Hooker because in 1864 he described a new species of *Abrotanella* from New Zealand and transferred *Trineuron* and *Ceratella* to *Abrotanella*. In the Flora of Australia, Bentham (1866) also transferred *Scleroleima* and the species of *Trineuron* described by Mueller (1855) to *Abrotanella*.

As presently circumscribed the genus *Abrotanella* includes 20 species that are distributed in Australia, New Guinea, New Zealand including Auckland, Campbell, and Stewart islands, and southern South America including the Falkland Islands (Swenson 1995; Swenson & Bremer 1997a; Heads 1999) (Fig. 1).

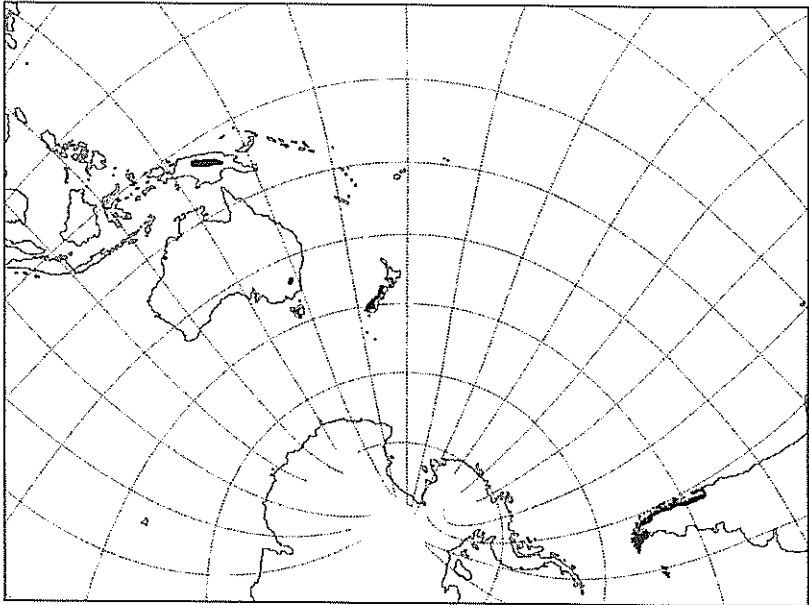


Figure 1. Distribution of *Abrotanella*.



**Figure 2.** Habit drawings from some of the New Zealand species of *Abrotanella*. **A.** *A. linearis* ( $\times 2$ ). **B.** *A. caespitosa* ( $\times 2$ ). **C.** *A. pusilla* ( $\times 2$ ). **D.** *A. inconspicua* ( $\times 2$ ). **E.** *A. rosulata*, endemic to the subantarctic islands ( $\times 1.5$ ). **F.** *A. spathulata*, endemic to the subantarctic islands ( $\times 1.5$ ). **G.** *A. muscosa* endemic to Stewart Island ( $\times 2$ ). A thorough taxonomic account and a key to the species is provided in Swenson (1995, 1996). Illustrations by Pollyanna von Knorring.

Ten species are described for New Zealand. They are usually small plants (Fig. 2A–G), sometimes not reaching more than a few millimetres above the ground, although some form cushions up to a metre in diameter. Often they form almost continuous communities with a few associated species representing other plant families. The leaves are entire and somewhat coriaceous with petioles that are often purple, sheathing, and widening at the base. In general, they have sessile capitula, and the capitula are disciform and heterogamous with slightly dimorphic florets. Central florets are of two types, perfect or functionally male. The corolla is generally 4-lobed (occasionally 2-, 3-, or 5-lobed) and white, purple, pale green, or yellowish. The cypsela (i.e. fruits typical of many Asteraceae, in which the achene is fused with a persistent calyx) lack a true pappus, but some species have a crowned apex or small horns.

The evolutionary relationships of this intriguing genus have puzzled botanists for the last 170 years. One view is that *Abrotanella* is a geographically isolated lineage whose evolution was coupled with the break-up of Gondwana, which included the separation of New Zealand during the late Cretaceous (Heads, 1999). Others have suggested that its evolution reflects a complex history of migration and long-distance dispersals along former antarctic archipelagos (Swenson & Bremer 1997b). In either case the study of the origin and diversification of *Abrotanella* is inextricably linked to its evolutionary history or phylogeny.

To reconstruct phylogenetic relationships in *Abrotanella*, we compared DNA sequences from 39 accessions that included most of the species and some of its putative relatives including *Blennosperma*, *Crocidium* and *Ischnea*. These four genera have been placed in subtribe Blennospermatinae (Senecioneae, Asteraceae). Our results were used to create the phylogeny shown in Fig. 3. In this tree the length of the branches reflects the number of accumulated mutations per million years. From the phylogeny presented in Fig. 3, we postulated the origin of the genus and estimated the timing of evolutionary events.

#### PHYLOGENY OF *ABROTANELLA*

Evolution of the Asteraceae very likely coincided with separation of South America from Antarctica, which occurred during the Eocene period of 35.5 to 30.5 million years ago (McLoughlin 2001). The place of origin is almost certainly South America (Bremer 1992, 1993). An Eocene origin of



Asteraceae is indicated by microfossils and general fossil flower morphology (DeVore & Stuessy 1995). Evidence for a South American origin is provided by subfamily Barnadesioideae (represented by the Chilean tree *Dasyphyllum dicanthoides* in Fig 3) which is restricted to South America, and is the sister group to all other Asteraceae (Bremer 1987; Jansen & Palmer 1998); that is, an ancestral member gave rise to one branch of the Asteraceae evolutionary tree consisting only of the Barnadesioideae and to another branch containing all other members of this large and diverse family.

The early appearance of comparatively specialized Asteraceae pollen suggests that the family radiated rapidly and was widely distributed by the Oligocene. The earliest reliable records of Asteraceae are microfossils from the mid-Oligocene of central Europe, although there are dubious records from the Eocene of South America (Graham 1996). Fossil pollen attributable to the Asteraceae first appears in Oligocene deposits in Eastern Australia and late Oligocene deposits in New Zealand (Macphail 1997). We used these fossil dates to calculate the mutation rate for the DNA sequences that we compared.

Our results suggest that *Abrotanella* was among a group of well-defined Asteraceae lineages that radiated during the mid- to late-Tertiary. Fig 3 suggests that the origin of the *Abrotanella* lineage dates back 19.4 million years. We propose that *Abrotanella* was widely distributed in Antarctica during the mid-Tertiary and became extinct there during the last glaciation, but their descendants persisted in lands to the north where they have since radiated. If this is a correct interpretation, Antarctica may in fact have been the ancestral area for *Abrotanella*. The radiation may have occurred via stepping stones along the Antarctic coastline and long-distance dispersal (Swenson & Bremer 1997b). However, this hypothesis is hard to test without fossil evidence from the different areas of endemism. The present disjunct distribution of *Abrotanella* in South America, New Zealand and Australia make reconstruction of the origin equivocal.

The main radiation in *Abrotanella* occurred about 4.2 million years ago (Fig. 3), which suggests that it accompanied mountain building and episodes of glaciation during the Pliocene and Pleistocene. *Abrotanella fosteroides* is restricted to Tasmania and is sister to the remaining species of *Abrotanella*. This is a surprising result, because it is the only tetraploid species in the genus (Swenson, 1995) and a more derived position, i.e. a more recent

origin, would be expected. Apart from *A. forsteroides*, the species form two distinct branches of the evolutionary tree that diverged approximately 3.1 million years ago, with one being confined to Australasia and the other, with the exception of *A. muscosa*, being confined to South America (Fig. 3). The timing is compatible with an Antarctic origin of the genus, as it coincides with recent fossil discoveries from the Meyer Desert Formation in the Transantarctic Mountains at latitude 85° 07' S, where tundra-like vegetation was present as late as 3 million years ago (Ashworth & Cantrill 2004). This vegetation had members of the angiosperm families Cyperaceae (sedges), Nothofagaceae, Poaceae (grasses) and Ranunculaceae. Perhaps the most interesting fossil is a cushion plant not determined to plant family, but similar in habit to extant cushion-forming plants found in southern South America, New Zealand and Tasmania.

*Abrotanella muscosa* is nested within the South American lineage, thus suggesting recent long-distance dispersal between South America and Stewart Island (New Zealand) after the two main branches split 3.1 million years ago, as first proposed by Swenson & Bremer (1997b). In other genera there apparently has also been considerable exchange between Australia (including Tasmania) New Guinea and New Zealand. Numerous examples of long-distance dispersal in southern hemisphere plant groups have been documented, and these are reviewed in Winkworth et al. (2002).

## CONCLUSION

*Abrotanella* is an intriguing genus restricted to the southern hemisphere. It is only distantly related to *Blennosperma*, *Crocidium* and *Ischnea*, the genera with which it was placed in the Blennospermatinae. However, its affinities within the Asteraceae are still in doubt. Our findings suggest *Abrotanella* is descended from a distinct lineage that initially diverged during the mid-Tertiary. The disjunct distributions of the species reflect a convoluted history of dispersal and extinction, which may include migration along the Antarctic coast and long-distance dispersal between South America and New Zealand. Recent speciation in *Abrotanella* has accompanied mountain building and episodes of glaciation. However, the divergence estimates calculated here should be viewed as preliminary and await the discovery of more detailed fossil evidence to establish multiple calibration points.

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