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THE HISTORY OF *BANKSIA* IN TASMANIA

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INTRODUCTION

The genus *Banksia*, in the family Proteaceae, is a prominent member of the Tasmanian flora today, but has a relatively low diversity, with only *Banksia marginata* having a widespread distribution. The other species of *Banksia* on mainland Tasmania, *B. serrata*, is restricted to only a few populations in the north west. Both Tasmanian species are widespread on mainland Australia. The fossil history of *Banksia* in Tasmania is relatively abundant, and demonstrates a much more diverse suite of species than today's remnants would indicate. In this paper we summarise the fossil history of *Banksia* and its near relatives in the state and consider the reason for the relatively low species diversity here today.

THE CURRENT DIVERSITY OF *BANKSIA*

Banksia is a widespread plant genus which characterises much of Australia's so-called "heathland"—areas with a classic mediterranean climate with hot dry summers and cool wet winters. More importantly, it is an integral part of the sclerophyllous flora, which is believed to have evolved primarily in response to soils with low nutrient levels, and in particular low levels of phosphorus and nitrogen. There are currently about 73 species of *Banksia* (Wrigley and Fagg 1989), with the greatest concentration of species being in southwestern Australia (more than 60 species). However, along the east coast of Australia there are 14 species, and, more importantly, it is not uncommon to see three or more species growing in close contact in the same ecosystems.

Related to *Banksia* (in the tribe Banksieae) are the genera *Dryandra*, which has at least 72 species, and is restricted to Western Australia; *Musgravea*, with two species in north Queensland rainforest; and *Austromuellera* with at least one and possibly two species, also in north Queensland rainforest. *Banksia* is occasionally found on rainforest margins, but apart from possibly one taxon, *B. integrifolia* var. *compar*, it is not recognised as a rainforest plant today.

Thus the diversity of *Banksia* in Tasmania today is relatively low compared to similar habitats in other parts of Australia. An intriguing aspect of this low diversity is that *Banksia marginata*, the common species in Tasmania, occurs in a very wide variety of habitats, from the alpine zone to coastal heath. A similar diversity of habitats is filled by several *Banksia* species in Victoria. This makes the history of the genus very important, since there are at least two options to account for this present day anomaly:

1. *Banksia* has always been relatively depauperate in Tasmania; or
2. *Banksia* was once much more common in Tasmania but has been restricted in diversity by one or more factors.

THE FOSSIL RECORD

One of the problems with the *Banksia* macrofossil record is that most specimens are leaves. While the leaves of *Banksia* are quite distinctive, it is difficult (and sometimes impossible) to separate them from *Dryandra*. Because of this, the fossils are put into the noncommittal genus *Banksieaephyllum* (see Hill and Christophel (1988) for a discussion of this). Each of the types of leaf which are assigned to *Banksieaephyllum* could have come from a true *Banksia*, an ancestor to *Banksia*, an extinct near relative of *Banksia*, or *Dryandra*. The first three options are quite likely in Tasmania, the last is less so, although even the possibility of finding a genus now restricted to Western Australia in Tasmania cannot be discounted.

The oldest evidence of *Banksia* comes from moulds of cones in Western Australia, which date from about 40–50 million years ago (McNamara and Scott 1983). The preservation of these cones is very good and there is no doubt about their identity. This provides the present benchmark for the maximum age of *Banksia*, which should be kept in mind during the following discussion. The oldest leaves of *Banksieaephyllum* are from slightly older sediments in southern New South Wales (about 55–60 million years), where two species occur, one of which probably represents an extinct genus, while the other is very similar to living *Banksia* species in Western Australia.

Fossil localities in Tasmania which contain *Banksia*-like leaves are shown on Fig. 1. The oldest fossils which resemble *Banksia* in Tasmania are leaf impressions which occur in sediments on the west coast (Regatta Point) which are about 50-55 million years old. There are at least two distinct leaf forms present. These do not have adequate organic preservation to fully confirm the generic identity, but

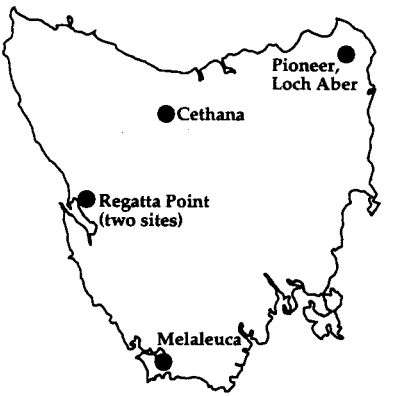

Fig. 1. Map of Tasmania showing the sites which have yielded *Banksia*-like fossils. There are two sites at Regatta Point that are mentioned in the text. Sites at Pioneer and Loch Aber, which are close together, are approximately 20-25 and 40-45 million years old respectively.

there is no doubt that they are of the *Banksia*-type, and can be placed in the genus *Banksieaeformis*, which is reserved for leaves of the *Banksieaephyllum*-type that have no organic preservation.

From this time onwards *Banksia*-like fossils are relatively common, but one site deserves special mention. The Cethana sediments in north central Tasmania, which are about 35 million years old, contain a very diverse flora, including at least seven species of *Banksia*-type leaves. Given that all species are well preserved it is reasonable to conclude that these species were growing within reasonable proximity of one another and thus represent a larger species diversity within a small region than in any similar area of the living Australian vegetation. It is also interesting to consider the form of the leaves that are present at about this time in Tasmania. Among the living species there are basically three main leaf types. Some species are entire margined, some are relatively finely serrate, and a third group are heavily serrate, sometimes with the serrations reaching right in to the mid-vein of the leaf (Fig. 2). All three leaf types occur in Western Australia, but in eastern Australia only the former two types are found. That is, the deeply serrate *Banksia* leaves are now totally restricted to Western Australia. It is therefore of great interest that leaves of this type commonly occur in the fossil record of south-eastern Australia, including Tasmania. One of the species at Cethana very clearly illustrates this type. Thus a leaf type which, on the basis of

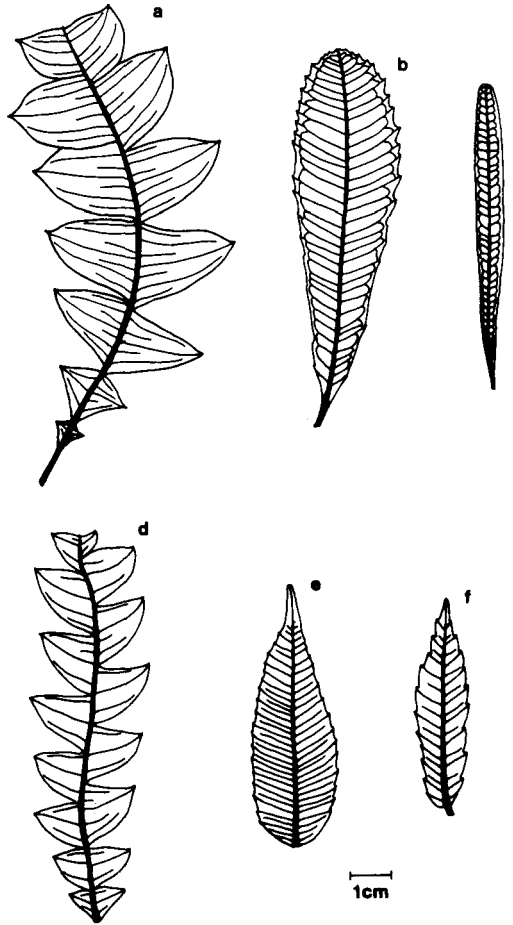

Fig. 2. (a-c) Living *Banksia* species: a,*B. grandis*.; b,*B. conferta* var. *conferta*.; c, *B. marginata*. These three leaves illustrate the range from very deeply serrate through to entire margined. (d-e) Tasmanian fossil leaves refereable to a *Banksia*-type: d, Undescribed *Banksieaephyllum* leaf from Cethana; e. *Banksieaephyllum attenuatum* from Loch Aber; f. *Banksieaephyllum regularis* from Pioneer.

living plant distribution, may have been predicted to have always been restricted to Western Australia, was once more widespread. The reason for the restriction of this type to Western Australia is unknown, but offers a particularly challenging palaeoecological problem.

There is a gap in the Tasmanian fossil record from about 25 to about 2.5 million years ago. However, the record of *Banksia* in Tasmania over the last approximately 2 million years is particularly interesting. The oldest macrofossil-bearing Quaternary sediments in Tasmania are mudstones at Regatta Point on Macquarie Harbour (about 0·7 to 2·5 million years old). These mudstones contain beautifully preserved leaves of two species of *Banksia*, both of which are extinct in Tasmania today (Jordan and Hill 1991). One, *B. strahanensis*, is typical of a group of species which have long, thin leaves with highly revolute margins. The most familiar example of this type in the living flora is *Banksia ericifolia*, which is a common garden plant which copes very well with the Tasmanian climate. The other is a large, broad-leaved species which is similar to *B. saxicola*, which is found today at high altitudes in the Grampian Mountains in Victoria. The interesting feature of these two species is that both are related to living species that could be expected to survive well in Tasmania today. This poses a pertinent question about the change in environment which brought about the relatively recent demise of such species here.

The Melaleuca sediments (approximately 40 000–150 000 years old) have yielded both leaves and cones of an extinct species of *Banksia* which may be the same as the broad-leaved species at Regatta Point. This places the time of extinction of this species very close to the present.

These records bring the glaciations of the last 2 million years sharply into focus as a possible cause of extinction of *Banksia* species. Some aspects of the fossil record are beyond dispute:

1. Prior to 25 million years ago, *Banksia* or *Banksia*-like plants were diverse in Tasmania.
2. Even since the onset of glacial cycles there were at least two species of *Banksia* in Tasmania which are now extinct.
3. Two species of *Banksia* remain in Tasmania today.

These points can be briefly discussed sequentially. The large number of older species is proven beyond doubt, but it is not certain when they began to decline. However, it is probable that there were less species present by about 25 million years ago. Part of the reason for this seems to be a shift in ecological preference among the taxa involved. At least some of the older taxa (which may or may not have been true *Banksia* species) were clear rainforest elements, having leaves with long drip tips (e.g. Fig. 2e,f) and very thin cuticles, whereas *Banksia* species today are predominantly members of open vegetation, although the related genera *Austromuellera* and *Musgravea* retain the rainforest habitat. The reasons for this shift from rainforest habitats to open vegetation are uncertain. One

possibility is that the rainforests prior to 25 million years ago had a different canopy structure to those of today, without a closed upper layer, but more conical forms suited to the capture of incoming radiant energy at a low angle and from a continuously varying direction at the prevailing very high latitudes. This would have suited mid-sized trees or shrubs which are shade intolerant and/or animal pollinated. A rainforest structure with the canopy spread vertically rather than horizontally would allow efficient capture of energy from a sun which is continually low in the sky. In such a forest, shade intolerant small trees or shrubs have access to direct sunlight, but as the landmass moved into lower latitudes and the sun appeared at a relatively higher angle, the tops of the forests would have closed over and smaller plants would have been disadvantaged because they no longer received high loads of direct sunlight. Another option is that in a more stratified rainforest, pollinating animals (especially birds) have much freer access to plants at lower levels, whereas they may be less frequent visitors beneath a closed canopy. Thus the closure of the rainforest canopy at the uppermost level may have excluded normally smaller plants like *Banksia*, and restricted them to more open (drier) habitats. This offers a possible explanation for the demise of at least some of the older species.

By the onset of the glaciations it is probable that the *Banksia* species present had a similar niche to that occupied by extant species, given their close morphological similarity to living forms. Why then did some species become extinct while others did not? One possibility is that all *Banksia* species became extinct from Tasmania during glaciations, but only some dispersed back. A more probable option lies in adaptability. *Banksia marginata* is an extremely adaptable and tolerant species in Tasmania (and other areas) today. This poses a "chicken or the egg" type of question. Is *B. marginata* adaptable and thus able to survive while other *Banksia* species became extinct, or has *B. marginata* evolved rapidly in recent time into a number of empty niches left by species which became extinct in the region? The former is the most likely. In difficult times it is the adaptable that survive rather than the adapted. *Banksia marginata* had the advantage of being relatively adaptable and thus was able to survive the rapid changes which occurred during the glaciations, whereas other species became extinct. During relatively mild times, like the present interglacial period, such a species does particularly well, expanding into a wide range of habitats. During the height of a glaciation it may be much more restricted, presumably to that end of its range which is most tolerant of cold and probably dry conditions, but its genetic flexibility has apparently been retained and it is able to expand rapidly when conditions permit.

Thus in Tasmania today *Banksia* is, in terms of numbers of species, a relatively unimportant genus. However, the species which occur here now and which occurred here in the past, reveal important aspects of the history of this characteristically Australian genus.

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METALLIC SKINKS *NIVEOSCINCUS METALLICUS* SAMPLED BY A CATTLE EGRET *ARDEOLA IBIS* IN HOBART

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A cattle egret, *Ardeola ibis*, crippled due to a wing injury, was found on a highway near Fitzroy Gardens in Hobart late in the morning of 15 September 1982. When rescued the egret regurgitated a food bolus composed entirely of 25 small freshly eaten metallic skinks, *Niveoscincus metallicus* . The recorded diet of cattle egrets in Australia is diverse: a very wide variety of arthropods, as well as frogs, reptiles and a few small mammals. These are taken from the surface of pasture or in shallow water (Hindwood 1971; McKilligan 1984). Egrets are catholic and opportunistic feeders in pasture. Lizards, especially small skinks, are the main veretbrate food of cattle egret chicks in a breeding colony near Gatton in south-eastern Queensland (McKilligan 1984). It appears lizards are a significant part of the diet only in Australia (McKilligan 1984).

The cattle egret is from Asia and is only recently naturalized in Australia. Its spread in Australasia is well recorded (Blakers *et al.* 1984). It was first reported as a visitor to Tasmania in 1965 (Thomas 1966). Since then some cattle egrets have regularly migrated to Tasmania spending winter here and then returning to breed in northern New South Wales and Queensland (Maddock 1990).

The recording of the egret eating lizards in Tasmania is not in itself remarkable; unless this was causing damage to lizard populations through added predation.