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The Cenozoic macrofossil record of the Cupressaceae in the Southern Hemisphere*

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ABSTRACT. Cupressaceae macrofossils are difficult to identify in older sediments, but the extant southern genera begin their record in the Cretaceous (*Athrotaxis*) and become more diverse and extensive during the Cenozoic. Several extinct genera of Cupressaceae also occur in Cretaceous and Cenozoic sediments, especially in Australasia, and some Cretaceous fossils appear to be more closely related to extant Northern rather than Southern Hemisphere genera. However, information about the history of the dry forest Cupressaceae is extremely limited due to a lack of fossilisation in such environments. The southern Cupressaceae, past and present, demonstrate an ability to compete effectively with angiosperms and have co-existed with them for tens of millions of years. In south-eastern Australia and New Zealand at least, the generic diversity and probably the geographic extent of the Cupressaceae has declined since the Early Oligocene. This decline was probably directly tied to climate change, with the Neogene changes in rainfall (in particular increasing seasonality and aridity) having a marked effect. However, in at least some genera (e.g. the dry-adapted *Callitris* in Australia) there appears to have been an increase in diversity following continental drying.

KEY WORDS: macrofossils, Cupressaceae, Cretaceous, Cenozoic, Southern Hemisphere

INTRODUCTION

The Southern Hemisphere vegetation is particularly interesting because of the wide distances separating most of the major land masses. Now that the history of fragmentation of the supercontinent Gondwana is relatively well known, it is clear that these ocean gaps are, by geological standards, relatively recent. Along with the separation of the continents, there have been massive climate changes that have led to much of the Southern Hemisphere now existing under a very different climate to that prevailing before rifting began (e.g. Frakes 1999). In some cases the magnitude of these climate changes has led to major vegetation change. The best example of this is Antarctica, where the climate has cooled to the point where the once forested landscape is now devoid of woody vegetation and is mostly ice-covered (see Hill & Scriven 1995) for a review of Antarctic vegetation history).

In other southern land masses the climate changes have been more subtle, and forested vegetation still occurs on all of them, making it more difficult to appreciate the magnitude of any changes that have occurred since rifting began. The conifers are an excellent group to use to examine vegetation changes, since many extant conifer genera have been in place for at least 50 million years, and thus encompass the time when Gondwana finished fragmenting and major climate change took place. Past conifer distribution gives a good indication of the magnitude of these changes, since the species concerned were and are an adaptable group of plants that have survived and sometimes flourished throughout this period of considerable turmoil.

Three major conifer families are present in the Southern Hemisphere today (along with one species in the Taxaceae). The Podocarpa-

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ceae have a well understood fossil record, while the Araucariaceae has only three extant genera (one of which is the very restricted, monospecific *Wollemia nobilis* W.G. Jones, K.D. Hill & J.M. Allen), which limits what can be said about major distributional changes (see Hill & Brodribb 1999). However, the Cupressaceae is more generically diverse than the Araucariaceae, but has not been as seriously considered in terms of its contribution to our understanding of changing environments in the Southern Hemisphere as the Podocarpaceae. My intention here is to examine the Cupressaceae macrofossil record, including the Taxodiaceae as recommended originally by Eckenwalder (1976 a,b) and recently supported by molecular phylogenetic research (Price & Lowenstein 1989, Chase et al. 1993, Gadek & Quinn 1993). Not all macrofossil records are mentioned, since many are difficult to substantiate, are very likely to be misidentifications, or are too poorly preserved to be useful. Zastawniak (1981) highlighted the problems involved by concluding that the Cupressaceae species cf. *Sequoia fastigiata* (Sternberg) Nathorst from Upper Cretaceous sediments on Snow Hill Island, Antarctica, and *Fitzroya tertiaria* Berry from Eocene sediments from Rio Pichileufu, Argentina, were probably better considered as the Podocarpaceae genera *Dacrydium* Sol. ex Lambert and *Dacrycarpus* (Endl.) de Laubenf. respectively. In most cases if a fossil lacks organic preservation, and especially cuticular detail, it is difficult to be precise about its placement within the family and the record loses much of its utility.

The fossil wood record of the Cupressaceae in the Southern Hemisphere is badly in need of critical review to determine reliable occurrence. Such a review is beyond the scope of this paper.

ECOLOGY OF EXTANT SOUTHERN CUPRESSACEAE

In order to fully appreciate the fossil record of the southern Cupressaceae, it is important to summarise what is known about the ecology of the living members of the family in the Southern Hemisphere. There are currently 11 Southern Hemisphere Cupressaceae genera, occurring in South America, Australia, New Zealand, New Guinea and South Africa. The separate generic status of *Papuacedrus* H.-L.Li, *Libocedrus* Endl. and *Austrocedrus* Florin & Boutelje is not accepted by everyone, but given the presence of all three genera as distinct entities in the fossil record back to at least the Early Oligocene (Hill & Carpenter 1989, Hill & Brodribb 1999), their separate identities are accepted here.

The southern Cupressaceae today express an enormous range of physiological tolerances, much wider than the Araucariaceae or Podocarpaceae. Some taxa grow in the extremes of drought and high temperature and exhibit extreme drought tolerance, e.g. *Actinostrobus* Miq. ex Lehm. and *Callitris* Vent. in Australia, *Widdringtonia* Endl. in South Africa (Brodribb & Hill 1997), low temperature (e.g. *Diselma* Hook.f. in Tasmania) and extremely wet and shady conditions (e.g. some *Papuacedrus* H.-L.Li, in Papua New Guinea and *Libocedrus* Endl. in New Zealand and New Caledonia, Hill & Brodribb 1999). Only about half of the 39 species of Southern Hemisphere Cupressaceae occur in wet forests, while the remainder grow in seasonally dry to arid woodland, with the bulk belonging to the genus *Callitris* Vent. in Australia. *Actinostrobus* Miq. ex Lehm., *Callitris* Vent. and *Widdringtonia* Endl. regenerate by continuous recruitment or in response to infrequent wildfire (Bowman & Harris 1995, Midgley et al. 1995), and one *Widdringtonia* Endl. species can resprout from an underground lignotuber (Midgley et al. 1995).

The monospecific *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri is the only Cupressaceae species spanning the gap from wet to dry forest, although even its driest occurrence in the Andean steppe is more mesic than the dry extremes of *Actinostrobus* Miq. ex Lehm., *Callitris* Vent. and *Widdringtonia* Endl. *Austrocedrus* Florin & Boutelje regenerates continuously at the dry and cold ends of its distribution (Villalba & Veblen 1997), but in more mesic mixed *Nothofagus* forest, regeneration relies on disturbance caused primarily by fire, but also by earthquakes, land slides and wind-throw (Veblen et al. 1995).

The other Southern Hemisphere Cupressaceae occur in wet forest, the majority in montane environments. *Fitzroya* Hook.f. ex Lindl. and *Athrotaxis* D. Don (Chile, Argentina and Tasmania respectively) fill similar niches by inhabiting a large altitudinal range and becoming increasingly dependent on disturbance for regeneration in lower altitude forest (Cullen 1987, Cullen & Kirkpatrick 1988a, b, Donoso et al. 1993). *Pilgerodendron* Florin and *Diselma* Hook.f. (also Chile, Argentina and Tasmania respectively) usually occur as shrubs and small trees on infertile substrata, and both have colonised subalpine areas in postglacial times (Villagran 1990). Extant *Libocedrus* Endl. species occur from near sea level to near the tree line in New Zealand and New Caledonia and the closely related *Papuacedrus* H.-L.Li is an abundant conifer in mid-montane to subalpine rainforest in Papua New Guinea (Hope 1980). The most restricted extant southern Cupressaceae genus is the monospecific *Neocallitropsis* Florin, which occurs as a few gregarious communities in the New Caledonian maquis (Hill & Brodribb 1999).

FOSSIL RECORD

The early fossil record of the Cupressaceae is obscure, since nearly all Mesozoic fossils originally assigned to the Cupressaceae having since been reassigned to the extinct family Cheirolepidiaceae (Miller 1988). Fossil pollen of the Cupressaceae is also generally uninformative, usually being identified only to family level (Hill & Brodribb 1999). The macrofossil record of unequivocal Southern Hemisphere Cupressaceae is mostly from south-eastern Australia, probably because so much well preserved Cenozoic plant material occurs there, but some very significant fossils are present elsewhere in the Southern Hemisphere. Macrofossils include relatively abundant foliage and occasional ovuliferous cones, although unfortunately the two are only rarely found in organic connection. Macrofossils of Cupressaceae from Cretaceous and Cenozoic sediments that are based on well preserved material that has been adequately identified were listed by Hill and Brodribb (1999).

The oldest unequivocal Cupressaceae macrofossil is permineralised foliage and attached ovuliferous cones assigned to *Austrosequoia wintonensis* M.D. Peters & D.C. Christophel, from the mid-Cretaceous of Queensland, Australia. Peters and Christophel (1978) described this material as a new, extinct genus because they considered the cone to be similar to extant *Sequoia* Endl., but the foliage to be similar to extant *Athrotaxis cupressoides* D. Don. Unfortunately the petrified foliage did not allow cuticular morphology of these fossil to be examined. Hill et al. (1993) described a second *Austrosequoia* species from Early Oligocene sediments in Tasmania, also based on ovulate cones and foliage, although this material is organically preserved. The cuticular micromorphology of the Tasmanian *Austrosequoia* species demonstrates that it is distinct from *Athrotaxis*, and Hill et al. (1993) concluded that the difference between the *Austrosequoia* species and *Sequoia* could be at the specific rather than the generic level. This is a particularly interesting fossil find, since it demonstrates a possible Cretaceous and Cenozoic distribution of a Cupressaceae genus in both hemispheres, something that does not occur today.

Pole (1995) described the extinct genus *Otokauia*, based on detached, organically preserved leaves from the Late Cretaceous of New Zealand. The cuticular micromorphology of these leaves matches *Austrosequoia* M.D. Peters & Christophel (Hill & Brodribb 1999), but the general leaf morphology does not. According to Hill and Brodribb (1999), this fossil genus may be closely related to *Austrosequoia* M.D. Peters & Christophel, and it falls within the range of cuticular morphology displayed by extant Northern Hemisphere genera such as *Cryptomeria* D. Don, *Sequoia* Endl., *Sequoiadendron* Buchholz and *Taiwania* Hayata. This may represent another example of a fossil record of a northern member of the Cupressaceae with a much wider past distribution, extending well into the Southern Hemisphere, in the past.

Other potentially ancient records of Cupressaceae in the Southern Hemisphere include the extant Tasmanian genus *Athrotaxis* D. Don. Florin (1960) reviewed the fossil record of this genus and rejected all Northern Hemisphere records, a conclusion since confirmed by other researchers (e.g. Miller & LaPasha 1983). Florin also concluded that the only Southern Hemisphere fossil species worth considering are *A. ungeri* (Halle) Florin, *A. australis* Bose, *A. novae-zeelandiae* (Ett.) Florin and *A. ?tamarensis* R.M. Johnst. Townrow (1965) rejected *A. australis* Bose and *A. ?tamarensis* R.M. Johnst. as being too poorly preserved to be determinable, but considered *A. ungeri* (Halle) Florin and *A. novae-zeelan-*

diae (Ett.) Florin to belong to *Athrotaxis*. *A. ungeri* (Halle) Florin consists of shoot and cone impressions from probable Early Cretaceous sediments in Patagonia. The foliage resembles that of extant *A. cupressoides* D. Don, and the cuticular morphology of Late Jurassic-Early Cretaceous specimens of this species from Argentina are consistent with *Athrotaxis* (Archangelsky 1963), but to be certain of the identification scanning electron microscopy of the cuticle is required (Hill & Brodribb 1999). Villar de Seoane (1998) re-investigated *A. ungeri* (Halle) Florin using scanning and transmission electron microscopy, but she did not illustrate the internal cuticular view of the stomatal complex, which is unique in *Athrotaxis* (Hill et al. 1993). However, on the basis of other characters she concluded that the leaves of *A. ungeri* (Halle) Florin are similar to those of *A. cupressoides* D. Don in size and shape, and in the anatomy and ultrastructure of the cuticle, although there are differences between the two species.

Athrotaxis novae-zeelandiae (Ett.) Florin is known only as vegetative shoots from the Late Cretaceous of New Zealand, and Pole (1995) transferred it to the extant genus *Sequoiadendron*. Pole illustrated both a shoot fragment with several attached leaves and the cuticular micromorphology with scanning electron microscopy. Hill and Brodribb (1999) concluded that the subsidiary cell arrangement in his illustrations is much more similar to the *Athrotaxis* type than to *Sequoiadendron* and they rejected Pole's transfer and retained the fossil in *Athrotaxis*. They also noted that the foliage of *A. novae-zeelaniae* (Ett.) Florin is extremely slender compared to extant *Athrotaxis* D. Don (and also *Sequoiadendron* Buchholz), but it is similar in dimension to an Oligocene species from Tasmania, *A. rhomboidea* (Wells & R.S. Hill) R.S. Hill, G. Jordan & Carpenter (Hill et al. 1993, see below).

The oldest *Athrotaxis* D. Don fossils from its current range (Tasmania) were described by Townrow (1965) from Early Eocene sediments. These specimens, consisting of leafy shoots with closely appressed leaves that are of about the same size and shape as extant *A. cupressoides* D. Don, have only been illustrated by line drawings. The cuticular morphology is consistent with *Athrotaxis*, but again, re-examination with scanning electron microscopy is necessary to confirm this (Hill & Brodribb 1999). Townrow (1965) initially assigned these fossils to *A. ungeri* (Halle) Florin, but later (Townrow 1967) he included them within *A. tasmanica* Townrow, which he described based on probable Tertiary macrofossils from Queensland. The identity of the Queensland fossils as *Athrotaxis* D. Don is even less certain, since they are more fragmentary than the Tasmanian specimens and again are only illustrated by line drawings (Hill & Brodribb 1999). *Athrotaxis* leafy shoots and ovulate cones (Fig. 1: 1) are relatively common in Tasmania from the Early Oligocene onwards (Hill et al. 1993). Most resemble the extant species quite closely, but *A. rhomboidea* (Wells & R.S. Hill) R.S. Hill, G. Jordan & Carpenter has foliage that is very slender in comparison with the extant species (Fig. 1: 1).

Late Paleocene sediments in south-eastern Australia have yielded vegetative remains of Cupressaceae that cannot be assigned to an extant genus. The extinct genera *Bungarbia* S.S. Whang & R.S. Hill and *Monarophyllum* S.S. Whang & R.S. Hill (Whang & Hill 1999) have the papillate cuticular micromorphology that is typical of most southern (and northern) genera of extant Cupressaceae, especially if the extant members of the old Taxodiaceae are not considered. Unfortunately, these fossils are quite fragmentary and much remains to be discovered about them.

The same Late Paleocene sediments have yielded vegetative material that has been assigned to two species of the extant genus *Libocedrus* Endl. (Whang & Hill 1999), and this represents the oldest record of the complex of three closely related genera, *Austrocedrus*, Florin & Boutelje, *Libocedrus* Endl. and *Papuacedrus* H.-L.Li. These two fossil species share some characters with *Austrocedrus* and may represent part of an ancestral complex that soon afterwards diverged into the genera *Austrocedrus*, *Libocedrus* and *Papuacedrus*. *Libocedrus* has also been recorded in Early Eocene sediments from Tasmania (Hill & Brodribb 1999). Zhou and Li (1994) described *Papuacedrus shenii* Zhou from Eocene sediments on the Antarctic Peninsula, but the specimens are fragmentary and so it is difficult to tell which of *Papuacedrus* H.-L.Li, *Libocedrus* Endl. and *Austrocedrus* Florin & Boutelje they should be assigned to.

Libocedrus Endl. was relatively common by the Early Oligocene in Tasmania, with both fo-

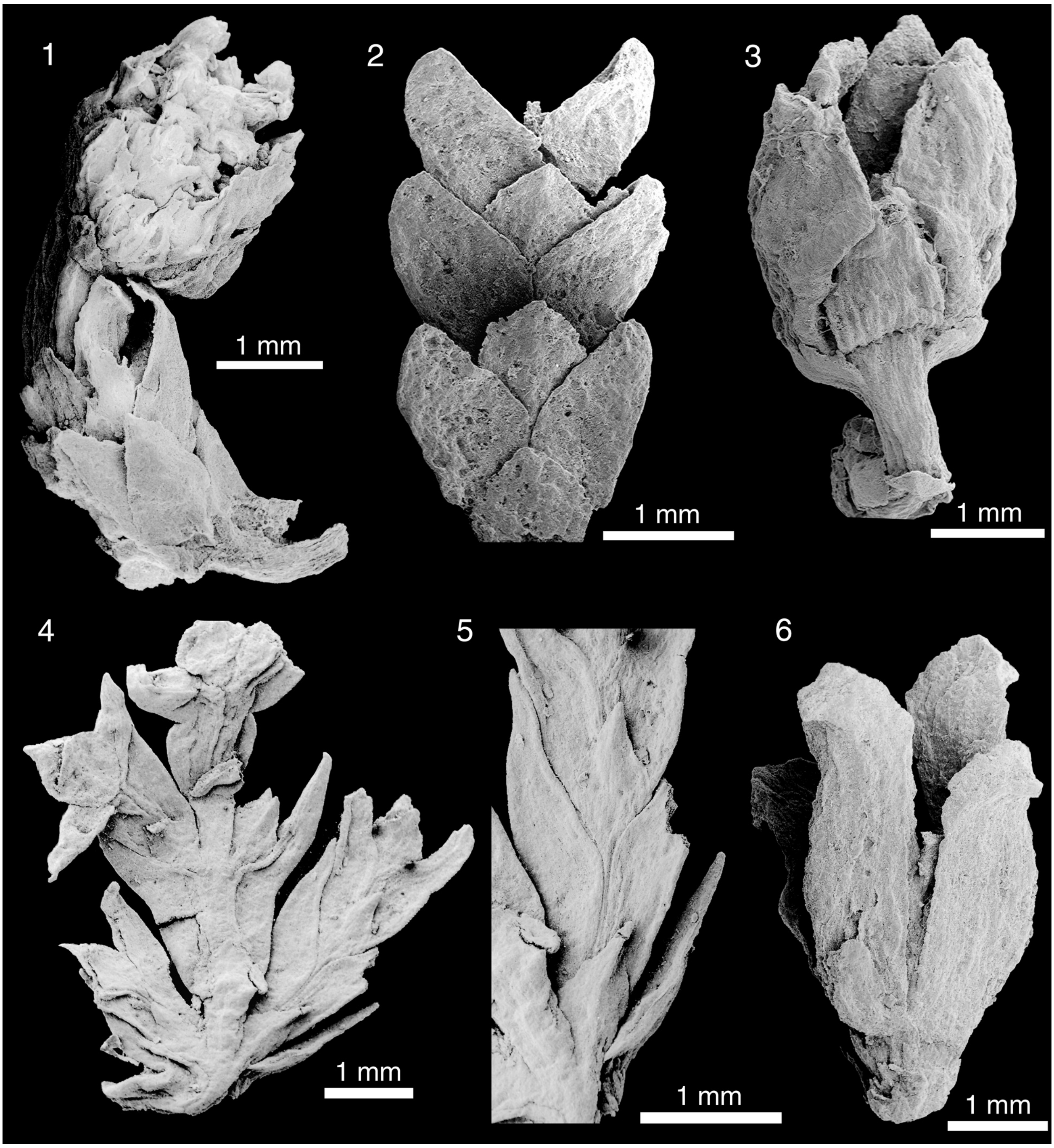

Fig. 1. **1** – scanning electron micrograph (SEM) of a shoot of *Athrotaxis rhomboidea* (Wells & R.S. Hill), R.S. Hill, G. Jordan & Carpenter with an immature ovulate cone attached from the Early Oligocene of Tasmania. Modified from Hill et al. (1993), **2** – SEM of a shoot of *Libocedrus jacksonii* R.S. Hill & Carpenter from the Early Oligocene of Tasmania, modified from Hill & Carpenter (1989), **3** – SEM of an ovulate cone of *Libocedrus mesibovii* R.S. Hill & Carpenter from the Early Oligocene of Tasmania, modified from Hill & Carpenter (1989), **4** – SEM of a shoot of *Papuacedrus australis* R.S. Hill & Carpenter from the Late Oligocene-Early Miocene of Tasmania, modified from Hill & Carpenter (1989), **5** – close up of part of the specimen shown in Fig. 4, showing detail of the leaf arrangement, modified from Hill & Carpenter (1989), **6** – SEM of an ovulate cone of *Austrocedrus tasmanica* R.S. Hill & Carpenter from the Late Oligocene-Early Miocene of Tasmania, modified from Hill & Carpenter (1989)

liage and ovuliferous cones (Fig. 1: 2,3) recorded (Hill & Carpenter 1989). *Papuacedrus* foliage (Fig. 1: 4,5) has also been recorded in the Tasmanian Early Oligocene and it persists until at least the Early Miocene (Hill & Carpenter 1989). Ovuliferous cones of *Austrocedrus* (Fig. 1: 6) have been recorded from Late Oligocene-Early Miocene Tasmanian sediments (Hill & Carpenter 1989). However, outside Tasmania these genera are rare in the fossil record. *Libocedrus* has one other published record in the Southern Hemisphere, that being foliage assigned to the extant *L. plumosa* (D. Don) Sarg. from the Late Miocene-Pliocene of New Zealand (Couper & McQueen 1954). Berry (1938) described impression fossils from the Miocene of Argentina as *Libocedrus prechilensis* E.W. Berry. He considered that they closely resembled *L. chilensis* (D. Don) Endl. (now *Austrocedrus* Florin & Boutelje), but this determination was made without preserved cuticular morphology.

A single fossil species of *Fitzroya* Hook.f. ex Lindl. (Fig. 2: 1) has been described from Early Oligocene sediments in Tasmania based on vegetative material (Hill & Whang 1996). It is similar to the only extant species, the South American endemic *F. cupressoides* (Molina) I.M. Johnst., but is clearly a distinct species. Other *Fitzroya* fossils have been located in Oligocene-Miocene sites in Tasmania, but they have not yet been described (Hill & Brodribb 1999).

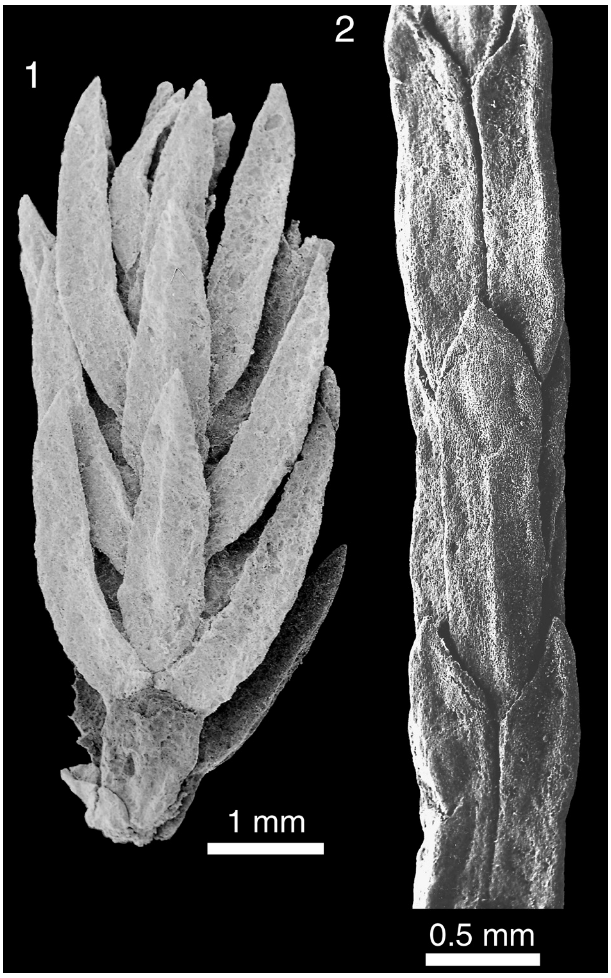

Fig. 2. **1** – scanning electron micrograph (SEM) of a shoot of *Fitzroya tasmanensis* R.S. Hill & S.S. Whang from the Early Oligocene of Tasmania, modified from Hill & Whang (1996), **2** – SEM of a shoot of *Callitris strahanensis* G. Jordan from the Early-Middle Pleistocene of Tasmania, modified from Jordan (1995)

The only other genus of the Cupressaceae in the Southern Hemisphere with a macrofossil record is *Callitris* Vent. This genus is the dominant member of the Cupressaceae in the living Australian vegetation, but it is very rare in the fossil record, with stem fragments and dispersed cuticle in the mid-Tertiary Latrobe Valley coal (Blackburn 1985) being the oldest record. Jordan (1995) described an extinct *Callitris* species from Early Pleistocene Tasmanian sediments (Fig. 2: 2).

GENERAL FEATURES OF THE CUPRESSACEAE FOSSIL RECORD

An interesting, but so far unexplained feature of the fossil record of the Cupressaceae is the extinction of many genera in Australia while other genera have survived through to the present. Extant genera that have become extinct in Australia are *Austrocedrus* Florin & Boutelje, *Libocedrus* Endl., *Papuacedrus* H.-L.Li and *Fitzroya* Hook.f., while *Athrotaxis* D. Don, *Diselma* Hook.f. and *Callitris* Vent. have survived. The two latter genera occur in specialised environments (alpine and arid respectively), which may offer a reason for their persistence, but the survival of *Athrotaxis* at the expense of other genera in Cupressaceae in Tasmania is enigmatic. Unfortunately we have no real idea what the patterns of extinction were elsewhere in the Southern Hemisphere, because the macrofossil record is not detailed enough to provide relevant data. However, we can see the survival patterns, and with the exception of *Libocedrus* it is interesting that no extant genus now exists on more than one landmass, whereas there are four extant genera that were present once in Australia that now only occur elsewhere. This suggests a very traumatic history for this family, with massive extinction over much of the range during the latter part of the Cenozoic.

There are also some interesting patterns in foliage evolution among the Southern Hemisphere Cupressaceae. Among extant taxa, two foliage types predominate. Several genera have relatively small bifacial leaves arranged three dimensionally around the axis (e.g. *Acti-*

nostrobus Miq. ex Lehm. *Athrotaxis* D. Don, *Callitris* Vent., *Diselma* Hook.f., *Fitzroya* Hook.f. ex Lindl., *Neocallitropsis* Florin, *Pilgerodendron* Florin and *Widdringtonia* Endl., Fig. 1: 1, Fig. 2: 1,2), and all of them either occur in open forests or are strongly disturbance dependent, suggesting that their leaf morphology is a factor in limiting the success of these taxa in closed forests (Hill & Brodribb 1999).

However, the other three, closely related genera, *Austrocedrus* Florin & Boutelje, *Libocedrus* Endl. and *Papuacedrus* H.-L.Li, have a similar leaf morphology that is very distinct from the other southern genera. The juvenile leaves are narrow and spirally arranged, while the adult leaves are in opposite pairs, with the lateral pair usually relatively large and bilaterally flattened, whereas the other pair are bifacially flattened to give an overall relatively two dimensional shoot with a broad, flat photosynthetic area (Fig. 1: 2). Stomata occur on the shoot undersurface, meaning that on the lateral leaves they cover one half of the abaxial surface, but not the other. This adult foliage form provides a very efficient means of light interception and may be important in improving growth rates when seedlings are in competition with angiosperms during regeneration (Hill & Brodribb 1999). Fossil species in these genera have similar foliage types as far back in time as they can be traced (Late Paleocene), and this possibly represents evolution in response to the presence of diverse broad-leaved angiosperms in closed forest canopies on a broad scale (Hill & Brodribb 1999).

Survival in closed, wet forest where large scale disturbance is infrequent requires shade tolerance and a high growth rate potential in order to capture space when canopy gaps are

Table 1. Conifer diversity in selected Cenozoic localities in south-eastern Australia and New Zealand. In each family for each location the number of species is given followed by the number of genera in brackets. Modified from Hill and Brodribb (1999), with updates where appropriate

Site	Age	Araucariaceae	Cupressaceae	Podocarpaceae	Unknown	Total
SE mainland Australia						
Lake Bungarby	Late Paleocene	3 (2)	4 (3)	6 (4)	0	13 (9)
Anglesea	Middle Eocene	0	0	5 (4)	0	5 (4)
Golden Grove	Middle Eocene	0	0	2 (2)	0	2 (2)
Nelly Creek	Middle Eocene	1 (1)	0	2 (1)	0	3 (2)
Nerriga	Middle Eocene	0	0	*1 (1)	0	1 (1)
Berwick Quarry	Late Oligocene-earliest Early Miocene	1 (1)	0	1 (1)	0	2 (2)
Latrobe Valley	Oligocene-Miocene	3 (2)	1 (1)	5 (4)	0	9 (7)
Tasmania						
Buckland	Early Eocene	0	1 (1)	7 (4)	0	8 (5)
Regatta Point	Early Eocene	5 (2)	1 (1)	5 (4)	0	11 (7)
Hasties	mid-Late Eocene	2 (1)	0	10 (7)	0	12 (8)
Loch Aber	mid-Late Eocene	1 (1)	0	4 (4)	0	5 (5)
Cethana	Early Oligocene	4 (2)	2 (2)	10 (6)	0	16 (10)
Lea River	Early Oligocene	3 (2)	5 (4)	6 (4)	0	14 (10)
Little Rapid River	Early Oligocene	3 (2)	4 (3)	19 (9)	0	26 (14)
Monpeelyata	Late Oligocene-earliest Miocene	3 (1)	2 (2)	2 (2)	0	7 (5)
Pioneer	Late Oligocene-earliest Miocene	2 (2)	5 (4)	7 (5)	0	14 (11)
Regatta Point	Early Pleistocene	0	2 (2)	5 (5)	0	7 (7)
New Zealand						
Kakahu	Paleocene	0	0	2 (2)	3	5 (>2)
Mt Somers	Paleocene	1 (1)	2 (2)	10 (4)	0	13 (7)
Livingstone	Middle Eocene	0	0	0	2	2 (?2)
Manuherika	Miocene	1 (1)	0	4 (4)	1	5 (>5)

[*] identification as a conifer not confirmed

formed. Shoot flattening in the Cupressaceae combines with a strong plagiotropic response in the shade to produce seedlings with a high ratio of leaf area to plant mass, and thus a potentially high growth rate under limiting light conditions.

Fossil conifer diversity is difficult to reconstruct in the Southern Hemisphere because data are rare, but some inferences can be drawn from south-eastern Australia and New Zealand. Table 1 shows the diversity of Cupressaceae and other conifer families in this region of southern Australasia. The general trend is for a high diversity of conifers at cooler locations throughout the region from the Late Paleocene through to the present day, although there has been an obvious decline in diversity since the peaks of the Early Oligocene. However, the warmer Middle Eocene sites on mainland south-eastern Australia are anomalous, with very low conifer diversity. Extant conifers have only very limited success in such lowland broad-leaf forest, and this may be due to mechanical limitations on the maximum size of leaves and shoots.

DISCUSSION

The ability of at least some Cupressaceae species to flatten their photosynthetic organs has enabled them to compete effectively with angiosperms in mesic conditions where disturbance is infrequent. This competition is facilitated by the long lifespans of Cupressaceae in the Southern Hemisphere (e.g. over 3,500 years in temperate regions, Lara & Villalba 1993). This gives shade tolerant species a long time to reach the canopy and disturbance-dependent species a higher probability of an appropriate disturbance event for seedling recruitment and establishment. Nevertheless, in south-eastern Australia and New Zealand, and probably many other parts of the Southern Hemisphere as well, the generic diversity and probably the extent of Cupressaceae has declined since the Early Oligocene. This decline was not a direct result of changes in angiosperm diversity, since they have also declined in wet environments over the same time period. Significant climate changes since Australia separated from Antarctica provide a more convincing explanation for conifer decline, but in some cases (e.g. the dry-adapted *Callitris* in Australia) there appears to have been an increase in diversity following continental drying.

The drought response of leaves of some extant Southern Hemisphere Cupressaceae and Podocarpaceae is closely correlated to the dry season rainfall experienced by these species (Brodribb & Hill 1998), suggesting that the current distribution of these species is constrained by water availability. Furthermore, the order of declining drought tolerance is approximately the same as the chronological order of conifer extinctions in south-eastern Australia (Hill & Brodribb 1999). Clearly, changes in rainfall, and in particular increased seasonality and aridity, had a marked effect on the distribution of conifers in the past. Angiosperms may also have contributed to conifer extinction in productive environments by lowering sub-canopy light levels and forcing conifers into a trade off between shade tolerance and drought tolerance where they do not perform as well as angiosperms. This may explain the current success of conifers in very wet and very dry habitats, but this hypothesis has not yet been tested (Hill & Brodribb 1999).

The fossil record of the Cupressaceae in the Southern Hemisphere remains sparse, but it demonstrates that the family has been an integral part of many plant communities for tens of millions of years leading up to the present. Many taxa in the Cupressaceae have been able to adapt to changing environments and especially to changing light climates as a result of the increase in angiosperm diversity coupled with relatively warm and wet climates in the Paleogene. However, climate change during the Neogene, and especially drying and cooling on a large scale at mid-high southern latitudes, has seen a major reduction in distribution and some extinction amonst the Cupressaceae.

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