Eucalyptus phylogeny and history: a brief summary

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Abstract

A brief summary of the systematic placement of Tasmanian species of the genus Eucalyptus *is provided. The fossil history of the genus in Australia is reviewed and previously undescribed Myrtaceae capsules are illustrated from the Eocene Redbank Plains Formation of south-eastern Queensland.*

Introduction

Eucalyptus is considered by many to be the quintessential Australian plant because of its history and long association with Australian folklore. It has been an extraordinarily successful group, in terms of its dominance of many plant communities and its high number of taxa (c. 500 species, Chippendale 1988; c. 700 species, Brooker and Kleinig 1994). Eucalypts vary in architecture and form, from the majestic *E. regnans* in tall forests of Victoria and Tasmania, to multi-stemmed species in mallee vegetation, and dwarf shrubs in alpine Tasmania. They occupy a diverse range of habitats, from high altitude meadows to the coast, from rainforest margins to watercourses in the Australian desert.

The name *Eucalyptus* was coined by the French Botanist, Charles Louis L'Héritier de Brutelle in 1788 to describe what was then a new genus of plants from Adventure Bay in Tasmania (see Kantvilas 1996). The name refers to the operculate nature of the flower which lacks conspicuous petals and sepals.

Eucalyptus belongs to the Myrtaceae family which also includes rainforest genera such as *Syzygium* and *Acmena*, and sclerophyllous taxa such as *Leptospermum* and *Melaleuca*. The Myrtaceae is characterised by oil glands, epigynous[1] or more rarely perigynous[2] flowers and a distinct pollen morphology. It is an essentially Southern Hemisphere family as shown by its modern distribution and extensive fossil record in Australia, South America and New Zealand. A few genera also occur in the Indo-Malaysian region. *Eucalyptus* itself has a narrow range compared to the Myrtaceae. Its present-day, natural distribution is essentially Australian although a few taxa occur in Indonesia, Philippines, Timor and nearby islands, New Guinea and New Britain. It is also widely cultivated throughout the world, with large plantations in Brazil, Africa, south-east Asia, southern Europe and elsewhere. Genera considered closely related to *Eucalyptus*, apart from *Corymbia* and *Angophora* (see below), include *Arillastrum* from New Caledonia, *Eucalyptopsis* from Australia and New Guinea, *Allosyncarpia* (Australia) and an undescribed genus from northern Australia (Johnson and Briggs 1984).

Classification of *Eucalyptus*

It has become increasingly evident that the genus *Eucalyptus* as originally defined over 200 years ago is not a natural grouping of taxa

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[1] Epigynous: The wall of the receptacle is fused to the ovary. The ovary is inferior and lies below or is level with the point where the anthers and petals are attached.

[2] Perigynous: The wall of the receptacle surrounds but is not fused to the ovary. The floral parts are raised on the walls of the receptacle.

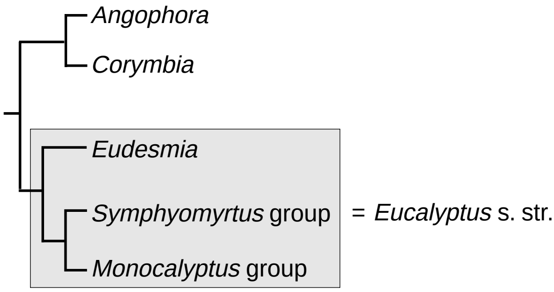

Figure 1. Simplified diagram showing the phylogenetic relationships between Eucalyptus, Angophora *and* Corymbia *(based upon Ladiges* et al. *1995).*

(Pryor and Johnson 1971, 1981). Recent research has resulted in a renaissance in the understanding of relationships within the genus (Pryor and Johnson 1971, 1981; Ladiges and Humphries 1983; Ladiges *et al.* 1995; Udovicic *et al.* 1995). The most recent study using results from molecular and morphological research identifies two major lineages. One lineage includes *Angophora* and *Corymbia* (bloodwoods, ghost gums), and the second (*Eucalyptus sensu stricto*) includes all the subgenera of *Eucalyptus* (Ladiges *et al.* 1995; Hill and Johnson 1995) (Figure 1). In *Eucalyptus*, the sepals and / or petals are fused into one or two caps (opercula) that cover the stamens and ovary, and when the flowers are mature the operculum is shed. The blood-woods and ghost gums (*Corymbia*) also have an operculum but the development of flowers shows that the operculum has evolved independently from that in *Eucalyptus*. In *Angophora*, a small genus of trees confined to eastern Australia, the petals and sepals are free.

Within *Eucalyptus sensu stricto*, three major groups are recognised: *Symphyomyrtus*, *Eudesmia* and *Monocalyptus*[3] (Figure 1) (e.g. Ladiges *et al.* 1995). The *Symphyomyrtus* group includes a number of smaller informal taxa; that is, subgenera *Symphyomyrtus*, *Telocalyptus* and a few isolated taxa. The *Monocalyptus* group also includes a number of informal taxa such as *Gaubaea*, *Idiogenes* and subgenus *Monocalyptus*.

[3] The nomenclature used for these taxonomic groupings generally follows Pryor and Johnson (1971), although the taxa have not been formally described.

Tasmanian eucalypts

Two of the informal subgenera of *Eucalyptus*, *Symphyomyrtus* and *Monocalyptus*, are represented in Tasmania. They can be identified by a range of characters including operculum characteristics, ovule and seed morphology (Boland *et al.* 1980), and the cotyledons (Table 1). An outer and inner operculum, derived from the sepals and petals, occurs in *Symphyomyrtus*. In *Monocalyptus*, the sepals are reduced or absent and the single operculum is considered to be formed from the petals that fuse early in development (Drinnan and Ladiges 1989).

The subgenus *Monocalyptus* is represented by 12 taxa in Tasmania (Table 1). The species have reniform (kidney-shaped) anthers with oblique, confluent slits (Brooker and Kleinig 1983). They include the peppermints, a group which is characterised by raised oil glands on seedling stems, stringy bark, and numerous oil glands on the mature leaves (> 600 / cm^2). The large number of oil glands on the leaves accounts for the common name of this group of trees (Ladiges *et al.* 1983).

The subgenus *Symphyomyrtus* is represented by 17 taxa in Tasmania (Table 1). The species have oblong anthers with longitudinal slits (Brooker and Kleinig 1983) and most belong to the series *Viminales* which is characterised by sessile seedling leaves, dimorphic juvenile and adult foliage, simple umbels and fruits with more-or-less exserted valves (Chippendale 1988).

Fossil history

Why is the fossil record of any group important? Fossils can provide information on the history and past distribution of taxa. Interpretation of fossils may be difficult, however, because characters that are considered crucial in recognising a group of

Table 1. Differences between the two informal subgenera Monocalyptus *and* Symphyomyrtus *in floral morphology, ovules and cotyledons, and the composition of the two subgenera in Tasmania. (The number of taxa and their nomenclature follows Williams and Potts 1996).*

	Monocalyptus	*Symphyomyrtus*
Morphological characters		
opercula	single operculum	two opercula derived from petals and sepals
ovules[4]	anatropous	hemitropous
ovule rows	two rows	four to five rows
seed testa	formed from two integuments	formed from a single integument
seed surface	smooth or irregularly sculptured	reticulate
cotyledons	emarginate	bilobed
Number of taxa		
worldwide	140+	300+
Tasmania	12	17
Tasmanian taxa		
	E. amygdalina Labill.	*E. archeri* Maiden & Blakely
	E. coccifera Hook. f.	*E. barberi* L. Johnson & Blaxell
	E. delegatensis R. Barker subsp. *tasmaniensis* Boland	*E. brookeriana* A.M. Gray
	E. nitida Hook. f.	*E. cordata* Labill.
	E. obliqua L' Hérit.	*E. dalrympleana* Maiden subsp. *dalrympleana*
	E. pauciflora Sieber ex Sprengel subsp. *pauciflora*	*E. globulus* Labill. subsp. *globulus*
	E. pulchella Desf.	*E. gunnii* Hook. f.
	E. aff. *radiata* Sieber ex DC.	*E. johnstonii* Maiden
	E. regnans F. Muell.	*E. morrisbyi* Brett
	E. risdonii Hook. f.	*E. ovata* Labill.
	E. sieberi L. Johnson	*E. perriniana* F. Muell. ex Rodway
	E. tenuiramis Miq.	*E. rodwayi* R. Barker & H.G. Smith
		E. rubida Deane & Maiden
		E. subcrenulata Maiden & Blakely
		E. urnigera Hook. f.
		E. vernicosa Hook. f.
		E. viminalis Labill.

[4] The terms 'anatropous' and 'hemitropous' refer to the orientation of the ovule in relation to the placenta (tissue where the ovules are attached). In anatropous ovules, the pore (micropyle) through which the pollen tube enters the ovule faces the placenta whereas in hemitropous ovules the micropyle is orientated perpendicular to the placenta.

taxa are often not preserved; for example, evidence of operculate flowers, numbers of ovule rows, anther morphology, or juvenile foliage characters. With *Eucalyptus*, identification of the genus and its separation from other Myrtaceae genera rely on features such as the presence of an operculum, a character which is rarely preserved in fossils. Sufficiently detailed phylogenetic studies of extant taxa using the parts of the plant most commonly found as fossils; for example, leaves, cuticle, pollen, or wood, have not been undertaken in many cases. Therefore, critical assessment of relationships between a fossil

PERIOD	EPOCH/STAGE	AGE*	STRATIGRAPHIC RECORD
TERTIARY	PLEISTOCENE	2.5	
	PLIOCENE	10	Bacchus Marsh fruits
	MIOCENE	27	Chalk Mountain Locality Lachlan Valley wood New Zealand 'Eucalyptus' Berwick Quarry
	OLIGOCENE	38	Silicified South Australian fruits ★
	EOCENE	54	Silicified South Australian fruits ★ South American 'Eucalyptus' Redbank Plains fruits
	PALEOCENE	65	Earliest record of eucalypt-group pollen for Australia Earliest record of Myrtaceae pollen for Australia
CRETACEOUS (SENONIAN)	MAASTRICHTIAN	70	Myrtaceae pollen (South Amercia)
	CAMPANIAN	80	Myrtaceae pollen (Africa)
	SANTONIAN	85	Myrtaceae pollen (Borneo)
	CONIACIAN	90	

Figure 2. Age and important records of Myrtaceae fossils. The age of the silicified fruits from South Australia is uncertain; two possible dates for this material are shown by a star. (= x 1 000 000 years)*

taxon and extant groups within *Eucalyptus* is often impossible.

Myrtaceae fossils

The oldest records of Myrtaceae pollen (microfossils) are from the lower Senonian (Santonian) of Borneo (Muller 1981; Figure 2). Myrtaceae pollen is also known from the Campanian of Africa and the Maastrichtian of South America (Muller 1981). These records all predate the earliest Myrtaceae pollen records from Australia which are Paleocene in age (Martin 1994; Figure 2). Pollen of non-eucalypt groups occur frequently in the Eocene, where the Myrtaceae is an important element in the floras (Christophel *et al.* 1987). These pollen records cannot be ascribed to any particular genus but, in general, the floras appear to be largely dominated by rainforest taxa.

Some of the oldest macrofossil evidence of the family is obtained from leaves, of uncertain affinity, from the Eocene Anglesea Locality in Victoria (Christophel *et al.* 1987; Christophel and Lys 1986). Hill and Merrifield (1993) also described a diverse Myrtaceae flora from West Dale in Western Australia, which may be of comparable age. Most of the Myrtaceae leaves were not identifiable beyond family, although Hill and Merrifield (1993) compared one of the fossil taxa they described with *Rhodomyrtus* and another with *Agonis*.

Myrtaceae leaf fossils are also known from Tasmania. Pole (1992) has recorded Eocene Myrtaceae leaves from Hasties in north-eastern Tasmania, which he compared with *Xanthomyrtus*, a rainforest genus occurring today from Borneo to New Caledonia. Myrtaceae leaves of uncertain affinity were also recorded from the Oligocene Pioneer Locality in Tasmania (Hill and Macphail 1983). However, these sites have not yielded macrofossils that could be compared with genera of the eucalypt group.

Fossil eucalypts from outside Australia

Since the eucalypt group today is essentially an Australian genus, except for a few taxa that occur in Indonesia, New Guinea and the Philippines, it might seem unnecessary to look outside Australia to trace the history of this plant group. Records of fossil 'eucalypt' leaves from the Northern Hemisphere appear to be in error, as does the record of putative eucalypt fossil wood from India (see below). However, records from South America and New Zealand suggest that the history of the eucalypt group may not be a strictly Australian event.

The fossil wood from India (Bande *et al.* 1986) has features that are shared with genera in the Myrtaceae including predominantly solitary vessels, vasicentric tracheids and diffuse parenchyma. Bande *et al.* (1986) did not record the presence of vestured pits in their sample. This character, while difficult to observe or confirm in fossil material, is important for identifying Myrtaceae wood. Bande *et al.* (1986) also recorded the rays as being homogeneous to weakly heterogeneous, but true homogeneous rays (i.e. all ray cells procumbent) were considered by Ingle and Dadswell (1953) not to occur in the Myrtaceae. Considerable doubt remains as to the affinities of this material.

Impressions of eucalypt-like fruits and foliage are known from the Early Miocene in New Zealand (Pole 1993). This material was considered by Johnson and Hill (pers. comm. in Pole 1993) to be consistent with *Symphyomyrtus* or possibly an extinct, early offshoot of this group. Evidence of important diagnostic features, including an operculum, was lacking and better preserved material is needed to unequivocally refer this material to *Symphyomyrtus* or to the eucalypt group generally. Pole (1993) also drew attention to the falcate leaf morphology that he considered indicative of the eucalypt group. Mildenhall (1980) tentatively recorded *Eucalyptus* pollen from the Miocene through to the Pleistocene of New Zealand.

The South American connection is also tantalising. Frenguelli (1953) described fruits that he considered referable to *Eucalyptus*. Johnson and Briggs (1984) considered that

Frenguelli's material was consistent with *Symphyomyrtus*, while other South American material was only comparable to the Myrtaceae generally. Like the New Zealand material, evidence of operculate flowers in the South American material is missing. The absence today of *Eucalyptus* in both South America and New Zealand may seem to negate any likelihood of *Eucalyptus* ever having been there. However, the same situation is apparent with another typically Australian group, the she-oaks (Casuarinaceae). The Casuarinaceae was in New Zealand and South America during the Tertiary but is absent from both regions today.

Fossil eucalypts from mainland Australia

Eucalypts are dominant elements of the Australian flora, particularly in sclerophyll forest communities but, for such an important group in the extant flora, there is surprisingly little well-substantiated evidence in the fossil record. The Australian fossil record is based on pollen, fruit and flowers, leaves and wood.

Pollen—Pollen from the mid Paleocene provides the earliest evidence of the Myrtaceae in Australia (Martin 1994) (Figure 2). The earliest record of eucalypt-type pollen, *Myrtaceidites eucalyptoides*, is from the late Paleocene Lake Eyre Basin of South Australia (Sluiter and Alley, pers. comm., in Hill 1994). The pollen record shows that the relative abundance of Myrtaceae pollen increased rapidly during the late Tertiary which is presumably coincident with the rise of the eucalypt group. However, Martin (1994) also pointed out that a detailed study of Tertiary Myrtaceae pollen has yet to be undertaken and the affinities of most Myrtaceae taxa have not been critically established.

The palynomorph *Myrtaceidites eucalyptoides* has been considered to have affinities with the eucalypt group as a whole (Martin 1994). Thus, at present, it provides little information about the evolution of the different genera and subgenera within the group. If *M. eucalyptoides* is definitely referable to this group, then the pollen record does show that the eucalypt group appeared shortly after the Myrtaceae is first recorded in Australia. This also suggests that the group is not a relatively recent radiation but, instead, has a long history on the Australian continent.

The earlier pollen records of *Eucalyptus* were assigned to the genus in the traditional broad sense and even quite recent research often leaves the status of material loosely defined; that is, '*sensu* eucalypt group' which would include *Angophora*, *Corymbia* and *Eucalyptus* (Martin 1994; Macphail *et al.* 1994). At present, it is not possible to identify taxa in the eucalypt group using pollen characters, although some individual taxa (e.g. *E. spathulata*) were considered distinctive by Martin and Gadek (1988). Churchill (1970) similarly claimed to be able to differentiate *Eucalyptus* species using pollen morphology. Whether phylogenetic groups within the eucalypt group can also be identified using pollen ultrastructure and / or scanning electron microscopy is yet to be shown.

Fruits—Eucalypt-like fruits and inflorescences have been described from a number of Tertiary localities in Australia. Fruits are particularly important because in well-preserved material it is possible to identify features that are known to occur only in certain taxa in the eucalypt group. New sites are also yielding additional material for study.

One of the oldest records is previously undescribed eucalypt-like fruits from the Redbank Plains Formation in south-eastern Queensland. This material was discovered by Robert Knezour in 1990. It is considered to be Paleocene or Eocene in age (Day *et al.* 1983), although a younger age is also possible. At least six, possibly seven, fruits are preserved as impressions and partial impressions in a fine-grained, red-brown mudstone. The fruits are not in organic connection but appear to have been originally grouped into a probable umbellaster (Photo 1). They are urceolate, with weak longitudinal ridges, the disc is descending and valves are not evident but are presumably deeply recessed. A sediment plug fills the opening of the fruit (Figure 3). Only the external morphology is preserved so information on the ovule morphology, number of ovule rows, and presence of an operculum is missing. The material can be compared to fruits in the eucalypt group in the broad sense and particularly with *Corymbia* or *Angophora*, but it is not possible to provide a more definitive identification. Myrtaceae leaves have not been found associated with the fruits.

Convincing evidence of *Eucalyptus* fruits was presented by Holmes *et al.* (1982) (Photo 2). They described a new species, *E. bugaldiensis*, for fruits from Chalk Mountain, a site in northern New South Wales, and compared these fruits with *E. microtheca* F. Muell. and *E. raveretiana* F. Muell. The site has been dated as 17–14 m.y. B.P. based upon absolute K/Ar dates for nearby volcanics. Holmes

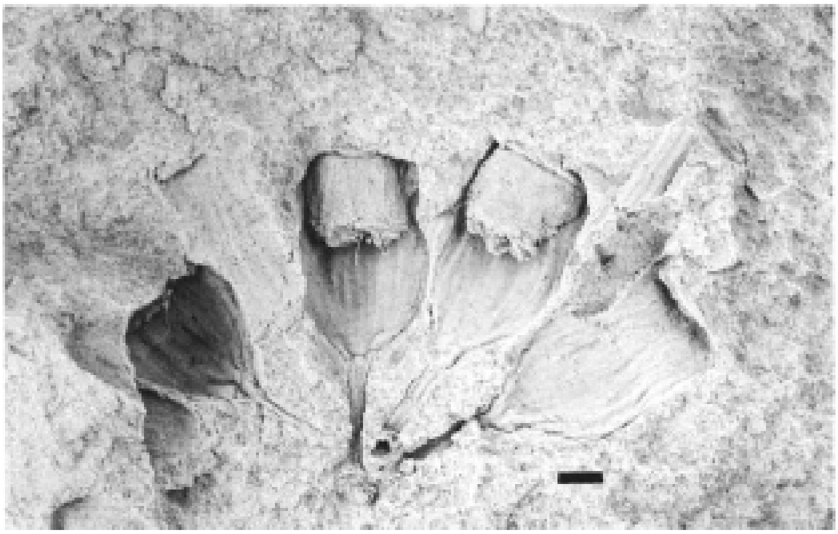

Photo 1. Impressions of Myrtaceae fruits from the Redbank Plains Formation, south-eastern Queensland. (Queensland Museum Specimen QMF16780.) Scale bar = 1 mm.

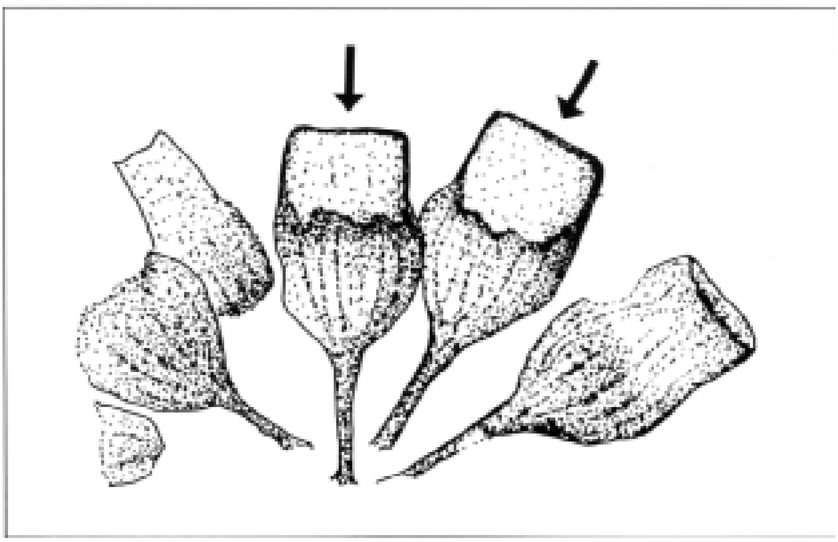

Figure 3. Drawing of Redbank Plains fruits (sediment plugs shown with arrows).

et al. (1982) also described eucalypt-like leaves of two types from the same flora which they considered were comparable with the *Eucalyptus* and *Angophora* / *Corymbia* groups. If this is correct, then the Chalk Mountain site indicates that *Eucalyptus* and *Angophora* / *Corymbia* lineages were separate by at least the mid Miocene.

Lange (1978) described a diverse and important flora of *Eucalyptus* and other Myrtaceae fruits from South Australia. The problem with this flora is that the site has not been accurately dated (Lange 1978). This fossil locality and others in Central and South Australia are silicified surface deposits that are stratigraphically isolated due to weathering, and cannot be confidently related to the surrounding geological units. There is also no pollen in the flora so the sites cannot be dated biostratigraphically. Ambrose *et al.* (1979), studying a nearby site, suggested either an Oligocene / Miocene age or Eocene age for these silcrete floras (see Figure 2). A Miocene age was favoured by Truswell and Harris (1982) and recent research by Greenwood *et al.* (1990) has not provided a more definitive dating of this flora. Further fieldwork planned by researchers at the Mines and Energy Department, South Australia, may help to resolve the age of these floras.

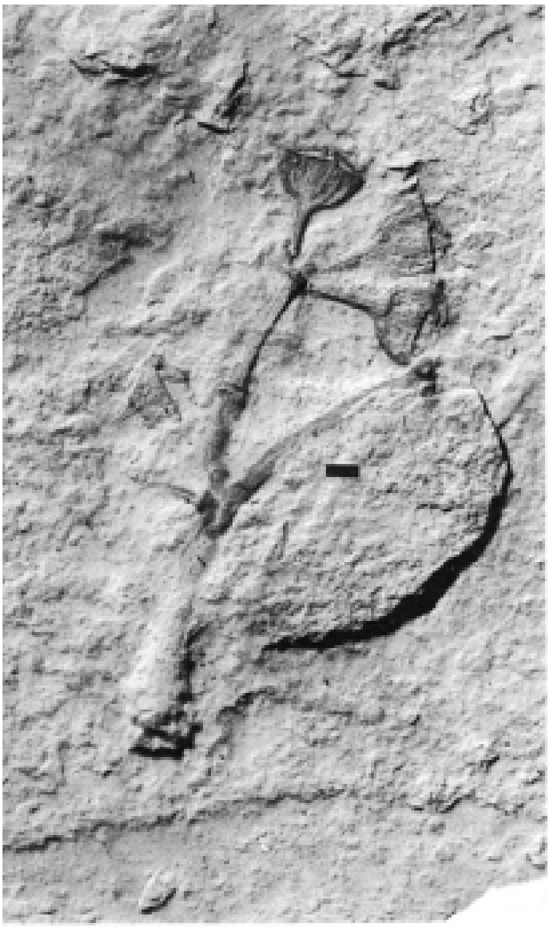

Photo 2. Eucalyptus bugaldiensis *Holmes and Holmes from the Chalk Mountain, New South Wales. Scale bar = 1 mm. (Photo supplied by W.B.K. Holmes.)*

Researchers at the University of Melbourne are presently studying immaculately preserved mummified *Eucalyptus* fruits from a late Miocene Bacchus Marsh locality in Victoria (Photos 3, 4). These operculate fruits are clearly referable to a number of eucalypts and can be compared to extant taxa in *Eucalyptus* because anatomical features, including the number of ovule rows and anther morphology, are preserved (J. Blazey, pers. comm. 1995).

Leaves—Early literature exists detailing fossil records of *Eucalyptus* leaves (e.g. Ettingshausen 1888; Deane 1902a, b) but, as Hill (1994) pointed out, the status of much of this material has not been critically re-examined. Some material previously referred to *Eucalyptus*, for example *E. praecoriacea* by Deane (1902a), has been shown to be in error (Hill 1980).

Leaves from the Berwick Quarry near Melbourne in Victoria were referred to seven *Eucalyptus* taxa by Deane (1902b). Pole *et al.* (1993) accepted the referral of these leaves to *Eucalyptus* but considered that all seven taxa could be placed into a single taxon. The authors considered that the leaves were comparable to a number of extant taxa but were unable to suggest links to any particular taxon in the eucalypt group. White (1984) illustrated Myrtaceae fruits from presumably the same site which she referred to *Tristania*, although no reason for this assessment was provided.

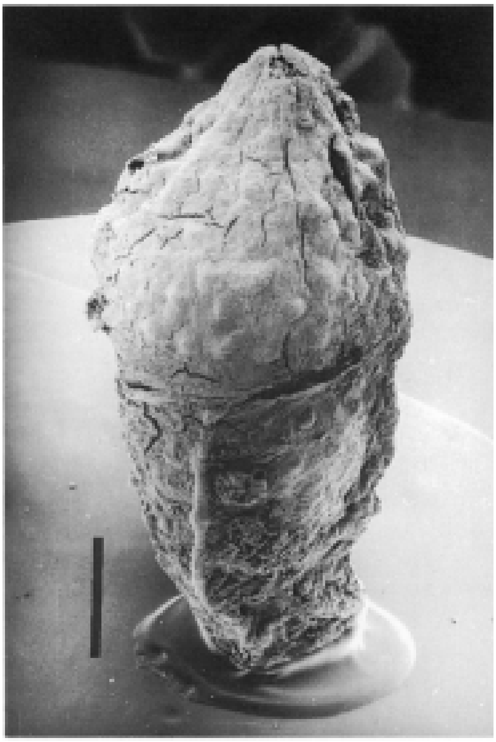

Photo 3. Eucalyptus *fruit from Bacchus Marsh with operculum in place. Scale bar = 1 mm. (Photo supplied by J. Blazey.)*

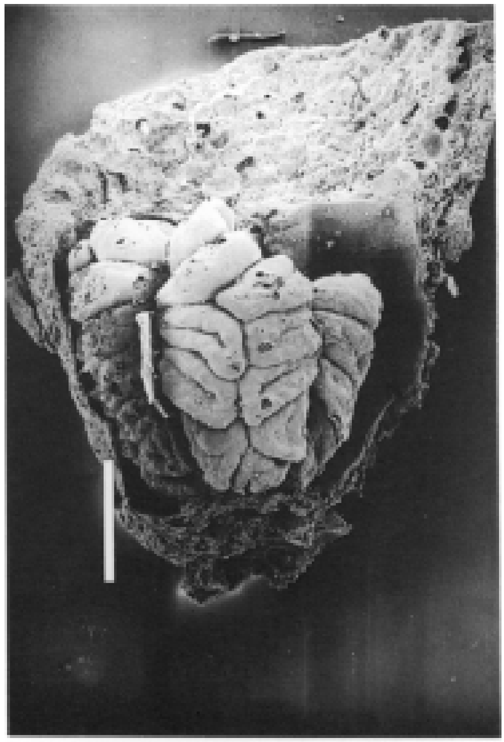

Photo 4. Eucalyptus *fruit from Bacchus Marsh, with ovule rows visible. Scale bar = 0.5 mm. (Photo supplied by J. Blazey.)*

Wood—Differences in wood anatomy between *Angophora* / *Corymbia* and *Eucalyptus* occur in the arrangement of vessels and parenchyma distribution. In *Eucalyptus*, the vessels tend to be solitary while in *Corymbia* and *Angophora* the vessels occur in radial multiples or vessel clusters (Ingle and Dadswell 1953). Parenchyma is usually abundant, often vasicentric, and aliform or confluent in *Corymbia* and *Angophora*, while in *Eucalyptus* it is generally diffuse, or occasionally vasicentric in some species (Ingle and Dadswell 1953). Considerable potential therefore exists to document the history of these two groups using wood anatomical features (Dadswell 1972). There are, however, surprisingly few published records of eucalypt-like wood in the fossil record.

Bishop and Bamber (1985) described Myrtaceae wood which they considered had affinities with *Eucalyptus* B (i.e. either *Angophora* or the bloodwoods, *sensu* Ingle and Dadswell 1953) from the upper Lachlan River area of New South Wales. Features used to identify the sample as Myrtaceae wood included vessels in clusters to short radial multiples, and vestured pits. An important additional character to identify positively the fossil sample as *Eucalyptus* B wood is the presence of abundant parenchyma cells (Ingle and Dadswell 1953). However, Bishop and Bamber (1985) were unable to confirm their identification due to the parenchyma cells not being preserved. The site has an absolute date of 21 m.y. B.P. (Early Miocene) based upon associated volcanics, and is potentially very important if better preserved wood samples can be located.

Fossil eucalypts in Tasmania

Johnston (1885a, b) described fossil *'Eucalyptus'* leaves from localities in Tasmania. Unfortunately, much of this material has not been located and is presumed to be lost. The

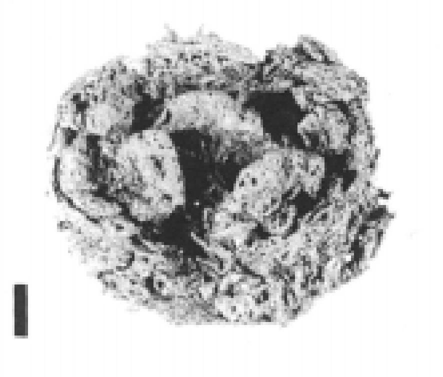

Photo 5. Pleistocene Eucalyptus *capsule from Regency, western Tasmania. Scale bar = 1 mm. (Photo supplied by G. Jordan.)*

Photos 6. Pleistocene Eucalyptus *leaf from Regatta Point, western Tasmania. Scale bar = 1 cm. (Photo supplied by G. Jordan.)*

oldest pollen records of the eucalypt group (*Myrtaceidites eucalyptoides*) in Tasmania are Oligocene in age (Hill and Macphail 1983). Myrtaceae leaves of uncertain affinity are also recorded from this flora (Hill and Macphail 1983). *Eucalyptus* leaves and fruits have been recently recognized from Pleistocene sites at Regatta Point and Regency in western Tasmania (G. Jordan, pers. comm. 1995) (Photos 5, 6).

Conclusion

There is an extensive fossil record of the Myrtaceae in Australia. While fossil leaves, wood, pollen and fruits have been compared with the eucalypt group generally, there is a paucity of well-substantiated records that can be assigned to particular genera or subgenera. New fossil localities, better preserved material like that at Bacchus Marsh, and restudy of existing material will allow a clearer picture to be developed of the history and past distribution of these genera in Australia. New discoveries of eucalypt-like fruits; for example, from the Redbank Plains in Queensland, are adding to the recorded history of this group.

Eucalyptus occurs in less mesic forest communities. It seems likely that the limited fossil record of *Eucalyptus* is due, in part, to the relative paucity of suitable depositional environments in these habitats. Also, to date, the majority of Tertiary floras studied in Australia have been interpreted as rainforest; that is, mesic forest floras. The eucalypt group is generally not considered characteristic of typical rainforest communities and it would be unexpected to find *Eucalyptus* fossils in these assemblages. The Bacchus Marsh fossil flora of Victoria and the silcrete floras of central South Australia are sites where eucalypt remains have been recorded, but are unlikely to be rainforest communities (J. Blazey, pers. comm.; Lange 1978). Other sites where eucalypt fossils are known, for example from Chalk Mountain and Berwick, suggest a mosaic of rainforest and sclerophyllous community types (Holmes *et al.* 1982; Pole *et al.* 1993).

In Tasmania, two groups, *Symphyomyrtus* and *Monocalyptus*, are widespread but there is no palaeontological evidence to show if other eucalypt groups were ever present. Eucalypt-type pollen is recorded from the Oligocene onwards, and Pleistocene leaves and fruits have been recently discovered in western Tasmania. The pollen record suggests that the eucalypts were in Tasmania for at least the last 20 million years.

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Robert Knezour collected the Myrtaceae capsules from the Redbank Plains Formation in Queensland and made them available for study. My thanks go to the following researchers for their assistance: Keith Holmes, Jolyon Blazey and Dr Greg Jordan provided photographs of the Chalk Mountain, Bacchus Marsh, and Pleistocene Tasmanian eucalypts respectively. Dr Mike Pole provided literature and advice on the New Zealand 'eucalypt' record. Dr N. Alley kindly made available unpublished information on the age of the silcrete floras of South Australia.

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