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Can Myrtaceae pollen of the Holocene from Bega Swamp (New South Wales, Australia) be compared with extant taxa?

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Introduction

Bega Swamp (Figure 1) is a seldom disturbed restiad-shrub bog (Hope et al. 2000) located 50 km inland at the eastern side of the Southern Tablelands in Wadbilliga National Park, New South Wales (36° 31' S, 149° 30' E) at an altitude of around 1080 m and with a mean annual rainfall of 800 mm to 1200 mm (Polach and Singh 1980). Rainfall is a limiting factor to plant growth in the region (Donders et al. 2007). It is thought that the swamp originated as a valley fill between Yankee Creek and Bemboka River (Polach and Singh 1980) and occupies an elongated north-south valley on a heavily forested granitic plateau (Hope et al. 2000). The site was selected by Dr Gurdhip Singh to represent montane southeastern Australia as it was a Holocene site with continuous sedimentation that would allow near annual resolution analysis as well as being surrounded by relatively undisturbed natural vegetation, providing the possibility of relating the modern pollen deposition to climatic conditions (Hope 1995).

The surrounding catchment area of Bega Swamp is predominantly a wet, tall, open sclerophyll forest, with dominant *Eucalyptus* tree species being *E. fraxinoides*, *E. fastigata*, *E. radiata* and *E. dalrympleana*, along with a rich shrub and herb understorey containing genera such as *Epacris*, *Leptospermum*, Asteraceae, *Acaena*, *Ranunculus*, *Hydrocotyle*, *Plantago*, *Wahlenbergia*, *Gonocarpus*, *Blechnum* and *Pteridium* (Green et al. 1988; Hope et al. 2000). The swamp area has a zone of *E. pauciflora* (snowgum) and *E. rubida* woodlands with a grassy shrubland suggesting that this is a frost hollow (Hope et al. 2000). *Poa* grasslands occur in the western area of the swamp, while the majority of it is thickly overgrown with *Empodisma* and *Restio*, with scattered aquatic sedges and ericaceous and myrtaceous shrubs (Hope et al. 2000). It was noted by Hope et al. (2000) that *Leptospermum lanigerum* would probably occupy parts of the swamp but had been partly removed by fire.

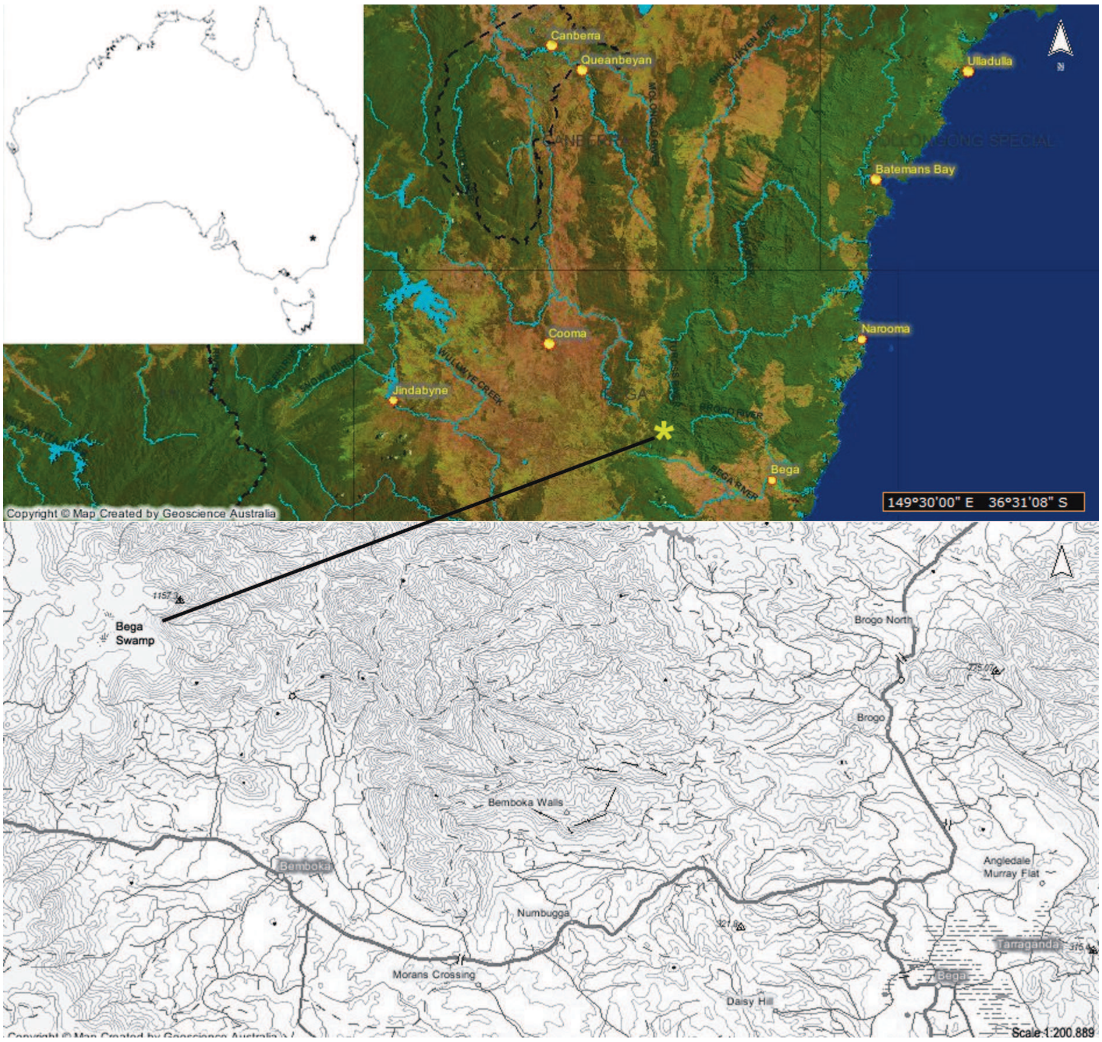

Figure 1. Locality map of Bega Swamp

Detailed pollen counts from the past 12,000 years have previously been conducted (Green et al. 1988; Hope 1995; Hope et al. 2000, 2004; Donders et al. 2007), from which 35 Myrtaceae-type pollen grains have been identified (Hope et al. 2000), with these various pollen types appearing at different times (Figure 2). Interestingly, the number of recorded Myrtaceae species housed at the Australian National Herbarium that come from the Wadbilliga National Park region is 37 (see Table 1 for species list). Various assumptions have been made about the identities of the pollen types, first by Gurdhip Singh (unpublished data) and then by Geoff Hope (Figure 2). One notable assumption is that *E. pauciflora* was a dominant eucalypt in the past, associated with a cooler and wetter climate at Bega Swamp. This is illustrated in Figure 2, which distinguishes five groups of *Eucalyptus* appearing and disappearing through the past 12,000 years. It was assumed that *Eucalyptus* 2 represented a high altitude group such as *E. pauciflora*, while *Eucalyptus* 3 and 4 were wet forest groups such as *E. fastigata* and *E. fraxinoides* (Hope 1995). The present study examined extant Myrtaceae taxa from the Bega Swamp area with light microscopy and compared images of Myrtaceae pollen grains from various sections of Singh's 1980 core using visual character comparison and a Lucid key of extant Myrtaceae pollen morphology (Thornhill unpublished) with the aim of correlating extant and fossil pollen.

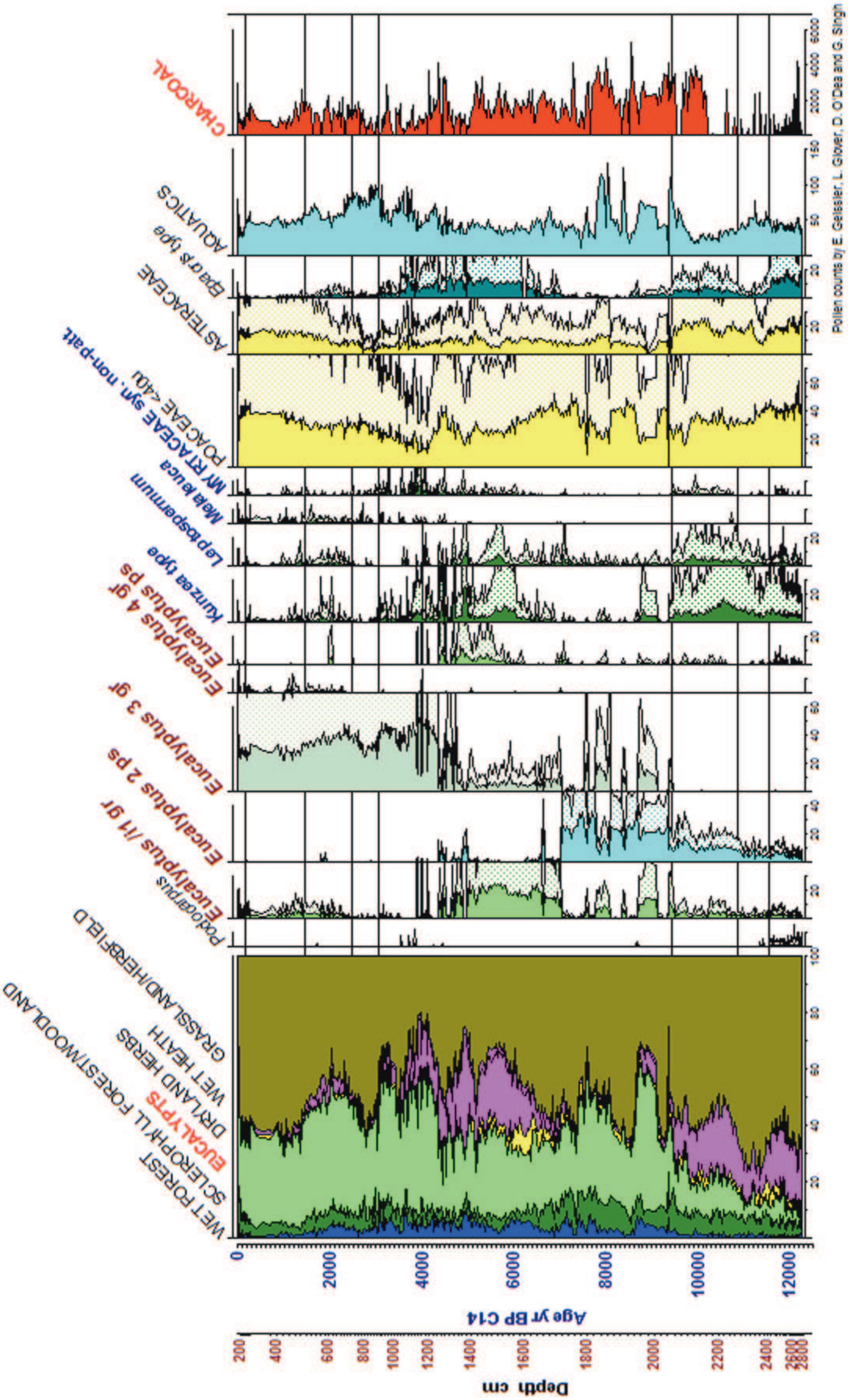

Figure 2a. Pollen diagrams from a 1980 core of Bega Swamp showing various plant families and genera found in the core

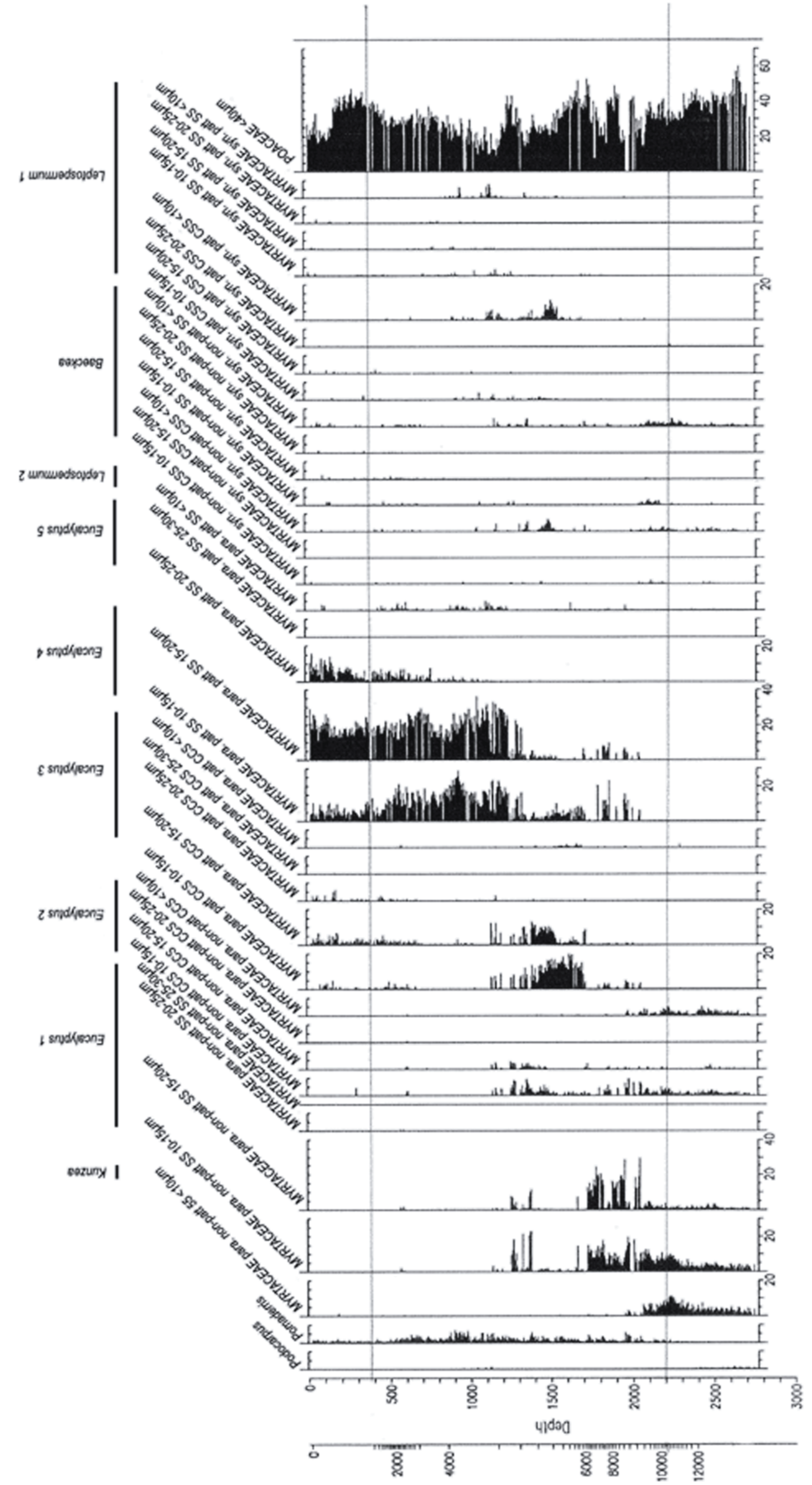

Figure 2b. Pollen diagrams from a 1980 core of Bega Swamp showing the presence of 35 Myrtaceae pollen grains and how they were grouped by Hope et al. in 2000

Table 1. Species list of Myrtaceae taxa from the area surrounding Bega Swamp (Table 1 continues on page 410)

Myrtaceae taxa	Taxa from Wadbilliga National Park recorded in Australian herbaria	Other taxa listed to occur in the area	Taxa that Gurdhip Singh suggested resembled fossil pollen
Acmena smithii (Poir.) Merr. & L.M.Perry	x		
Angophora floribunda (Sm.) Sweet			x
Babingtonia pluriflora (F.Muell.) A.R.Bean ex Govaerts & al.		x	
Backhousia myrtifolia Hook. & Harv.	x		
Baeckea gunniana Schauer ex Walp., Repert			x
Baeckea linifolia Rudge		x	
Baeckea utilis F.Muell. ex Miq.	x		
Baeckea virgata (J.R.Forst. & G.Forst.) Andrews (now Sannantha)		x	
Callistemon citrinus (Curtis) Skeels		x	
Callistemon salignus (Sm.) Colv. ex Sweet		x	
Callistemon sieberi DC.	x		
Callistemon subulatus Cheel		x	
Calytrix tetragona Labill.		x	
Corymbia gummifera (Gaertn.) K.D.Hill & L.A.S.Johnson		x	
Corymbia maculata (Hook.) K.D.Hill & L.A.S.Johnson		x	
Eucalyptus badjensis Beuzev. & M.B.Welch	x		
Eucalyptus baeuerlenii F.Muell.	x		
Eucalyptus dalrympleana Maiden	x		
Eucalyptus elata Dehnh.	x		
Eucalyptus fastigata H.Deane & Maiden			x
Eucalyptus fraxinoides H.Deane & Maiden	x		x
Eucalyptus kybeanensis Maiden & Cambage	x		
Eucalyptus moorei Maiden & Cambage subsp. *moorei*	x		
Eucalyptus nitens (H.Deane & Maiden) Maiden	x		
Eucalyptus olsenii L.A.S.Johnson & Blaxell	x		
Eucalyptus paliformis L.A.S.Johnson & Blaxell	x		
Eucalyptus parvula L.A.S.Johnson & K.D.Hill	x		
Eucalyptus pauciflora Sieber ex Spreng.	x		x
Eucalyptus radiata Sieber ex DC. subsp. *radiata*	x		
Eucalyptus smithii R.T.Baker	x		
Eucalyptus stellulata Sieber ex DC.	x		x

Myrtaceae taxa	Taxa from Wadbilliga National Park recorded in Australian herbaria	Other taxa listed to occur in the area	Taxa that Gurdhip Singh suggested resembled fossil pollen
Eucalyptus stenostoma L.A.S.Johnson & Blaxell	x		
Eucalyptus viminalis Labill.			x
Eucalyptus wilcoxii Boland & Kleinig	x		
Euryomyrtus denticulata (Maiden & Betche) Trudgen	x		
Kunzea ambigua (Sm.) Druce		x	
Kunzea ericoides (A.Rich.) Joy Thomps.		x	
Kunzea parvifolia Schauer		x	
Kunzea sp. 'Wadbilliga' (Rodd 6168)	x		
Leptospermum brevipes F.Muell.	x		
Leptospermum grandifolium Sm.	x		
Leptospermum morrisonii Joy Thomps.	x		
Leptospermum myrtifolium Sieber ex DC.	x		x
Leptospermum obovatum Sweet	x		
Leptospermum polygalifolium Salisb. subsp. *polygalifolium*	x		
Leptospermum scoparium J.R.Forst. & G.Forst.			x
Melaleuca armillaris (Sol. ex Gaertn.) Sm. subsp. *armillaris*	x		
Melaleuca citrina (Curtis) Dum. Cours.	x		
Melaleuca hypericifolia Sm.	x		
Melaleuca pityoides (F.Muell.) Craven	x		
Melaleuca subulata (Cheel) Craven	x		
Tristania neriifolia (Sieber ex Sims) R.Br.			x
Tristaniopsis laurina (Sm.) Peter G.Wilson & J.T.Waterh.	x		x

Pollen of the plant family Myrtaceae is characterised by a syncolpate or parasyncolpate appearance, although some Myrtaceae tribes are brevicolpate and asyncolpate (Thornhill unpublished data), with many studies conducted on the pollen of the family or specific groups within (Pike 1956; McIntyre 1963; Churchill 1968; Barth and Barbosa 1973; Graham 1980; Gadek and Martin 1981; Gadek and Martin 1982; Patel et al. 1984; Van Wyk and Dedekind 1985; Martin and Gadek 1988; Chalson and Martin 1995; Pickett and Newsome 1997; Parnell 2003; Eliseu and Dinis 2008). It has been said that at the generic and species levels, separation of taxa can be difficult or impossible (Pickett and Newsome 1997), but a number of useful and distinctive characters have been created to tackle the task (Dodson 1974; Chalson and Martin 1995). The high significance that is placed on Myrtaceae, especially *Eucalyptus*, when identifying pollen to interpret past vegetation and climatic conditions means that the ability to differentiate Myrtaceae into distinct pollen groups is of great value. Most important, as Pickett and Newsome (1997) noted, is whether *Eucalyptus* pollen might be identifiable to species, or groups of species.

Methods

As many extant Myrtaceae genera and species as were readily available were imaged with light microscopy. Images were taken from existing slides sourced from the pollen slide collection in the Department of Archaeology and Natural History (ANH), Australian National University, and from slides made by Kathleen Pike in the 1940s and '50s (many of which are line illustrated in Pike 1956) housed at the School of Botany, University of Melbourne, and the School of Land and Environment, University of Melbourne. Taxa used for extant reference pollen were selected by searching a species list of Wadbilliga National Park housed in the Australian National Herbarium, Canberra, and from a Bega Swamp species list compiled by Gurdhip Singh (unpublished). New slides were created for the Bega Swamp fossil pollen from archived residues, as the slides used in previous studies had been lost. The original core was taken in 1980 by Gurdhip Singh who froze the core on site and then sliced it with a fine bandsaw into a series of 500 discs of 20 cm diameter and approximately 2.5 mm thickness, resulting in a sample every 4 mm (Hope 1995). The archived acetolysed samples are stored in silicone oil at ANH. Peaks in concentration of fossil Myrtaceae pollen grains were recognised from the pollen diagram (Figure 2), and from these peaks archived samples were selected for the new slides. The chronology used in this study comes from several previous published studies (Hope et al. 2000; Wheeler et al. 2001), as well as unpublished dates provided by Dr Nick Porch from ANH. This chronology is summarised in Table 2 and it is worth noting that the chronology is now the highest resolution sequence in Australia. Specimens for new slides were mounted in silicone oil and all images were captured using a Zeiss (Oberkochen) Microscope, objective lens x63 and the image capturing software Axiovision.

Table 2. Depth and age of core sample numbers

Sample number	Depth (mm)	Age
54, 55, 56	302–316	~ 400 years
81, 82, 83	400-419	850 years
115, 116, 117, 118	583-606	2300 years
194, 195	980-1002	3400 years
202	1006-1009	3500 years
238, 239, 240	1197-1213	4300 years
269, 270, 271	1369-1386	4700 years
274	1399-1404	4800 years
290, 291	1494-1505	5000 years
344, 345, 346	1796-1814	8500 years
374	1971-1975	8800 years
440, 441, 442	2199-2213	10,900 years
498, 499, 500	2497-2511	12,500 years

Both extant and fossil pollen grains were scored using the characters described by Chalson and Martin (1995) and descriptions followed the terminology of Punt et al. (2007). Pollen measurements were also made in Adobe Photoshop. A Lucid key was created compiling character scores of extant Myrtaceae pollen. The key, which contains 329 Myrtaceae taxa that have been imaged with light microscopy (and another 220 with scanning electron microscopy), was then used to search for similarities with the fossil pollen by entering the characters of each individual fossil pollen grain (more than 400 grains in total).

Results

Extant Myrtaceae

In total, 25 Myrtaceae taxa representing 10 genera were used as a reference for extant pollen, and in most instances, pollen grains could be sorted down to a species level using a total of 15 morphological characters and image measurements (Figure 3).

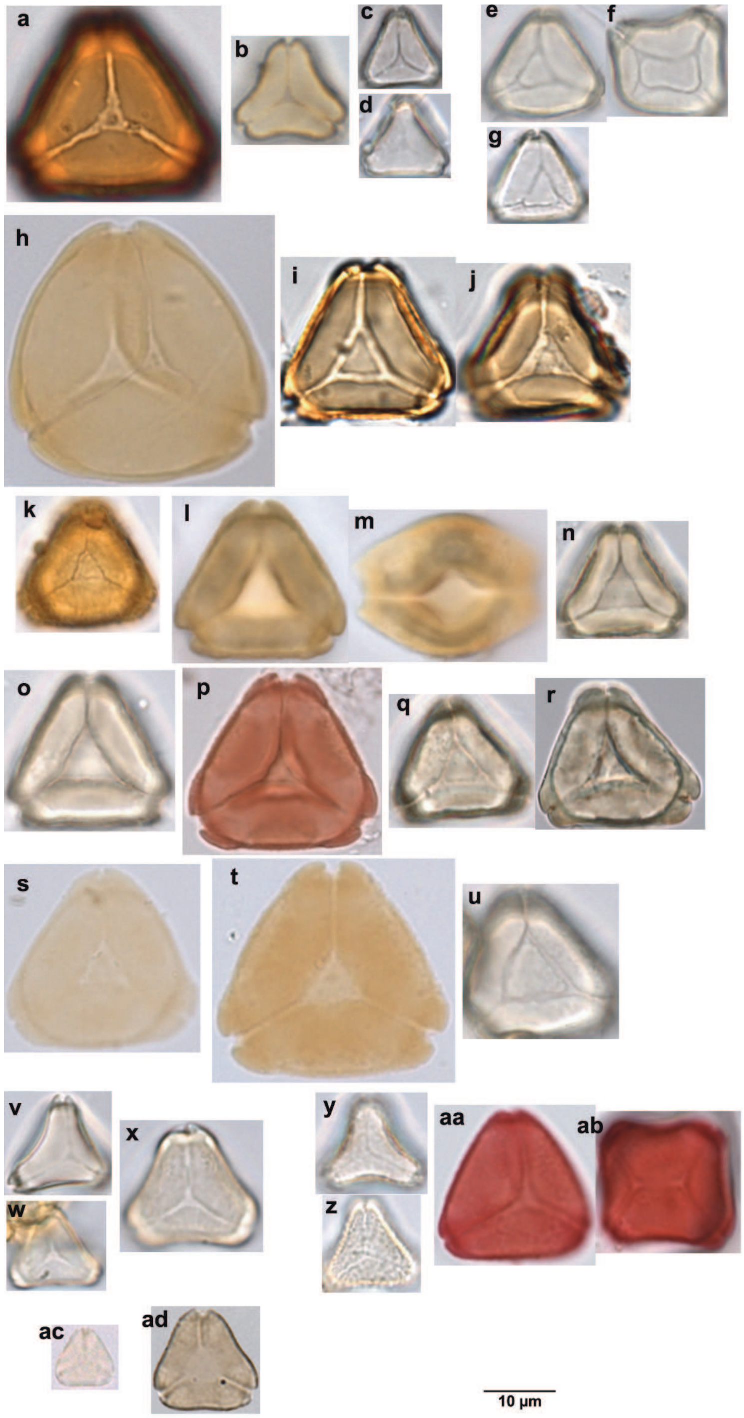

Figure 3. Extant Myrtaceae pollen of Bega Swamp (a) *Angophora floribunda*; (b) *Backhousia myrtifolia*; (c) *Baeckea gunniana*; (d) *Baeckea utilis*; (e) and (f) *Callistemon citrinus*; (g) *Callistemon sieberi*; (h) *Corymbia gummifera*; (i) and (j) *Corymbia maculata*; (k) *Eucalyptus dalrympleana*; (l) and (m) *E. fastigata*; (n) *E. fraxinoides*; (o) *E. pauciflora*; (p) *E. radiata*; (q) and (r) *E. rubida*; (s) *E. smithii*; (t) *E. stellulata*; (u) *E. viminalis*; (v) *Kunzea ambigua*; (w) *K. ericoides*; (x) *K. parvifolia*; (y) *Leptospermum grandifolium*; (z) *L. lanigerum*; (aa) and (ab) *L. scoparium*; (ac) *Tristania neriifolia*; (ad) *Tristaniopsis laurina*

Scale bar – 10 µm

Eucalyptus and allies

Nine *Eucalyptus* species (Figure 3 k-u) were sampled, representing five eucalypt groups: peppermints (*E. radiata*), longitudinale (*E. stellulata*), symphomyrtus (*E. smithii*, *E. viminalis*, *E. rubida* and *E. dalrympleana*), snowgum (*E. pauciflora*) and ashes (*E. fastigata* and *E. fraxinoides*), showing a variation in pollen length among species (16-25.7 µm). *Eucalyptus pauciflora* and *E. fraxinoides* exhibited pollen grains which were parasyncolpate with straight sides and had psilate/scabrate exine patterning, with *E. pauciflora* appearing slightly larger on average (20.4 µm compared with 16 µm). *Eucalyptus fastigata* was also straight sided, but had psilate exine patterning. *Eucalyptus rubida* showed presence of an apocolpial island, as did *E. viminalis*. *Eucalyptus dalrympleana* had scabrate exine patterning, while *E. stellulata* was large in size with convex pollen sides and psilate/scabrate patterning. The pollen grains of genera *Angophora* and *Corymbia* (Figure 3 a, h-j), which are in the same Myrtaceae tribe as *Eucalyptus*, could be distinguished by their larger size (pollen length of 18-34 µm) and arcuate-shaped colpi. The majority of *Angophora* and *Corymbia* also had apocolpial islands present.

Other Myrtaceae

Nine other Myrtaceae genera were used as reference pollen. Grains of *Callistemon* (now *Melaleuca*) were parasyncolpate with straight edges and a large closely fitting island present and had a pollen length range of 12-15.6 µm (Figure 3 e-g). The majority of other Myrtaceae genera exhibited small pollen grains (pollen length <15 µm). *Kunzea* and *Leptospermum*, which are both in the Leptospermeae tribe, had syncolpate grains with straight or concave edges and arcuate colpi, the difference being that *Leptospermum* pollen had granulate/scabrate exine patterning while *Kunzea* was psilate (Figure 3 v-ab). *Baeckea* pollen (Figure 3 c and d) was also syncolpate with arcuate colpi making it difficult to separate from *Kunzea* pollen, the most notable difference being that *Kunzea* were less syncolpate than *Baeckea*. *Backhousia myrtifolia* (Figure 3 b) and *Tristaniopsis laurina* pollen (Figure 3 ad) looked similar, both being parasyncolpate with concave sides, while pollen from *Tristania neriifolia* (Figure 3 ac) was extremely small, on average being less than 8 µm in length.

Fossil Myrtaceae

A total of 428 Myrtaceae pollen grains was recognised from the 32 core sections sampled. Comparison of the fossil pollen with extant specimens showed trends in the genera and species that were present at Bega Swamp at various times (Table 3). *Eucalyptus* pollen grains were found in every sample examined but the total number of eucalypt grains per sample, as well as the number of eucalypt 'species' identified per sample, varied through time. The results given by entering pollen characters into the Lucid key and by simply looking at the grains were compared and found to be compatible. Sixty-nine (16%) Lucid key suggestions did not match visual assumptions. Three-hundred-and-fifty-nine (84%) Lucid suggestions matched to at least genera visual judgements; of these, 119 (28%) Lucid suggestions gave matching species.

Core samples 54-56, depth 302-316 mm, age ~400 BP

52 grains, 8 unmatched between Lucid and visual, 34 generically matched, 10 fully matched.

The youngest core samples investigated, approximately 400 years old, presented a variety of pollen types, the most dominant being similar to *E. rubida* (Figure 4 h) and *E. pauciflora* (Figure 4 a, g and j). Seven other *Eucalyptus* pollen types were identified in smaller numbers. One diporate grain (Figure 4 d) was found and attributed to *E. fastigata*, although it is possible that other *Eucalyptus* species have diporate pollen grains. Pollen thought to belong to *Callistemon* (Figure 4 m) was present, as were *Kunzea* (Figure 4 i), *Tristania* (Figure 4 n), *Baeckea* (Figure 4 i) and *Leptospermum*.

Table 3. Grain numbers of various core sections attributed to Myrtaceous pollen types using visual judgement

	Core sample numbers												
Genus	**54-56**	**81-83**	**115-118**	**194-195**	**202**	**238-240**	**269-271**	**274**	**290-291**	**344-346**	**374**	**440-442**	**498-500**
Eucalyptus fraxinoides	3	2	11	4	0	11	14	5	5	5	0	5	3
Eucalyptus pauciflora	8	0	8	2	0	2	7	1	5	7	1	10	7
Eucalyptus fastigata	4	4	9	0	1	3	6	1	6	5	1	1	7
Eucalyptus rubida	14	3	12	3	0	5	6	2	6	1	1	4	3
Eucalyptus dalrympleana	2	2	3	0	0	1	3	1	1	0	0	1	0
Eucalyptus viminalis	6	1	2	0	0	1	1	1	0	2	0	2	1
Eucalyptus smithii	1	2	5	1	0	2	2	0	0	0	0	0	1
Eucalyptus radiata	1	0	0	0	0	0	0	0	0	0	0	0	
Eucalyptus stellulata	1	1	2	1	0	1	2	0	0	1	0	0	1
Angophora/Corymbia	0	0	2	0	0	0	0	0	0	0	0	0	0
Callistemon	7	1	3	1	1	2	6	0	0	0	1	1	1
Kunzea	4	1	6	0	1	5	9	2	15	0	3	1	3
Leptospermum	1	0	1	0	0	6	8	1	1	0	2	1	1
Baeckea	1	0	5	1	1	5	6	1	8	0	1	1	3
Tristania neriifolia	1	1	2	0	0	2	1	0	1	0	0	0	1
Tristaniopsis laurina	0	0	1	0	0	1	0	0	0	0	0	0	0

Core samples 81-83, depth 400-419 mm, age 850 BP

22 grains, 2 unmatched, 16 generically matched, 4 fully matched.

Seven *Eucalyptus* pollen grains were identified but no species appeared dominant and grains from *E. pauciflora* were not seen. One pollen grain from an *Angophora* or *Corymbia* (Figure 4 t) was observed, as well as grains from *Callistemon* (Figure 4 v), *Kunzea* (Figure 4 w) and *Tristania* (Figure 4 s, overleaf).

Core samples 115-118, depth 583-606 mm, age 2300 BP

74 grains, 9 unmatched, 43 generically matched, 22 fully matched.

Eucalyptus rubida (Figure 5 o, overleaf), *E. fraxinoides* (Figure 5 c, d i, s and t), *E. fastigata* (Figure 5 h) and *E. pauciflora* (Figure 5 k and n) all had many grains attributed to them during this time period. Another four *Eucalyptus* species had pollen grains attributed to them and grains from *Angophora* or *Corymbia* (Figure 5 q) were identified. *Kunzea* and/or *Baeckea* pollen grains (Figure 5 f, p and u) showed an increased number, while grains from *Tristania*, *Leptospermum* and *Tristaniopsis* were found.

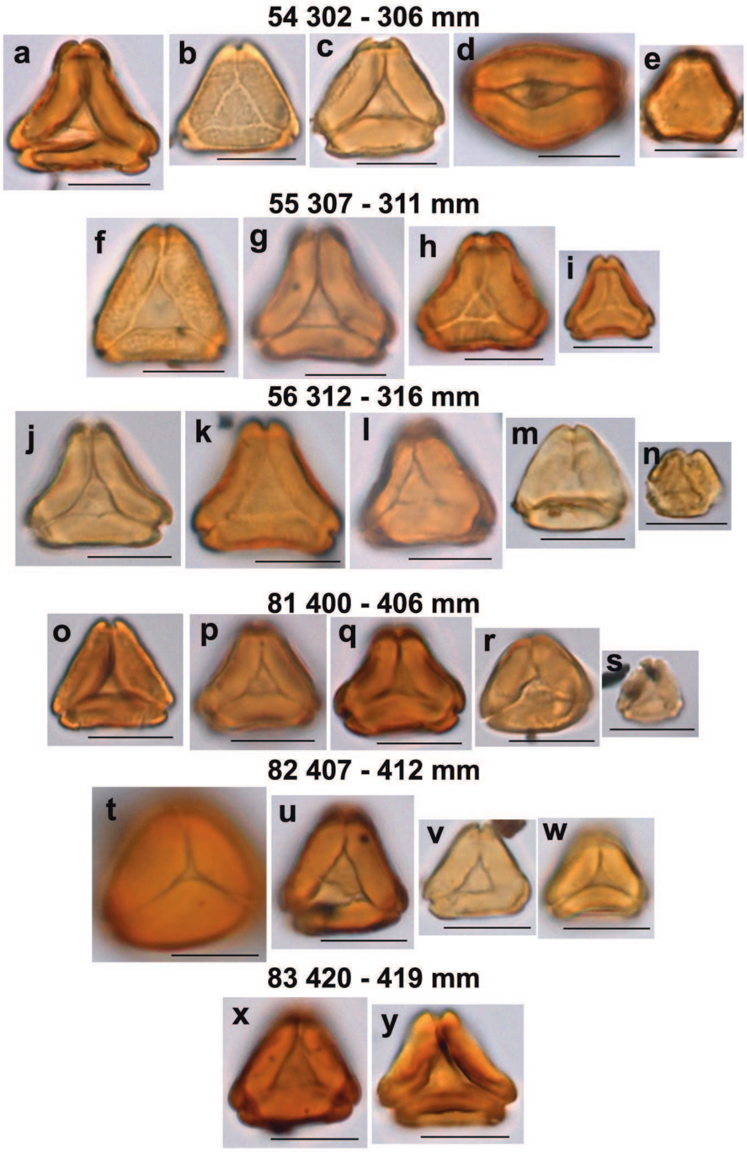

Figure 4. Examples of fossil pollen types from Bega Swamp core sections 54-56 and 81-83 with related core depth. 54 (a) *E. pauciflora*; (b); (c) *E. fastigata*; (d) Diporate *E. fastigata*; (e) *Kunzea*; 55 (f) *E. viminalis*; (g) *E. pauciflora*; (h) *E. rubida*; (i) *Baeckea;* 56 (j) *E. pauciflora*; (k) *E. fastigata*; (l) *E. rubida*; (m) *Callistemon*; (n) *Tristania*; 81 (o) *E. fraxinoides*; (p) *E. dalrympleana*; (q) *E. pauciflora*; (r) *E. rubida*; (s) *Tristania*; 82 (t) *Angophora/Corymbia*; (u) *E. viminalis*; (v) *Callistemon*; (w) *Kunzea*; 83 (x) *E. smithii*; (y) *E. fastigata*

Scale bar – 10 µm

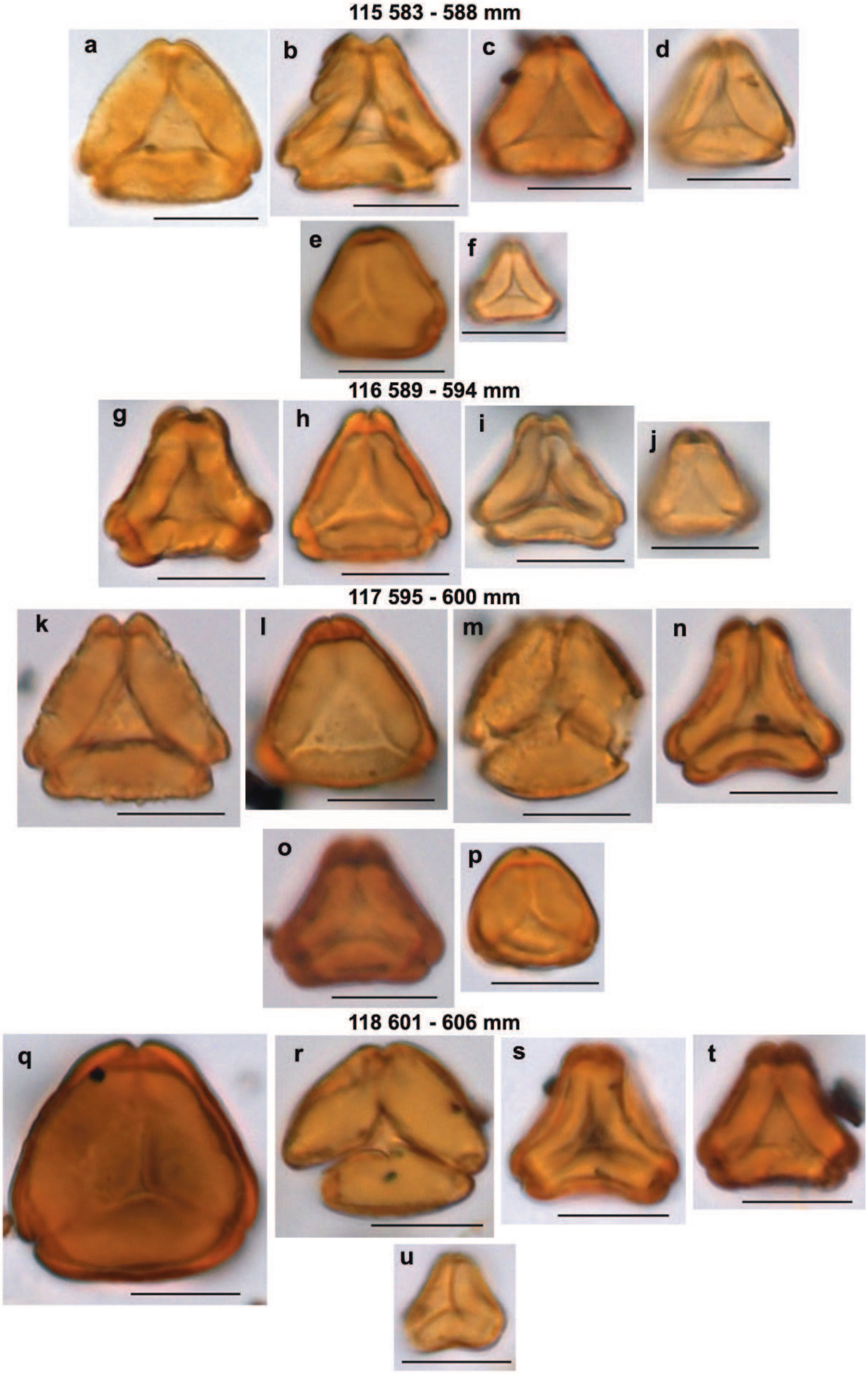

Figure 5. Examples of fossil pollen from Bega Swamp core sections 115-118 with related core depth. 115 (a) *E. stellulata*; (b) *E. pauciflora*; (c) and (d) *E. fraxinoides*; (e) *Kunzea*; (f) *Baeckea*; 116 (g) *E. pauciflora*; (h) *E. fastigata*; (i) *E. fraxinoides*; (j) *Callistemon*; 117 (k) *E. pauciflora*; (l) *E. viminalis*; (m) *Angophora/Corymbia*; (n) *E. pauciflora*; (o) *E. rubida*; (p) *Kunzea/Baeckea*; 118 (q) *Angophora/Corymbia*; (r) *Eucalyptus* sp.; (s) and (t) *E. fraxinoides*; (u) *Kunzea/Baeckea*

Scale bar – 10 μm

Core samples 194, 195, depth 980-1002 mm, age 3400 BP

14 grains, 1 unmatched, 7 generically matched, 6 fully matched.

Five *Eucalyptus* species were identified in samples from 3400 years ago (Figure 6), with one pollen grain each being attributed to *Callistemon* (Figure 6 e) and *Baeckea*.

Core sample 202, depth 1006-1009 mm, age 3500 BP

3 grains, 1 unmatched, 1 generically matched, 1 fully matched.

Three grains in total were found, with one thought to be similar to *E. fastigata* (Figure 6 g), one *Callistemon* and one *Kunzea* or *Baeckea*.

Core samples 238-240, depth 1197-1213 mm, age 4300 BP

47 grains, 6 unmatched, 19 generically matched, 22 fully matched.

A marked increase in smaller grains was seen from 4300 years ago. *Leptospermum* (Figure 6 q and w), *Kunzea* (Figure 6 r and x) and *Baeckea* (Figure 6 l and p) grain types all appeared more prevalent, suggesting that vegetation composition was different during this time. *Eucalyptus fraxinoides* (Figure 6 i, m and t) pollen type was abundant. Seven other *Eucalyptus* grains were identified, as well as *Callistemon*, *Tristania* and *Tristaniopsis*.

Core samples 269-271, depth 1369-1386 mm, age 4700 BP

69 grains, 15 unmatched, 33 generically matched, 21 fully matched.

Eucalyptus fraxinoides (Figure 7 c and k) and *E. pauciflora* (Figure 7 p) type pollen were the most common seen in samples from 4700 years. *Eucalyptus fastigata* (Figure 7 a) and *E. rubida* (Figure 7 r) also had a number of pollen grains identified, while four other *Eucalyptus* species were found. The number of *Callistemon* (Figure 7 g and m) pollen grains increased in this time period and many smaller pollen grains from *Kunzea* (Figure 7 o and u), *Leptospermum* (Figure 7 f, n, s and t) and *Baeckea* (Figure 7 v) were seen.

Core sample 274, depth 1399-1404 mm, age 4800 BP

15 grains, 2 unmatched, 9 generically matched, 4 fully matched.

Eucalyptus fraxinoides type grains (Figure 7 y, overleaf) were most prevalent and five other *Eucalyptus* species were found in small numbers. Smaller grains from *Kunzea* (Figure 7 aa), *Baeckea* (Figure 7 z) and *Leptospermum* (Figure ab) were found in smaller numbers.

Core samples 290, 291, depth 1494-1505 mm, age 5000 BP

42 grains, 9 unmatched, 18 generically matched, 15 fully matched.

Four *Eucalyptus* species, *E. fraxinoides* (Figure 8 h), *E. pauciflora* (Figure 8 a), *E. fastigata* (Figure 8 c) and *E. rubida* had similar numbers of pollen types identified. One tetraporate grain (Figure 8 j) was found and attributed to *Eucalyptus*. The most common pollen grains were small syncolpate grains of *Kunzea* (Figure 8 m) and *Baeckea* (Figure 8 n), while one grain each of *Tristania* (Figure 8 g) and *Leptospermum* was found.

Core samples 344-346, depth 1796-1814 mm, age 8500 BP

19 grains, 2 unmatched, 15 generically matched, 2 fully matched.

Grains from *Eucalyptus* species were the only pollen identified in this period, *Eucalyptus fraxinoides* (Figure 8 v), *E. pauciflora* (Figure 8 s) and *E. fastigata* (Figure 8 o) being the most abundant, with three other species also being recognised.

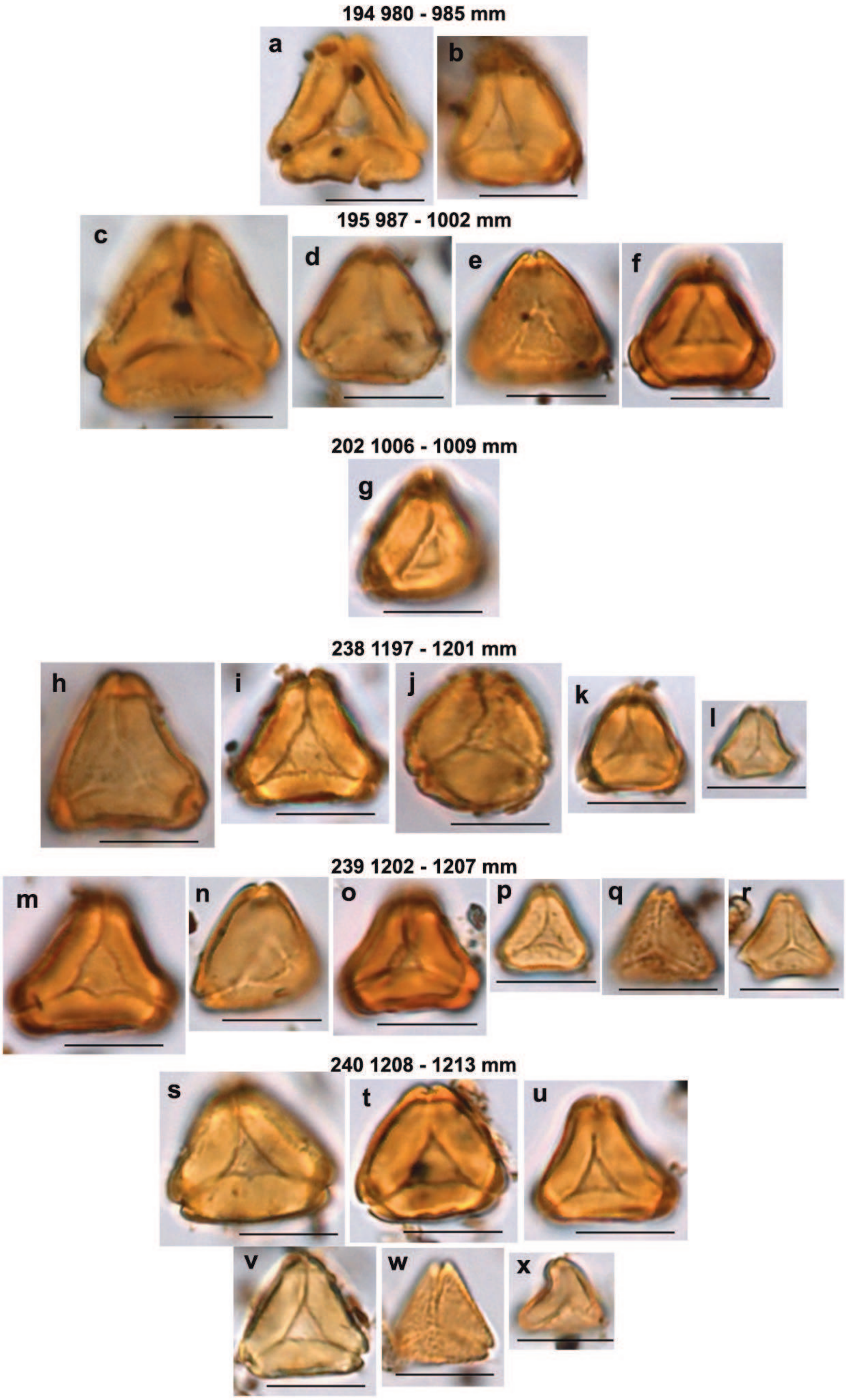

Figure 6. Examples of fossil pollen types from Bega Swamp core sections 194, 195, 202 and 238-240 with related core depth. 194 (a) *E. pauciflora*; (b) *E. fraxinoides*; 195 (c) *E. stellulata*; (d) *E. rubida*; (e) *Callistemon*; (f) *E. smithii*; 202 (g) *E. fastigata*; 238 (h) *E. viminalis*; (i) *E. fraxinoides*; (j) *E. dalrympleana*; (k) *E. radiata/rubida*; (l) *Baeckea*; 239 (m) *E. fraxinoides*; (n) *E. viminalis*; (o) *E. rubida*; (p) *Baeckea*; (q) *Leptospermum*; (r) *Kunzea*; 240 (s) *E. stellulata*; (t) *E. fastigata*; (u) and (v) *E. fraxinoides*; (w) *Leptospermum*; (x) *Baeckea/Kunzea*

Scale bar – 10 μm

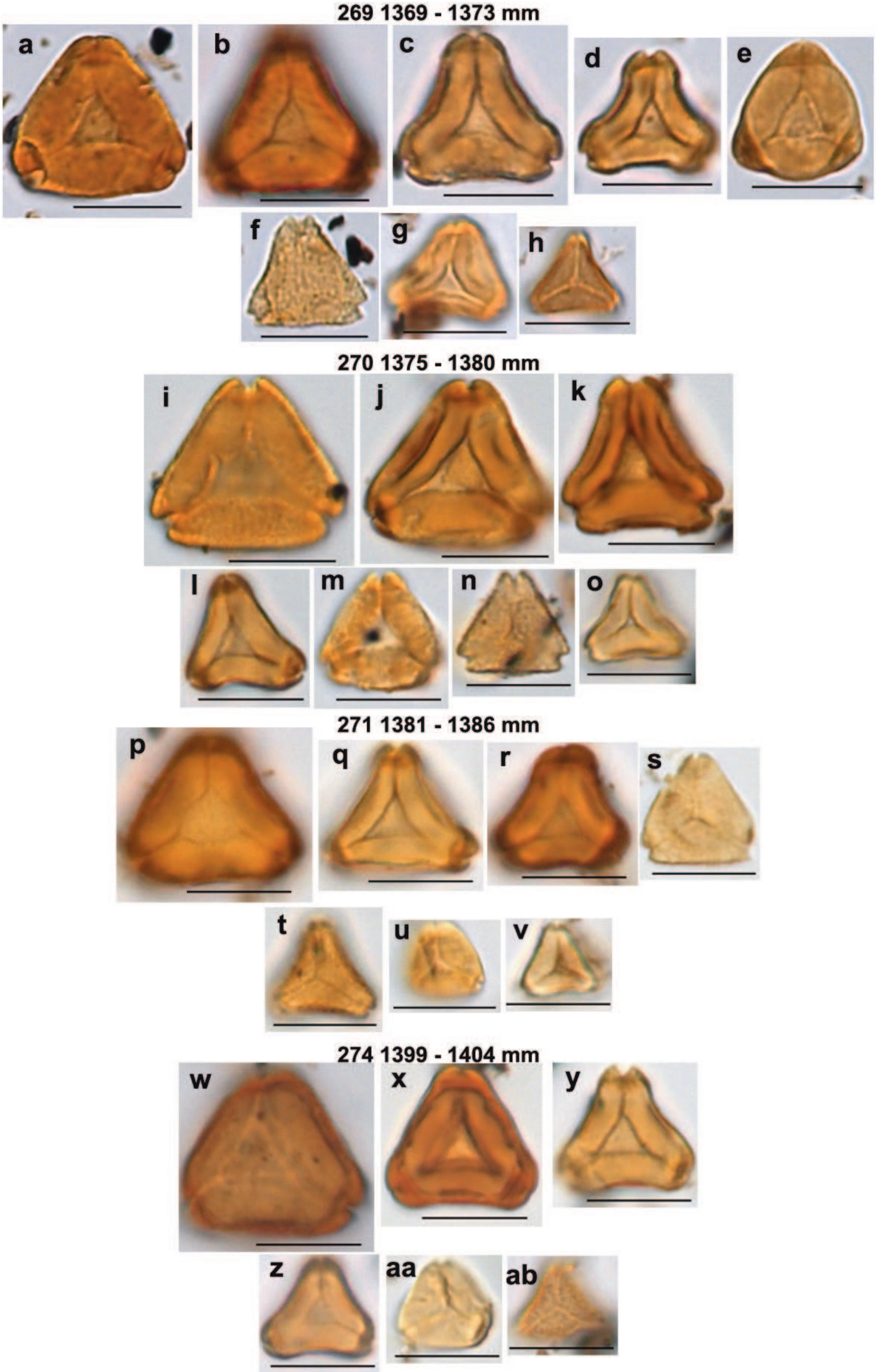

Figure 7. Examples of fossil pollen types from Bega Swamp core sections 269-271 and 274 with related core depth. 269 (a) *E. fastigata*; (b) *E. dalrympleana*; (c) *E. fraxinoides/pauciflora*; (d) *E. fastigata*; (e) *E. smithii*; (f) *Leptospermum*; (g) *Callistemon*; (h) *Kunzea/Baeckea*; 270 (i) *E. stellulata*; (j) *E. viminalis*; (k) *E. fraxinoides*; (l) *Kunzea*; (m) *Callistemon*; (n) *Leptospermum*; (o) *Kunzea*; 271 (p) & (q) *E. pauciflora*; (r) *E. smithii*; (s) *Leptospermum*; (t) *Leptospermum*; (u) *Kunzea*; (v) *Baeckea*; 274 (w) *E. viminalis*; (x) *E. fastigata;* (y) *E. fraxinoides*; (z) *Baeckea*; (aa) *Kunzea*; (ab) *Leptospermum*

Scale bar – 10 µm

Core sample 374, depth 1971-1975 mm, age 8800 BP

12 grains, 4 unmatched, 5 generically matched, 3 fully matched.

Around half the grains identified in this section were small syncolpate grains of *Kunzea* (Figure 8 z), *Baeckea* and *Leptospermum* (Figure 8 aa, overleaf). Three *Eucalyptus* species were identified, as was one *Callistemon* (Figure 8 y) grain.

Core samples 440-442, depth 2199-2213 mm, age 10,900 BP

33 grains, 4 unmatched, 24 generically matched, 5 fully matched.

Six *Eucalyptus* species were found, *E. pauciflora* (Figure 9 i, overleaf) and *E. fraxinoides* (Figure 9 j) types being the most common. A tetraporate pollen grain with an apocolpial island (Figure 9 b) was found and appeared similar to extant tetraporate grains of *Callistemon* (Figure 3 f). Smaller syncolpate grains were less abundant.

Core samples 498-500, depth 2497-2511 mm, age 12,500 BP

26 grains, 6 unmatched, 16 generically matched, 4 fully matched.

Eucalyptus viminalis (Figure 9 q) and *E. fastigata* (Figure 9 n) grains were identified as the most common grains from the oldest samples analysed. *Eucalyptus* type pollen was more diverse in this section, with five other pollen types being identified. The number for *Kunzea* (Figure 9 u) and *Baeckea* (Figure 9 w) pollen was slightly higher, and one grain each of *Callistemon* (Figure 9 z) and *Leptospermum* was found.

Validating fossil data

Images of fossil pollen were shown to Geoff Hope to establish which pollen types represented Myrtaceae groups from the Hope et al. (2000) pollen diagram (Figure 2). *Eucalyptus* type 1 grains were best illustrated by Figure 5 k. *Eucalyptus* type 2 pollen were similar to Figure 4 a and j. *Eucalyptus* type 3 pollen was similar to Figure 5 n. *Eucalyptus* type 4 was most like Figure 4 b and *Eucalyptus* type 5 like Figure 4 f. The smaller pollen grains were attributed to *Kunzea* (Figure 5 e), *Baeckea* (Figure 5 f) and *Leptospermum* (Figure 6 q). When comparing the Hope et al. (2000) *Eucalyptus* types to extant grains it was seen that *Eucalyptus* 1 looked similar to *E. pauciflora* (Figure 3 o). *Eucalyptus* 2 grains, which were thought to belong to *E. pauciflora,* looked similar to *E. fraxinoides* (Figure 3 n), *E. pauciflora* (Figure 3 o) and *E. fastigata* (Figure 3 m). *Eucalyptus* type 3 grains appeared most like *E. dalrympleana* (Figure 3 k), *E. radiata* (Figure 3 p) and *E. smithii* (Figure 3 s). *Eucalyptus* type 4 was very similar to *E. viminalis* (Figure 3 u), as was *Eucalyptus* type 5.

Discussion

The vegetation history of Bega Swamp interpreted from pollen diagrams by Hope et al. (2000) observes a transition from shrubby daisy-grass steppe to a low eucalypt (presumed snowgum) woodland by about 11,800 BP and then a phase of herbfield development. Eucalypt forest appeared abruptly around 9400 BP and increased in diversity. Changes in eucalypt dominance occurred around 7000 and 4000 BP, which may represent shifts to the *E. fastigata/E. dalrympleana* forest of the present day. The centre of a possible 'wet phase' happened between 6000 BP and 3300 BP. The present study searched selected core samples for Myrtaceae pollen which could correlate with this vegetation history interpretation. It was found that younger core samples contained higher concentrations and a wider variety of *Eucalyptus* type pollen than older sections. The dominant pollen type fluctuated through the core and this was also stated by Hope et al. (2004), who suggested that this may represent quite minor transitions across environmental limits or even autogenic processes that are not driven by external changes.

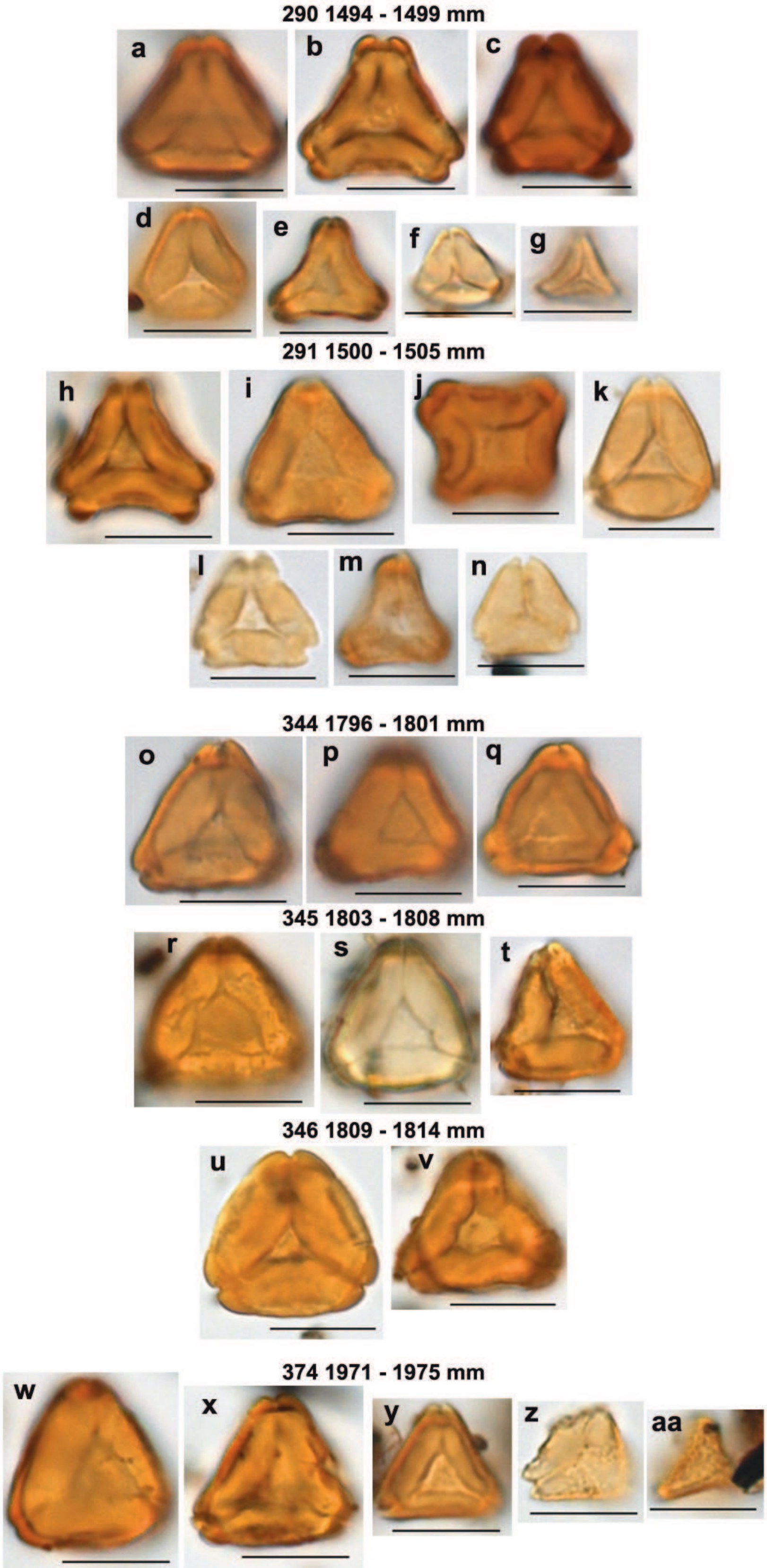

Figure 8. Examples of fossil pollen types from Bega Swamp core sections 290, 291, 344-346 and 374 with related core depth. 290 (a) *E. pauciflora*; (b) *E. fraxinoides*; (c) *E. fastigata*; (d) and (e) *Kunzea*; (f) *Baeckea*; (g) *Baeckea/Kunzea*; 291 (h) *E. pauciflora*; (i) *E. dalrympleana*; (j) Tetraporate *Eucalyptus*; (k) *E. smithii*; (l) *E. pauciflora*; (m) *Kunzea*; (n) *Baeckea*; 344 (o) *E. fastigata*; (p) *E. viminalis*; (q) *E. rubida*; 345 (r) *E. fastigata*; (s) *E. pauciflora*; (t) *E. fastigata*; 346 (u) *E. stellulata*; (v) *E. fraxinoides*; 374 (w) *E. fastigata*; (x) *E. pauciflora*; (y) *Callistemon*; (z) *Kunzea/Leptospermum*; (aa) *Leptospermum*

Scale bar – 10 µm

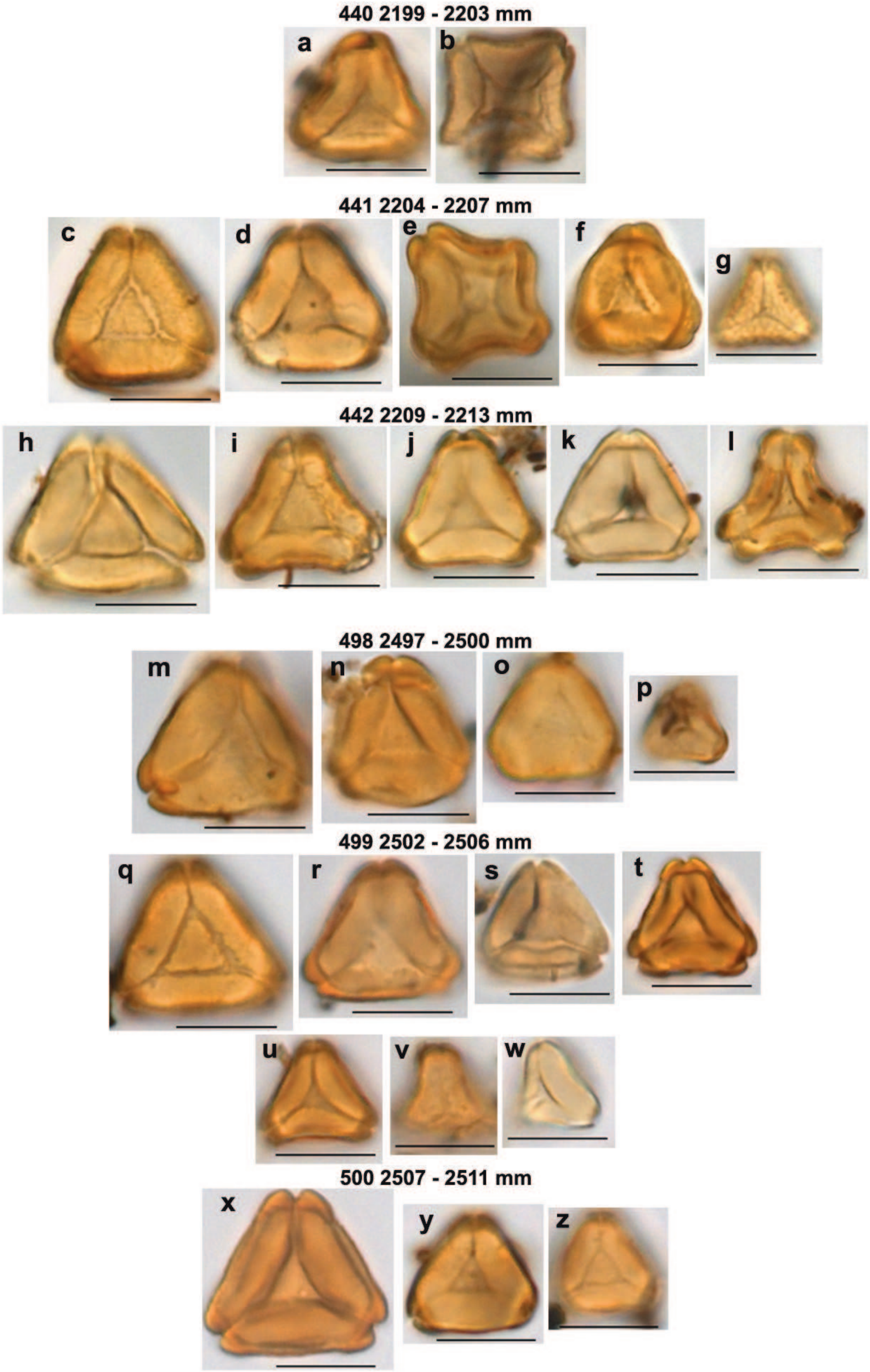

Figure 9. Examples of fossil pollen types from Bega Swamp core sections 440-442 and 498-500 with related core depth. 440 (a) *E. rubida*; (b) Tetraporate *Callistemon*; 441 (c) *E. viminalis*; (d) *E. fastigata*; (e) Tetraporate *Eucalyptus*; (f) *E. rubida*; (g) *Leptospermum*; 442 (h) and (i) *E. pauciflora*; (j) *E. fraxinoides*; (k) *E. pauciflora*; (l) *E. fraxinoides*; 498 (m) *E. stellulata*; (n) *E. fastigata*; (o) *E. fraxinoides*; (p) *Baeckea/Kunzea*; 499 (q) *E. viminalis*; (r) *E. fastigata*; (s) *Eucalyptus* sp.; (t) *E. fraxinoides*; (u) *Baeckea/Kunzea*; (v) *Kunzea*; (w) *Baeckea*; 500 (x) *E. fastigata*; (y) *E. pauciflora*; (z) *Callistemon*

Scale bar – 10 µm

Eucalyptus pauciflora (snowgum) pollen was found in all but two of the sections sampled and in higher concentrations in older and younger samples, with lower values in between. However, *E. fraxinoides (*white ash) type pollen, which looks very similar to *E. pauciflora* but is smaller, was found in high concentrations when the larger *E. pauciflora* type was not as abundant (4300 to 4700 BP). If these fossil grains are indeed *E. fraxinoides*, it would suggest a wet, tall eucalypt forest present at Bega Swamp during this time. *E. dalrympleana*, *E. rubida*, *E. smithii* and *E. viminalis* pollen types all began showing higher concentrations in mid-core sections, starting around 5000 BP, matching suggestions that dominant present-day vegetation emerged somewhere between 6000 BP and 3300 BP. *Eucalyptus fastigata*, however, was found in high concentrations in the oldest core samples, differing from previous pollen studies, suggesting that components of a tall eucalypt forest have existed in the Bega Swamp area for longer than has been assumed.

Comparing the suggested eucalypt groups of Hope et al. (2000) with extant pollen presented problems with the interpretation. Nine extant *Eucalyptus* species were used as reference material in the present study, which contrasted with Hope et al. (2000) who had five distinct eucalypt pollen groups. While the idea of having five groups would concur with the morphological and ecological groups that occur in the Bega Swamp area (i.e. snowgum, ashes, peppermints etc) and create a neat vegetation transition history as shown in the pollen diagram (Figure 2), the extant pollen morphology did not give full support to the morphological eucalypt pollen groups created by Hope et al. (2000). Eucalypt pollen types 2, 3 and 5 have similarities with extant *Eucalyptus* pollen across multiple morphological groups – for instance, eucalypt group 2 pollen could belong to the snowgums or ashes, and eucalypt type 3 could belong to ashes or peppermints. To create a vegetation history based on the occurrence of various eucalypt pollen type groups would thus seem implausible.

There have been previous attempts to find distinctive *Eucalyptus/*Myrtaceae pollen groups (Dodson 1974; Chalson and Martin 1995; Pickett and Newsome 1997). Dodson (1974) identified four types of *Eucalyptus* pollen from Lake Leake in South Australia and related these pollen types to eucalypt groups comprising 11 extant *Eucalyptus* species, although how this was done is not exactly clear as the results are published as an appendix. Chalson and Martin (1995) created the characters used in this study and worked only on extant Myrtaceae pollen of the Blue Mountains, finding that all but two taxa could be sorted to a species level. This study showed that there is the ability to separate Myrtaceae pollen to a species level if a wide range of genera and a low number of species from each genus is selected. Pickett and Newsome (1997) used nine *Eucalyptus* species and fossils from a Holocene swamp at Walpole, Western Australia, finding that extant species could be differentiated to pollen types with some confidence so long as suites of morphological characters, rather than single characters, were used, and that much of the fossil pollen could be allocated to a pollen type if the necessary features were preserved in the pollen grain. However, they also stated that 'a basic pre-requisite is that the area under study has a relatively small number of *Eucalyptus* species and that these can be separated to a satisfactory extent, on the basis of pollen morphology' (Pickett and Newsome 1997:203). This study also showed that when a small number of known taxa is used as a pollen reference, comparisons with fossil pollen can be more confidently made as there is likely to have been minimal floral composition change during the Holocene and known pollen synapomorphies can be discounted. However, it was not *Eucalyptus* pollen, but other representatives of the Myrtaceae family that best illustrated this concept.

Sections sampled between 4300 and 5000 BP showed a dramatic increase in the number of smaller syncolpate pollen grains found, representing the wet phase that has been suggested by previous studies (Hope et al. 2000; Donders et al. 2007). While much focus at Bega Swamp has been on what type of *Eucalyptus* was present throughout the Holocene, little has been mentioned about the smaller Myrtaceae pollen grains present in the core, which may be more indicative and less difficult to interpret than the various *Eucalyptus* species. The smallest of these grains most likely belongs to *Tristania neriifolia* (water gum), which occurs along rocky creek beds and banks on sandstone. The presence of this grain in core sections suggests that there was running water at or into Bega Swamp at various stages. Pollen grains sized 10-15 µm that were psilate and syncolpate most likely came from the genera *Baeckea* and *Kunzea*. Differentiating between the grains of these two genera is not easy, so most fossil grains with these characters were assigned to a combined genera type. However, they are both myrtaceous shrubs that occur in bogs and smaller heathland communities and the presence of these pollen grains suggests a more open vegetation type community. The quantity of *Eucalyptus* pollen types was lower in sections where *Baeckea*/*Kunzea* and *Leptospermum* pollen grains show a marked increase. While this could be interpreted as a reduction in the area of the surrounding tree forest community during these phases, it could be attributed alternatively to pollen filtration caused by shrub cover. Hope (1968) showed from traps in Wilson's Promontory that shrub cover intercepts pollen from nearby communities, which is then presumably destroyed by sunlight. This was also demonstrated by Tauber (1967) in shrubland surrounding a pond in Denmark. This suggests that while the Bega Swamp bog area may have been dominated by an open heathland community during this time, the surrounding vegetation would most likely have remained a eucalypt forest type.

Pollen grains sized 10-15 µm that were granulate or scabrate and syncolpate closely matched extant grains of *Leptospermum* species. The presence of these grains also suggests a more open heathland type community. It can also be noted from the Bega Swamp pollen diagram (Figure 2) that there is a decrease in charcoal found around the same time of the *Leptospermum* and *Baeckea*/*Kunzea* increase. Bickford and Gell (2005) suggested that the presence of *Leptospermum* at around 6500 BP in a core from the Fleurieu Peninsula, South Australia, combined with the presence of Cyperaceae, *Allocasuarina* (*paludosa* or *robusta*) and *Banksia marginata* represented a wet-heath community. This concurs with the previous studies on Bega Swamp that suggest a mid-Holocene wet phase, characterised by expansion of wet heath and ferns, starting around 7500 BP (Donders et al. 2007). Bickford and Gell (2005) also suggested that the dramatic increase in *Leptospermum* pollen could be accounted for in part by the reduction of *Acacia* present in the wetlands and surrounding vegetation following clearance and the cessation of regular burning. Other research has shown that *Leptospermum* benefits from a lack of fire (Bennet 1994; Johnson 2001), while it has also been suggested that fire benefits *Leptospermum*, which is tolerant of high-intensity fires (Morrison and Renwick 2000; Bond et al. 2004). This result suggests that *Leptospermum* and *Kunzea*/*Baeckea* pollen are better vegetation and climate indicators than separating *Eucalyptus* pollen into different sub-genera or species types.

Using size as a sorting characteristic did not prove efficient when using the Lucid key. Entering morphological characteristics of fossil pollen into the Lucid key often resulted in close matches with extant Myrtaceae pollen, but when measurements were combined with morphology no matches were commonly encountered. This may be explained by the use of different mounting media. The Bega Swamp samples were mounted in silicone oil; extant samples in a variety of substrates such as syn-matrix and glycerine, and differing sizes in relation to mounting media and acetolysis treatment has been noted before (Deuse 1960; Drugg 1962). To rely on size as a characteristic when searching for possible fossil-extant matches thus involves greater ranges depending on how many mounting substrates have been used, and creates less certainty.

Conclusion

Eucalyptus pollen morphology of the extant taxa did not consistently match morphological or ecological groups. Pollen grains of the symphomyrtus group did not look the same (*E.*

dalrympleana, *E. rubida*, *E. smithii* and *E. viminalis*), but similarities could be found within the group, such as the presence of a large apocolpial island (*E. rubida* and *E. viminalis*). Another important pollen morphology similarity in *Eucalyptus* was that seen between *E. pauciflora* (snowgum) and *E. fraxinoides* (white ash).

This raises doubts about using *Eucalyptus* pollen types when interpreting past vegetation and climatic conditions. On the other hand, Myrtaceae genera such as *Leptospermum*, *Kunzea*, *Baeckea*, *Melaleuca* (*Callistemon*), *Angophora*/*Corymbia*, *Tristaniopsis* and *Tristania* are more easily identifiable, especially when known pollen synapomorphies do not occur in the area. While it would be foolish to announce with complete certainty that fossil pollen grains match extant pollen grains, sentiments that have been expressed before by Joosten and de Klerk (2002), it is not unreasonable to suggest that pollen grains from the Holocene that display similar characteristics as extant pollen are most likely the same genus, or more safely, tribe within the Myrtaceae family. The confidence in comparing fossil and extant pollen increases when an extant taxa sample size is small and the extant taxa have distinct pollen characteristic suites such as observed in *Leptospermum*, which has small, granulate/scabrate patterned grains, *Kunzea*, which is syncolpate and less patterned than *Leptospermum*, or *Callistemon*, which always has a polar island, and *Tristania*, which has very small pollen grains (less than 8 μm).

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