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Pollen morphology of the Myrtaceae. Part 2: tribes Backhousieae, Melaleuceae, Metrosidereae, Osbornieae and Syzygieae

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Abstract. Pollen morphology of 16 genera and 101 species from the Myrtaceae tribes Backhousieae, Melaleuceae, Metrosidereae, Osbornieae and Syzygieae was surveyed using scanning electron microscopy (SEM) and light microscopy (LM). The most common pollen type observed in these tribes was parasyncolpate with arcuate or angular colpi, and a rugulate exine pattern. There was little size variation in observed pollen, except for larger pollen in tribe Melaleuceae. All *Metrosideros* pollen grains had apocolpial islands, as well as all *Callistemon* species viewed by LM. *Choricarpia* of tribe Backhousieae had pollen with a distinctive exine pattern. Dicolporate pollen were observed in two tribes, Metrosidereae (*Tepualia*) and Syzygieae (*Acmena*), and may be of systematic value. The dicolporate grains of these two genera were also easily distinguishable from each other by using size and pollen side shape as diagnostic characters. Two pollen types were observed within the genus *Melaleuca*, and a number of pollen types were observed within the species-rich genus *Syzygium*.

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Introduction

Tribes of the Myrtaceae subfamily Myrtoideae, namely Backhousieae, Melaleuceae, Metrosidereae, Osbornieae and Syzygieae, are found in Australia, New Zealand, New Caledonia, South-east Asia, South Pacific islands, Hawaii, southern South America and Africa. Melaleuceae and Osbornieae are sister tribes (Wilson *et al*. 2005), whereas sister tribes Backhousieae and Syzygieae are closely related to Metrosidereae (Biffin *et al*. 2010). These two groups are distantly related to each other, but the pollen of these tribes, in particular the presence of a large apocolpial island, are very similar. Previous palynological work on members of these tribes has been conducted by Pike (1956), McIntyre (1963), Gadek and Martin (1981), Patel *et al*. (1984), Moar (1993) and Parnell (2003). These studies have shown that pollen is oblate and parasyncolpate. Parnell (2003) investigated 57 species of *Syzygium*, mainly from South-east Asia, by SEM and found it difficult to separate species on the basis of pollen characters, but also noted that pollen from *Jambosa*-type species were larger than pollen from most other *Syzygium* species.

Materials and methods

Methods and terminology used in the present study are detailed in Thornhill *et al*. (2012*a*). In figures and tables, the current accepted species name is applied and the previous name appears in parentheses. The list of taxa used for the study includes previous and current accepted names to enable cross-referencing to past palynological work (Tables S1 and S2, available as Supplementary Material).

Results

Pollen descriptions

Tribe Backhousieae

Two genera are included in Backhousieae, both of which occur only in Australia. *Backhousia* and *Choricarpia* species grow in rainforest and dry forest areas of Queensland and New South Wales, and one species of *Backhousia* occurs in the Kimberley region of Western Australia. Pollen measurements for Backhousieae are summarised in Tables 1 and 2.

Genus ***Backhousia***

Number of species: 10.

Distribution: eastern and north-western Australia.

Species examined: SEM – 2; LM – 2.

Previous pollen studies: Pike (1956); Gadek and Martin (1981).

Table 1. Backhousieae scanning electron microscopy sample measurements

Pollen shape: Ob, oblate; Pro, prolate. *Pore no*.: Di, dicolporate; Tri, tricolporate; Tet, tetracolporate; Hex, hexacolporate. *Colpal morphology*: Syn, syncolpate; Arc, parasyncolpate arcuate; Ang, parasyncolpate angular; Inv, parasyncolpate inverse arcuate; Bre, brevicolpate; Aco, acolpate; Synd, syndemicolpate; Di, Dicolpate. *Shape of side*: Str, straight; Conv, convex; GC, greatly convex; Conc, concave; DC, deeply concave. *Exine*: Psi, psilate; Rug, rugulate; Ver, verrucate; Sca, scabrate; Gra, granulate; Verm, vermiculate. *Amb shape*: R, round; P, pointed; F, flat; N, notched. *Colpal edge*: S, smooth; R, rough; B, broken; N, none. *Apocolpial field*: Gra, granulate; Psi, psilate; Rug, rugulate; Sca, scabrate; Ver, verrucate; N, none. *Island type*: N, none; S, small/irregular; C, closely fitting; G, globular. Length and width columns show minimum (mean) maximum

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Backhousia citriodora	Ob	Tri	Arc, Ang	Str, Conc	Rug	R, P	S	Psi	N	13.9 (14.5) 15.1	13.6 (14.4) 14.8	6.4 (6.9) 7.4	45.7 (47.9) 49.7
Backhousia myrtifolia	Ob	Tri	Arc	Conc	Sca	R, P	S	Psi	N	13.5 (14.2) 14.7	13.5 (14.3) 14.9	7.4 (7.6) 7.8	53.2 (54) 54.9
Choricarpia subargentea	Ob	Tri	Syn, Arc	DC, Conc	Sca	R, P, F	B, S	Sca, Psi	N	14.3 (15.8) 17.2	15.5 (16.4) 17.5	8 (8.5) 9	46.3 (54.2) 57.6

Table 2. Backhousieae light microscopy sample measurements

See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Backhousia citriodora	Ob	Tri	Arc, Ang	Str, Conv	Psi, Rug	R, P	S, R	Psi	N, C	14.1 (15.6) 19.1	13.6 (14.6) 18.2	5.6 (6.2) 6.9	29.2 (40.7) 48
Backhousia myrtifolia	Ob	Tri	Arc	Conc	Psi	R, P	S, R	Psi		12 (12.6) 13.5	12.7 (13.2) 13.8	6.1 (6.3) 6.6	48.6 (50.3) 54.4
Choricarpia leptopatala[A]	Ob	Tri	Arc, Ang	Str, Conv	Sca	R, P	R, S	Psi, Sca	N, C	11.5 (13.3) 15.1	11.8 (13) 14.4	2.6 (3.1) 3.7	22.3 (23.4) 24.4
Metrosideros (*Choricarpia*) *leptopetala*[A]	Ob	Tri	Ang	Str, Conv	Sca	R	S	N	C	18.5 (22.2) 24.2	16.7 (21.1) 23.1	4.8 (7.6) 9.1	26.2 (33.7) 39.1
Choricarpia subargentea	Ob	Tri	Arc, Ang	Conc	Sca	R	R	Psi	N	13.4 (14) 15	13.9 (14.9) 15.9	6.1 (6.8) 7.8	40.7 (48.6) 54.5

[A]Slide from Pike collection.

Images: SEM polar view – Fig. 1*a*, *b*; SEM exine pattern – Fig. 2*a*, *b*; SEM equatorial view – Fig. 13*h*; LM polar view – Fig. 3*a*, *b*.

SEM: *Backhousia* pollen were tricolporate with a rugulate or scabrate exine, partially similar to the findings of Gadek and Martin (1981). Pollen sides were concave or straight and colpal morphology was parasyncolpate with arcuate or angular colpi. Pollen ambs were round or pointed, colpal edges were smooth and the apocolpial field was psilate. Pollen length ranged from 13.5 to 15.1 µm. Colpus/length ratio ranged from 45.7 to 54.9%.

LM: the exine of *Backhousia* was psilate or sometimes rugulate. Pollen sides were straight, concave or convex. Colpal morphology was parasyncolpate with arcuate, or more rarely, angular colpi. Pollen ambs were round or pointed, colpal edges were smooth or rough, and the apocolpial field was psilate. Pollen length ranged from 12 to 19.1 µm. Colpus/length ratio ranged from 29.23 to 54.4%.

Genus ***Choricarpia***

Number of species: 2.

Distribution: eastern Australia.

Species examined: SEM – 1; LM – 2 (3 samples).

Previous pollen studies: Pike (1956); Gadek and Martin (1981).

Images: SEM polar view – Fig. 1*c*; SEM exine pattern – Fig. 2*c*; LM polar view – Fig. 3*c–f*.

SEM: *Choricarpia* pollen were tricolporate with a scabrate exine. Pollen sides were deeply concave or concave and colpal morphology was syncolpate or parasyncolpate with arcuate colpi. All possible pollen amb states were scored for *Choricarpia*. Colpus edges were broken or sometimes smooth, and there was a scabrate or psilate apocolpial field. Pollen length ranged from 14.3 to 17.2 µm. Colpus/length ranged from 35.6 to 45%.

LM: exine patterns of *Choricarpia* were scabrate. Pollen sides were straight, concave or convex and colpal morphology was parasyncolpate with arcuate or angular colpi. Pollen ambs were round or occasionally pointed, colpal edges were rough or smooth and the apocolpial field was psilate or scabrate. Closely fitting apocolpial islands were sometimes present. Pollen length ranged from 11.5 to 24.2 µm. Colpus/length ratio ranged from 22.3 to 54.5%.

Tribe Metrosidereae

There are two genera included in Metrosidereae, both of which occur in the Malesian–Pacific region, with one species of *Metrosideros* occurring in South Africa. The previously recognised *Mearnsia*, now part of *Metrosideros* (Wright *et al*. 2000), is discussed as a separate genus in the present paper, for ease of reference to past palynology papers. All species of *Metrosideros* are found in rainforests, whereas the monotypic genus *Tepualia* occurs in marshes, bogs and river banks of Chile

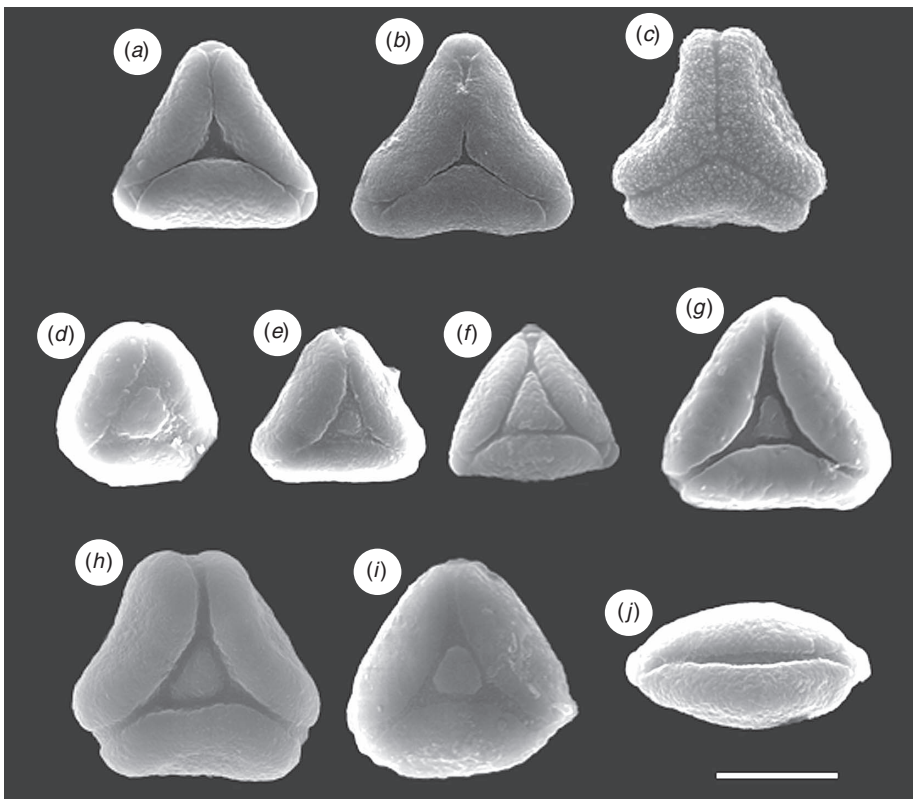

Fig. 1. Polar view of Backhousieae and Metrosidereae under scanning electron microscope. Scale bar = 10 µm. (*a*) *Backhousia citriodora*, (*b*) *B. myrtifolia*, (*c*) *Choricarpia subargentea*, (*d*) *Mearnsia cordata*, (*e*) *Metrosideros carminea*, (*f*) *M. diffusa*, (*g*) *M. macropus*, (*h*) *M. nervulosa*, (*i*) *M. nitida* and (*j*) *Tepualia stipularis*.

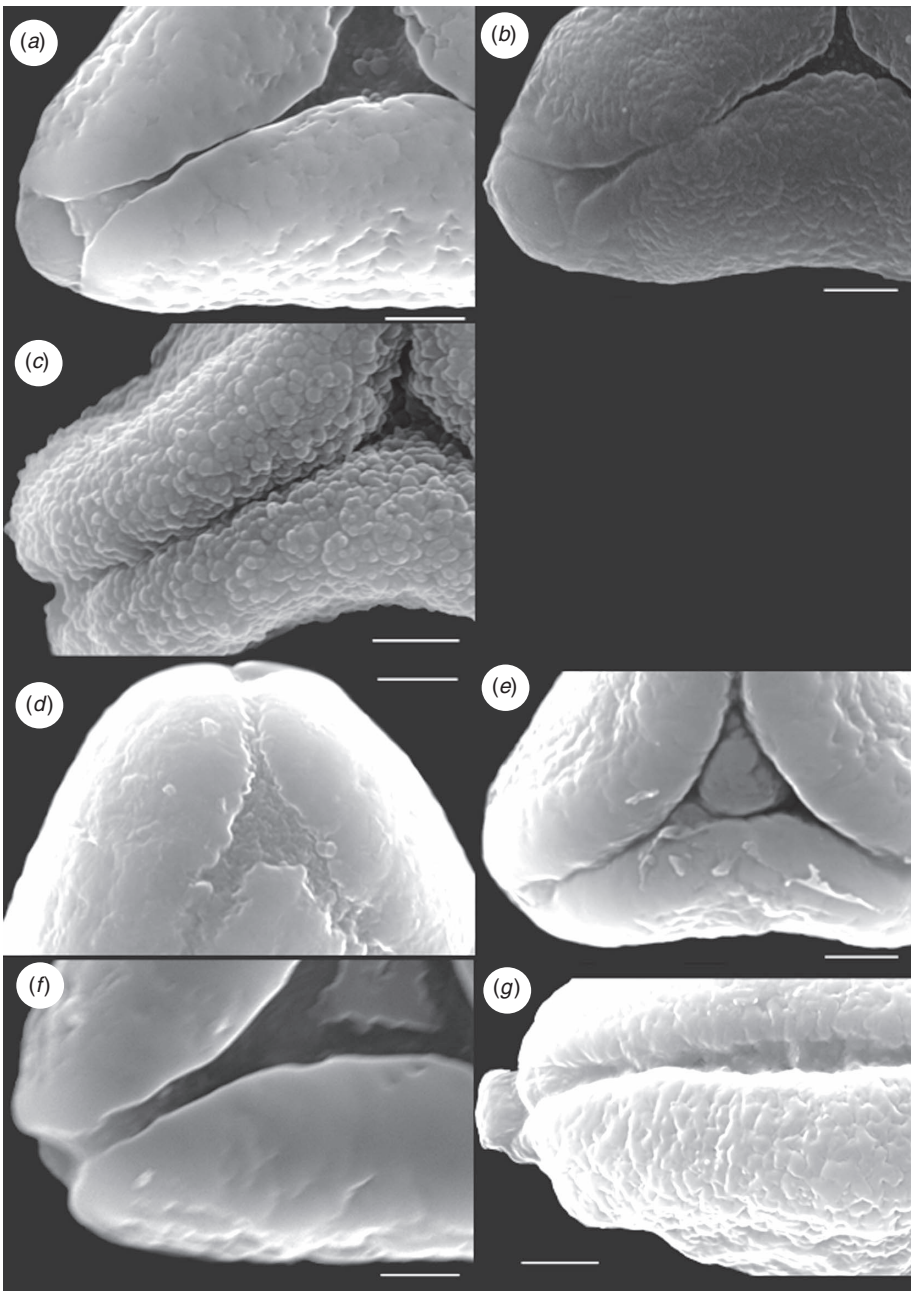

Fig. 2. Exine pattern of Backhousieae and Metrosidereae under scanning electron microscope. Scale bar = 2 µm. (*a*) *Backhousia citriodora*, (*b*) *B. myrtifolia*, (*c*) *Choricarpia subargentea*, (*d*) *Mearnsia cordata*, (*e*) *Metrosideros carminea*, (*f*) *M. macrocarpus* and (*g*) *Tepualia stipularis*.

and Argentina in South America. Pollen measurements for Metrosidereae are summarised in Tables 5 and 6.

Genus ***Mearnsia***

Number of species: ~18.

Distribution: Malesia.

Species examined: SEM –1; LM –1.

Previous pollen studies: Pike (1956).

Images: SEM polar view – Fig. 1*d*; SEM exine pattern – Fig. 2*d*; LM polar view – Fig. 3*g*.

SEM: *Mearnsia* pollen were tricolporate with a psilate/rugulate exine. Pollen sides were convex and colpal morphology was parasyncolpate with angular colpi. Pollen ambs were round or flat, colpal edges were rough and the apocolpial field was psilate or scabrate. Closely fitting polar islands were present at the polar regions of all grains. Pollen length ranged from 12.6 to 13.7 µm. Colpus/length ratio ranged from 27.4 to 32%.

LM: the exine of *Mearnsia* was psilate. Pollen sides were convex and colpal morphology was parasyncolpate with angular colpi. Pollen ambs were round, colpus edges were smooth, and all pollen had closely fitting apocolpial islands. Pollen length ranged

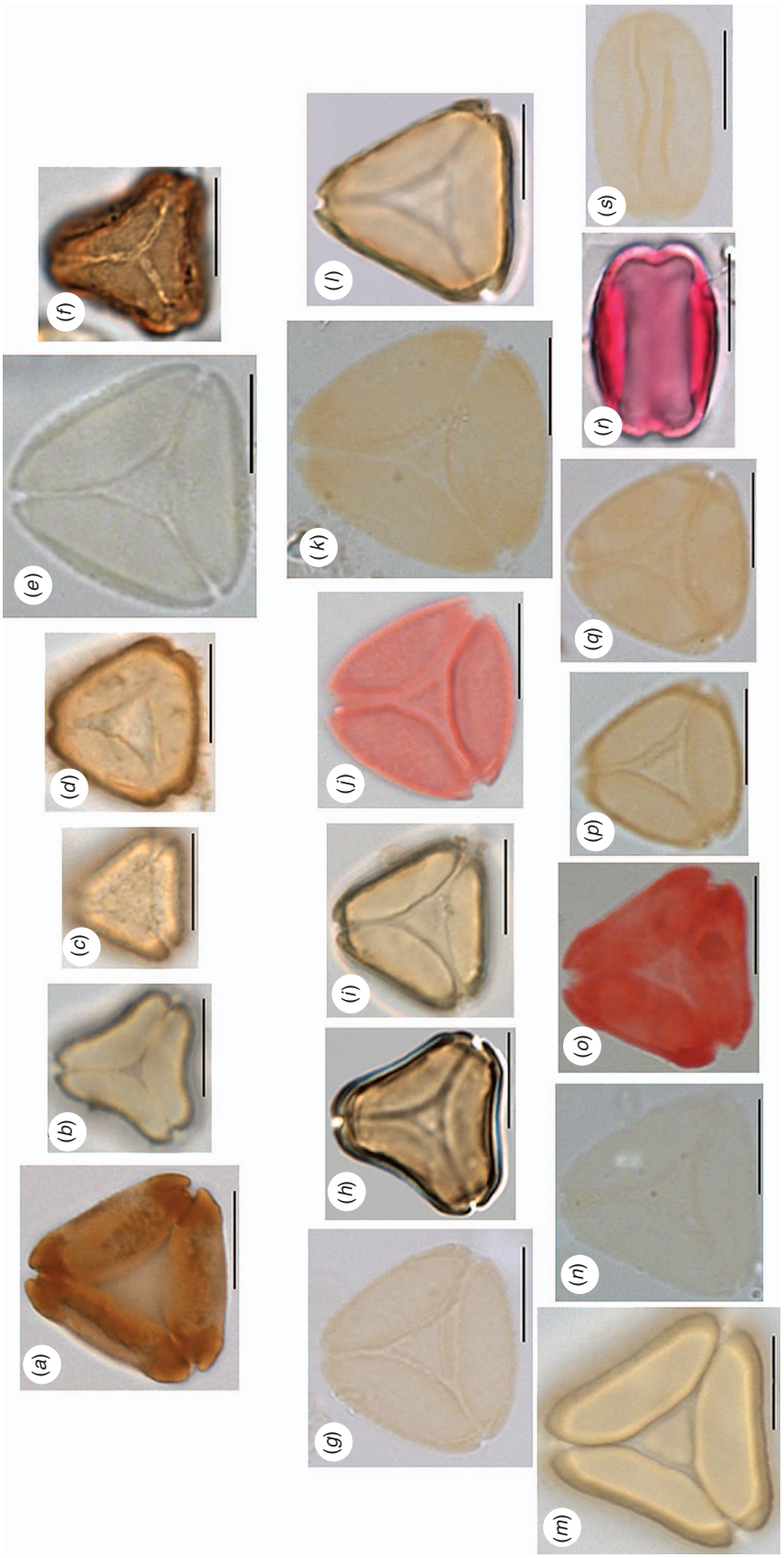

Fig. 3. Polar view of Backhousieae and Metrosidereae as viewed under light microscope. Scale bar = 10 µm. (*a*) *Backhousia citriodora*, (*b*) *B. myrtifolia*, (c) *Choricarpia leptopatala**, (*d*) *C. leptopatala**, (*e*) *C.* (*Metrosideros*) *leptopetala**, (*f*) *C. subargentea*, (*g*) *Mearnsia ramiflora**, (*h*) *Metrosideros carminea*, (*i*) *M. collina*, (*j*) *M. diffusa*, (*k*) *M. excelsa**, (*l*) *M. macropus*, (*m*) *M. nervulosa* (*n*) *M. perforata**, (*o*) *M. salomonensis**, (*p*) *M. perforata* (*scandens*)*, (*q*) *M. umbellata**, (*r*) *Tepualia stipularis** and (*s*) *T. stipularis**. Slides indicated with asterisk are from Pike collection.

from 19.2 to 21.6 µm. Colpus/length ratio ranged from 31.3 to 35.4%.

Genus ***Metrosideros***

Number of species: ~74.

Distribution: New Caledonia, New Zealand, Hawaii, New Guinea, south Pacific Islands and South Africa.

Species examined: SEM –5; LM – 10.

Previous pollen studies: Pike (1956); McIntyre (1963); Gadek and Martin (1981); Moar (1993).

Images: SEM polar view – Fig. 1*e–i*; SEM exine pattern – Fig. 2*e*, *f*; SEM equatorial view – Fig. 13*i*; LM polar view – Fig. 3*h–q*.

SEM: *Metrosideros* pollen were tricolporate. The majority of grains had a rugulate exine, and a lesser number possessed a vermiculate or verrucate/scabrate exine. Pollen sides were concave, convex or straight, and colpal morphology was consistently parasyncolpate with angular colpi. Pollen ambs were round, pointed or sometimes flat, colpal edges were smooth or rough and the apocolpial field was either psilate, scabrate or not visible because of apocolpial island presence. Most observed apocolpial islands were closely fitting, but small irregular islands were observed in *M.carminea*, *M. macropus* and *M. nervulosa*, and apocolpial islands have been observed in all previous palynology studies of *Metrosideros*. Pollen length ranged from 11.1 to 20.9 µm. Colpus/length ratio ranged from 27.3 to 46.5%.

LM: the exine of *Metrosideros* was psilate or at times scabrate. Most grains were tricolporate, except for some dicolporate grains of *M.umbellata*. Pollen sides were straight or convex or intermittently greatly convex. Colpal morphology was consistently parasyncolpate with angular colpi, except for *M. carminea* and *M. macropus* which had arcuate colpi. Pollen ambs were primarily round, or less often pointed, and colpal edges were smooth. The majority of observed apocolpial islands were closely fitting, although small irregular islands were observed on *M. salomonensis* grains. Pollen length ranged from 13 to 30.6 µm. Colpus/length ratio ranged from 26.8 to 42.8%.

Genus ***Tepualia***

Number of species: 1.

Distribution: Argentina and Chile.

Species examined: SEM – 1; LM – 1 (2 samples).

Previous pollen studies: Pike (1956); Zhou and Heusser (1996).

Images: SEM polar view – Fig. 1*j*; SEM exine pattern – Fig. 2*g*; LM polar view – Fig. 3*r*, *s*.

SEM: *Tepualia* pollen were dicolporate with a rugulate or verrucate exine. Pollen sides were convex and colpal morphology was dicolpate with the colpi fused together to give the appearance of one functional unit. Pollen ambs were round or pointed, colpal edges were smooth and the apocolpial field was psilate or scabrate. Pollen length ranged from 10.6 to 11.8 µm. The colpus/length ratio was 100%.

Table 3. Melaleuceae scanning electron microscopy sample measurements
See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Beaufortia orbifolia	Ob	Tri	Arc	DC	Sca, Gra/Sca	P	S, R	Psi, Sca	S	18.4 (19.2) 19.9	20.2 (21.5) 23.1	7.9 (9.2) 10.8	42.6 (47.9) 54.9
Melaleuca (Callistemon) polandii	Ob	Tri	Ang	Conc, Str	Rug	R	S	Psi	N, C	13.5 (14.7) 15.4	14.3 (15.3) 16.4	6.2 (7.3) 8.2	42.8 (49.8) 54.9
Melaleuca (Callistemon) viminalis	Ob	Tri	Ang	Conv, Str	Rug	R, P	S	Psi	S, C	15.3 (16.2) 16.9	14.7 (16.1) 17.9	5.1 (6.3) 7.6	31.3 (38.9) 44.9
Calothamnus macropus	Ob	Tri	Arc	Conc	Gra/Sca	N, P	S, R	Psi, Sca	N	13.5 (13.9) 14.1	14.3 (14.7) 15	7.3 (7.6) 7.8	52.7 (54.8) 57.7
Calothamnus quadrifidus	Ob	Tri	Ang	Str	Rug, Sca	R, P	R, S	N, Psi	S, N	12.8 (13.5) 14.1	13.4 (13.8) 14.5	6.2 (6.7) 7.3	45.7 (49.7) 54.1
Calothamnus validus	Ob	Tri	Syn	Conc	Sca, Rug	P	S	Psi	N	12.9 (13.2) 13.5	13.9 (14.4) 15	7.2 (7.6) 8.2	53.5 (58.1) 61.1
Lamarchea sulcata	Ob	Tri	Arc, Ang	Conc, Str	Sca	P, R	S, B, R	Sca, Psi	C, S, N	20 (22.2) 23.6	21.3 (23.1) 24.3	9.8 (10.3) 11	43.7 (46.8) 50.8
Melaleuca citrolens	Ob	Tri	Ang	Str, Conv	Rug	P, R	S, R	N	C	11.4 (12.6) 14.9	11.8 (12.5) 14.3	3.7 (4.3) 5	26.4 (34.2) 43.5
Melaleuca deanei	Ob	Tri	Ang	Str, Conc	Rug	R	S	N	C	15 (16.3) 18.3	14.5 (16.1) 18.1	5.6 (6.2) 6.5	35.6 (37.9) 40.4
Melaleuca nesophila	Ob	Tri	Ang	Str	Gra/Sca	R	R, B, S	N	C	11 (11.9) 12.7	11.1 (11.6) 12.2	3.8 (4.4) 4.7	32.4 (37.2) 42.9
Melaleuca steedmanii	Ob	Tri	Ang	Str	Rug	R, P, N	S	Psi	C	19 (19.6) 20	19.7 (20.1) 20.8	8.03 (8.4) 8.8	40.1 (43) 44.8
Melaleuca viridiflora	Ob	Tri	Ang	Str, Conc	Rug	R, P	S, R	N	C	16.3 (17.5) 18.8	16.8 (17.8) 19.6	5.9 (6.6) 7.6	33.2 (38) 46.3
Petraeomyrtus punicea	Ob	Tri	Arc	Conv	Ver	R, P	S	Psi, Sca	N	16.8 (18.8) 19.7	17 (18.7) 19.6	8.9 (9.3) 9.8	47.7 (49.8) 52.9
Phymatocarpus maxwellii	Ob	Tri	Syn	Conc	Gra/Sca	R, P	S, R	Psi	N	15.9 (16.4) 17.3	16.5 (17.1) 17.8	9.2 (9.5) 10.1	56.3 (57.9) 59.9
Regelia punicea	Ob	Tri	Syn	Conc	Ver	R, F	S	Psi, N	N	17.3 (19.3) 20.7	17.6 (19.8) 21.6	9.8 (11) 12.3	53.5 (56.9) 59.5

Table 4. Melaleuceae light microscopy sample measurements
See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Beaufortia anisandra[A]	Ob	Tri	Ang	Str	Psi	R	S	N	C	19.7 (22.9) 24.5	18.9 (22.4) 24.4	6.1 (8.1) 9.1	30.8 (35.2) 37.3
Beaufortia decussata[A]	Ob	Tri	Syn	Str	Sca	R	S	Psi	N	32.6 (33.8) 34.5	32.9 (34.1) 34.7	17.7 (18.4) 19.3	53 (54.4) 55.8
Beaufortia heterophylla[A]	Ob	Tri	Ang	Str	Psi	R	S	N	S	30	29.4	11.8	39.3
Beaufortia orbifolia	Ob	Tri	Ang, Arc	Str	Sca	R, P, F	S, R	Psi, N	C, S	17.9 (21.7) 27.2	18.3 (21.8) 27.5	8.8 (10.3) 12.8	42.4 (47.8) 52
Beaufortia squarrosa[A]	Ob	Tri	Arc	Conc, DC	Gra/Sca	P, N	S	Psi	N, S	22.1 (26.1) 28.5	26.4 (29.8) 32.2	14 (15.7) 17.1	56.1 (60.1) 63.2
Melaleuca citrina (*Callistemon citrinus*)	Ob	Tri, Tet	Ang	Conv	Sca	R	R	N	C	14.6 (15.6) 16.8	14.8 (15.6) 16.6	5.4 (5.6) 6.1	35.3 (36.1) 36.9
Melaleuca citrina (*Callistemon lanceolatus*)[A]	Ob	Tri	Ang	Str	Psi	R, P	S, R	N	C	18.2 (19.4) 20.6	17.9 (19) 20.1	5.3 (5.8) 6.7	27.7 (29.7) 34.1
Melaleuca (*Callistemon*) *polandii*	Ob	Tri	Ang	Str, Conv	Sca, Psi	R, P	S, R	Psi	C	12.6 (14.8) 16.8	13.2 (14.5) 15.7	5.4 (6) 7	32.1 (41.4) 49
Melaleuca paludicola (*Callistemon sieberi*)	Ob	Tri	Ang	Str	Sca	P, N	R, S	N., Psi	C, N	10.7 (11.9) 12.8	10.9 (12.1) 12.7	2.9 (3.7) 4.2	26.7 (31.1) 34
Melaleuca virens (*Callistemon viridiflorus*)[A]	Ob	Tri	Ang, Arc	Conc, Str, Conc	Psi	P, R, N	R, S	Psi	S, N	15 (17.4) 19.8	16.7 (18.3) 19.6	6.4 (7.3) 8	32.3 (43) 51.6
Calothamnus chrysantherus[A]	Ob	Tri	Syn	Str, Conc	Psi	R, P	S	N	N	21.2 (22.1) 22.9	21.3 (22.4) 23.5	12.4 (12.6) 12.9	56.2 (57.3) 58.3
Calothamnus sanguineus[A]	Ob	Tri	Syn	Str, Conv	Sca/Psi, Psi	P	S	Psi, N	N	18.5 (19.7) 20.8	17.6 (18.7) 19.6	9.5 (10.1) 10.8	49.6 (51.2) 5
Calothamnus torulosus[A]	Ob	Tri	Arc, Syn	Str	Psi	R	S	Psi	N	16.5 (17.1) 17.5	15 (15.9) 16.4	6.9 (7.9) 8.7	41.4 (46.3) 51.2
Calothamnus validus	Ob	Tri	Arc	Conc, DC	Sca	N, R	S	Psi	N	10.8 (13.2) 16.7	12.1 (14.4) 17	6.1 (7.2) 8.9	53.2 (54.6) 56.2
Conothamnus trinervis[A]	Ob	Tri	Arc	Str	Gra/Sca	R, F	S	Psi	N	24.3 (25.6) 28	22.8 (24.2) 27	12.2 (12.7) 14.1	47.2 (49.8) 52.1
Eremaea acutifolia	Ob	Tri	Syn	Conv	Sca, Psi	R	S	Psi	N	24.3 (25) 26.4	22.3 (23.8) 25.9	11.3 (12.5) 14	46.4 (49.8) 53.2
Eremaea beaufortioides	Ob	Tri	Syn	Str, Conv	Sca, Psi	R, P	S	Psi	N	21.2 (22.4) 23.4	20.5 (22) 23.6	11.1 (11.9) 13	51.6 (53.1) 55.4
Eremaea ebracteata	Ob	Tri	Syn	Conv	Psi	R	S	Psi	N	23.5 (25) 25.6	22.4 (24.3) 25.6	12.1 (13) 13.7	50.1 (51.7) 53.6
Eremaea fimbriata	Ob	Tri	Syn	Conv	Sca	R	S, R	Psi	N	26.1 (27.1) 27.7	25.1 (25.9) 26.7	13.7 (14.1) 14.5	51.3 (52.3) 53.2
Eremaea pilosa (*pauciflora*)	Ob	Tri	Syn	Str, Conv	Sca	R, R/F	S	Psi	N	20.8 (22.8) 23.8	19.9 (22) 23.1	10.6 (11.8) 12.6	50.9 (51.7) 53.1
Lamarchea hakeifolia[A]	Ob	Tri	Ang	Str	Psi, Sca	R	S	Psi	C	29.2 (30.6) 31.4	28.9 (30.2) 30.8	9.2 (10.5) 11.1	31.6 (34.3) 36.2
Melaleuca adnata var. aspera[A]	Ob	Tri	Arc	Str	Psi	R	S	Psi	N	14.5 (15) 15.8	13.4 (14.2) 15.1	2.7 (6.6) 7.8	18.3 (44.1) 50.3
Melaleuca argentea	Ob	Tri	Ang	Str	Psi	R, P, N	S	N	C	14.6 (16.6) 18.8	15.2 (17.2) 19.1	7.27 (7.9) 8.9	43.3 (47.4) 52.9
Melaleuca ericifolia[A]	Ob	Tri	Arc	Str, Conv	Psi, Sca	R	S	Psi	N	16.2 (16.9) 18.1	15.7 (16.4) 17.3	7 (8) 8.9	41.4 (47.3) 54.7
Melaleuca erubescens[A]	Ob	Tri	Syn	Str	Psi	R	S	Psi	N	15.2 (17.5) 19.3	14.3 (16.6) 18.1	7.2 (8.9) 10	46.6 (50.8) 53.7
Melaleuca leucadendra[A]	Ob	Tri	Ang	Str	Psi, Sca	R, P, F	S	N	C	14.1 (14.7) 15.6	14.6 (14.9) 15.9	5.9 (6.4) 6.8	40.9 (43.3) 45.9
Melaleuca nesophila	Ob	Tri	Ang	Conv	Sca	R, P	N	N	C	13.3 (14.6) 16.5	12.3 (13.8) 15.5	5.3 (6.1) 6.7	39.7 (41.6) 43.6
Melaleuca pauciflora[A]	Ob	Tri	Syn	Str	Sca	R	S	Psi	N	16.7 (20.5) 24.8	17.2 (20.3) 24.5	8.6 (10.8) 13.2	51.6 (52.7) 53.5
Melaleuca pubescens[A]	Ob	Tri	Syn	Str	Sca	R, P	S	Psi	N	15 (15.9) 17.2	14.9 (15.7) 17.2	8.1 (8.6) 9.8	52.9 (54.4) 56.8
Melaleuca quinquenervia[A]	Ob	Tri	Ang	Conv	Sca	R	S	N	C	16.6 (17.9) 19.1	16.1 (16.9) 17.6	7.9 (7.9) 8	41.3 (44.6) 47.9
Melaleuca radula[A]	Ob	Tri	Arc	Str	Psi	R	S	Psi	N	24.9 (27.4) 29.5	24 (26.5) 28.1	10.8 (12.8) 14.6	40.1 (46.7) 52.6
Melaleuca squamea[A]	Ob	Tri	Arc	Str	Sca	R	S	Psi	N	25 (26.9) 28.1	25.8 (27.2) 28.7	12.7 (14.2) 15.7	50.6 (52.7) 56.3
Melaleuca squarrosa[A]	Ob	Tri	Arc, Ang	Conv	Gra/Sca	R, P	S, R	N	C, N	20.2 (21.8) 24.6	19.3 (21) 24.2	9.1 (10.1) 11	43.5 (46.5) 51.2
Melaleuca steedmanii	Ob	Tri	Ang	Conv	Gra/Sca, Psi	R	R	N, Psi	C	21.7 (22.7) 23.5	20.3 (21.2) 21.6	8.1 (8.7) 9.8	34.2 (38.5) 42.8
Melaleuca viridiflora	Ob	Tri	Arc, Ang	GC, Conv	Gra/Sca	R	S, R	N, Psi	C	17.8 (19.1) 20	17.4 (17.8) 18.2	6.5 (7.3) 8.1	36.1 (38.3) 41.1
Phymatocarpus porphyrocephalus[A]	Ob	Tri	Syn	Str	Sca	P, R	S	Psi	N	20.3 (23.8) 25.6	19.3 (22.8) 24.5	11.1 (13) 14.4	52.2 (54.6) 56.8
Regelia ciliata[A]	Ob	Tri	Ang	Str, Conc	Psi	R	S	Psi	N	26.1 (28) 29.1	26.3 (28.4) 29.5	8.5 (9.6) 10.9	29.2 (34.5) 39
Regelia grandiflora (*velutina*)[A]	Ob	Tri	Ang	Str	Psi, Sca	R	S	Psi	N	33.7 (39.4) 46.7	33.7 (39.5) 47	11.6 (15.3) 18.8	34.3 (38.7) 40.3
Regelia inops[A]	Ob	Tri	Arc/Syn	Str	Sca	R	S	Psi	N	28.3 (32.9) 36.9	29.2 (33.8) 38.5	16.1 (18.3) 20.7	53.6 (55.5) 56.9

[A]Slide from Pike collection.

LM: the exine of *Tepualia* was psilate. Pollen sides were convex and colpal morphology was dicolpate. Pollen ambs were round, colpi edges were smooth, and the apocolpial field was psilate. Pollen length ranged from 11.8 to 12.5 µm. The colpus/length ratio was 100%.

Tribe Melaleuceae

Representatives of Melaleuceae are predominantly found in Australia, but also occur in Malesia, Lord Howe Island and New Caledonia. There were nine genera recognised in tribe Melaleuceae; however, recent phylogenetic work has shown that all genera are nested within *Melaleuca*, which now encompasses ~380 species (Edwards *et al*. 2010). Melaleuceae taxa occur in many vegetation types, especially heathlands, woodlands and swamp. For ease of cross referencing to past palynology studies, we have retained the former generic names in the present paper. Pollen measurements for Melaleuceae are summarised in Tables 3 and 4.

Genus ***Beaufortia***

Number of species: 21.

Distribution: south-western Australia.

Species examined: SEM – 1; LM – 5.

Previous pollen studies: Pike (1956).

Images: SEM polar view – Fig. 4*a*; SEM exine pattern – Fig. 5*a*; SEM equatorial view – Fig. 7*a*; LM polar view – Fig. 8*a–f*.

SEM: *Beaufortia* pollen were tricolporate with a scabrate to granulate/scabrate exine. Pollen sides were deeply concave and the colpal morphology was parasyncolpate with arcuate colpi. Small irregular islands occurred on every grain. Pollen ambs were pointed, colpal edges were smooth or rough and the apocolpial field was psilate or scabrate. Pollen length ranged from 18.4 to 19.9 µm. Colpus/length percentage ranged from 42.6% to 54.9%.

LM: exine patterns of *Beaufortia* were either psilate, scabrate or granulate/scabrate. Most observed grains had straight sides, except for *B. squarrosa* which had either concave or deeply concave sides. Colpal morphology was predominantly parasyncolpate with angular colpi, but *B. squarrosa* had arcuate colpi, and *B. decussata* had syncolpate pollen. Pollen ambs were round, or less often pointed, flat or notched. Colpal edges were smooth and the apocolpial field was psilate, or not visible because of a closely fitting apocolpial island. Apocolpial islands were present on the pollen of all species except for *B. decussata*. Pollen length ranged from 17.9 to 34.5 µm. Colpus/length ratio ranged from 30.8% to 63.2%.

Genus ***Callistemon***

Number of species: 39.

Distribution: Australia.

Species examined: SEM – 2; LM – 5.

Previous pollen studies: Pike (1956); Patel *et al*. (1984); Boyd (1992).

Images: SEM polar view – Fig. 4*b*, *c*; SEM exine pattern – Fig. 5*b*; LM polar view – Fig. 8*g–l*.

SEM: *Callistemon* grains were tricolporate with a rugulate exine. Pollen sides were concave, convex or straight and colpal morphology was parasyncolpate with angular colpi. Pollen ambs were round or pointed, colpal edges were smooth and the apocolpial field was psilate. Some pollen lacked an apocolpial island but the majority of grains possessed a closely fitting or sometimes small irregular polar island. Pollen length ranged from 13.5 to 16.9 µm. Colpus/length ratio ranged from 31.3% to 54.9%.

LM: the exine of *Callistemon* was scabrate or psilate. Pollen sides were straight or convex or occasionally concave. Some pollen of *C. citrinus* was tetracolporate. Colpal morphology was parasyncolpate with angular colpi, except for some grains of *C.viridiflorus* which had arcuate colpi. Pollen ambs were round, pointed or sometimes notched, colpal edges were smooth or rough, and the apocolpial field was either psilate or not visible because of an apocolpial island. All examined slides had pollen with closely fitting apocolpial islands, except for *C.viridiflorus* which had small irregular islands. Pollen length ranged from 10.7 to 20.6 µm. Colpus/length ratio ranged from 26.7% to 51.6%.

Genus ***Calothamnus***

Number of species: 40.

Distribution: south-western Australia.

Species examined: SEM – 3; LM – 4.

Previous pollen studies: Pike (1956); Patel *et al*. (1984).

Images: SEM polar view – Fig. 4*d–f*; SEM exine pattern – Fig. 5*c*, *d*; SEM equatorial view – Fig. 7*b*; LM polar view – Fig. 8*m–p*.

SEM: *Calothamnus* pollen were tricolporate with a rugulate or scabrate exine. Pollen sides were concave or straight and colpal morphology was parasyncolpate with arcuate or angular colpi or syncolpate. Pollen ambs were pointed, round or notched, colpus edges were smooth or round and the apocolpial field pattern was psilate or scabrate. Most pollen grains lacked an apocolpial island, except for those of *C.quadrifidus* which had small irregular islands. Pollen length ranged from 12.8 to 14.1 µm. Colpus/length ratio ranged from 45.7% to 61.1%.

LM: exine patterns of *Calothamnus* were psilate or scabrate. Pollen sides were straight or sometimes convex or concave. Colpal morphology was mainly syncolpate or occasionally parasyncolpate with arcuate colpi. Pollen ambs were round or pointed, colpal edges were smooth and the apocolpial field was psilate. Pollen length ranged from 10.8 to 22.9 µm. Colpus/length ratio ranged from 41.4 to 58.3%.

Genus ***Conothamnus***

Number of species: 3.

Distribution: south-western Australia.

Species examined: SEM – not observed; LM – 1.

Previous pollen studies: Pike (1956).

Images: LM polar view – Fig. 8*q*.

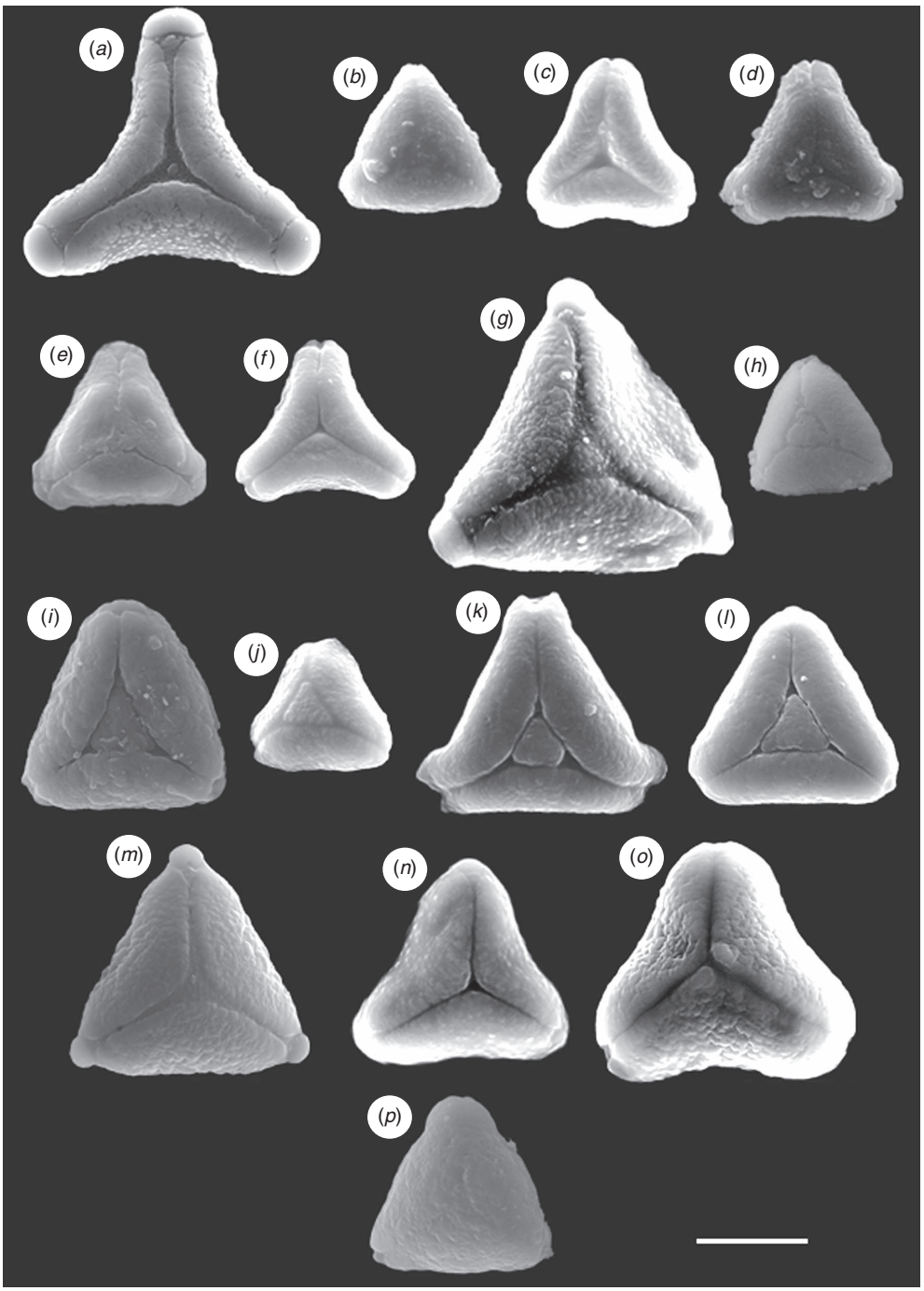

Fig. 4. Polar view of Melaleuceae and Osbornieae under scanning electron microscope. Scale bar = 10 µm. (*a*) *Beaufortia orbifolia*, (*b*) *Melaleuca* (*Callistemon*) *polandii*, (*c*) *M.* (*Callistemon*) *viminalis*, (*d*) *Calothamnus macrocarpus*, (*e*) *C. quadrifidus*, (*f*) *C. validus*, (*g*) *Lamarchea sulcata*, (*h*) *Melaleuca citrolens*, (*i*) *M. deanei*, (*j*) *M. nesophila*, (*k*) *M. steedmanii*, (*l*) *M. viridiflora*, (*m*) *Petraeomyrtus punicea*, (*n*) *Phymatocarpus maxwellii*, (*o*) *Petraeomyrtus* (*Regelia*) *punicea* and (*p*) *Osbornia octodonta*.

LM: *Conothamnus* pollen were tricolporate with a granulate/scabrate exine. Pollen sides were straight and colpal morphology was parasyncolpate with arcuate colpi. Pollen ambs were notched or round, colpus edges were smooth and the apocolpial field was psilate. Pollen length ranged from 24.3 to 28 µm. Colpus/length ratio ranged from 47.2 to 52.1%.

Genus ***Eremaea***

Number of species: 15.

Distribution: south-western Australia.

Species examined: SEM – not observed; LM – 5.

Previous pollen studies: Pike (1956); Patel *et al*. (1984).

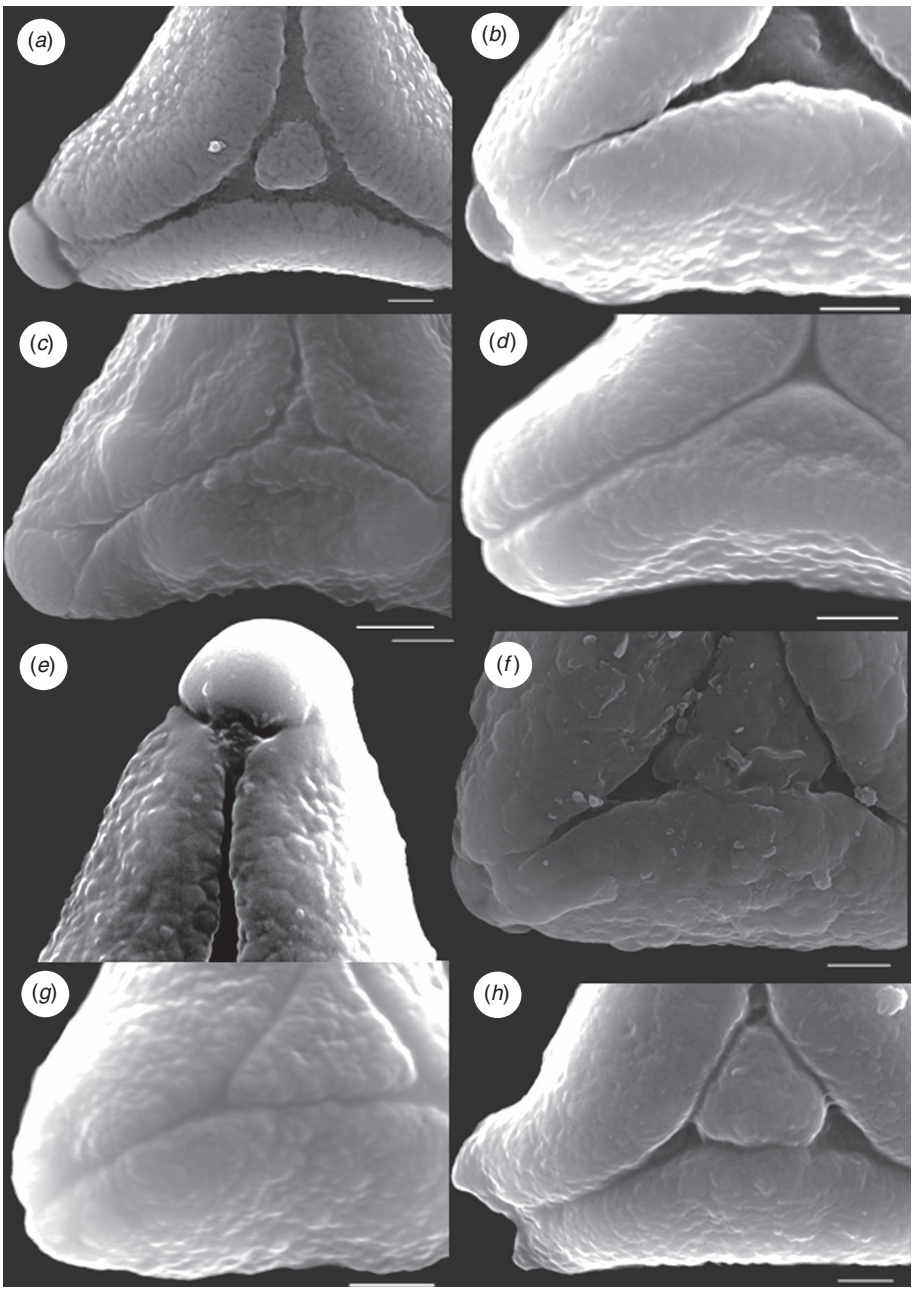

Fig. 5. Exine pattern of Melaleuceae under scanning electron microscope. Scale bar = 2 µm. (*a*) *Beaufortia orbifolia*, (*b*) *Melaleuca* (*Callistemon*) *polandii*, (*c*) *Calothamnus quadrifidus*, (*d*) *C. validus*, (*e*) *Lamarchea sulcata*, (*f*) *Melaleuca deanei*, (*g*) *M. nesophila* and (*h*) *M. steedmanii*.

Images: LM polar view – Fig. 8*r*–*w*.

LM: *Eremaea* pollen were tricolporate with a scabrate or psilate exine. Pollen sides were convex or straight and the colpal morphology was syncolpate. Pollen ambs were round or less often pointed or flat, colpal edges were smooth and the apocolpial field was psilate. Pollen length ranged from 20.8 to 27.7 µm. Colpus/length ratio ranged from 46.4 to 55.4%.

Genus ***Lamarchea***

Number of species: 2.

Distribution: south-western Australia.

Species examined: SEM – 1; LM – 1.

Previous pollen studies: Pike (1956); Boyd (1992).

Images: SEM polar view – Fig. 4*g*; SEM exine pattern – Fig. 5*e*; LM polar view – Fig. 8*x*.

SEM: *Lamarchea* pollen were tricolporate with a verrucate/scabrate exine. Pollen sides were concave or straight and colpal morphology was parasyncolpate with arcuate or angular colpi. Pollen ambs were pointed or round, colpal edges were smooth, broken or rough and the apocolpial field was scabrate or

psilate. Closely fitting or small irregular islands were noted, but some *Lamarchea* grains did not have an island. Pollen length ranged from 20 to 26.6 µm. Colpus/length ratio ranged from 43.7 to 50.8%.

LM: exine patterns of *Lamarchea* were psilate or scabrate. Pollen sides were straight and the colpal morphology was parasyncolpate with angular colpi. Pollen ambs were round, colpal edges were smooth and the apocolpial field was psilate.

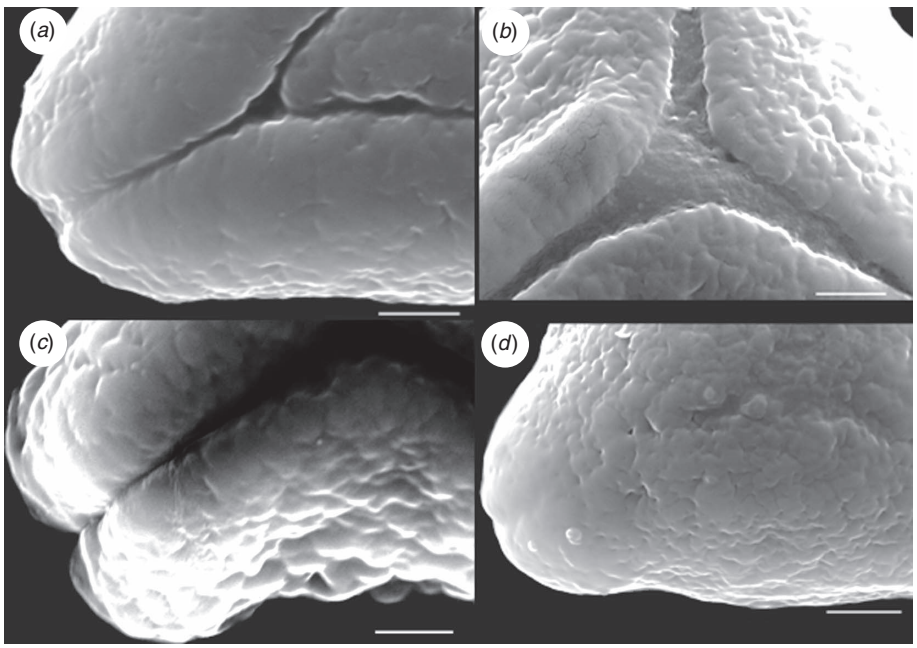

Fig. 6. Exine pattern of Melaleuceae and Osbornieae under scanning electron microscope. Scale bar = 2 µm. (*a*) *Melaleuca viridiflora*, (*b*) *Petraeomyrtus punicea*, (*c*) *P*. (*Regelia*) *punicea* and (*d*) *Osbornia octodonta*.

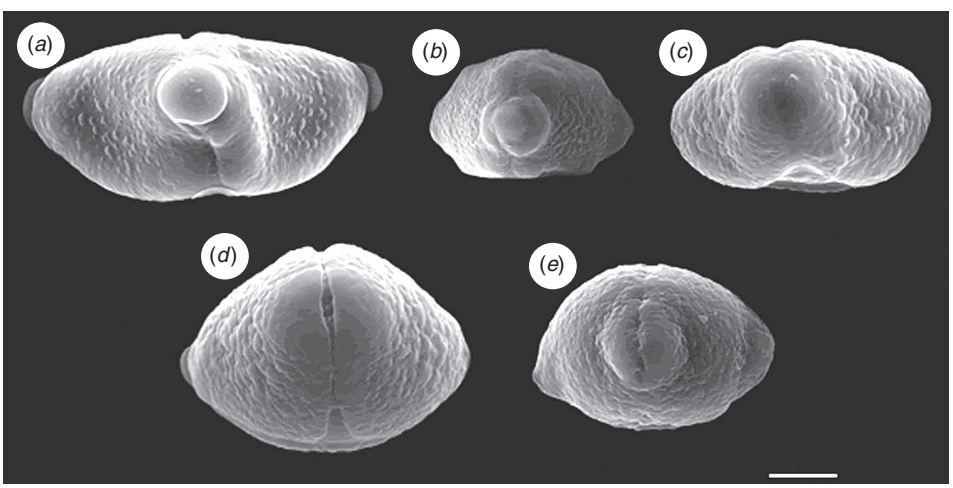

Fig. 7. Equatorial view of Melaleuceae and Osbornieae under scanning electron microscope. Scale bar = 5 µm. (*a*) *Beaufortia orbifolia*, (*b*) *Calothamnus quadrifidus*, (*c*) *Melaleuca viridiflora*, (*d*) *Petraeomyrtus punicea* and (*e*) *Osbornia octodonta*.

Fig. 8. Polar view of Melaleuceae as viewed under light microscope. Scale bar = 10 µm. (*a*) *Beaufortia anisandra**, (*b*) *B. decussata**, (*c*) *B. heterophylla**, (*d*) *B. orbifolia*, (*e*) *B. squarrosa**, (*f*) *B. squarrosa**, (*g*) *Melaleuca citrina* (*Callistemon citrinus*), (*h*) *M. citrina* (*Callistemon citrinus*), (*i*) *M. citrina* (*Callistemon lanceolatus*), (*j*) *M.* (*Callistemon*) *polandii*, (*k*) *M. paludicola* (*Callistemon sieberi*), (*l*) *M. virens* (*Callistemon viridiflorus*)*, (*m*) *Calothamnus chrysantherus**, (*n*) *C. sanguineus**, (*o*) *C. torulosus**, (*p*) *C. validus*, (*q*) *Conothamnus trinervis**, (*r*) *Eremaea acutifolia*, (*s*) *E. beaufortioides*, (*t*) *E. beaufortioides*, (*u*) *E. ebracteata*, (*v*) *Eremaea fimbriata*, (*w*) *E. pilosa*, (*x*) *Lamarchea hakeifolia**, (*y*) *Melaleuca adnata var. aspera**, (*z*) *M. argentea*, (*aa*) *M. ericifolia**, (*bb*) *M. erubescens**, (*cc*) *M. leucadendra**, (*dd*) *M. nesophila*, (*ee*) *M. pauciflora**, (*ff*) *M. pubescens** and (*gg*) *M. quinquenervia**. Slides indicated with asterisk are from Pike collection.


(a)
(b)
(c)
(d)
(e)
(f)
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Table 5. Metrosidereae scanning electron microscopy sample measurements
See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Mearnsia cordata	Ob	Tri	Ang	Conv	Psi, Rug	R, F	R	Psi, Sca	C	12.6 (13.2) 13.7	11.4 (12) 12.4	3.8 (4) 4.3	27.4 (29.8) 32
Metrosideros carminea	Ob	Tri	Ang	Conc	Rug, Ver, Sca	R	S, R	Psi, Sca, N	S, C	12.5 (12.9) 13.4	12.5 (13.1) 13.8	4.6 (5.5) 6.2	37.1 (42.3) 46.5
Metrosideros diffusa	Ob	Tri	Ang	Str, Conv	Rug	P, R	R, S	N	C	11.1 (11.9) 12.5	11.2 (11.7) 12.1	3.1 (3.7) 4.2	27.3 (31.3) 35
Metrosideros macropus	Ob	Tri	Ang	Conv	Verm, Rug	R	S	Psi, N	C, S	16.2 (17.1) 17.6	15.7 (16.9) 17.6	6.7 (7.2) 7.9	40 (41.9) 45.1
Metrosideros nervulosa	Ob	Tri	Ang	Conc, Str, Conv	Rug	R, F	S, B	Psi, Sca	S	17.2 (19.4) 20.9	17.1 (18.9) 20.3	7.3 (8.2) 9	39.3 (42.1) 44.8
Metrosideros nitida	Ob	Tri	Ang	Conv	Rug	R/F	S	Sca, Psi	C	15.3 (16.1) 17.4	14.2 (14.9) 15.9	5.7 (6) 6.8	36.7 (37.4) 38.9
Tepualia stipularis	Pro	Di	Di	Conv	Rug, Ver	R, P	S	Psi, Sca	N	10.6 (10.9) 11.8	17.2 (18.4) 19.7	17.2 (18.4) 19.7	100

Table 6. Metrosidereae light microscopy sample measurements
See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Mearnsia ramiflora[A]	Ob	Tri	Ang	Conv	Psi	R	S	N	C	19.2 (20.1) 21.6	18.2 (19) 20.3	6.2 (6.7) 7.3	31.3 (33.3) 35.4
Metrosideros carminea	Ob	Tri	Arc	Conc	Psi	R	S	N	S	13 (14) 15.4	13 (14.2) 16.1	6.1 (6.6) 7.3	46.5 (47.1) 47.5
Metrosideros collina	Ob	Tri	Ang	Str	Psi	R	S	Psi, N	S	14.6 (15.3) 15.9	13.8 (14.9) 15.6	4.1 (4.8) 5.3	26.8 (31.1) 34.2
Metrosideros diffusa	Ob	Tri	Ang	Conv, GC	Sca	R	S	N	C	18.9 (19.2) 19.6	17.5 (17.9) 18.3	5.4 (6.7) 7.6	28.5 (34.9) 39.3
Metrosideros excelsa[A]	Ob	Tri	Ang	Conv	Psi	R	S	N	C	22.5 (25.7) 30.6	20.1 (23.4) 28	8.5 (10) 12.1	37.1 (39) 42.8
Metrosideros macropus	Ob	Tri	Arc	Str, Conv	Psi, Sca	P, R	S	N	N, C	18.4 (19.9) 21.2	17.1 (19.4) 20.7	5.7 (7.1) 7.9	31 (35.4) 38.8
Metrosideros nervulosa	Ob	Tri	Ang	Str	Psi	R	S	Psi	C	21.2 (22) 22.8	21.2 (21.7) 22.5	7.2 (8.2) 8.7	32.7 (37.1) 40.9
Metrosideros perforata[A]	Ob	Tri	Ang	Str, Conv	Psi	R, P	S	N	C	17.1 (18.7) 19.8	16.4 (18.1) 19.4	6.2 (6.9) 8.1	33.5 (36.8) 42.1
Metrosideros salomonensis[A]	Ob	Tri	Ang	Str	Psi	R	S	Psi	S	17.9 (19.7) 20.8	16.8 (18.8) 19.4	6.5 (7.5) 8.3	35.5 (38.1) 42
Metrosideros perforata (*scandens*)[A]	Ob	Tri	Ang	Conv	Psi	R	S	N	C	15.8 (16.9) 18	14.8 (15.9) 17.3	4.7 (5.9) 6.7	29.6 (34.7) 38.7
Metrosideros umbellata[A]	Ob, Pro	Tri, Di	Ang	Conv	Psi	R	S	N	C	18.8 (20.2) 22.2	17.2 (18.9) 20.5	6.2 (7.1) 8.8	32.8 (35.1) 39.4
Tepualia stipularis	Pro	Di	Di	Conv	Psi	R	S	Psi	N	11.8 (12.1) 12.5	18.5 (19.9) 21.2	0	100
Tepualia stipularis[A]	Pro	Di	Di	Conv	Psi	R	S	Psi	N	11.8 (11.9) 12.1	20.2 (20.4) 20.7	0	100

[A]Slide from Pike collection.

Table 7. Osbornieae scanning electron microscopy sample measurements
See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Osbornia octodonta	Ob	Tri, Tet	Ang	Str	Rug	R, P	R, S	Sca	N	14.6 (15.2) 16	14.8 (15.4) 16.5	6 (7.9) 9.5	40.9 (51.9) 59.2

Table 8. Osbornieae light microscopy sample measurements
See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Osbornia octodonta	Ob	Tri	Syn	Conv	Psi	P	S, R	N	N, S	16.6 (17.3) 18.2	16 (16.8) 18.2	7.6 (8.2) 8.8	44.6 (47.1) 48.5
Osbornia octodonta[A]	Ob	Tri	Ang	Str	Psi	R	S	Psi	N	20.1 (22.7) 24.6	19.5 (21.8) 23.7	8.1 (9.3) 11.7	35.7 (40.9) 47.5

[A]Slide from Pike collection.

Closely fitting apocolpial islands were observed on all grains. Pollen length ranged from 30 to 31.4 µm. Colpus/length ratio ranged from 31.6 to 36.2%.

Genus ***Melaleuca***

Number of species: 251.

Distribution: Australia, Malesia, and New Caledonia.

Species examined: SEM – 5; LM – 14.

Previous pollen studies: Pike (1956); Martin (1973); Patel *et al.* (1984); Boyd (1992); Chalson and Martin (1995).

Images: SEM polar view – Fig. 4*h*–*l*; SEM exine pattern – Figs 5*f*–*h*, 6*a*; SEM equatorial view – Fig. 7*c*; LM polar view – Figs 8*y*–*gg*, 9*a*–*f*.

SEM: *Melaleuca* pollen were tricolporate with a rugulate exine, except for *M. nesophila* grains that had a granulate/scabrate exine. Pollen sides were straight, or less commonly convex or concave, and the colpal morphology was consistently parasyncolpate with angular colpi. Pollen ambs were round or pointed, or less commonly notched, colpal edges were smooth or occasionally rough and the apocolpial field was not visible or psilate. Closely fitting apocolpial islands were present for pollen of all observed *Melaleuca* species. Pollen length ranged from 11 to 20 µm. Colpus/length ratio ranged from 26.4% to 46.3%.

LM: exine patterns of *Melaleuca* were scabrate, psilate or, less often, granulate/scabrate. Pollen sides were straight or convex, and the colpal morphology was parasyncolpate with angular or arcuate colpi, or occasionally syncolpate. Pollen ambs were round or less commonly pointed or flat. Colpal edges were smooth or rough and the apocolpial field was psilate. Pollen length ranged from 13.3 to 29.5 µm. Colpus/length ratio ranged from 34.2 to 56.8%.

Genus ***Petraeomyrtus***

Number of species: 1.

Distribution: northern Australia.

Species examined: SEM – 1; LM – not observed.

Previous pollen studies: none.

Images: SEM polar view – Fig. 4*m*; SEM exine pattern – Fig. 6*b*; SEM equatorial view – Fig. 7*d*.

SEM: *Petraeomyrtus* pollen were tricolporate with a verrucate exine. Pollen sides were convex and colpal morphology was parasyncolpate with arcuate colpi. Pollen ambs were round or pointed, colpal edges were smooth and the apocolpial field was psilate or scabrate. Pollen length ranged from 16.8 to 19.7 µm. Colpus/length ratio ranged from 47.7 to 52.9%.

Genus ***Phymatocarpus***

Number of species: 3.

Distribution: south-western Australia.

Species examined: SEM – 1; LM – 1.

Previous pollen studies: Pike (1956).

Images: SEM polar view – Fig. 4*n*; LM polar view – Fig. 9*g*.

SEM: *Phymatocarpus* pollen were tricolporate with a granulate/scabrate exine. Pollen sides were concave and colpal morphology was syncolpate. Pollen ambs were round or pointed, colpal edges

Table 9. Syzygieae scanning electron microscopy sample measurements
See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Syzygium divaricatum (*Acmena divaricata*)	Pro	Di	Di	Conv	Psi, Rug	R	S, R	Psi	N	15.2 (15.8) 16.8	14.8 (15.8) 16.6	0	100
Syzygium (*Acmena*) *graveolens*	Pro	Di	Di	Conv	Psi	R	S	Psi	N	15.3 (15.4) 15.5	16.1 (16.9) 17.7	0	100
Syzygium mackinnonianum (*Acmena mackinnoniana*)	Pro	Di	Di	Conv	Psi, Rug	R	S, R	Psi	N	15 (15.7) 16.4	16.3 (17.1) 18.4	0	100
Syzygium (*Acmena*) *smithii*	Pro, Ob	Di, Tri	Di, Ang, Arc	GC	Psi, Psi, Rug	R, P	S, R	Psi	N	13.3 (14.7) 18.3	14.1 (16.6) 18.6	0 (3.8) 7.4	32.9 (98.5) 100
Syzygium anisatum (*Anetholea anisata*)	Ob	Tri	Arc	Conv, Str	Gra	R, P	S	Sca, Psi	S	11.7 (12.1) 12.7	11.2 (11.7) 12.1	6.5 (6.6) 7	54.1 (55.2) 56.5
Syzygium sp. (*Piliocalyx boudoninii*)	Ob	Tri, Tet	Arc	Str, Conc	Psi, Rug	R	S	Psi, Sca	N	19.2 (20.3) 21.5	18.6 (19.5) 21	8.4 (9) 9.7	43.9 (44.6) 45.7
Syzygium aromaticum	Ob	Tri	Ang	Conv	Ver, Ver, Sca	R	R, B	N	C	15 (16.7) 18.4	14.6 (16) 17.5	4.5 (4.8) 5.1	24.2 (29) 33.7
Syzygium australe	Ob	Tri	Arc	DC	Psi, Rug	R	S	Psi, Sca	N	11.5 (12.1) 12.7	12.6 (13.2) 13.9	6.3 (6.7) 7.1	52.5 (55.1) 57.6
Syzygium claviflorum	Ob	Tri	Ang	Str, Conc	Sca, Ver	R, P	S, R, B	Psi, N	C	13.4 (14.1) 14.7	13.6 (14.3) 14.9	4.5 (5.3) 6.1	32.7 (37.4) 41.5
Syzygium cumini	Ob	Tri	Ang	Conc, Str	Psi, Rug, Rug	R	S	Psi	N	11.3 (11.9) 13.1	11.5 (12) 13.3	4.1 (4.9) 5.6	35.2 (41.7) 46.7
Syzygium eucalyptoides	Ob	Tri	Arc	Str, Conc	Psi, Sca	R, P	S	Psi, N	C	11.3 (11.6) 12.4	11.5 (11.9) 12.9	3.6 (4.6) 5.7	31.1 (40) 45.7
Syzygium samarangense	Ob	Tri	Arc, Syn	GC	Psi, Rug	R	B, S	Sca	N	11.8 (12.1) 12.5	10.5 (10.9) 11.3	4.3 (5.1) 5.8	35.9 (42) 48.3
Syzygium wilsonii	Ob	Tri	Ang	Str, Conc	Rug, Sca	R, P	S	N	C	12.1 (13.8) 14.9	13 (14) 14.7	5.1 (5.7) 6.1	35.7 (41) 45
Syzygium floribundum (*Waterhousea floribunda*)	Ob	Tri	Arc	Str	Ver, Sca, Rug	R, P	R, S	Psi, Sca	S, G	11.4 (11.8) 12.2	11.4 (12) 12.6	4.6 (5) 5.3	39.5 (42.2) 45.3
Syzygium hedraiophyllum (*Waterhousea hedraiophylla*)	Ob	Tri	Arc	Str, Conv	Rug	R, P	R, S	Sca, Psi	N	11.5 (11.8) 12.2	11.5 (11.8) 12.2	5.4 (5.7) 6.2	46.9 (48.8) 51.4

Table 10. Syzygieae light microscopy sample measurements

See Table 1 for explanation of abbreviations and length and width data

Species	Pollen shape	Pore no.	Colpal morph.	Shape of side	Exine	Amb shape	Colpal edge	Apocolpial field	Island type	Length (µm)	Width (µm)	Colpus length (µm)	Colpus/length (%)
Syzygium acuminatissimum (*Acmena acuminatissima*)[A]	Pro, Ob	Di, Tri	Arc, Di	GC	Psi, Sca	R	S	Psi	N	18.4 (19.5) 23.8	19 (20.2) 20.9	0 (8.1) 11.1	0 (35.4) 46.8
Syzygium piluliferum (*Acmena caudata*)[A]	Ob	Tri	Arc	GC	Psi, Sca	R	S	Psi	N	18.3 (19.7) 21.6	16.1 (17) 18.3	7.4 (8.6) 9.6	39.5 (44) 47.2
Syzygium divaricatum (*Acmena divaricata*)[A]	Pro	Di	Di	GC	Psi, Sca	R, P	S	Psi	N	15.4 (16.6) 17.5	16.1 (18.4) 21.2	0 (1.2) 8	100
Syzygium (*Acmena*) *graveolens*	Pro	Di	Di	Conv	Psi	R, P	S	Psi	N	12.6 (13.3) 14.4	15.8 (17.7) 21.7	0	100
Syzygium hemilamprum (*Acmena hemilampra*)[A]	Ob	Tri	Arc	GC, Conv	Psi	R	S	Psi	N	17.2 (18.3) 19.2	15.6 (16.4) 17	6.9 (8.1) 9.1	40.2 (44.4) 48
Syzygium acuminatissimum (*Acmena laevifolia*)[A]	Ob, Pro	Di, Tri	Arc, Di	GC, Conv	Psi, Gra/Sca	R	S	Psi	N	15 (16) 16.8	13.1 (15.6) 16.2	0 (4.6) 8.1	100
Syzygium graveolens (*Acmena macrocarpa*)[A]	Pro	Di	Di	GC, Conv	Psi	R, P	S	Psi	N	19 (20) 20.5	23.1 (23.8) 25.4	0	100
Syzygium (*Acmena*) *smithii*	Pro, Ob	Di, Tri	Arc, Di	GC	Psi	R	S	Psi	N	14 (15.7) 18	14.2 (15.2) 16	0 (5.2) 8.1	0 (30.5) 46.3
Syzygium (*Acmena*) *smithii*[A]	Ob, Pro	Tri, Di	Arc, Di	GC, Conv	Psi	R	S, R	Psi	N	18.3 (20.1) 21.6	16.2 (18.1) 19.4	6.9 (8.3) 9.9	36.5 (40.9) 46
Syzygium anisatum (*Anetholea anisata*)	Ob	Tri, Tet	Arc	Conv	Psi	R	S	Psi	N	12 (13.4) 14.5	11.4 (12.3) 13.1	4.5 (5.5) 6.3	37.7 (41.1) 44.1
Syzygium arcuatinervium Cleistocalyx arcuatinervius[A]	Ob	Tri	Inv, Ang	Str	Psi	R, F	R, S	Psi	S	13.1 (14.1) 15.5	12.3 (12.9) 13.8	4.4 (4.7) 5	29.9 (33.3) 38.1
Syzygium seemannii (*Cleistocalyx ellipticus*)[A]	Ob, Pro	Tri, Di	Ang	Str	Psi	R	S	Psi	N	10.5 (11.3) 12.1	11.2 (11.6) 12.2	0 (2.8) 4.6	34.2 (57.4) 100
Syzygium (*Cleistocalyx*) *eugenioides*[A]	Ob	Tri	Inv, Ang	Conv	Psi	R	R	Psi	N	11.8 (12.3) 12.7	11.5 (11.7) 12	3.5 (3.9) 4.2	27.4 (31.6) 33.8
Syzygium (*Cleistocalyx*) *gustavioides*[A]	Ob, Pro	Di, Tri	Arc, Di	GC, Conv	Psi	R	S	Psi	N	26 (28.8) 31.7	24.3 (27) 29.6	12.9 (14.7) 16.4	49.6 (50.7) 51.8
Syzygium seemannii (*Cleistocalyx longiflorus*)[A]	Ob	Tri	Ang	Conv	Psi	R	S	Psi	N	11.7 (12.4) 13.1	11 (11.7) 12.2	3.7 (4.3) 4.7	32 (34.4) 37.9
Syzygium retinervium (*Cleistocalyx retinervius*)[A]	Ob	Tri	Arc, Ang, Inv	Conv	Psi	R	S, B	Psi	N	13.8 (14.9) 16.3	12.7 (14) 15.5	3.8 (5) 6	27.8 (33.4) 36.5
Syzygium (*Cleistocalyx*) *seemannii*[A]	Ob	Tri	Ang	Conv, Str	Psi	R	S	Psi	N	14 (14.8) 15.5	13.6 (14.1) 14.4	4.4 (4.9) 5.2	31.2 (32.9) 35.1
Syzygium sp. (*Piliocalyx boudoninii*)[A]	Ob	Tri	Arc	Conv	Psi	R	S	Psi	N	19.8 (22.5) 24.5	17.7 (20.2) 21.8	7.5 (10) 11.1	38 (44.4) 48.5
Syzygium sp. (*Piliocalyx wagapensis*)[A]	Ob	Tri	Arc	Conv	Psi	R	S	Psi	N	18.7	17.7	9.2	49.3
Syzygium angophoroides	Ob	Tri	Arc, Ang	Conv, GC	Psi, Sca	R, F	S	Psi, N	N, C	10.4 (11.7) 13	10.2 (10.9) 11.5	4.4 (4.9) 5.2	40.2 (42.3) 43.5
Syzygium (*Eugenia*) *angophoroides*[A]	Ob	Tri, Tet	Ang	Conv	Psi	R	S, R	Psi	N	12.8 (14) 15.1	11.6 (12.6) 13.4	3.9 (4.2) 4.6	25.6 (30.4) 35
Syzygium australe	Ob	Tri	Arc	Conc, Conv	Psi	R	S	Psi	N	9.7 (11) 12.6	9.3 (11.1) 12.6	4.5 (4.9) 5.6	39.5 (44.8) 49.2
Syzygium (*Eugenia*) *australe*[A]	Ob, Pro	Tri, Di	Arc, Di	Conv	Sca	R	S	Psi	N	20 (20.3) 20.5	18.6 (18.9) 19.3	9.6 (9.8) 10	47.8 (48.3) 48.7
Syzygium (*Eugenia*) *coolminiana*[A]	Ob	Tri	Arc	Conv	Psi	R	S	Psi	N	12 (12.6) 13.3	11.3 (11.9) 12.5	4.5 (4.8) 5.1	35.5 (37.9) 42.3
Syzygium corticosum[A]	Ob	Tri	Ang	Conv	Psi	R	S	Psi	N	15	14.3	5.7	38
Syzygium (*Eugenia*) *crebrinervis*[A]	Ob	Tri	Arc	Conv	Psi	R	S	Psi	N	12.4 (13.2) 13.6	11.1 (11.8) 12.2	4.6 (5.1) 5.6	35.2 (38.7) 44.9
Syzygium cumini	Ob	Tri	Ang	Str, Conv	Psi, Sca	P, R, F	R, S	Psi, N	S, C	10.5 (11.2) 12.6	10.6 (11) 11.7	3.3 (3.8) 4.3	31.6 (34.1) 37.7
Syzygium (*Eugenia*) *cyanocarpa*[A]	Ob	Tri	Ang	Conv	Psi	R	S	Psi	N	17.3 (18.6) 19.8	16.2 (17.3) 18.3	7.6 (7.6) 7.6	38.3 (41) 43.8
Syzygium (*Eugenia*) *hodgkinsoniae*[A]	Ob	Tri	Arc	Conv, Str	Psi, Sca	R	S	Psi	N, S	16.8 (17.5) 18.6	16 (16.8) 17.9	7.2 (7.7) 8.3	40.4 (44.4) 47.4
Syzygium (*Eugenia*) *luehmanni*[A]	Ob	Tri	Ang	Conv	Psi	R	S	Psi	N	18.1	16.6	5.1	28.4
Syzygium maire	Ob	Tri	Ang	Str, Conv	Psi	R, F	S	Psi	C	12.4 (13.8) 15.1	12.2 (13.1) 13.8	3.6 (4.3) 4.7	25.8 (30.9) 36.6
Syzygium (*Eugenia*) *moorei*[A]	Ob	Tri	Ang	Conv	Psi	R	S	Psi	N	13.6 (14) 14.6	12.4 (13.1) 13.8	3.9 (4.2) 4.4	29 (30) 31.4
Syzygium (*Eugenia*) *suberlox*[A]	Ob	Tri	Arc	Str	Psi	R	S	Psi	N	16.3	16.5	7.6	46.9
Syzygium floribundum (*ventenatii*)[A]	Ob	Tri	Ang	Conv	Psi	R	S	Psi	N	15.1 (15.8) 16.5	14.1 (14.9) 15.8	5.1 (5.6) 6.1	33.7 (35.3) 37
Syzygium wilsonii	Ob	Tri, Tet	Ang	Str	Psil	R, F	S	Psi	C, N	11.8 (12.7) 13.8	11.7 (12.6) 13.6	3 (3.9) 4.4	24.5 (30.8) 37.6
Syzygium zeylanicum[A]	Ob, Pro	Tri, Di	Ang, Di	Conv	Psi, Sca	R	S	Psi	S	4.2 (12.5) 15.5	11.9 (11.9) 14.7	4.1 (5) 5.8	29.5 (34.1) 39.8
Syzygium floribundum (*Waterhousea floribunda*)	Ob	Tri	Arc, Ang	GC, Conv, Str	Sca. Psi	R, P	S, R, B	Psi	N, S	11.6 (12.6) 14.7	11 (11.8) 13	4.3 (5.1) 6.5	35.6 (40.5) 45

[A]Slide from Pike collection.

were smooth or rough and a psilate apocolpial field was present. Pollen length ranged from 15.9 to 17.2 µm. Colpus/length ratio ranged from 56.3 to 59.9%.

LM: exine of *Phymatocarpus* was scabrate. Pollen sides were straight and colpal morphology was syncolpate. Pollen ambs were pointed or round, colpal edges were smooth and the apocolpial field was psilate. Pollen length ranged from 20.3 to 25.6 µm. Colpus/length ratio ranged from 52.2 to 56.8%.

Genus ***Regelia***

Number of species: 5.

Distribution: south-western Australia.

Species examined: SEM – 1; LM – 2 (3 taxon).

Previous pollen studies: Pike (1956).

Images: SEM polar view – Fig. 4*o*; SEM exine pattern – Fig. 6*c*; LM polar view – Fig. 9*h–j*.

SEM: *Regelia* pollen were tricolporate with a verrucate exine. Pollen sides were concave and colpal morphology was syncolpate. Pollen ambs were round or occasionally flat, colpal edges were smooth and the apocolpial field was psilate. Pollen length ranged from 17.3 to 20.7 µm. Colpus/length ratio ranged from 53.5 to 59.5%.

LM: the exine of *Regelia* was psilate or scabrate. Pollen sides were straight and occasionally concave and colpal morphology was parasyncolpate with angular colpi or parasyncolpate with arcuate colpi, tending to be almost syncolpate, as exemplified by the pollen of *R. inops*. Pollen ambs were round, colpal edges were smooth and the apocolpial field was psilate. Pollen length ranged from 26.1 to 46.7 µm. Colpus/length ratio ranged from 29.9 to 56.9%.

Tribe Osbornieae

Osbornieae is monotypic and contains the mangrove species *Osbornia octodonta*, which is found in northern Australia and the Philippines. Pollen measurements for Osbornieae are summarised in Tables 7 and 8.

Genus ***Osbornia***

Number of species: 1.

Distribution: northern Australia and Philippines.

Species examined: SEM – 1; LM – 1 (2 specimens).

Previous pollen studies: Pike (1956); Patel *et al*. (1984).

Images: SEM polar view – Fig. 4*p*; SEM exine pattern – Fig. 6*d*; SEM equatorial view – Fig. 7*e*; LM polar view – Fig. 9*k*, *l*.

SEM: *Osbornia* pollen were tricolporate, or sometimes tetracolporate, with a consistent rugulate exine. Pollen sides were straight and colpal morphology was parasyncolpate with

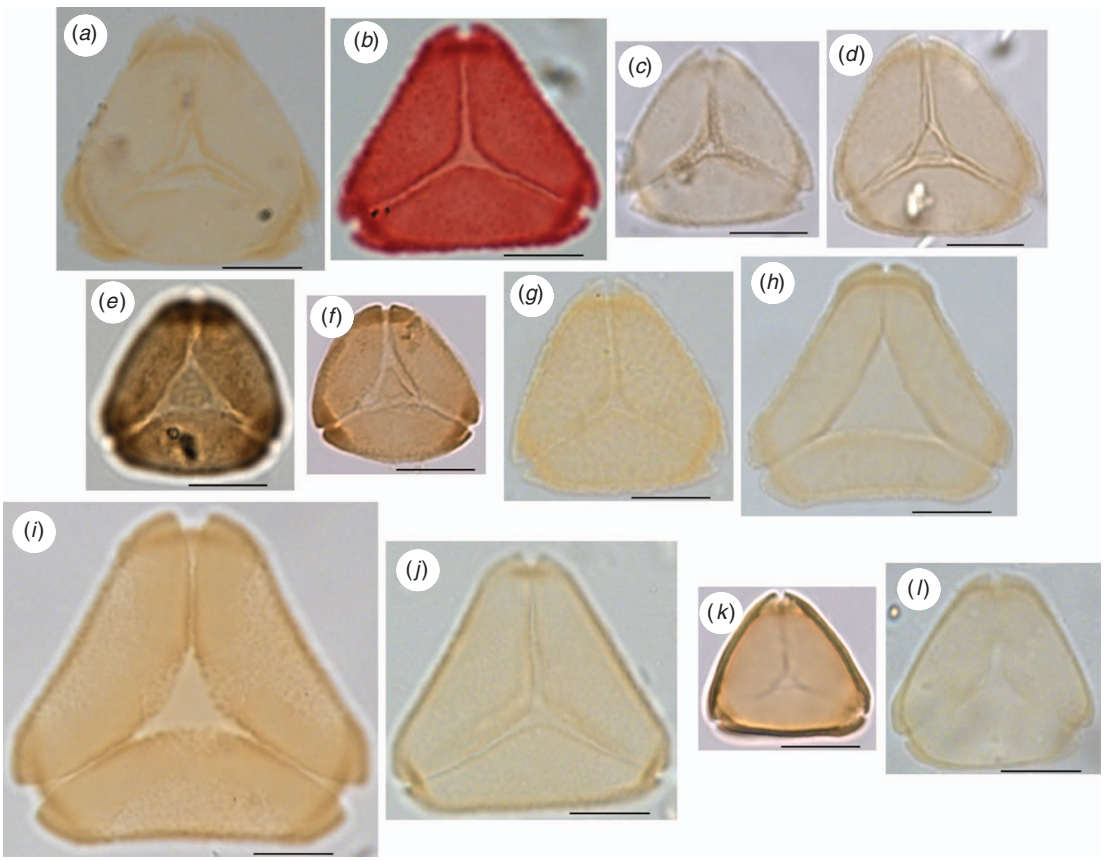


Fig. 9. Polar view of Melaleuceae and Osbornieae as viewed under light microscope. Scale bar = 10 µm. (*a*) *Melaleuca radula**, (*b*) *M. squamea**, (*c*) *M. squarrosa**, (*d*) *M. squarrosa**, (*e*) *M. steedmanii*, (*f*) *M. viridiflora*, (g) *Phymatocarpus porphyrocephalus**, (*h*) *Regelia ciliata**, (*i*) *R. grandiflora**, (*j*) *R. inops**, (*k*) *Osbornia octodonta* and (*l*) *O. octodonta**. Slides indicated with asterisk are from Pike collection.

angular colpi. Pollen length ranged from 14.6 to 16 µm. Colpus/length ratio ranged from 40.9 to 59.2%.

LM: exine patterns of *Osbornia* were psilate. Pollen sides ranged from straight to convex and colpal morphology was syncolpate in pollen prepared for the present study and parasyncolpate with angular colpi in pollen from the Pike collection slide. The majority of pollen lacked a polar island, but a small number of grains had a small irregular apocolpial island. Pollen length ranged from 16.6 to 24.6 µm. Colpus/length ratio ranged from 35.7 to 48.5%.

Tribe Syzygieae

Taxa of Syzygieae occur in Australia, New Zealand, Malesia, southern Asia, India, southern China, Africa and many South Pacific islands (especially the Solomon Islands, New Caledonia, Vanuatu and Fiji). It is one of six higher-level Myrtaceae taxa that contain species producing fleshy fruit, the others being Psiloxyloideae (*Psiloxylon*), Leptospermeae (*Kunzea pomifera* and *Leptospermum semibaccatum*), Myrteae, Lophostemoneae (*Kjellbergiodendron*) and Tristanieae (*Xanthomyrtus*) (Wilson 2011). Syzygieae species occur predominantly in rainforest, woodlands and seasonally dry monsoonal forest. There is now only one genus in Syzygieae, after reclassification by Craven and Biffin (2010) on the basis of an analysis of DNA sequence data. For ease of reference to past studies, we have used several of the previously recognised genera of Syzygieae for presentation of the pollen descriptions. Pollen measurements for Syzygieae are summarised in Tables 9 and 10.

Genus ***Acmena***

Number of species: ~39.

Distribution: northern and eastern Australia, Malesia, South-east Asia, southern China and the Solomon Islands.

Species examined: SEM – 4; LM – 8 (9 samples).

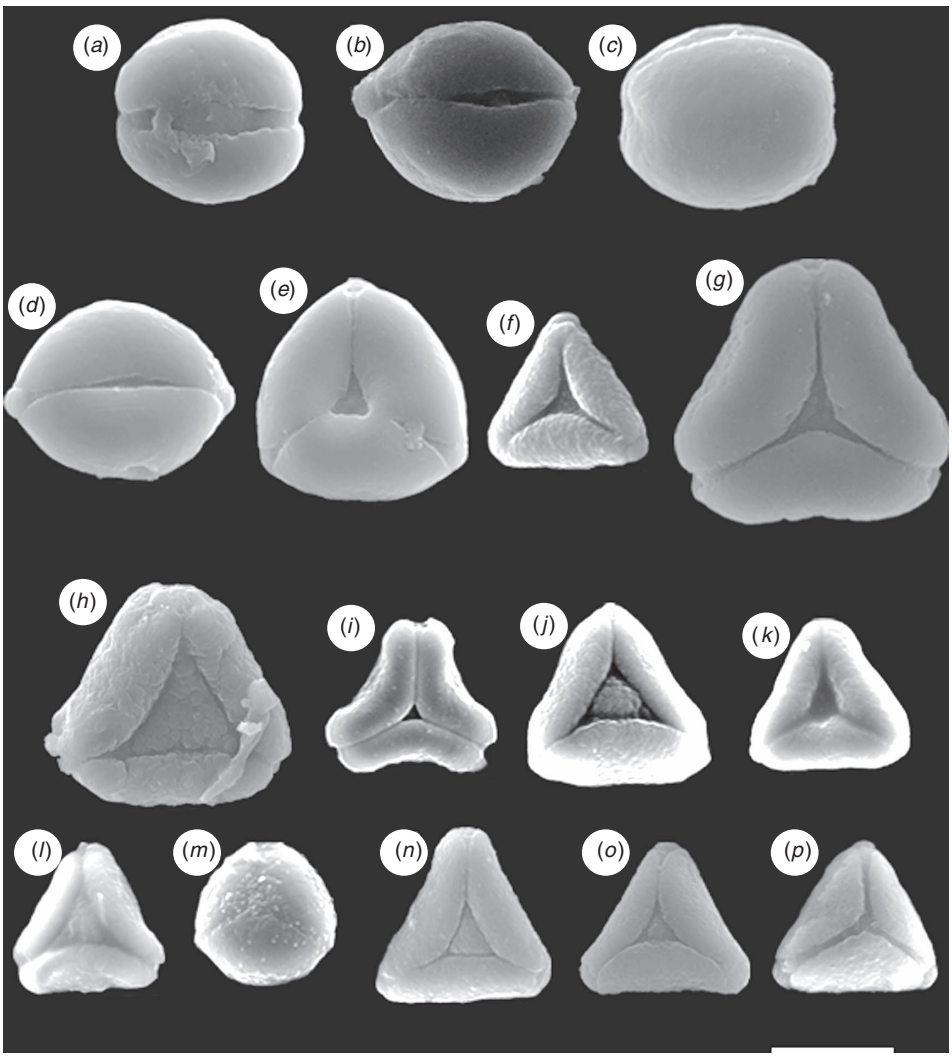


Fig. 10. Polar view of Syzygieae under scanning electron microscope. Scale bar = 10 µm. (*a*) *Syzygium divaricatum* (*Acmena divaricata*), (*b*) *S.* (*Acmena*) *graveolens*, (*c*) *S. mackinnonianum* (*Acmena mackinnoniana*), (*d*) *S.* (*Acmena*) *smithii*, (*e*) *S.* (*Acmena*) *smithii*, (*f*) *S. anisatum* (*Anetholea anisata*), (*g*) *S.* sp. (*Piliocalyx boudoninii*), (*h*) *S. aromaticum*, (*i*) *S. australe*, (*j*) *S. claviflorum*, (*k*) *S. cumini*, (*l*) *S. eucalyptoides*, (*m*) *S. samarangense*, (*n*) *S. wilsonii*, (*o*) *S. floribundum* (*Waterhousea floribunda*) and (*p*) *S. hedraiophyllum* (*Waterhousea hedraiophylla*).

Previous pollen studies: Pike (1956).

Images: SEM polar view – Fig. 10*a–e*; SEM exine pattern – Fig. 11*a–d*; SEM equatorial view – Fig. 13*a*, *b*; LM polar view – Fig. 14*a–m*.

SEM: *Acmena* pollen were dicolporate in the majority of species, except for *A. smithii*, which produced an equal proportion of dicolporate and tricolporate pollen. A psilate/rugulate exine was observed on all grains. Pollen sides were convex or sometimes greatly convex and colpal morphology was monocolpate or parasyncolpate with angular or arcuate colpi. Pollen ambs were round or sometimes pointed, colpal edges were smooth or rough and the apocolpial field was psilate. Pollen length ranged from 15 to 18.3 µm Colpus/length ratio ranged from 33 to 100%.

LM: the exine of *Acmena* was psilate, scabrate or, less often, granulate/scabrate. Either dicolporate or tricolporate pollen were observed in *Acmena* LM samples. Three species, *A. acuminatissima*, *A. laevifolia* and *A. smithii* produced pollen that were both dicolporate and tricolporate. Pollen sides were greatly convex or convex and colpal morphology was monocolpate, or parasyncolpate with arcuate colpi. Pollen

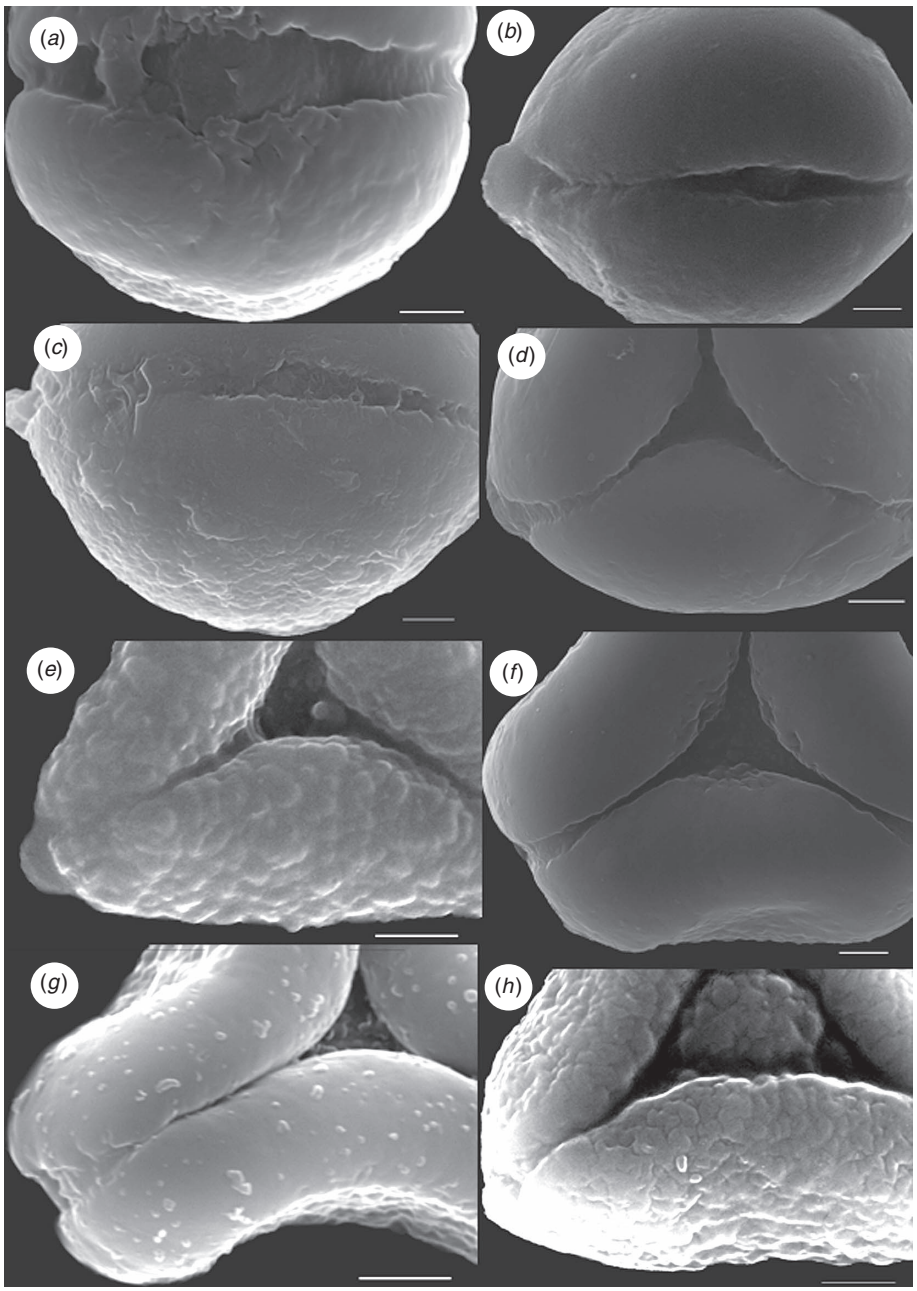


Fig. 11. Exine pattern of Syzygieae under scanning electron microscope. Scale bar = 2 µm. (*a*) *Syzygium divaricatum* (*Acmena divaricata*), (*b*) *S.* (*Acmena*) *graveolens*, (*c*) *S. mackinnonianum* (*Acmena mackinnoniana*), (*d*) *S.* (*Acmena*) *smithii*, (*e*) *S. anisatum* (*Anetholea anisata*), (*f*) *Piliocalyx boudoninii*, (*g*) *Syzygium australe* and (*h*) *S. claviflorum*.

ambs were round or pointed, colpal edges were smooth and the apocolpial field pattern was psilate. Pollen length ranged from 12.6 to 23.8 µm. Colpus/length ratio ranged from 36.5 to 100%.

Genus ***Anetholea***

Number of species: 1.

Distribution: eastern Australia.

Species examined: SEM –1; LM – 1.

Previous pollen studies: none.

Images: SEM polar view – Fig. 10*f*; SEM exine pattern – Fig. 11*e*; LM polar view – Fig. 14*n*.

SEM: *Anetholea* pollen were tricolporate with a granulate exine. Pollen sides were convex or straight, and the colpal morphology was parasyncolpate with arcuate colpi. Pollen ambs were round or pointed, colpal edges were smooth and the apocolpial field was scabrate or psilate. Small apocolpial islands were observed on most grains. Polar length ranged from 11.7 to 12.7 µm. Colpus/length ratio ranged from 54.1 to 56.5%.

LM: exine patterns of *Anetholea* were psilate. Most grains were tricolporate, or on rare occasions, tetracolporate. Pollen sides were convex and colpal morphology was parasyncolpate with arcuate colpi. Pollen ambs were round, colpal edges were smooth and the apocolpial field was psilate. Pollen length ranged from 12 to 14.5 µm. Colpus/length ratio ranged from 37.7 to 44.1%.

Genus ***Cleistocalyx***

Number of species: ~33.

Distribution: Pacific Islands (especially New Caledonia and Fiji), Australia, Malesia, and South-east Asia.

Species examined: SEM – not observed; LM –7.

Previous pollen studies: Pike (1956); Patel *et al*. (1984).

Images: LM polar view – Fig. 14*o–w*.

LM: *Cleistocalyx* pollen were tricolporate, except for some grains of *C. ellipticus* and *C. gustavoides*, which were dicolporate. The exine of all grains was psilate. Pollen sides were convex or straight and, less often, greatly convex. Colpal morphology was parasyncolpate with arcuate, inverse arcuate or angular colpi, except for dicolporate grains that had colpi that were fused and presented the appearance of a single colpus. Pollen ambs were round and colpal edges were mostly smooth, but were

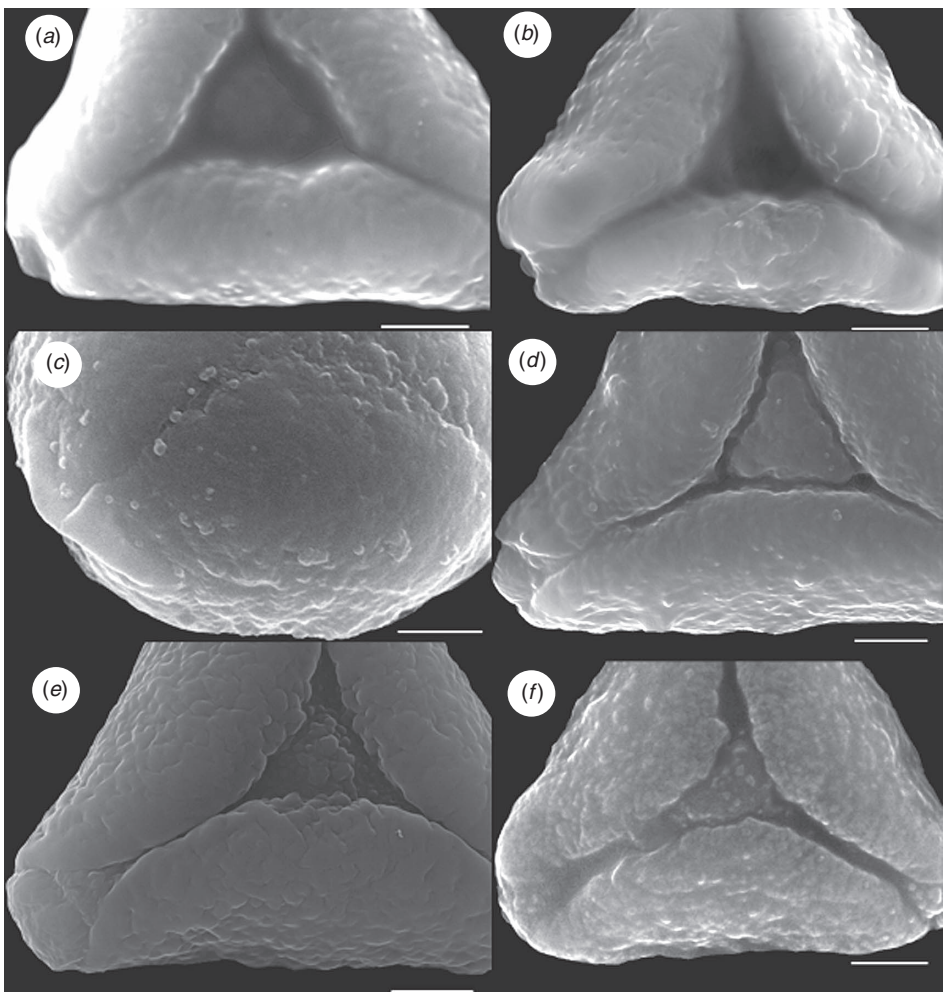


Fig. 12. Exine pattern 2 of Syzygieae under scanning electron microscope. Scale bar = 2 µm. (*a*) *Syzygium cumini*, (*b*) *S. eucalyptoides*, (*c*) *S. samarangense*, (*d*) *S. wilsonii*, (*e*) *S. floribundum* (*Waterhousea floribunda*) and (*f*) *S. hedraiophyllum* (*Waterhousea hedraiophylla*).

occasionally rough or broken, and the apocolpial field was psilate. All species lacked an apocolpial island, except for *C. arcuatinervius*, which had a small apocolpial island. Pollen length ranged from 10.5 to 16.3 µm. Colpus/length ratio ranged from 27.4 to 100%.

Genus ***Piliocalyx***

Number of species: ~20.

Distribution: New Caledonia, Vanuatu and Fiji.

Species examined: SEM –1; LM – 2.

Previous pollen studies: Pike (1956).

Images: SEM polar view – Fig. 10*g*; SEM exine pattern – Fig. 11*f*; SEM equatorial view – Fig. 13*c*; LM polar view – Fig. 14*ii*, *jj*.

SEM: *Piliocalyx* pollen were tricolporate, or less often tetracolporate, and the exine was psilate/rugulate. Pollen sides were straight or concave and colpal morphology was parasyncolpate with arcuate colpi. Pollen ambs were round, colpal edges were smooth and the apocolpial field was psilate or scabrate. Pollen length ranged from 11.7 to 12.7 µm. Colpus/length ratio ranged from 35.7 to 43.9%.

LM: the exine of *Piliocalyx* was psilate. Pollen sides were convex and colpal morphology was parasyncolpate with arcuate colpi. Pollen ambs were round, colpal edges were smooth and the apocolpial field was psilate. Pollen length ranged from 18.7 to 24.5 µm. Colpus/length ratio ranged from 38 to 49.3%.

Genus ***Syzygium***

Number of species: ~1200.

Distribution: Australia, Pacific Islands (especially the Solomon Islands, New Caledonia, Vanuatu and Fiji), Malesia, South-east Asia, southern Asia, New Zealand, Africa, Madagascar and the Mascarenes.

Species examined: SEM – 7; LM – 15 (17 samples).

Previous pollen studies: Pike (1956); McIntyre (1963); Moar (1993); Premathilake and Nilsson (2001); Parnell (2003); Fujiki and Ozawa (2007).

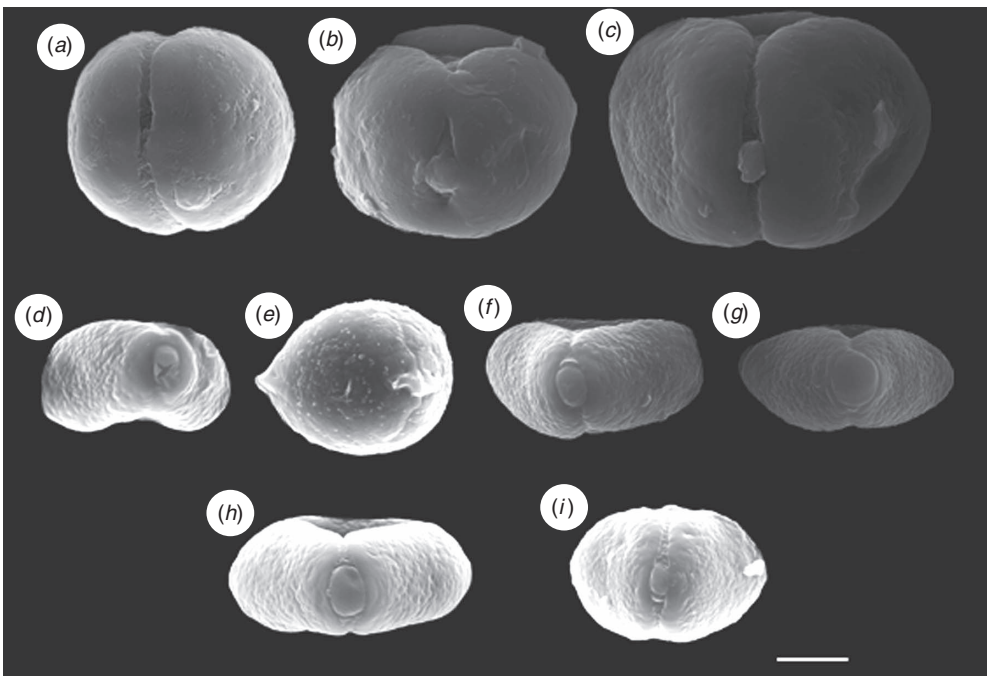
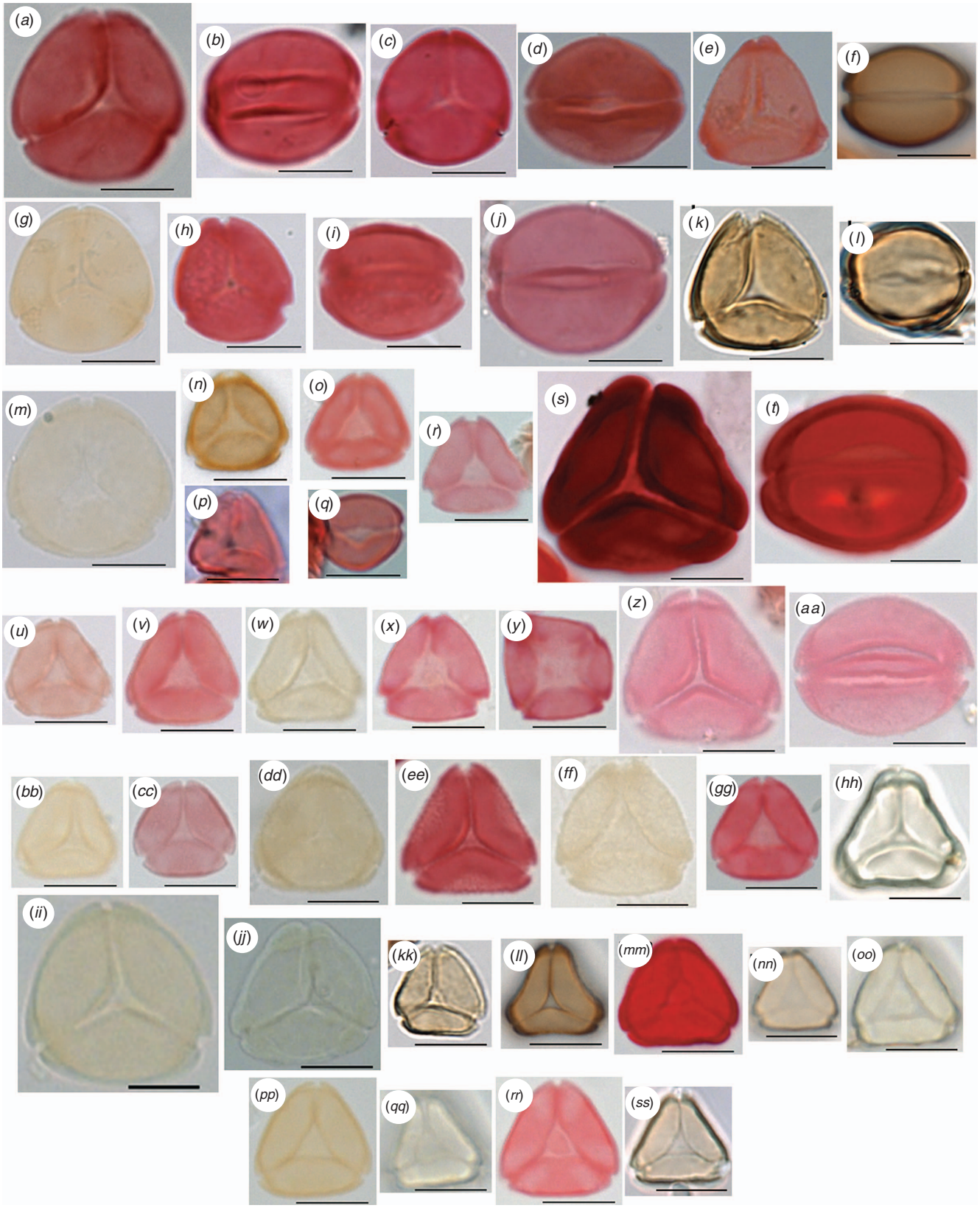


Fig. 13. Equatorial view of Syzygieae, Backhousieae and Metrosiderea under scanning electron microscope. Scale bar = 5 µm. (*a*) *Syzygium mackinnonianum* (*Acmena mackinnoniana*), (*b*) *S.* (*Acmena*) *smithii*, (*c*) *Piliocalyx boudoninii*, (*d*) *Syzygium cumini*, (*e*) *S. samarangense*, (*f*) *S. wilsonii*, (*g*) *S. floribundum* (*Waterhousea floribunda*), (*h*) *Backhousia citriodora* and (*i*) *Metrosideros carmine*.

Fig. 14. Polar view of Syzygieae as viewed under light microscope. Scale bar = 10 µm. (*a*) *Syzygium acuminatissimum* (*Acmena acuminatissima*)*, (*b*) *S. acuminatissimum* (*Acmena acuminatissima*)*, (*c*) *S. piluliferum* (*Acmena caudata*)*, (*d*) *S. divaricatum* (*Acmena divaricata*)*, (*e*) *S. divaricatum* (*Acmena divaricata*)*, (*f*) *S.* (*Acmena*) *graveolens*, (*g*) *S. hemilamprum* (*Acmena hemilampra*)*, (*h*) *S. acuminatissimum* (*Acmena laevifolia*)*, (*i*) *S. acuminatissimum* (*Acmena laevifolia*)*, (*j*) *S. graveolens* (*Acmena macrocarpa*)*, (*k*) *S.* (*Acmena*) *smithii*, (*l*) *S.* (*Acmena*) *smithii*, (*m*) *S.* (*Acmena*) *smithii**, (*n*) *S. anisatum* (*Anetholea anisata*), (*o*) *S. arcuatinervium* (*Cleistocalyx arcuatinervius*)*, (*p*) *S. seemannii* (*Cleistocalyx ellipticus*)*, (*q*) *S. seemannii* (*Cleistocalyx ellipticus*)*, (*r*) *S.* (*Cleistocalyx*) *eugenioides**, (*s*) *S.* (*Cleistocalyx*) *gustavioides**, (*t*) *S.* (*Cleistocalyx*) *gustavioides**, (*u*) *S. seemannii* (*Cleistocalyx longiflorus*)*, (*v*) *S. retinervium* (*Cleistocalyx retinervius*)*, (*w*) *S.* (*Cleistocalyx*) *seemannii**, (*x*) *S.* (*Eugenia*) *angophoroides**, (*y*) *S.* (*Eugenia*) *angophoroides**, (*z*) *S.* (*Eugenia*) *australis**, (*aa*) *S.* (*Eugenia*) *australis**, (*bb*) *S.* (*Eugenia*) *coolminiana**, (*cc*) *S.* (*Eugenia*) *crebrinervis**, (*dd*) *S.* (*Eugenia*) *cyanocarpa**, (*ee*) *S.* (*Eugenia*) *hodgkinsoniae**, (*ff*) *S.* (*Eugenia*) *luehmanni**, (*gg*) *S.* (*Eugenia*) *moorei**, (*hh*) *S.* (*Eugenia*) *suberlox**, (*ii*) *S.* sp. (*Piliocalyx boudoninii*)*, (*jj*) *S.* sp. (*Piliocalyx wagapensis*)*, (*kk*) *S. angophoroides*, (*ll*) *S. australe*, (*mm*) *S. corticosum**, (*nn*) *S. cumini*, (*oo*) *S. maire*, (*pp*) *S. floribundum* (*ventenatii*)*, (*qq*) *S. wilsonii*, (*rr*) *S. zeylanicum** and (*ss*) *S. floribundum* (*Waterhousea floribunda*). Slides indicated with asterisk are from Pike collection.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Images: SEM polar view – Fig. 10*h–n*; SEM exine pattern – Figs 11*g*, *h*, 12*a–d*; SEM equatorial view – Fig. 13*d–f*; LM polar view – Fig. 14*kk–rr*.

SEM: *Syzygium* pollen were tricolporate with a psilate/rugulate or verrucate/scabrate exine. Pollen sides were convex, straight or concave and the colpal morphology was parasyncolpate with angular or arcuate colpi. Pollen ambs were round or pointed, colpal edges were smooth, broken or rough and the apocolpial field was psilate or less often scabrate. Closely fitting apocolpial islands were observed on half of the *Syzygium* species. Pollen length ranged from 11.3 to 18.4 μm. Colpus/length ratio ranged from 24.2 to 57.6%.

LM: the exine of *Syzygium* was psilate or, less commonly, scabrate. Most pollen were tricolporate, but four species produced occasional tetracolporate or dicolporate grains. Pollen sides were convex or straight, and colpal morphology was parasyncolpate with angular or arcuate colpi. Pollen ambs were round, or lest often flat or pointed, colpal edges were smooth or sometimes rough, and the apocolpial field was psilate. Some species had closely fitting or small irregular apocolpial islands. Pollen length ranged from 10.4 to 20.5 μm. Colpus/length ratio ranged from 24.5 to 49.2%.

Genus ***Waterhousea***

Number of species: 4.

Distribution: eastern Australia.

Species examined: SEM –2; LM – 1.

Previous pollen studies: none.

Images: SEM polar view – Fig. 10*o*, *p*; SEM exine pattern – Fig. 12*e*, *f*; SEM equatorial view – Fig. 13*g*; LM polar view – Fig. 14*ss*.

SEM: *Waterhousea* pollen were tricolporate with a rugulate or verrucate/scabrate exine. Pollen sides were straight, or sometimes convex, and colpal morphology was parasyncolpate with arcuate colpi. Pollen ambs were round or pointed, colpal edges were rough or smooth and the apocolpial field was psilate or scabrate. No apocolpial islands were observed on *W.hedraiophylla* grains, whereas small irregular or globular islands occurred in *W. floribunda*. Pollen length ranged from 11.4 to 12.2 μm. Colpus/length ratio ranged from 39.5 to 51.4%.

LM: exine patterns of *Waterhousea* were scabrate or psilate. Pollen sides were greatly convex, convex or straight and colpal morphology was parasyncolpate with arcuate or angular colpi. Pollen ambs were round and occasionally pointed. Colpal edges were smooth or rough and the apocolpial field was psilate. The majority of pollen grains lacked an apocolpial island; however, some small irregular islands were seen. Pollen length ranged from 11.6 to 14.7 μm. Colpus/length ratio ranged from 35.6 to 45%.

Summary of tribes Backhousieae, Melaleuceae, Metrosidereae, Osbornieae and Syzygieae

Backhousieae

Backhousieae pollen were generally parasyncolpate with arcuate colpi, and occasionally syncolpate (*Choricarpia*). The difference in exine patterns clearly separated the pollen of the two Backhousieae genera, with *Backhousia* being psilate and having insignificant patterns, whereas, in contrast, *Choricarpia* was scabrate and highly ornate. Apocolpial islands were not seen in SEM but in LM one *Choricarpia* species (*C. leptopetala*) had closely fitting apocolpial islands. There was no major difference in pollen length within the tribe (~14 μm).

Melaleuceae

Melaleuceae pollen were most commonly parasyncolpate with angular colpi; however, taxa belonging to some former genera had arcuate colpi or were syncolpate (*Calothamnus*, *Eremaea*, *Phymatocarpus* and *Regelia*), which differed from most members of Melaleuceae, but were not dissimilar to pollen produced by taxa of Leptospermeae and Chamelaucieae. Exine patterns were primarily rugulate, but there were occasional occurrences of more ornate granulate/scabrate or verrucate/scabrate patterns. All *Melaleuca* species observed by SEM had closely fitting islands, as well as did *Callistemon* and *Lamarchea* species. *Beaufortia* pollen had small irregular apocolpial islands, whereas the other Melaleuceae genera pollen lacked an island. Pollen size was variable in Melaleuceae, with smaller-sized pollen grains occurring in *Callistemon*, *Melaleuca* and *Calothamnus*, larger-sized pollen occurring in *Beaufortia*, *Lamarchea* and *Regelia* (~17–20 μm) and very large pollen were observed in LM samples of *Eremaea* (~25 μm).

Metrosidereae

Metrosidereae pollen were parasyncolpate with angular colpi (similar to the pollen of some Melaleuceae), with the exception of *Tepualia*, which was dicolporate. Most pollen had a rugulate exine, with some pollen appearing verrucate or vermiculate. All Metrosidereae pollen, except *Tepualia*, possessed an apocolpial island, and closely fitting was the most common type. Pollen size was variable, but most recorded pollen lengths were average size for Myrtaceae pollen (~15 μm).

Osbornieae

Osbornieae is monotypic and very little variation was observed. However, the two LM samples used for the present study displayed different colpal morphologies. Pollen of the Pike collection slide appeared parasyncolpate with arcuate colpi and the pollen prepared for the present study had pollen that were syncolpate. The Osbornieae exine pattern was rugulate, which was commonly observed in many other Myrtaceae tribes. Pollen size varied between microscopy methods and among LM samples, with the pollen observed by SEM being about 15 μm, whereas those in LM samples ranged from 17 to 22 μm.

Syzygieae

Syzygieae pollen were most commonly parasyncolpate with arcuate or sometimes angular colpi. Some *Acmena* species (*A. divaricata*, *A. graveolens*, *A. mackinnoniana*, and *A. macrocarpa*) had dicolporate pollen, whereas other species (*A. acuminatissima*, *A. laevifolia*, and *A. smithii*) produced pollen that were either dicolporate or tricolporate. Syzygieae exines were consistently psilate or rugulate. Closely fitting pollen apocolpial islands were seen in many *Syzygium* species and small irregular islands were observed on the pollen of

Anetholea and *Waterhousea*. Pollen size was generally consistent within Syzygieae (~11–13 μm); however, large pollen were observed in *Piliocalyx* (~20 μm) and in one *Cleistocalyx* species (*C. gustavioides*, ~28 μm).

Discussion

Distinct pollen morphology in phylogenetic groups

A number of phylogenetic studies of the individual tribes in the present study allows us to compare the association of distinct pollen types or characters with systematic groups (Wright *et al*. 2000, 2001; Biffin *et al*. 2006; Cook *et al*. 2008; Edwards *et al*. 2010). Similar to the taxa of tribes presented in Thornhill *et al*. (2012*a*), most described pollen were parasyncolpate with arcuate or angular colpi, making differentiating pollen among tribes difficult. There was also little variation in pollen size, although some pollen of tribe Melaleuceae species (*Beaufortia*, *Eremaea*, *Lamarchea* and *Regelia*) appeared moderately larger. Pollen grains of the monophyletic group *Metrosideros* (including *Mearnsia*) (Wright *et al*. 2000, 2001) all had apocolpial islands and this may be of some benefit to New Zealand palynologists because the other endemic New Zealand Myrtaceae taxa, with the exception of *Syzygium maire*, have morphologically different pollen. However, in comparison with other tribes of Myrtaceae, *Metrosideros* pollen are not dissimilar to Melaleuceae, Syzygieae, Eucalypteae and Xanthostemoneae. All *Callistemon* species had large closely fitting apocolpial islands when viewed by LM, similar to previous observations of the genus (Pike 1956; Binder 1978), and island presence appears to be characteristic of this group, although pollen of *C. sieberi* and *C. viridiflorus* viewed by SEM did not consistently have this feature. This may be because *Callistemon* has been shown to be paraphyletic and also nested within *Melaleuca* (Edwards *et al*. 2010). The monophyletic group of *Beaufortia* (Edwards *et al*. 2010) had pollen that were granulate and had a prominent margo (thickened exine near the colpus and aperture regions). *Lamarchea* and *Regelia* pollen were large compared with those of *Beaufortia*, but also displayed the same prominent margo. The pollen of *Calothamnus* and *Eremaea* species appeared similar and all had syncolpate pollen; however, this cannot be linked to a monophyletic clade of Melaleuceae (Edwards *et al*. 2010).

Within tribe Backhousieae, *Choricarpia* pollen had a distinctive exine pattern when viewed under SEM, in comparison to its sister genus *Backhousia*. This pattern was still noticeable in LM but could be confused as scabrate, and its use as a diagnostic character is therefore not as powerful. Dicolporate pollen were observed in two tribes, Metrosidereae (*Tepualia*) and Syzygieae (*Acmena*), and this feature may be of systematic value. The dicolporate grains of these two genera were also easily distinguishable. *Tepualia* grains were small (10 μm) in length and had straight sides, compared with those of *Acmena* which were longer (15 μm) and had round convex sides. Dicolporate pollen are also characteristic of *Pileanthus* (see Thornhill *et al*. 2012*b*); however, again, this can be discerned from the other two genera by the fact that the genus has a psilate exine and colpi do not always fuse together to give the appearance of a single colpus. Interestingly, three species of *Acmena* that produce dicolporate pollen (*A. divaricata*, *A. graveolens* and *A. mackinnoniana*) form a monophyletic group in Biffin *et al*'s (2006) Syzygieae phylogeny, that is sister to another group of *Acmena* species that produces both dicolporate and tricolporate pollen species (*A. acuminatissima* and *A. smithii*), suggesting that a total shift to dicolporate grains has been made within part of the *Acmena* clade.

The exine pattern did not show much variability in the observed tribes. One feature that may have phylogenetic significance is the psilate exine of *Acmena* and *Piliocalyx*; the latter of these two genera nest within the traditional circumscription of *Acmena* (Biffin *et al*. 2006) but is sister to *Acmena sensu stricto* in the classification of Craven and Biffin (2010). Very small pollen were observed in many species of Syzygieae; however, they were not consistently observed in the tribe to be of any systematic value.

Pollen types within genera

Melaleuca

Different pollen types were observed within *Melaleuca*. Many species of the *M. leucadendra* complex (Cook *et al*. 2008; Edwards *et al*. 2010) had pollen with large apocolpial islands and appeared similar to pollen of *Callistemon*. This is interesting, considering the similar 'bottle-brush' floral structure of these two groups, and the shared pollen characters may reflect possible similarities in modes of pollen dispersal or a shared pollinator group. The other main pollen type of *Melaleuca* was medium-sized, syncolpate pollen with faint granulate patterning (e.g. *M. squamea*). In light of recent phylogenetic work (Edwards *et al*. 2010), it appears that the two *Melaleuca* pollen types are homoplasious within the genus.

Syzygium

Syzygium pollen, in general, were smaller than pollen from most other tribes of the present study; however, no other characters were useful in delineating the tribe from other Myrtaceae tribes with similar pollen. Apocolpial islands occurred in some members of Syzygieae, but were not consistent in relation to any phylogenetic groups as defined by Biffin *et al*. (2006); such a lack of correlation has previously been noted by (Parnell 2003). The shape of pollen sides was very variable within *Syzygium* and this character also appears to not be of any systematic value.

Supplementary Material

Supplementary Material for this article is available on the Journal's website.

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