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# Pollen morphology of the subfamily Aurantioideae (Rutaceae)

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The Aurantioideae is one of seven subfamilies of the Rutaceae consisting of two tribes, the Clauseneae, containing five genera, and the Citreae, with 28 genera. Each tribe contains three subtribes. The pollen morphology of the subfamily Aurantioideae is described and illustrated for the first time based on light and scanning electron microscopy. Five pollen types have been recognised in the subfamily, based mainly on aperture number and exine ornamentation. The pollen grains show a high degree of intergeneric variation. Pollen grains of Clauseneae are 3-colporate, microstriate or microstriato-reticulate, whereas pollen grains of Citreae are almost always 4/5 colporate with exines varying from microperforate to coarsely reticulate. Congruence between pollen types and the currently accepted classification is discussed, as well as the systematic implications of pollen morphology for the subfamily.

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The 33 genera of the subfamily Aurantioideae are divided into two tribes, the Clauseneae, containing five genera, and the Citreae, containing 28 genera (Swingle & Reece 1967). Each of these two tribes is divided into three subtribes (see Table II). All species are trees, shrubs or lianas and the flowers are usually white and very often fragrant. Many of the genera bear subglobose fruits with a green, yellow or orange peel dotted with numerous oil glands which often release an aroma when handled.

Of the 33 genera belonging to the Aurantioideae, 29 are native to the Monsoon region extending from west Pakistan to north-central China and from there south through the East Indian Archipelago to New Guinea and the Bismark Archipelago, Australia, New Caledonia, Melanesia and the western Polynesian islands (Swingle 1943). Five genera are native to tropical Africa. Only one genus, *Clausena*, is native to both the Monsoon region and tropical Africa.

The tribe Clauseneae contains five genera (Swingle 1943). All lack axillary spines, and have odd-pinnate leaves with leaflets alternately attached to the rachis. The fruits are usually small, semi-dry or juicy berries, except in *Merrillia*, which has ovoid fruits with a thick, radially lacunose leathery exocarp, unique in the subfamily. *Merrillia* is also the only genus in the subfamily with zygomorphic flowers, and these are also the largest in the subfamily. Some Clauseneae are economically important: *Murraya paniculata*, which has fragrant flowers and small red fruits, is grown as an ornamental (Spiegel-Roy & Goldschmidt 1996, Tolkowsky 1938). *Clausena lansium* (the Chinese wampee) is cultivated for its edible fruit in southern China (Swingle & Reece 1967).

In the tribe Citreae nearly all the species develop axillary spines, which are either single or paired, sometimes curved

as in *Luvunga* and *Paramignya*. The leaves are either simple, unifoliolate or trifoliolate, but a few genera have odd pinnate, opposite leaves. The subtribe Citrinae differs from all the other subtribes in the subfamily by having pulp vesicles which arise from the dorsal wall of the locule, growing into the locular cavity and developing into sacs filled with large, thin walled cells containing watery juice. No such structures have been found in any other Rutaceae or related families. No close homologies are known in any of the higher plants. However some of the other genera of the Aurantioideae have secretory glands on the walls of the locules, giving rise to mucilaginous gum, which fills the locular cavity of the fruit. The genera of the subtribe Balsamocitrinae have woody shelled fruits, containing resin-like gum.

The current classification of Swingle & Reece (1967) is based on morphology, and traditional taxonomic methods, but includes no data from palynology. The aims of this study are to examine the variation in pollen morphology, and to consider its systematic implications in relation to the existing classification. Five pollen types are described and illustrated, followed by descriptions for each of the taxa studied.

## MATERIALS AND METHODS

At least one species in every currently recognised genus (Swingle & Reece 1967, Chase et al. 1999) was examined except *Wenzelia*, *Monanthocitrus* and *Merope* in the subtribe Triphasiinae, and *Atalantia*, *Clymenia* and *Burkillanthus* in the subtribe Citrinae, for which polliniferous material was not available. More samples were taken from the larger genera, although 14 of the 33 genera are currently circumscribed as monotypic (Swingle & Reece 1967). The

genera examined are listed in Table II, and a full list of specimens examined is given in the appendix. Pollen was obtained from specimens in the Herbaria of the Natural History Museum, London (BM) and the Royal Botanic Gardens Kew (K), as well as from various living collections (see list of Specimens Examined). All samples were prepared by acetolysis (Erdtman 1960). For examination in LM, the pollen was mounted in glycerine jelly. Measurements were taken from at least ten grains of each sample. For examination in SEM pollen was air dried from 95% ethanol onto specimen stubs covered with negative photographic film, coated with gold palladium, and examined in a Hitachi H2500 SEM.

Exine structure was studied by making sections of acetolysed pollen grains of 10–20 µm in thickness using a Leitz MGW Lauda Kryomat freezing microtome.

The terminology used follows Punt et al. (1994).

## RESULTS

### Description of the pollen of the subfamily Aurantioideae

The pollen types are based on observations from light microscopy (see Table I), but features seen in SEM are also mentioned where appropriate. Five pollen types are

recognized in the subfamily Aurantioideae. All grains in the subfamily are isopolar, but with some showing a slight heteropolarity (for example *Citrus medica*), and colpiate, with a colpus number of three, four or five. Some genera have 4 and 5 colpiate grains occurring in a single anther. In all instances where this has been observed, the more frequent number is four, with approximately 20% of grains having five apertures. Size varies from small to medium, shape classes range from oblate spheroidal to subprolate. Polar outline may be circular to almost triangular, angulaperturate or planaperturate where the outline is angular, with the colpi sunken or not sunken. Equatorial outline elliptical, circular or angular. Exine from <2 µm to 8 µm thick, and of uniform thickness throughout each grain, except around endoapertures, where thickening is present. Nexine varying from having almost no thickening to distinct thickening around endoapertures (Fig. 17). Sexine from <1 µm to 2 µm thick, divisible into two layers. Sexine 1 of short or very short columellae. Sexine 2 a semi-tectum. All grains are tectate with either a reticulate, microreticulate, microperforate or microstriate tectum.

Table I. Observations from LM.

TAXON	Aperture	P (µm)	E (µm)	P/E
<b>Tribe Clauseneae</b>				
<b>Subtribe Micromelinae</b>				
<i>Micromelum minutum</i>	3 colpiate	32(35.6)38	26(27.1)28	1.31
<b>Subtribe Clauseninae</b>				
<i>Glycosmis pentaphylla</i>	3 colpiate	24(27.0)30	20(23.5)26	1.14
<i>Clausena inequalis</i>	3 colpiate	26(27.5)28	22(22.6)24	1.27
<i>Murraya paniculata</i>	3 colpiate	33(33.9)37	30(31.1)32	1.09
<b>Subtribe Merrillinae</b>				
<i>Merrillia caloxylon</i>	3 colpiate	32(35.5)37	30(31.3)32	1.13
<b>Tribe Citreae</b>				
<b>Subtribe Triphasiinae</b>				
<i>Oxanthera fragrans</i>	4 colpiate	30(34.6)36	29(33.4)36	1.02
<i>Triphasia trifolia</i>	3 colpiate	40(42.4)45	33(35.0)39	1.21
<i>Pamburus missionis</i>	5 colpiate	29(30.4)32	26(27.4)29	1.11
<i>Luvunga scandens</i>	4/5 colpiate	39(40.9)43	37(38.3)41	1.07
<i>Paramignya trimera</i>	4/5 colpiate	34(35.5)37	30(30.4)31	1.17
<b>Subtribe Citrinae</b>				
<i>Severinia</i> sp.	4 colpiate	36(37.5)39	26(34.1)37	1.10
<i>Pleiospermium alatum</i>	4/5 colpiate	25(28.2)30	24(26.8)30	1.05
<i>Limnocitrus littoralis</i>	4 colpiate	35(36.7)38	31(34.4)36	1.07
<i>Hesperethusa crenulata</i>	4/5 colpiate	33(34.9)36	23(25.1)27	1.39
<i>Citropsis schweinfurthii</i>	4/5 colpiate	17(18.5)21	16(16.8)18	1.10
<i>Fortunella japonica</i>	4 colpiate	28(29.1)32	23(24.6)26	1.18
<i>Eremocitrus glauca</i>	4/5 colpiate	25(26.3)27	21(22.4)24	1.16
<i>Poncirus trifoliata</i>	4/5 colpiate	34(37.4)40	28(31.2)37	1.19
<i>Microcitrus australis</i>	4 colpiate	22(24.8)29	21(25.4)27	1.10
<i>Citrus medica</i>	4/5 colpiate	16(17.9)19	18(18.2)19	0.98
<b>Subtribe Balsamocitrinae</b>				
<i>Swinglea glutinosa</i>	4 colpiate	37(39.9)45	33(35.4)38	1.12
<i>Aegle marmelos</i>	4 colpiate	23(24.7)26	21(21.7)22	1.14
<i>Afraegle paniculata</i>	4/5/6 colpiate	39(39.7)41	35(36.5)38	1.09
<i>Aeglopsis chevalieri</i>	4/5 colpiate	36(36.8)38	37(38.5)40	0.96
<i>Balsamocitrus paniculata</i>	4 colpiate	45(48.9)53	48(55.9)55	0.87
<i>Feronia limonia</i>	4 colpiate	22(22.6)24	21(21.8)23	1.04
<i>Feroniella pubescens</i>	3 colpiate	43(44.8)47	35(36.0)40	1.24

Table I. Continued

TAXON	Ectoapertures		Endoapertures		Nexine Thickness ( $\mu\text{m}$ )	Sesine ( $\mu\text{m}$ )
	Length ( $\mu\text{m}$ )	Width ( $\mu\text{m}$ )	Length ( $\mu\text{m}$ )	Width ( $\mu\text{m}$ )		
<b>Tribe Clauseneae</b>						
<b>Subtribe Micromelinae</b>						
<i>Micromelum minutum</i>	18(24.1)28	2	10(11.2)12	2	1	1
<b>Subtribe Clauseninae</b>						
<i>Glycosmis pentaphylla</i>	indistinct	indistinct	indistinct	indistinct	1–2	1
<i>Clausena inequalis</i>	17(19.3)21	2	8(8.5)9	2	1–2	1
<i>Murraya paniculata</i>	21(23.9)27	2	9(10.1)11	2	1–3	1
<b>Subtribe Merrillinae</b>						
<i>Merrillia caloxylon</i>	22(24.5)27	2	8(11.4)14	2	1–3	1
<b>Tribe Citreae</b>						
<b>Subtribe Triphasiinae</b>						
<i>Oxanthera fragrans</i>	17(22.9)26	2	6(6.2)7	1(1.9)2	1–3	1
<i>Triphasia trifolia</i>	28(31.5)35	2	8(9.4)12	2	<1–3	<1
<i>Pamburus missionis</i>	19(21.8)24	1(1.3)2	5(6.3)8	1(1.8)2	<1–2	<1
<i>Luvunga scandens</i>	25(27.4)30	2	13(14.5)16	2	1–5	1
<i>Paramignya trimera</i>	15(17.9)22	1	10(11.8)14	1	1–4	1
<b>Subtribe Citrinae</b>						
<i>Severinia</i> sp.	21(23.4)26	3(5.6)7	12(13.5)15	3(4.5)5	1–5	<1–1
<i>Pleiospermium alatum</i>	14(18.8)21	2	6(8.4)10	2	1–2	1
<i>Linnocitrus littoralis</i>	23(24.7)26	2	9(9.7)11	2	2–4	1
<i>Hesperethusa crenulata</i>	24(26.0)28	1	4(6.3)7	3(3.5)4	1–4	1
<i>Citropsis schweinfurthii</i>	10(12.0)14	1	5(5.1)6	1	<1–1	1
<i>Fortunella japonica</i>	17(19.6)21	1(1.1)2	7(7.9)9	1	1–3	1
<i>Eremocitrus glauca</i>	17(19.9)21	1	5(6.0)7	1(1.8)2	<1–3	1
<i>Poncirus trifoliata</i>	22(27.5)30		5(6.4)8	2	1–4	1
<i>Microcitrus australis</i>	15(17.2)20	1(2.1)3	3(5.8)7	2(2.5)3	1–2	1
<i>Citrus medica</i>	11(13.4)15	2(2.5)3	indistinct	indistinct	<1–1	1
<b>Subtribe Balsamocitrinae</b>						
<i>Swinglea glutinosa</i>	21(23.3)28	1(1.8)2	10(11.6)14	2	<1–3	1
<i>Aegle marmelos</i>	14(15.6)17	2	6(6.5)8	2	1–6	2
<i>Afraegle paniculata</i>	19(20.8)25	1(1.2)2	8(9.6)12	2	1–4	1
<i>Aeglopsis chevalieri</i>	13(15.5)17	2(2.1)3	6(7.7)10	4(4.2)5	1–7	1
<i>Balsamocitrus paniculata</i>	12(16.5)21	1	9(12.5)17	1(1.1)2	2–6	1
<i>Feronia limonia</i>	14(15.2)16	1	indistinct	indistinct	1–2	1
<i>Feroniella pubescens</i>	32(33.5)35	1	7(7.7)9	1	1	1

Where solid, the tectum usually shows striations. Muri rounded, with or without suprategal ornamentation. Ectocolpus long, narrow, sometimes narrower at centre, slightly sunken, length 14(21.9)32.6  $\mu\text{m}$ , and width 1.2(1.6)3.0  $\mu\text{m}$ , margins distinct, regular. Granules present on ectocolpus membrane. Endoaperture a porus or a lalongate colpus, length 6.8(9.5)14  $\mu\text{m}$ , and width 1.2(1.9)2.8  $\mu\text{m}$ .

#### Description of the pollen types and species examined

##### Type 1. The *Micromelum minutum*-type (Figs. 1–6).

Pollen grains 3 colporate, P/E 32(36.9)45  $\times$  26(31.1)39  $\mu\text{m}$  (subprolate–prolate spheroidal). Mean P/E ratio 1.19. Polar outline circular to almost triangular (Fig. 1), angulaperturate where the outline is angular, with the colpi sunken or not sunken (Fig. 1). Equatorial outline elliptical, or elliptical with comparatively acute apices (Figs. 2, 3, 5). Nexine varying from having almost no thickening to distinct

thickening around endoapertures. Sesine of uniform thickness throughout, 1  $\mu\text{m}$  or <1  $\mu\text{m}$ . Sesine 1 of short or very short columellae. Sesine 2 a microstriate tectum, with or without microperforations (Figs. 4, 6), muri rounded, with no suprategal ornamentation. Ectocolpus long, narrow, sometimes narrower at centre, slightly sunken, length 18(26.0)35  $\mu\text{m}$ , and width 2  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endocolpus lalongate, very narrow in *Micromelum minutum*, length 8(10.5)12  $\mu\text{m}$ , and width 2(2.25)3  $\mu\text{m}$ . Present in *Micromelum*, *Murraya*, *Merrillia* and *Triphasia*.

*Micromelum minutum*.—Pollen grains 3 colporate, P/E 32(35.6)38  $\times$  26(27.1)28. Mean P/E ratio 1.31 (subprolate). Polar outline circular to almost triangular, angulaperturate. Equatorial outline elliptical (Figs. 2, 3). Nexine with almost no thickening around endocolpi. Sesine 1  $\mu\text{m}$  thick throughout. Sesine 1 of very short columellae. Sesine 2 a microstriate semi-tectum, with microperforations (Fig. 4), muri rounded. Ectocolpus long, narrower at centre, slightly sunken, margins distinct, regular, length 18(24.1)28  $\mu\text{m}$ , and

Table I. Continued

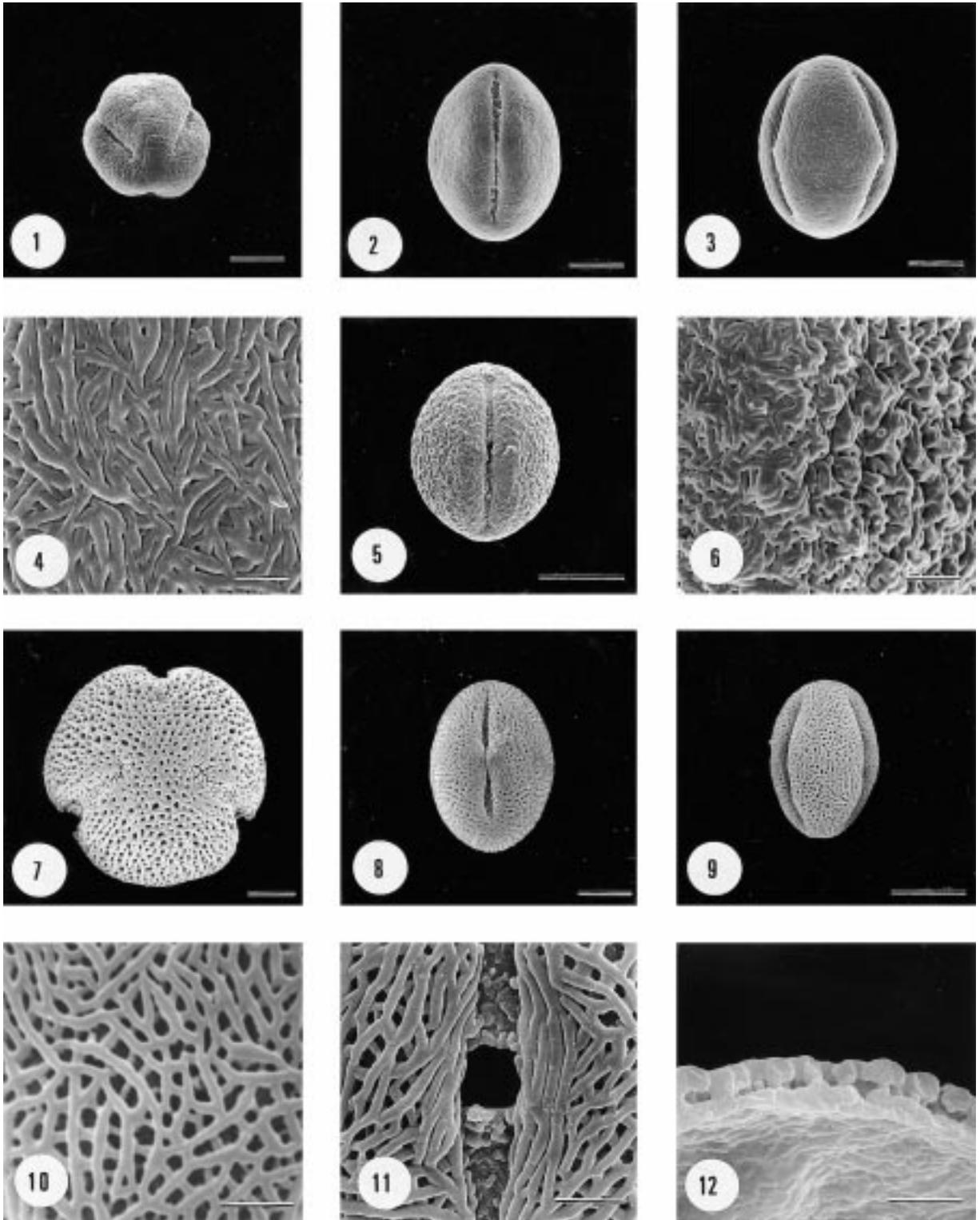
Taxon	Outline in polar view	Outline in equatorial view	Exine Thickening Around Endoapertures
<b>Tribe Clauseneae</b>			
<b>Subtribe Micromelinae</b>			
<i>Micromelum minutum</i>	Circular to almost triangular, angulaperturate, mesocolpium flattened	Elliptical	Almost none
<b>Subtribe Clauseninae</b>			
<i>Glycosmis pentaphylla</i>	Circular, but with the ectocolpi slightly indented	Elliptical, with quite sharp ends	Slight
<i>Clausena inequalis</i>	Circular, with the colpori quite sunken	Elliptical	Slight
<i>Murraya paniculata</i>	Circular, or slightly triangular	Elliptical, with sharp ends	Distinct
<b>Subtribe Merrillinae</b>			
<i>Merrillia caloxylon</i>	Circular, but with ectocolpi slightly sunken	Slightly elliptical	Distinct
<b>Tribe Citreae</b>			
<b>Subtribe Triphasiinae</b>			
<i>Oxanthera fragrans</i>	Circular, or slightly squared off with the most curvature in the mesocolpium	Slightly elliptical, or circular	Distinct
<i>Triphasia trifolia</i>	Slightly triangular	Elliptical	Distinct
<i>Pamburus missionis</i>	Circular, some grains flattened between colpori	Elliptical	Slight
<i>Luvunga scandens</i>	Circular with quite sunken ectocolpi	Elliptical	Distinct
<i>Paramignya trimeria</i>	Quite square profile, with the most curvature in the mesocolpial region	Elliptical, with quite straightened sides	Distinct
<b>Subtribe Citrinae</b>			
<i>Severinia</i> sp.	Circular, or slightly squared off, the most curvature at the colpori	Elliptical	Distinct
<i>Pleiospermium alatum</i>	Circular, with colpori slightly sunken	Elliptical	Distinct
<i>Limnocitrus littoralis</i>	Circular, with colpori slightly sunken	Elliptical	Distinct
<i>Hesperethusa crenulata</i>	Circular	Elliptical	Distinct
<i>Citropsis schweinfurthii</i>	Circular, with colpori slightly sunken	Elliptical	Almost none
<i>Fortunella japonica</i>	Circular, or slightly squared off, with the most curvature in the centre of the mesocolpium	Elliptical	Distinct
<i>Eremocitrus glauca</i>	Squared off with most curved part in the centre of the mesocolpium	Elliptical, with quite straightened sides	Distinct
<i>Poncirus trifoliata</i>	Circular but with a slight squaring off, with the most curvature in the centre of the mesocolpium	Elliptical, with quite sharp poles in some cases	Distinct
<i>Microcitrus australis</i>	Circular	Elliptical	Distinct
<i>Citrus medica</i>	Circular	Elliptical	Slight
<b>Subtribe Balsamocitrinae</b>			
<i>Swinglea glutinosa</i>	Circular, some grains with slightly irregular depressions in SEM	Elliptical	Distinct
<i>Aegle marmelos</i>	Circular	Elliptical, or occasionally almost circular	Distinct
<i>Afraegle paniculata</i>	Circular, with colpori slightly sunken	Circular, or slightly elliptical	Distinct
<i>Aeglopsis chevalieri</i>	Circular, with some grains showing flattening between colpori	Elliptical or circular	Distinct
<i>Balsamocitrus paniculata</i>	Circular, but squared off with the most curvature in the mesocolpial region	Circular, but quite squared off	Very slight
<i>Feronia limonia</i>	Circular	Circular or slightly elliptical	Virtually none
<i>Feroniella pubescens</i>	Circular, with colpori slightly sunken	Elliptical	None

width 2 µm. Endocolpus lalongate, margins distinct, regular, very narrow, length 10(11.2)12 µm, and width µm.

*Murraya paniculata*.—Pollen grains 3 colporate, P/E 33(33.9)37 × 30(31.1)32 µm. Mean P/E ratio 1.09 (prolate spheroidal). Polar outline circular, or slightly triangular. Equatorial outline elliptical, with comparatively acute apices. Nexine with distinct thickening around endocolpi, 1 µm thick at poles, 3 µm thick around endocolpi. Sexine 1 of short columellae. Sexine 2 a microstriate tectum.

Ectocolpus very long, narrow, sunken, margins distinct, regular, length 21(23.9)27 µm, and width 2 µm. Endocolpus lalongate, margins distinct, regular, length 9(10.1)11 µm, and width 3 µm.

*Merrillia caloxylon*.—Pollen grains 3 colporate, P/E 32(35.5)37 × 30(31.3)32 µm. Mean P/E ratio 1.13 (prolate spheroidal). Polar outline circular, but with ectocolpi slightly sunken. Equatorial outline slightly elliptical. Nexine with distinct thickening around endocolpi, 1 µm



Figs. 1–4. SEM of pollen of *Micromelum minutum*, type 1. (1) oblique polar view, scale bar 10  $\mu\text{m}$ ; (2) equatorial view, scale bar 10  $\mu\text{m}$ ; (3) equatorial view, scale bar 10  $\mu\text{m}$ ; (4) close up of mesocolpium, scale bar 2  $\mu\text{m}$ . Figs. 5, 6. SEM of pollen of *Triphasis trifolia*, type 1. (5) equatorial view, scale bar 20  $\mu\text{m}$ ; (6) close up of mesocolpium, scale bar 5  $\mu\text{m}$ . Figs 7–10. SEM of pollen of *Clausena inequalis*, type 2. (7) polar view, scale bar 5  $\mu\text{m}$ ; (8) equatorial view, scale bar 7  $\mu\text{m}$ ; (9) equatorial view, scale bar 10  $\mu\text{m}$ ; (10) close up of mesocolpium, scale bar 2  $\mu\text{m}$ . Fig. 11. SEM of pollen of *Glycosmis pentaphylla*, type 2; showing increasing density of sculpturing pattern around ectocolpus, scale bar 2  $\mu\text{m}$ . Fig. 12. SEM of pollen of *Clausena inequalis*, type 2; freeze section through exine, scale bar 1  $\mu\text{m}$ .

thick at poles, 3 µm thick around endocolpi. Sexine 1 of short columellae. Sexine 2 a microstriate semi-tectum, almost completely closed but with some microperforations. Ectocolpus very long, narrow, sunken, margins distinct, regular, length 22(24.5)27 µm, and width 2 µm. Endocolpus lalongate, margins distinct, regular, length 8(11.4)14 µm, and width 2 µm.

*Triphasia trifolia*.—Pollen grains 3 colporate, P/E 40(42.4)45 × 33(35.0)39 µm. Mean P/E ratio 1.21 (subprolate). Polar outline slightly triangular. Equatorial outline elliptical (Fig. 5). Exine very thin, especially sexine. Nexine with distinct thickening around endocolpi, <1 µm thick at poles, 3 µm thick around endocolpi. Sexine 1 of short columellae, more or less uniform in length. Sexine 2 a microstriate tectum, with short irregular striate elements (Fig. 6). Ectocolpus very long, narrow, sunken, length 28(31.5)35 µm, and width 2 µm. Some grains almost syncolporate. Granules present on ectocolpus membrane, margins distinct, regular. Endocolpus lalongate, margins distinct, regular, length 8(9.4)12 µm, and width 2 µm.

#### Type 2. The *Clausena inequalis*-type (Figs. 7–10, 12).

Pollen grains 3 colporate, P/E 24(33.1)47 × 20(27.3)40 µm, Mean P/E ratio 1.21 (subprolate). Polar outline circular, with the colpi sunken or slightly sunken (Fig. 7). Equatorial outline elliptical (Figs. 8, 9), with acute apices in *Glycosmis pentaphylla*. Exine thin (Fig. 12). Nexine with no thickening or only a little thickening around endoapertures, 1 µm thick at poles, 1–2 µm thick around endoapertures. Sexine 1 of short or very short columellae. Sexine 2 a microstriate or microstriato-reticulate semi-tectum, with two distinct layers to the muri (seen only in SEM) in *Clausena inequalis* (Fig. 10). Columellae thin, tectum with no supracteal ornamentation. No breakdown of ornamentation around ectocolpi. Ectocolpus long, quite narrow, sunken, length 17(26.4)35 µm, and width 1(1.5)2 µm. Ectocolpi narrower at centre in *Clausena inequalis* and *Glycosmis pentaphylla*. Few to many granules present on ectocolpus membrane, evenly distributed or more at ends in *Clausena inequalis*. Endocolpus lalongate, narrow or very narrow, length 7(8.1)9 µm, and width 1(1.5)2 µm. Present in *Clausena*, *Glycosmis* and *Feroniella*.

*Glycosmis pentaphylla*.—Pollen grains 3 colporate, P/E 24(27.0)30 × 20(23.5)26 µm. Mean P/E ratio 1.14 (prolate spheroidal). Polar outline circular, but with the ectocolpi slightly indented. Equatorial outline elliptical with acute apices. Nexine with only slight thickening around endoapertures. Nexine 1 µm thick at poles, 2 µm thick around endoapertures. Sexine 1 of very short columellae. Sexine 2 a microstriate semi-tectum with the area around the ectocolpi being more closed or almost completely solid (Fig. 11), unlike any of the other genera in the subfamily. Tectum relatively thick. Muri rounded. Ectocolpus long, slightly narrower at centre, slightly sunken, margins indistinct. Granules present on ectocolpus membrane. Endocolpus lalongate, margins indistinct, very narrow. Ectocolpus and endocolpus length and width measurements were not obtained.

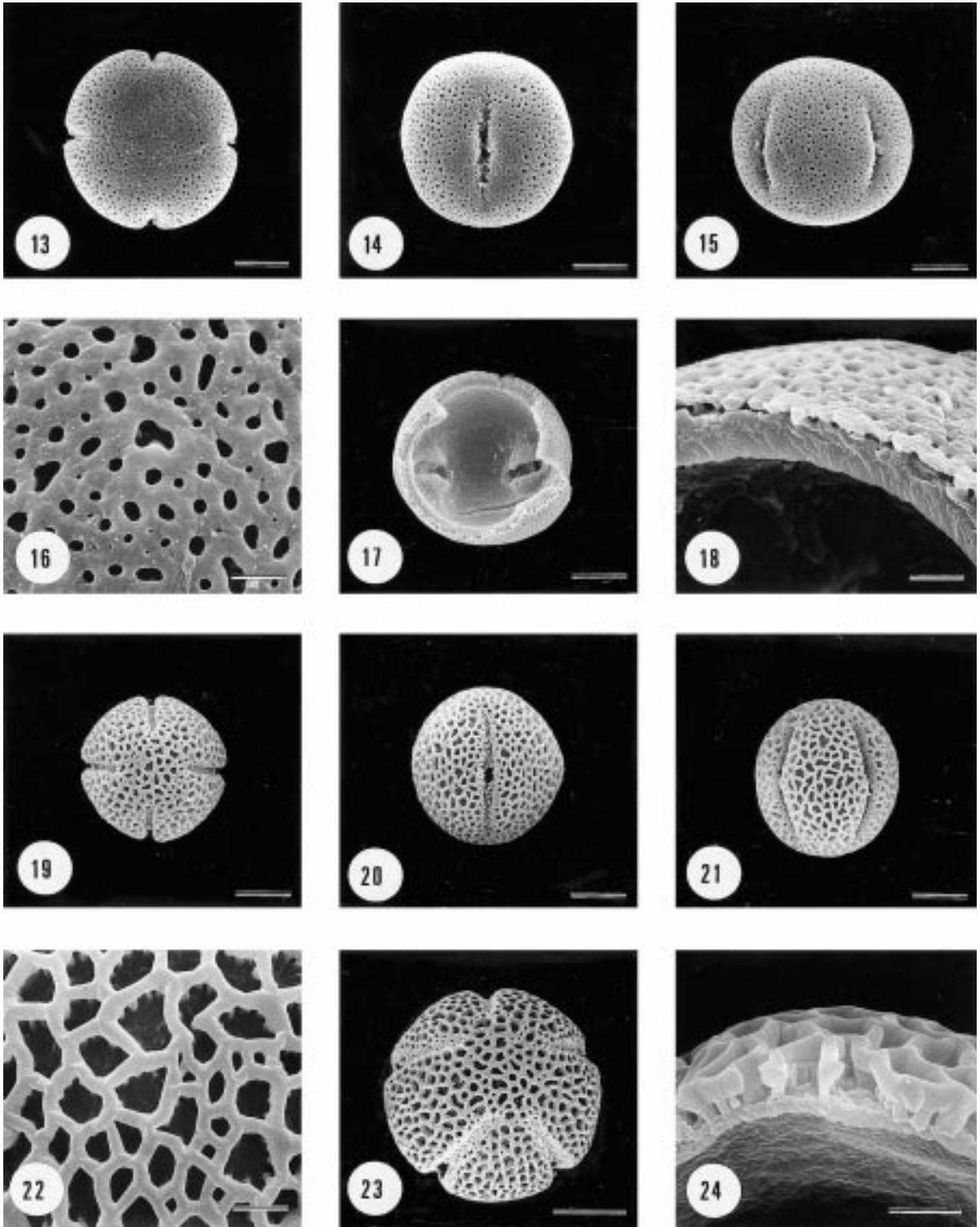
*Clausena inequalis*.—Pollen grains 3 colporate, P/E 26(27.5)28 × 22(22.6)24 µm. Mean P/E ratio 1.27 (subprolate). Polar outline circular, with the colpi sunken. Equatorial outline elliptical (Figs. 8, 9). Nexine with only a little thickening around endoapertures, 1 µm thick at poles, 2 µm thick around endoapertures. Sexine 1 of short columellae. Sexine 2 a microstriato-reticulate semi-tectum, with two distinct levels of muri, seen only in SEM (Fig. 10). Tectum thin. Columellae thin. Ectocolpus long, narrow, narrowest at centre, sunken, margins distinct, regular, length 17(19.3)21 µm, and width 2 µm. Granules present on ectocolpus membrane, more at ends. Endocolpus lalongate, margins distinct, regular, length 8(8.5)9 µm, and width 2 µm.

*Feroniella pubescens*.—Pollen grains 3 colporate, P/E 43(44.8)47 × 35(36.0)40 µm. Mean P/E ratio 1.24 (subprolate). Polar outline circular, with colpi slightly sunken. Equatorial outline elliptical, with the poles flattened. Nexine with no thickening around endoapertures. Nexine 1 µm thick. Sexine of uniform thickness (1 µm) throughout. Sexine 1 of short columellae. Sexine 2 a microstriato-reticulate semi-tectum with the muri all at the same level. Tectum thin, muri square in cross section. No breakdown of ornamentation around ectocolpi. Simplicolumellate. Ectocolpus very long, very narrow, sunken, margins distinct, regular, length 32(33.5)35 µm, and width 1 µm. Few granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular. Endocolpus also very narrow, length 7(7.7)9 µm, and width 1 µm.

#### Type 3. The *Balsamocitrus paniculata*-type (Figs. 13–18).

Pollen grains 4 or 4/5 colporate, P/E 36(41.8)53 × 35(42.6)55 µm (oblate-spheroidal–prolate spheroidal). Mean P/E ratio 0.97. Polar outline circular with flattening, planaperturate (Fig. 13). Equatorial outline also with flattening (Figs. 14, 15). Exine thick or thin. Nexine with thickening around endoapertures (Fig. 17), 1–2 µm thick at poles, up to 7 µm thick around endoapertures. Sexine 1 of short or very short columellae. Sexine 2 a microperforate semi-tectum (Fig. 16). Microperforations varying in size, and some of irregular shape. No supracteal ornamentation. Ectocolpus, short, quite narrow, sunken or not sunken, length 12(16.5)21 µm, and width 1 µm. Narrower at centre in *Balsamocitrus paniculata* (SEM). Granules present on ectocolpus membrane, with more at apices. Endocolpus lalongate, length 9(12.5)17 µm, and width 1(1.5)2 µm. Present in *Balsamocitrus*, *Aeglopsis* and *Afraegle*.

*Afraegle paniculata*.—Pollen grains 4/5/6 colporate (only one grain seen with 6 colpi), P/E 39(39.7)41 × 35(36.5)38 µm. Mean P/E ratio 1.09 (prolate spheroidal). Polar outline circular, with colpi slightly sunken. Equatorial outline circular, or slightly elliptical. Exine thin. Nexine with distinct thickening around endoapertures, 1 µm thick at poles, 4 µm thick around endoapertures. Sexine 1 of very short columellae. Sexine 2 a microperforate semi-tectum, microperforations varying in size and shape, especially around poles. Ectocolpus short, quite narrow, sunken, margins distinct, regular, length 19(20.8)25 µm, and



Figs. 13–18. SEM of pollen of *Aeglopsis chevalieri*, type 3. (13) polar view, scale bar 10 μm; (14) equatorial view, scale bar 10 μm; (15) equatorial view, scale bar 10 μm; (16) close up of mesocolpium, scale bar 2 μm; (17) fractured grain, showing thickening of endexine around endoapertures, scale bar 10μm; (18) freeze section through exine, scale bar 2 μm. Figs. 19–24. SEM of pollen of *Citrus medica*, type 4. (19) polar view, scale bar 10 μm; (20) equatorial view, scale bar 10 μm; (21) equatorial view, scale bar 10 μm; (22) close up of mesocolpium, scale bar 2 μm; (23) polar view of a five aperturate grain, showing asymmetry and near syncolporate apertures, scale bar 10 μm; (24) freeze section through exine, scale bar 2 μm.

width 1–2  $\mu\text{m}$ . Granules present on ectocolpus membrane, more densely distributed at ends. Endocolpus lalongate, margins distinct, regular, length 8(9.6)12  $\mu\text{m}$ , and width 2  $\mu\text{m}$ . Endocolpus quite wide, but not as wide as *Aeglopsis chevalieri*.

*Aeglopsis chevalieri*.—Pollen grains 4/5 colporate, P/E 36(36.8)38  $\times$  37(38.5)40  $\mu\text{m}$ . Mean P/E ratio 0.96 (oblate spheroidal). Polar outline circular, with some grains showing flattening between colpi (Fig. 13). Equatorial outline elliptical or circular (Figs. 14, 15). Exine thin (Fig. 18). Nexine 1  $\mu\text{m}$  thick at poles, up to 7  $\mu\text{m}$  thick around endoapertures (Fig. 17). Sexine of uniform thickness (1  $\mu\text{m}$ ) throughout. Sexine 1 of short columellae. Sexine 2 a microperforate semi-tectum (Fig. 16), microperforations varying in size, and some of irregular shape, especially around poles. Ectocolpus short, quite narrow, sunken, margins distinct, regular, length 13(15.5)17  $\mu\text{m}$ , and width 2–3  $\mu\text{m}$ . Granules present on ectocolpus membrane, more densely distributed at ends. Endocolpus lalongate, margins distinct, regular. Endocolpus wide, length 6(7.7)10  $\mu\text{m}$ , and width 4–5  $\mu\text{m}$ .

*Balsamocitrus paniculata*.—Pollen grains 4 colporate, P/E 45(48.9)53  $\times$  48(55.9)55  $\mu\text{m}$ . Mean P/E ratio 0.87 (suboblate). Polar outline circular, but squared off, with the most curvature in the mesocolpium region. Equatorial outline also squared off. Exine thick. Nexine 2  $\mu\text{m}$  thick at poles, up to 6  $\mu\text{m}$  thick around endoapertures. Sexine 1 of short columellae. Sexine 2 a microperforate semi-tectum, microperforations varying in size, with some being of irregular shape. Ectocolpus short, sunken, margins distinct, regular, length 12(16.5)21  $\mu\text{m}$ , and width 1  $\mu\text{m}$ . Granules present on ectocolpus membrane, more densely distributed at ends. Endocolpus lalongate, margins distinct, regular, length 9(12.5)17  $\mu\text{m}$ , and width 1–2  $\mu\text{m}$ .

#### Type 4. The *Citrus medica*-type (Figs. 19–24).

Pollen grains 4 or 4/5 colporate, P/E 16(27.2)40  $\times$  18(24.8)37  $\mu\text{m}$ . Mean P/E ratio 1.10 (oblate spheroidal–subprolate). Polar outline circular, or where angular, planaperturate (Figs. 19, 23). Colpori sunken. Equatorial outline elliptical or circular (Figs. 20, 21), apices acute in *Poncirus trifoliata*. Exine thin in cross section. Nexine with a little or much thickening around endoapertures. Nexine <1–1  $\mu\text{m}$  thick at poles, 1–6  $\mu\text{m}$  thick around endoapertures (Fig. 24). Sexine of uniform thickness throughout, 1  $\mu\text{m}$  except in *Aegle*. Sexine 1 of short columellae. Sexine 2 a heterobrochate semi-tectate reticulum (Fig. 22), muri thick, simplicolumellate, smooth, rounded, with no further ornamentation. Lumen quite small, of angular or rounded appearance. Ectocolpus, very long, narrow, slightly broader toward the equator, sunken, length 11(18.9)36  $\mu\text{m}$ , and width 1(1.7)3  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endoaperture a porus almost circular in shape, or a colpus, length 5(6.5)9  $\mu\text{m}$ , and width 1(1.7)2  $\mu\text{m}$ . Present in *Oxanthera*, *Citrus*, *Microcitrus*, *Poncirus*, *Eremocitrus*, *Feronia*, *Fortunella* and *Aegle*.

*Oxanthera fragrans*.—Pollen grains 4 colporate, P/E 30(34.6)36  $\times$  29(33.4)36  $\mu\text{m}$ . Mean P/E ratio 1.02 (prolate

spheroidal). Polar outline circular, or slightly squared off, planaperturate. Equatorial outline slightly elliptical, or circular. Exine thin. Nexine 1  $\mu\text{m}$  thick at poles, 3  $\mu\text{m}$  thick around endoapertures. Sexine 1 of short columellae. Sexine 2 a heterobrochate microreticulate/microperforate semi-tectum. Lumen larger at equator, smaller at poles, muri rounded. Ectocolpus long, narrow, sunken, margins distinct, regular, length 17(22.9)26  $\mu\text{m}$ , and width 2  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular, length 6(6.2)7  $\mu\text{m}$ , and width 1–2  $\mu\text{m}$ .

*Fortunella japonica*.—Pollen grains 4 colporate, P/E 28(29.1)32  $\times$  23(24.6)26  $\mu\text{m}$ . Mean P/E ratio 1.18 (subprolate). Polar outline circular, or slightly squared off, planaperturate. Equatorial outline elliptical. Nexine with distinct thickening round the apertures. Nexine 1  $\mu\text{m}$  thick at poles, 3  $\mu\text{m}$  thick around endoapertures. Sexine 1 columellate, sexine 2 a heterobrochate semitectate microreticulum, muri thick, smooth, rounded, with height greater than width. Ectocolpus long, narrow, sunken, margins distinct, regular, length 17(19.6)21  $\mu\text{m}$ , and width 1(1.1)2  $\mu\text{m}$ . Only a few granules present on ectocolpus membrane mostly near ends. Endocolpus lalongate, margins distinct, regular, length 7(7.9)9  $\mu\text{m}$ , and width 1  $\mu\text{m}$ .

*Eremocitrus glauca*.—Pollen grains 4/5 colporate, P/E 25(26.3)27  $\times$  21(22.4)24  $\mu\text{m}$ . Mean P/E ratio 1.16 (subprolate). Polar outline squared off, planaperturate. Equatorial outline elliptical, with some flattening. Exine thin. Nexine <1  $\mu\text{m}$  thick at poles, 3  $\mu\text{m}$  thick around endoapertures. Sexine 1 of very short uniform columellae. Sexine 2 a heterobrochate semi tectate microreticulum, muri thick, simplicolumellate. Tectum smooth, muri height greater than width, no supracteal ornamentation. Ectocolpus very long, narrow, sunken, margins distinct, regular, length 17(19.9)21  $\mu\text{m}$ , and width 1  $\mu\text{m}$ . Ectocolpi almost join at poles in some cases. Granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular, length 5(6.0)7  $\mu\text{m}$ , and width 1(1.8)2  $\mu\text{m}$ .

*Poncirus trifoliata*.—Pollen grains 4/5 colporate, P/E 34(37.4)40  $\times$  28(31.2)37  $\mu\text{m}$ . Mean P/E ratio 1.19 (subprolate). Polar outline circular but with a slight squaring off, planaperturate. Equatorial outline elliptical, with quite acute apices in some cases. Exine thin. Nexine 1  $\mu\text{m}$  thick at poles, 4  $\mu\text{m}$  thick around endoapertures. Sexine 1 of short columellae. Sexine 2 a heterobrochate semi tectate microreticulum, muri quite thick, smooth, height greater than width, no supracteal ornamentation. Ectocolpus long, narrow, sunken, margins distinct, regular, length 22(27.5)30  $\mu\text{m}$ , and width 2  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular, length 5(6.4)8  $\mu\text{m}$ , and width 2  $\mu\text{m}$ .

*Microcitrus australis*.—Pollen grains 4 colporate, P/E 22(24.8)29  $\times$  21(25.4)27  $\mu\text{m}$ . Mean P/E ratio 1.10 (prolate spheroidal). Polar outline circular. Equatorial outline elliptical. Exine thin. Nexine with distinct thickening around endoapertures. Nexine 1  $\mu\text{m}$  thick at poles, 2  $\mu\text{m}$  thick around endoapertures. Sexine 1 of short columellae, more or less uniform in length. Sexine 2 a semitectate heterobrochate reticulum or microreticulum, muri thick, smooth, rounded, with no supracteal ornamentation. Ectocolpus long, narrow,

broader toward the equator, sunken. Margins distinct, regular, length 15(17.2)20  $\mu\text{m}$ , and width 1(2.1)3  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endoaperture a porus or a lalongate colpus, margins distinct, regular. Length 3(5.8)7  $\mu\text{m}$ , and width 2(2.5)3  $\mu\text{m}$ .

*Citrus medica*.—Pollen grains 4/5 colporate, P/E 16(17.9)19  $\times$  18(18.2)19  $\mu\text{m}$ . P/E ratio 0.98 (Oblate spheroidal). Polar outline circular (Fig. 19). Equatorial outline elliptical or circular (Figs. 20, 21). Exine thin (Fig. 24). Nexine with only a little thickening around endoapertures. Nexine <1  $\mu\text{m}$  thick at poles, 1  $\mu\text{m}$  thick around endoapertures. Sexine of uniform thickness (1  $\mu\text{m}$ ) throughout. Sexine 1 of short uniform columellae. Sexine 2 a heterobrochate semi-TECTATE reticulum (Fig. 22), muri thick, smooth, rounded, with no suprategal ornamentation. lumen 2–3  $\mu\text{m}$  at widest point. Ectocolpus very long, narrow, slightly broader toward the equator, sunken, margins distinct, regular, length 11(13.4)15  $\mu\text{m}$ , width 2(2.5)3  $\mu\text{m}$ . Some grains with a tendency toward syncolporate apertures (Fig. 23). Granules present on ectocolpus membrane. Endoaperture a porus almost circular in shape, margins indistinct.

*Feronia limonia*.—Pollen grains 4 colporate, P/E 22(22.6)24  $\times$  21(21.8)23  $\mu\text{m}$ . P/E ratio 1.04 (prolate spheroidal). Polar outline circular. Equatorial outline circular or slightly elliptical. Exine thin. Nexine with slight or virtually no thickening around endoapertures. Nexine 1  $\mu\text{m}$  thick at poles, 2  $\mu\text{m}$  thick around endoapertures. Sexine of uniform thickness (1  $\mu\text{m}$ ) throughout, sexine 1 of short thin columellae, more or less uniform in length, simpli-columellate, sexine 2 semi tectate, heterobrochate microreticulate/foveolate. Muri thick, smooth, rounded, with no suprategal ornamentation. Lumen of sharp angular appearance, 3-sided to many sided. Ectocolpus long, quite narrow, sunken. margins distinct, regular, length 14(15.2)16  $\mu\text{m}$ , width 1(1.0)1  $\mu\text{m}$ . Endoaperture a porus, margins indistinct.

*Aegle marmelos*.—Pollen grains 4 colporate, P/E 23(24.7)26  $\times$  21(21.7)22  $\mu\text{m}$ . P/E ratio 1.14 (prolate spheroidal). P/E ratios variable from spherical to prolate spheroidal. Polar outline circular. Equatorial outline elliptical, or occasionally almost circular. Nexine with much thickening around endoapertures. Nexine 1  $\mu\text{m}$  thick at poles, up to 6  $\mu\text{m}$  thick around endoapertures. Sexine of uniform thickness (2  $\mu\text{m}$ ) throughout. Sexine 1 of very short columellae, wider at base than at top. Sexine 2 a heterobrochate reticulum. Muri thick, smooth, with no suprategal ornamentation. Lumina of angular appearance, 3-sided to many sided. Ectocolpus long, almost joining at poles, narrow, sunken, margins distinct, regular, length 14(15.6)17  $\mu\text{m}$ , and width 2  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular, length 6(6.5)8  $\mu\text{m}$ , and width 2  $\mu\text{m}$ .

#### Type 5. The *Pleiospermium alatum*—type (Figs. 25–36).

Pollen grains 4/5 colporate, P/E 17(31.5)45  $\times$  16(29.8)41  $\mu\text{m}$ . P/E ratio 1.13 (prolate spheroidal–prolate). Polar outline circular, with colpi slightly sunken (Figs.

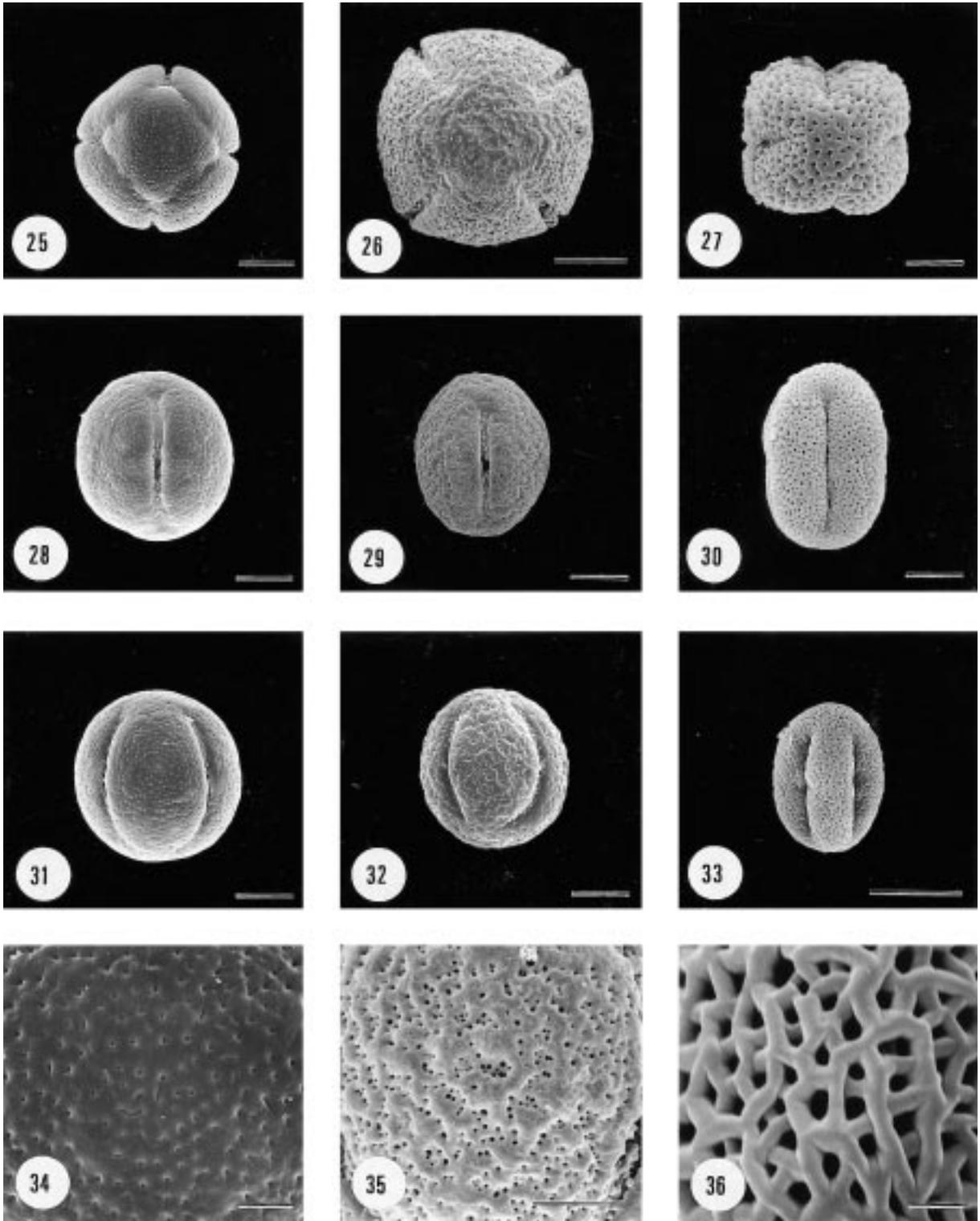
25–27). Equatorial outline elliptical (Figs. 28–33). Nexine with slight to distinct thickening round endoapertures. Nexine <1–1  $\mu\text{m}$  thick at poles, 2–5  $\mu\text{m}$  thick around endoapertures. Sexine of uniform thickness (<1–1  $\mu\text{m}$ ) throughout. Sexine 1 of short or very short columellae. Sexine 2 a microperforate tectum, or microreticulate (Figs. 34–36). Tectum almost solid. No suprategal ornamentation. Ectocolpus, long, very narrow, sunken, length 10(21.7)36  $\mu\text{m}$ , and width 1(1.9)7  $\mu\text{m}$ . Few granules present on ectocolpus membrane. Endocolpus lalongate, length 5(9.7)22  $\mu\text{m}$ , and width 1(2.2)5  $\mu\text{m}$ . This type has been further subdivided into types a, b and c on the grounds of overall similarity of exine morphology, as the variation was insufficient to designate separate types. Present in *Luvunga*, *Severinia*, *Swinglea*, *Pleiospermium*, *Limnocitrus*, *Citropsis*, *Hesperethusa*, *Pamburus* and *Paramignya*.

#### Type 5a

*Luvunga scandens*.—Pollen grains 4/5 colporate, P/E 39(40.9)43  $\times$  37(38.3)41  $\mu\text{m}$ . P/E ratio 1.07 (prolate spheroidal). Polar outline circular with quite sunken colpi (Fig. 25). Equatorial outline elliptical (Figs. 28, 31). Nexine with distinct thickening round endoapertures. Nexine 1  $\mu\text{m}$  thick at poles, up to 5  $\mu\text{m}$  thick around endoapertures. Sexine 1 of very short columellae. Sexine 2 a microperforate tectum (Fig. 34), microperforations fewer but larger around poles. Ectocolpus long, narrow, sunken, margins distinct, regular, length 25(27.4)30  $\mu\text{m}$ , and width 2  $\mu\text{m}$ . Very few granules present on ectocolpus membrane. Endocolpus lalongate, quite long, margins distinct, regular, length 13(14.5)16  $\mu\text{m}$ , and width 2  $\mu\text{m}$ .

*Swinglea glutinosa*.—Pollen grains 4 colporate, P/E 37(39.9)45  $\times$  33(35.4)38  $\mu\text{m}$ . P/E ratio 1.12 (prolate spheroidal). Polar outline circular, (some grains with slightly irregular depressions in SEM). Equatorial outline elliptical. Nexine with some thickening round endoapertures. Nexine <1  $\mu\text{m}$  thick at poles, 3  $\mu\text{m}$  thick around endoapertures. Sexine 1 of very short columellae. Sexine 2 a solid tectum. Tectum of microstriate appearance. No suprategal ornamentation. Ectocolpus long, narrow, sunken, margins distinct, regular, length 21(23.3)28  $\mu\text{m}$ , and width 1(1.5)2  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular, length 10(11.6)14  $\mu\text{m}$ , and width 2  $\mu\text{m}$ .

*Severinia buxifolia*.—Pollen grains 4 colporate, P/E 36(37.5)39  $\times$  26(34.1)37  $\mu\text{m}$ . P/E ratio 1.10 (prolate spheroidal). Polar outline circular, or slightly squared off, the most curvature at the colpi. Equatorial outline elliptical. Exine thin in cross section. Nexine with a lot of thickening around endoapertures. Nexine 1  $\mu\text{m}$  thick at poles, 5  $\mu\text{m}$  thick around endoapertures. Sexine <1 to 1  $\mu\text{m}$ . Sexine 1 of very short columellae. Sexine 2 heterobrochate, semitectate, microreticulate/foveolate. Muri thick, smooth, muri rounded, with no further ornamentation. Ectocolpus long, quite narrow, sunken, margins distinct, regular, length 21(23.4)26  $\mu\text{m}$ , and width 3(5.6)7  $\mu\text{m}$ . granules present on ectocolpus membrane, distributed unevenly, with more round the edge of colpus membrane. Endocolpus lalongate,



Figs. 25, 28, 31, 34. SEM of pollen of *Luvunga scandens*, type 5 (a). (25) polar view, scale bar 10  $\mu\text{m}$ ; (28) equatorial view, scale bar 10  $\mu\text{m}$ ; (31) equatorial view, scale bar 10  $\mu\text{m}$ ; (34) close up of mesocolpium, scale bar 2.5  $\mu\text{m}$ . Figs. 26, 29, 32, 35. SEM of pollen of *Citropsis schweinfurthii*, type 5 (b). (26) polar view, scale bar 10  $\mu\text{m}$ ; (29) equatorial view, scale bar 10  $\mu\text{m}$ ; (32) equatorial view, showing irregular colpi, scale bar 11  $\mu\text{m}$ ; (35) close up of mesocolpium, scale bar 5  $\mu\text{m}$ . Figs. 27, 30, 33, 36. SEM of pollen of *Paramignya trimera*, type 5 (c). (27) polar view, scale bar 5  $\mu\text{m}$ ; (30) equatorial view, scale bar 6  $\mu\text{m}$ ; (33) equatorial view, scale bar 10  $\mu\text{m}$ ; (36) close up of mesocolpium, scale bar 1  $\mu\text{m}$ .

margins distinct, regular, length 12(13.5)15  $\mu\text{m}$ , and width 3(4.5)5  $\mu\text{m}$ .

*Pleiospermium alatum*.—Pollen grains 4/5 colporate, P/E 25(28.2)30  $\times$  24(26.8)30  $\mu\text{m}$ . P/E ratio 1.05 (prolate spheroidal). Polar outline circular, with colpi slightly sunken. Equatorial outline elliptical. Nexine with distinct thickening round endoapertures. Nexine 1  $\mu\text{m}$  thick at poles, 2  $\mu\text{m}$  thick around endoapertures. Sexine 1 of very short columellae. Sexine 2 a microperforate tectum. Tectum almost solid. No suprategal ornamentation. Ectocolpus long, very narrow, sunken, margins distinct, regular, length 14(18.8)21  $\mu\text{m}$ , and width 2  $\mu\text{m}$ . Few granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular, length 6(8.4)10  $\mu\text{m}$ , and width 2  $\mu\text{m}$ .

*Pamburus missionis*.—Pollen grains 5 colporate, P/E 29(30.4)32  $\times$  26(27.4)29  $\mu\text{m}$ . P/E ratio 1.11 (prolate spheroidal). Polar outline circular, some grains with flattening in the mesocolpium. Equatorial outline elliptical. Exine very thin. Nexine with only slight thickening round endoapertures. Nexine <1  $\mu\text{m}$  thick at poles, 2  $\mu\text{m}$  thick around endoapertures. Sexine <1  $\mu\text{m}$  throughout. Sexine 1 of very short columellae. Sexine 2 a microperforate tectum. Microperforations more coarse than in *Luvunga scandens*. Tectum almost solid, no suprategal ornamentation. Ectocolpus long, narrow, sunken, margins distinct, regular, length 19(21.8)24  $\mu\text{m}$ , and width 1(1.3)2  $\mu\text{m}$ . Some grains with centre of ectocolpus raised slightly. Very few granules present on ectocolpus membrane. Endocolpus lalongate, quite long, margins distinct, regular, length 5(6.3)8  $\mu\text{m}$ , and width 1(1.5)2  $\mu\text{m}$ .

#### Type 5b

*Limmocitrus littoralis*.—Pollen grains 4 colporate, P/E 35(36.7)38  $\times$  31(34.4)36  $\mu\text{m}$ . P/E ratio 1.07 (prolate spheroidal). Polar outline circular, with colpi slightly sunken. Equatorial outline elliptical. Nexine 2  $\mu\text{m}$  thick at poles, 4  $\mu\text{m}$  thick around endoapertures. Nexine with distinct thickening around endoapertures. Nexine thicker than sexine. Sexine 1 of short columellae. Sexine 2 semi tectate, microperforate, with an irregular suprategal layer. Ectocolpus long, narrow, slightly sunken, margins distinct, regular, length 23(24.7)26  $\mu\text{m}$ , and width 2  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular, length 9(9.7)11  $\mu\text{m}$ , and width 2  $\mu\text{m}$ .

*Citropsis schweinfurthii*.—Pollen grains 4/5 colporate, P/E 17(18.5)21  $\times$  16(16.8)18  $\mu\text{m}$ . P/E ratio 1.10 (prolate spheroidal). Polar outline circular, with apertures slightly sunken (Fig. 26). Equatorial outline elliptical (Figs. 29, 32). Nexine <1  $\mu\text{m}$  thick at poles, 1  $\mu\text{m}$  thick around endoapertures. Nexine with almost no thickening around endoapertures. Nexine thicker than sexine. Sexine 1 of short columellae. Sexine 2 semi tectate, microperforate, with an irregular suprategal layer (Fig. 35), more coarse than in *Limmocitrus littoralis*. Ectocolpus long, narrow, sunken, margins distinct, regular, length 10(12.0)14  $\mu\text{m}$ , and width 1  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endocolpus lalongate, margins distinct, regular, length 5(5.1)6  $\mu\text{m}$ , and width 1  $\mu\text{m}$ .

*Hesperethusa crenulata*.—Pollen grains 4/5 colporate, P/E 33(34.9)36  $\times$  23(25.1)27  $\mu\text{m}$ . P/E ratio 1.39 (prolate). Polar outline circular. Equatorial outline elliptical. Nexine with distinct thickening round endoapertures. Nexine 1  $\mu\text{m}$  thick at poles, 4  $\mu\text{m}$  thick around endoapertures. Sexine 1 of very short columellae. Sexine 2 a microperforate tectum. Tectum almost solid, with an irregular suprategal layer. Ectocolpus long, very narrow, sunken, margins distinct, regular, length 24(26.0)28  $\mu\text{m}$ , and width 1  $\mu\text{m}$ . Few granules present on ectocolpus membrane. Endoaperture a porus, margins distinct, regular, length 4(6.3)7  $\mu\text{m}$ , and width 3(3.5)4  $\mu\text{m}$ .

#### Type 5c

*Paramignya trimera*.—Pollen grains 4/5 colporate, P/E 34(35.5)37  $\times$  30(30.4)31  $\mu\text{m}$ . P/E ratio 1.17 (subprolate). Polar outline planaperturate (Fig. 27). Colpi forming slight indentations. Equatorial outline elliptical, with the edges quite straight (Figs. 30, 33). Nexine with distinct thickening around endoapertures. Nexine 1  $\mu\text{m}$  thick at poles, 4  $\mu\text{m}$  thick around endoapertures. Sexine 1 of very short columellae. Sexine 2 a microstriae/microrugulate semi-nectum, with overlapping striae (Fig. 36). Muri rounded, with no suprategal ornamentation. Ectocolpus long, very narrow, sunken, margins distinct, regular, length 15(17.9)22  $\mu\text{m}$ , and width 1  $\mu\text{m}$ . Granules present on ectocolpus membrane. Endocolpus lalongate, very narrow, margins distinct, regular, length 10(11.8)14  $\mu\text{m}$ , and width 1  $\mu\text{m}$ .

## DISCUSSION

### Pollen morphology and systematic relationships

There is considerable variation in the pollen morphology of the Aurantioideae, which has been divided here into five pollen types. The differences include aperture number, ectocolpus shape and size, exine ornamentation and wall structure, in particular the presence of thickening of endexine around endoapertures. When designating pollen types for the subfamily Aurantioideae, the principal character used was the aperture number. This was due to the ease with which the states could be observed, so that the types could be readily distinguished and as useful as possible for identification purposes. Characters from ectexine sculpturing and wall stratification were much more difficult to use, and so were only emphasised where there were clear differences within the previous divisions based on aperture number. The distribution of the types in relation to the subfamilial classification can be seen in Table II.

The distribution of the pollen types, and of the characters supporting them was examined in relation to the classification of Swingle & Reece (1967). In general a high degree of congruence was found between pollen morphology and the classification. In particular:

1. The aperture number is highly congruent with the current classification. All genera of the tribe Clauseneae have 3 colporate, striate/striato-reticulate pollen, whereas 26 of the 28 genera of the tribe Citreae have pollen which is 4/5

Table II. Distribution of pollen types according to the classification of Swingle &amp; Reece (1967).

Tribe	Subtribe	Group (Swing 1967)	Genus	Pollen Type
Clauseneae	Micromelinae		<i>Micromelum</i>	Type 1
	Clauseninae		<i>Glycosmis</i>	Type 2
Citreae	Merrilliinae		<i>Clausena</i>	Type 2
			<i>Murraya</i>	Type 1
	Triphasiinae	(Group A)	<i>Merrillia</i>	Type 1
		(Group B)	<i>Oxanthera</i>	Type 4
			<i>Triphasia</i>	Type 1
			<i>Pamburus</i>	Type 5 (a)
		(Group C)	<i>Luvunga</i>	Type 5 (a)
			<i>Paramignya</i>	Type 5 (c)
			<i>Severinia</i>	Type 5 (a)
			<i>Pleiospermium</i>	Type 5 (a)
			<i>Limnocitrus</i>	Type 5 (b)
			<i>Hesperethusa</i>	Type 5 (b)
	Citrinae	(Group A)	<i>Citropsis</i>	Type 5 (b)
		(Group C)	<i>Fortunella</i>	Type 4
			<i>Eremocitrus</i>	Type 4
			<i>Poncirus</i>	Type 4
			<i>Microcitrus</i>	Type 4
			<i>Citrus</i>	Type 4
			<i>Swinglea</i>	Type 5 (a)
			<i>Aegle</i>	Type 4
		<i>Afraegle</i>	Type 3	
		<i>Aeglopsis</i>	Type 3	
Balsamocitrinae	(Group A)	<i>Balsamocitrus</i>	Type 3	
	(Group B)	<i>Feronia</i>	Type 4	
		<i>Feroniella</i>	Type 2	
	(Group C)			

colporate, with microperforate or reticulate ornamentation. This supports the existing tribal delimitation, except in the case of *Triphasia* (Citreae, Triphasiinae), and *Feroniella* (Citreae, Balsamocitrinae), which both have striate/striato-reticulate 3-colporate pollen.

- The presence of unique states of several characters including shape, exine ornamentation and colpus type, diagnostic of the type 3 pollen in *Afraegle*, *Aeglopsis* and *Balsamocitrus*, suggests that the three genera are closely related (see Table I). This is corroborated by other morphological evidence, including the presence of a large woody-shelled fruit, found only in these three African genera and the Indian genus *Aegle*. *Aegle* is the only other genus with this fruit type, which also is in the subtribe Balsamocitrinae. This genus has type 4 pollen, thus there is not total correspondence of fruit and pollen characters in the Balsamocitrinae.
- Type 4, with 4/5-colporate grains is found in all the members of the Citrinae group C, all genera sharing very similar coarsely reticulate sculpturing. However this type is also present in the genera *Oxanthera* (Triphasiinae group A), *Aegle* (Balsamocitrinae group B), and *Feronia* (Balsamocitrinae group C), thus type 4 pollen is represented in all three subtribes of the tribe Citreae.

Although in practice there is a good correlation between the existing classification and pollen morphology, there is no *a priori* reason why all of the character states should vary in a consistent manner or that this should correspond directly with the classification. Individual characters of the pollen

grains may exhibit either general or specialised character states depending on their phylogenetic history. To elucidate this more clearly, the next step in this study will be a phylogenetic analysis of the pollen and other morphological and molecular characters. (Grant et al., unpublished).

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#### SPECIMENS EXAMINED

##### Clauseneae, Micromelinae

*Micromelum minutum* (Forst.) Wt. & Arn. AUSTRALIA: Telford 9465, CBG; India: Ally B42, BM; S. AFRICA: Morton 8501640, Kirstenbosch Gardens Living Collection.

##### Clauseneae, Clauseninae

*Glycosmis pentaphylla* (Retz.) Correa. INDIA: B162, BM.

*Glycosmis angustifolia* Lindl. INDIA: Dumpiaz 8507, BM.

*Clausena anisata* (Willd.) Hook. S. AFRICA: Morton 33976, Kirstenbosch Gardens Living Collection; ZIMBABWE: Chase 1607, BM.

*Clausena indica* (Dalz.) Oliv. INDONESIA: Java: Morton III F 78, Bogor Gardens Living Collection.

*Clausena excavata* Burm. MALAYSIA Malaya Penins.: HCR B416, BM.

- Clausena inaequalis* (DC.) Benth. AUSTRALIA: Morton G875707, Adelaide Botanic Gardens Living Collection.
- Murraya paniculata* (Linn.) Jack. INDONESIA: Java Morton XXIVAI 20, Bogor Gardens Living Collection; AUSTRALIA: Morton G853900, Adelaide Botanic Gardens Living Collection; KENYA: Williams 408, K.
- Clauseneae, Merrilliinae
- Merrillia caloxylon* (Ridl.) Swing. MALAYSIA: Ridley 21149, K; SINGAPORE: Anon s.n. K.
- Citreae, Triphasiinae
- Oxanthera brevipes* Stone. AUSTRALIA: MacKee 40121, CBG.
- Oxanthera fragrans* Montr. NEW CALEDONIA: Anon. 288, K.
- Triphasia trifolia* Lour. INDONESIA: Java: Morton III G 140, Bogor Gardens Living Collection; AUSTRALIA: Williams 35, CBG; AUSTRALIA: Wilson s.n. UWA; INDIA: Wils Q1281, K; THAILAND: Bangkok: Kerr s.n. BM; MALAYA: Sandique B469, BM.
- Pamburus missionis* (Wt.) Swing. INDIA: Gamble 18171, BM; INDIA: Beddome B583, BM.
- Luvunga scandens* (Roxb.) Buch. CHINA: Hosseus B507, BM.
- Paramignya trimeria* (Oliv.) Burkill. AUSTRALIA: Fosberg 62185, CBG; AUSTRALIA: Hyland B21238V, UWA; AUSTRALIA: Latz 3433, UWA.
- Paramignya andamanica* (King) Tan. INDIA: Andemans B531, BM; INDIA: Floryking B532, BM.
- Citreae, Citrinae
- Severinia buxifolia* (Poir.) Tenore. AUSTRALIA: Morton 882074, AD-U; CHINA: Wilson B594, BM.
- Severinia* sp. PHILIPPINES: Abarez 18565, BM.
- Pleiospermium dubium* Swing. INDONESIA: Java: Morton III G 64a, Bogor Gardens Living Collection.
- Pleiospermium longisepalum* Swing. AUSTRALIA: Chew et al. RSNB2939, CBG.
- Pleiospermium alatum* (Wt. & Arn.) Swing. INDIA: Horder B486, BM.
- Limnocitrus littoralis* (Miq.) Swing. INDOCHINA: Clemens 3263, K; USA: Morton, Personal collection.
- Hesperethusa crenulata* (Roxb.) Roem. AUSTRALIA: Cole 1972, CBG; INDIA: Worthington 4591, BM; INDIA: Puniaz 9363, BM.
- Citropsis schweinfurthii* (Engl.) Swing. TROPICAL AFRICA: Swingle 2902, BM; USA (Cult): Swingle 2902, BM.
- Fortunella japonica* (Thunb.) Swing. JAPAN: Anon. B698, BM;
- Eremocitrus glauca* (Lindl.) Swing. AUSTRALIA: Morton 842564, SYD; AUSTRALIA: Brown B567, BM; AUSTRALIA: Mitchell B568, BM.
- Poncirus trifoliata* (Linn.) Raf. CHINA: Forbes 2217, BM.
- Microcitrus australasica* Swing. AUSTRALIA: Morton 8800855, CBG.
- Microcitrus australis* (Planch.) Swing. AUSTRALIA: Forster 12461, K; AUSTRALIA: Cunningham 163, BM.
- Citrus medica* Linn. WESTERN ASIA: Lindsay 856, BM; PHILIPPINES: Yates B755, BM.
- Citreae, Balsamocitrinae
- Swinglea glutinosa* (Blanco) Merr. INDONESIA: Java: Morton XXIVA44, Bogor Gardens Living Collection; MALAYSIA: Malaya Penins.: Anon. B761, BM; MALAYA: Merrill B761, BM.
- Aegle marmelos* (Linn.) Corr. NEPAL: Stainton 5849, BM; INDIA: Clarke B452, BM.
- Afraegle paniculata* (Schum.) Engl. NIGERIA: Keay 22491, K; Country unknown: Morton PI 0, Personal collection.
- Aeglopsis chevalieri* Swing. GHANA: Levique 656, K; Country unknown: Morton PI 539143, Personal collection.
- Balsamocitrus paniculata* Swing. CAMEROON: Bates B597, BM.
- Feronia limonia* (Linn.) Swing. INDIA: Bremer 93, K.
- Feronia limonia* (Linn.) Swing. ANTIGUA: Gabriel 1348, BM.
- Feroniella pubescens* Tan. MALAYSIA: Malaya Penins.: Calo. B438bis, BM. CHINA: Floryking B441, BM.

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