

## Pollen morphology of the family Polygalaceae (Fabales)

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An overview of pollen morphology from all genera in the family Polygalaceae is presented to assist systematic studies of the Fabales clade. The pollen of 72 species, representing 18 genera, in Polygalaceae was examined using light microscopy and scanning electron microscopy. In addition, the pollen of eight species, representing seven genera, was examined using transmission electron microscopy. Pollen is described and illustrated for each genus, and the first pollen descriptions and publication of photomicrographs are presented for seven genera: *Balgoya*, *Barnhartia*, *Comesperma*, *Diclidanthera*, *Eriandra*, *Moutabea*, plus *Polygala* subgenus *Badiera*, and species previously included in *Nylandtia* (now in *Muraltia*). Pollen morphological similarities and differences broadly correspond with relationships suggested by recent molecular phylogenies. The aperture number was also found to correlate with trees generated using molecular data; early branching taxa have lower aperture numbers than later branching ones. The overall range of ectoaperture numbers seen in Polygalaceae, excluding *Balgoya*, is between five and 33. The pollen of *Balgoya* is tricolporate; all other genera have pollen with a range of ectoaperture numbers within each sample. The degree of endoaperture fusion to form endocingula is variable at a subgeneric level. All pollen is isopolar, except for that of *Heterosamara* and *Polygala wattersii*. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 156, 253–289.

ADDITIONAL KEYWORDS: apertures – endocingula – heteropolar – isopolar – Leguminosae – phylogeny – Quillajaceae – Surianaceae – systematics.

### INTRODUCTION

The monophyly of the Fabales clade *sensu* Angiosperm Phylogeny Group (APG) II (2003) is strongly supported by molecular sequence data (Morgan, Soltis & Robertson, 1994; Källersjö *et al.*, 1998; Doyle *et al.*, 2000; Savolainen *et al.*, 2000; Soltis *et al.*, 2000; Kajita *et al.*, 2001; Persson, 2001; Bello, Hawkins & Rudall, 2007). The clade consists of four families: Leguminosae, Polygalaceae, Quillajaceae, and Surianaceae. Some relationships amongst major groups within this clade are currently unresolved, but the family Polygalaceae is well supported as a monophyletic group by morphological data (Eriksen, 1993), *trnL-F* region sequence data (Persson, 2001), *rbcL*

and *trnL-F* region sequences (Forest, 2004; Forest *et al.*, 2007), and *rbcL* and *matK* sequences (Bello *et al.*, 2007). The Polygalaceae comprises 18–20 genera and over 1000 species (Brummitt, 1992; Maberley, 1997; Persson, 2001) (Table 1). Members of the Polygalaceae are almost cosmopolitan in distribution, but are absent from New Zealand and Polynesia. Life forms include trees, shrubs, lianes, herbs, and parasites.

The pollen morphology of the Fabales clade is the subject of ongoing research at the Royal Botanic Gardens, Kew (for example, see Banks & Klitgaard, 2000; Banks *et al.*, 2003 for caesalpinoid legume pollen studies, and Claxton *et al.*, 2005 for a comprehensive account of Surianaceae and Quillajaceae pollen). A particular focus is to resolve phylogenetic relationships between the early diverging lineages of the Fabales clade. This study set out to examine and

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**Table 1.** Number of species recognized per genus, species sampled for pollen morphology in this study, and summary of previous Polygalaceae pollen literature

Genus	Number of species	Number of species sampled in this study	Specimens examined in this study Key to herbaria: K, RBG Kew; MEXU, Mexico; NSW, RBG Sydney	Descriptions in the pollen literature	Drawings in the pollen literature	LM images in the pollen literature	SEM images in the pollen literature	TEM images in the literature	Polygalaceae pollen literature
<i>Aroxima</i>	2 <sup>1</sup>	2	<i>A. afzeliana</i> Stapf, Aushoff 513, Ivory Coast, K; <i>A. liberia</i> Stapf, Breteler 5910, Ivory Coast, K	✓		✓			21
<i>Balgoya</i>	1 <sup>2,3</sup>	1	<i>Ba. pacifica</i> Morat & Meijden, McPherson 3394; McKee 24667, New Caledonia, K; <i>Ba. pacifica</i> , McPherson 3374, McPherson 3394, New Caledonia, NSW						None
<i>Barnhartia</i>	1 <sup>7,10</sup>	1	<i>Bm. floribunda</i> Gleason, Broom <i>et al.</i> 8594, Brazil, K						8
<i>Bredemeyera</i>	15–60 <sup>4,10,16</sup>	3	<i>Br. lucida</i> (Benth.) Benn., Ratter <i>et al.</i> R.6182, Brazil, E; <i>Br. microphylla</i> Hieron., Maas <i>et al.</i> 8181, Argentina, K; <i>Br. papuana</i> Steen., Ridsdale and Galore 33380, New Guinea, K	✓	✓		✓		22,23,24
<i>Carpolobia</i>	4 <sup>1</sup>	2	<i>C. alba</i> G. Don, Troupin 3888, Republic of Congo, K; <i>C. goetzii</i> Gürke, Goyder <i>et al.</i> 3722, Tanzania, K	✓		✓			25,26,27,28,29
<i>Comesperma</i>	24 <sup>17</sup>	5	<i>Co. calymega</i> Labill., R.M.L.G. 4274, Australia, K; <i>Co. ericinum</i> DC., Adams 1480, Australia, K; <i>Co. hispidum</i> Pedley, Jobson 5008, Australia, NSW; <i>Co. virgatum</i> Labill., Strid. 21356, Australia, K; <i>Co. volubile</i> Labill., Milligan s.n., Australia, K	✓					30
<i>Diclidanthera</i>	4–7 <sup>4,7,10</sup>	1	<i>D. penduliflora</i> Mart., Prance <i>et al.</i> 24657, Peru, K	✓					31,32

<i>Epirixanthes</i>	5–6 <sup>6,18</sup>	2	✓	✓	✓	33,34
<i>Eriandra</i>	1 <sup>6,8</sup>	1	✓	✓	✓	34
<i>Heterosamara</i>	14 <sup>19</sup>	4	✓	✓	✓	20
<i>Monnina</i>	c. 150 <sup>4,10,13</sup>	3	✓	✓	✓	30,31,32,35,36
<i>Moutabea</i>	8–10 <sup>4,9,10</sup>	1	✓	✓	✓	None
<i>Muraltia</i>	115–117 <sup>14</sup>	7	✓	✓	✓	31,32,36,37
<i>Nylandtia</i>	21 <sup>11,14,20</sup>	1	✓	✓	✓	30

Table 1. *Continued*

Genus	Number of species	Number of species sampled in this study	Specimens examined in this study	Key to herbaria: K, RBG Kew; MEXU, Mexico; NSW, RBG Sydney	Descriptions in the pollen literature	Drawings in the pollen literature	LM images in the pollen literature	SEM images in the pollen literature	TEM images in the literature	Polygalaceae pollen literature	
<i>Polygala</i>	c. 500 <sup>4,6,10,15,19</sup>	23	<p><i>Badiera acuminata</i> DC., Boom 4055, Bolivia, K;</p> <p><i>B. caracasana</i> (Kunth) C. Persson, 4796, Ecuador, K;</p> <p><i>B. diversifolia</i> DC., Harris 9651, Jamaica, K; <i>B. fuertesii</i> Urb., Ekman 13894, Greater Antilles, K; <i>B. oblongata</i> Britton, Ekman 18985, Cuba, K; <i>B. penaea</i> DC., Ekman 3982, Haiti (Hispaniola), K; <i>Phlebotania covellii</i> Britton, Britton and Stewardson Brown 5703, Porto Rico, K;</p> <p><i>Ph. cuneata</i> Griseb., Ekman 9236, Cuba, K; <i>Polygala arillata</i> Buch-Ham. ex D. Don, Sino-British Expedition 1175, China, K; <i>P. chamaebuxus</i> Linn., Jackson 6343, France, RNG; <i>P. cruciata</i> L., Godfrey 48200, USA, K; <i>P. hebeclada</i> DC., Irwin <i>et al.</i> 13559, Brazil, K; <i>P. klotzschii</i> Chodat, Hatchbach and Silva 69279, Brazil, MEXU; <i>P. laurocola</i> St Hil., Harley 20506, Brazil, K; <i>P. ligustrioides</i> A. St-Hil. &amp; Moq., Irwin <i>et al.</i> 34335, Brazil, K; <i>P. macroptera</i> DC., M. Kerandren-Aymonin 25295, Madagascar, K; <i>P. meridionalis</i> Levyns &amp; Salter 1802, South Africa, K; <i>P. microphylla</i> L., Reynolds and Frazer H649/57, Portugal, K; <i>P. obscura</i> Benth., Tenorio <i>et al.</i> 11788, Mexico, MEXU; <i>P. senega</i> DC., Kennedy and Ganders 4111, Canada, K; <i>P. uncinata</i> C. Wright, Irwin <i>et al.</i> 19528, Brazil, K; <i>P. vulgaris</i> L., Martineol 45, Yugoslavia, K; <i>P. wattersii</i> Hance, Hwa 416, China, K</p>								See Table 3

<i>Salomonina</i>	8 <sup>6</sup> ,11,12	2	✓	✓	✓	38,39
<p><i>Sa. ciliata</i> (L.) DC., Wallace 9187, Burma, K;  <i>Sa. longiciliata</i> Kurz., Thomas 252, Brunei, K</p>						
<i>Securidaca</i>	80 <sup>4</sup> ,6,10	6	✓	✓	✓	40,41
<p><i>S. diversifolia</i> (L.) Blake, Hartley 24719, Brazil, K;  <i>S. longipendunculata</i> Fresen., Mwasumbi <i>et al.</i> 16608,  Tanzania, K; <i>S. paniculata</i> L.C. Rich, Tillet and Tillet 45669, British Guiana, K;  <i>S. philippinensis</i> Chodat, Elmer 10851, Philippines, K;  <i>S. virgata</i> Sw., Ekman 8322, Hispaniola, K; <i>S. velutischi</i> Oliv., Fernandez Casas 11574, Equatorial Guinea, K</p>						
<i>Xanthophyllum</i>	93 <sup>5</sup> ,6	7	✓	✓	✓	5,13,31,34, 37,39,42,43
<p><i>X. affine</i> Korth.ex Miq., Ngadiman 36794, Singapore, K; <i>X. ameonum</i> Chod., Aban Gibot SAN. 66701, Sabah, K;  <i>X. fragrans</i> C.T.White, Hyland 8906, Australia, K;  <i>X. lanceatum</i> (Miq.) J.J.Smith, Garrett 163, Thailand, K;  <i>X. octandrum</i> (F.Muell.) Domin, Gray 1563, Australia, K; <i>X. papuanum</i> Meijden, Hartley 11385, Papua New Guinea, K; <i>X. vitellinum</i> D.Dietr., Bskar SAN. 28638, Sabah,</p>						

LM, light microscopy; SEM, scanning electron microscopy; TEM, transmission electron microscopy.

<sup>1</sup>Breteler & Smitsaert-Houwing (1977); <sup>2</sup>Persson (2001); <sup>3</sup>Morat & van der Meijden (1991); <sup>4</sup>Eriksen *et al.* (2000); <sup>5</sup>van der Meijden (1982); <sup>6</sup>van der Meijden (1988); <sup>7</sup>Gleason (1926); <sup>8</sup>van Royen & van Steenis (1952); <sup>9</sup>Wendt (2000); <sup>10</sup>Aymard & Berry (1997); <sup>11</sup>Goldblatt & Manning (2000); <sup>12</sup>Koyama (1995); <sup>13</sup>Eriksen (1993); <sup>14</sup>Forest (2004); <sup>15</sup>Bernardi (2000); <sup>16</sup>Marques (1980); <sup>17</sup>Pedley (1984); <sup>18</sup>Pendry (2001); <sup>19</sup>Paiva (1998); <sup>20</sup>Dumort (1823); <sup>21</sup>Fredoux (1977); <sup>22</sup>Gibbs & Ferguson (1987); <sup>23</sup>Labouriau (1973); <sup>24</sup>Labouriau & Morphy (1969); <sup>25</sup>De Leonardis *et al.* (1989); <sup>26</sup>Lobreau-Callen, Oltmann & Straka (1975); <sup>27</sup>Lobreau-Callen, Straka & Friedrich (1984); <sup>28</sup>Paiva & Santos Dias (1990); <sup>29</sup>Straka (1990); <sup>30</sup>Mohl (1835); <sup>31</sup>Erdtman (1952); <sup>32</sup>Sladkov (1967); <sup>33</sup>Hsieh, Hsieh & Lai (1995); <sup>34</sup>van der Ham (1988); <sup>35</sup>Arreguin-Sanchez *et al.* (1988); <sup>36</sup>Edgeworth (1877); <sup>37</sup>Simpson & Skvarla (1981); <sup>38</sup>Huang (1972); <sup>39</sup>Wang (1960); <sup>40</sup>Coetzee & Robbertse (1985); <sup>41</sup>Roubik & Moreno (1991); <sup>42</sup>Muller (1979); <sup>43</sup>Tissot, Chikhi & Nayar (1994).

describe the structure of Polygalaceae pollen using light microscopy (LM), scanning electron microscopy (SEM), and (selectively) transmission electron microscopy (TEM) in order to: (1) provide baseline data for studies on the ecology and evolution of pollen structure; (2) provide pollen data for phylogenetic analyses based on combined datasets; and (3) document the diversity of pollen structure in the family.

The pollen morphology of Polygalaceae has long been recognized as distinctive, and it has been used as a valuable diagnostic character at the family level (Chodat, 1896; Erdtman, 1952; van der Meijden, 1988). The pollen is polycolporate, often synorate (endocingulate), with between six and 30 ectoapertures (Erdtman, 1952; Eriksen, 1993; Furness & Stafford, 1995). However, until now, there has been no comprehensive, systematic survey of Polygalaceae pollen. In providing such a survey, this paper presents the first photomicrographs of the pollen of seven genera: *Balgoya*, *Barnhartia*, *Comesperma*, *Diclidanthera*, *Eriandra*, *Moutabea*, as well as *Polygala* subgenus *Badiera*, and species formerly included in *Nylandtia*, but now included in *Muraltia* (Forest & Manning, 2006). In addition, new information is presented for many species, such as *Polygala cruciata*, *P. meridionalis*, *P. uncinata*, *P. glochidiata*, *P. wattersii*, *P. hebeclada*, *P. macroptera*, and *P. obscura*. In this study, we sample the genus *Heterosamara* Kuntze, which was reinstated on the basis of flower morphology and pollen characters (Paiva, 1998). A summary of previous literature on the pollen of Polygalaceae is given in Tables 1 and 3.

## MATERIAL AND METHODS

### TAXON SAMPLING

The pollen of 73 species (Table 2), representing 18 genera, in Polygalaceae *sensu* Paiva (1998), Bernardi (2000), Eriksen, Staahl & Persson (2000), and Persson (2001) was examined using LM and SEM, and the pollen of eight species, representing seven genera, was examined using TEM. Taxon sampling was co-ordinated with that of the molecular studies by Forest (2004) and Forest *et al.* (2007) in order to facilitate future phylogenetic studies of combined datasets of the Fabales clade. All genera were sampled following the most recent authoritative taxonomic revisions available, and samples were chosen to be representative of geographical distributions, and biogeographical and morphological splits, within the genera. Sampling also sought to complement the pollen data already available from the literature (Tables 1 and 3; Table 1 lists the Polygalaceae genera recognized in this study, the total number of species per genus, and references to the taxonomic frame-

works that formed the basis of the sampling in each genus; Table 3 lists the literature for *Polygala*).

The three monotypic genera *Balgoya* P.Morat & Meijden (New Caledonia), *Barnhartia* Gleason (South America), and *Eriandra* P.Royen & Steenis (New Guinea) were all represented (Table 1). Both species of the West and Central African genus *Aroxima* Stapf were sampled to correspond with molecular studies. *Carpolobia* G.Don, also from Africa, is the sister taxon to *Aroxima*. It consists of four species, two of which were sampled to represent both savannah woodland (*C. goetzei*) and rain forest (*C. alba*). The Neotropical genus *Bredemeyera* Willd. has between 15 and 60 species depending on the taxonomic concepts followed (Marques, 1980; Eriksen *et al.*, 2000). Three species were sampled. Australian *Comesperma* Labill. includes 24 species, five of which were sampled, representing all three sections (Pedley, 1984). *Diclidanthera* Mart. is an Amazonian genus of four species, one of which was sampled. *Epirixanthes* Blume, with five to six species, has an Asian distribution (two species were sampled). Paiva (1998) recognized *Heterosamara* Kuntze as an African and Asian genus of 14 species, which is separated from *Polygala* mainly on the basis of pollen morphology. Four species were sampled to represent the geographical range.

Neotropical *Monnina* Ruiz & Pav. has about 150 species, and three species were sampled to reflect sections and geographical distribution. *Moutabea* Aubl. consists of eight to ten Central and South American species (Wendt, 2000), one of which was sampled. The mostly South African taxa *Muraltia* Neck. (117 species) and *Nylandtia* Dum. (two species) were sampled with seven and one species, respectively, to reflect the morphological and geographical ranges.

Sampling for *Polygala* L. follows the taxonomic frameworks of Paiva (1998). Paiva recognized about 500 species, divided into 12 subgenera, some of which were previously recognized as separate genera (i.e. the subgenera *Badiera* and *Phlebotaenia*). This study sampled 23 *Polygala s.l.* species representing ten of the 12 subgenera. The Asian *Salomonina* Lour. is a genus comprising six species, two of which were sampled to represent the geographical range. *Securidaca* L. is cosmopolitan (apart from Australia) and contains about 80 species, five of which were sampled to cover the geographical and morphological range. *Xanthophyllum* Roxb. has a geographical range from India across China and South-East Asia to Australia. The genus contains 93 species, seven of which were sampled to cover the seven sections recognized by van der Meijden (1982).

Pollen material was obtained from the herbaria of the Royal Botanic Gardens, Kew (K), the Mexican National Herbarium (MEXU), the Royal Botanic Garden, Sydney (NSW), and the Royal Botanic



**Table 2.** Polygalaceae pollen sampled, except for seven species which were not measured (*Aroxima afzeliana*, *Bredemeyera papuana*, *Muraltia alba*, *Muraltia serpylloides*, *Polygala* subgenus *Badiera panacea*, *Securidaca inappendiculata*, *Securidaca paniculata*)

Taxon	Average measurements $P \times E$ ( $\mu\text{m}$ )	$P/E$ ( $\mu\text{m}$ )	Polar wall ( $\mu\text{m}$ )	Excoapertures $l \times w$	Endoapertures $l \times w$	Aperture number
<i>Aroxima liberia</i> Stapf.	(29)–38.0–(38) × (31)–36.3–(40)	1.05	2	(17)–19.8–(24) × (2)–2.2–(3)	(3)–4–(6) × 5–8 or endocingulate	7–8
<i>Balgoya pacifica</i> Morat & Meijden (six collections examined)	(41)–45.9–(49) × (44)–45.3–(50)	1.01	1	(10)–21.4–(33) × (1)–2–(5)	(1)–3.6–(11) × 3–6	3
<i>Barnhartia floribunda</i> Gleason	(29)–30.4–(32) × (44)–45.2–(50)	0.67	2	(18)–19.6–(22) × (0.5)–2.5–(4)	(3)–3.2–(5) × endocingulate	7–10
<i>Bredemeyera lucida</i> (Benth.) Benn. (two collections examined)	23–24–(25) × (20)–21–(22)	1.14	1.5	(18)–18.7–(20) × (1)–1–(1)	(2)–2.7–(3) × (4)–4.5–(5)	10–11
<i>Bredemeyera microphylla</i> Hieron.	(26)–28.8–(32) × (20)–24–(29)	1.20	1.5–2	(19)–21.8–(23) × (1)–1.3–(2)	(2)–3.2–(4) × 3 or endocingulate	10–12
<i>Carpolobia alba</i> G.Don	(36)–45.9–(44) × (38)–41.7–(45)	1.10	1.5–2	(24)–28.4–(32) × (2)–2.8–(3)	(5)–7.7–(10) × endocingulate	12–15
<i>Carpolobia goetzii</i> Gurke	(34)–36.6–(40) × (34)–36.4–(40)	1.00	2–3	(21)–25.7–(30) × (1)–1.6–(3)	(4)–5.7–(7) × (3)–5.3–(8) or endocingulate	10–11
<i>Comesperma calymega</i> Labill.	(36)–39–(40) × (30)–35.5–(39)	1.11	2–3	(27)–30.8–(34) × (2)–2.2–(3)	(4)–5.2–(6) × endocingulate	12–13
<i>Comesperma ericinum</i> DC.	(41)–42.5–(50) × (35)–41.7–(44)	1.01	2	(31)–38–(47) × (2)–3.4–(5)	(7)–9.2–(11) × endocingulate	13–18
<i>Comesperma hispidulum</i> Pedley	(34)–41.4–(45) × (37)–44.7–(59)	0.99	2	(25)–30.8–(31) × (3)–3.4–(4)	(9)–9.4–(10) × endocingulate	15–17
<i>Comesperma virgatum</i> Labill.	(46)–50.1–(54) × (45)–50.5–(55)	0.93	1.5–2	(36)–37.8–(40) × (4)–4.2–(5)	(6)–7.8–(10) × endocingulate	14–17
<i>Comesperma volubile</i> Labill.	(51)–53.8–(58) × (41)–44.2–(47)	1.22	2	(37)–39–(42) × (2)–3–(4)	(6)–7.4–(10) × endocingulate	13–15
<i>Didclanthera penduliflora</i> Mart.	(34)–38–(40) × (32)–36.1–(40)	1.05	2–3	(22)–24.7–(27) × (1)–1.7–(2)	(2)–2.4–(3) × (4)–5.3–(7)	8–9
<i>Epirixanthes elongata</i> Bl.	Not available					
<i>Epirixanthes papuana</i> J.J.Sm.	(39)–39.8–(48) × (33)–37.8–(43)	1.05	1.5	(10)–13.4–(16) × 2	(1)–1.4–(3) × endocingulate	15–18
<i>Eriandra fragrans</i> P.Royen & Steenis	(27)–26.2–(32) × (25)–26.6–(30)	0.98	2	(17)–18.4–(20) × (1)–1.2–(2)	(4)–4.4–(5) × endocingulate	6–8
<i>Heterosamara cabrae</i> (Chodat) J.A.R. Paiva	(35)–39.8–(47) × (65)–72.4–(81)	0.55	8 at top pole, 4 at bottom pole	(16)–20.6–(27) × (1)–1.4–(2)	(1)–4–(6) × endocingulate	33
<i>Heterosamara carrissoana</i> (Exell & Mendonça) J.A.R. Paiva	(35)–37.5–(40) × (52)–60.5–(69)	0.62	3	15 × 2	2 × endocingulate	
<i>Heterosamara tatarinowii</i> (Regal) J.A.R. Paiva	20 × 46	0.43	2	(15)–15–(15) × (2)–2.5–(3)	(2)–2.5–(3) × endocingulate	24
<i>Heterosamara ubonata</i> (Craib) J.A.R. Paiva	(9)–16–(20) × (30)–39.6–(43)	0.40	2	(11)–12.8–(14) × 2	2 × endocingulate	30
<i>Monnina leptostachya</i> Benth.	(29)–37.3–(41) × (29)–34.5–(38)	1.08	2–3.5	(19)–22.2–(26) × (1)–1.4–(1.5)	(1)–1.6–(3) × (3)–3.6–(4)	13–15
<i>Monnina richardiana</i> A.St.Hil.	(40)–42.1–(49) × (37)–42.4–(45)	0.98	3	(31)–34.8–(40) × (2)–2.8–(3)	(5)–5.6–(6) × endocingulate	13–15
<i>Monnina xalapensis</i> HBK	(37)–41.1–(48) × (39)–42.9–(50)	0.95	3	(26)–28.6–(31) × (1)–2.2–(3)	(2)–2.4–(3) × 3–8 or endocingulate	12–16
<i>Moutabea guianensis</i> Aubl.	(25)–29.4–(36) × (24)–27.4–(32)	1.07	4	(20)–20.3–(21) × 1	(1)–1.6–(2) × (1)–1.5–(2)	11–13
<i>Muraltia filiformis</i> (Thunb.) DC.	(42)–42.2–(51) × (40)–44.4–(48)	0.95	1–2	(38)–40.8–(44) × (6)–8–(9)	(6)–6.7–(8) × 12 or endocingulate	8–9
<i>Muraltia flanaganii</i> Bolus	(23)–25–(28) × (21)–24.9–(28)	1.00	2	(14)–15.8–(18) × (1)–1.4–(3)	(3)–3.4–(4) × 4 or endocingulate	14–16
<i>Muraltia heisteria</i> (L.) DC.	(46)–52.3–(59) × (40)–47.1–(52)	1.11	3	(31)–36.2–(42) × (8)–9.4–(11)	(4)–4.8–(6) × 13 or endocingulate	8–9
<i>Muraltia mixta</i> (L.f.) DC.	21–28.8–(32) × (31)–34.8–(38)	0.83	1	(16)–19–(22) × (4)–4.7–(6)	5 × endocingulate	10–11
<i>Muraltia thunbergii</i> E. and Z.	36 × 33	1.09	2–3	24 × 3	4 × endocingulate	9
<i>Nylandtia spinosa</i> (L.) Dumort.	28–34.6–(38) × (26)–33.3–(35)	1.04	2	(24)–24.8–(26) × (3)–3.6–(4)	5 × 5 or endocingulate	12–14
<b>Polygala L.</b>	(32)–34.8–(40) × (26)–27.9–(29)	1.25	2	(24)–26.4–(31) × 1	(1)–2.6–(4) × 4 or endocingulate	10–12
<b>Subgenus I <i>Phlebotanien</i> (Griseb.) S.F. Blake (= genus <i>Phlebotanien sensu Griseb.</i>)</b>						
<i>Phlebotanien covellii</i> Britton	(32)–34.8–(40) × (26)–27.9–(29)	1.25	2	(24)–26.4–(31) × 1	(1)–2.6–(4) × 4 or endocingulate	10–12
<i>Phlebotanien cuneata</i> Griseb.	(26)–28.4–(31) × (21)–26.3–(30)	1.08	2	(17)–20.8–(23) × 1	(3)–3.6–(4) × (6)–6.6–(7)	10
<b>Subgenus II <i>Badiera</i> (DC.) S.F. Blake (= genus <i>Badiera sensu DC.</i>)</b>						
<i>Badiera acuminata</i> DC.	(33)–36.5–(39) × (32)–35.3–(38)	1.03	2–3	(26)–29.2–(31) × (3)–4.2–(5)	(4)–7.4–(11) × 5–6 or endocingulate	12–13
<i>Badiera caracasana</i> (Kunth) C. Persson	(37)–42.2–(49) × (31)–32.9–(37)	1.28	2	(28)–30.6–(33) × (1)–1.2–(2)	(4)–4.2–(5) × 4 or endocingulate	17–18
<i>Badiera diversifolia</i> DC.	(23)–25.9–(29) × (24)–25.9–(28)	1.00	1.5–2	(20)–21–(22) × (2)–2.8–(3)	4 × 5–8 or endocingulate	8–10
<i>Badiera fuertesii</i> Urb.	(25)–27–(29) × (24)–26.4–(29)	1.02	1	(15)–17.8–(20) × (1)–1.4–(2)	(2)–2.4–(3) × (3)–4.2–(6)	8–10
<i>Badiera oblongata</i> Britton	(20)–21.8–(23) × (20)–22.7–(24)	0.96	2	(10)–13.6–(15) × (1)–1.5–(2)	(1)–1.9–(3) × (3)–3.4–(4)	8–10
<i>Badiera penaea</i> DC.	(22)–23.5–(25) × (16)–18–(21)	1.30	1	(14)–16–(19) × (1)–1–(1)	(2)–2.2–(3) × (3)–3.6–(4)	8–9

Table 2. Continued

Taxon	Average measurements $P \times E$ ( $\mu\text{m}$ )	$P/E$	Polar wall ( $\mu\text{m}$ )	Ectoapertures $l \times w$	Endoapertures $l \times w$	Aperture number
<b>Subgenus III <i>Hebecarpa</i> (Chodat) S.F. Blake (= sect. <i>Hebecarpa</i> Chodat)</b>						
<i>Polygala obscura</i> Benth.	(36)–38.2–(41) $\times$ (27)–33.7–(35)	1.13	1.5	(26)–26.8–(28) $\times$ (1)–1.2–(2)	(4)–4.8–(5) $\times$ endocingulate	18–22
<b>Subgenus IV <i>Acanthocladius</i> (Klotzsch ex Hassk.) Paiva (= genus <i>Acanthocladius</i> Klotzsch ex Hassk.)</b>						
<i>Polygala klotzschii</i> Chodat	(24)–26–(27) $\times$ (23)–25.5–(28)	1.02	2	(18)–19.2–(20) $\times$ (2)–2.2–(3)	(4)–4.2–(5) $\times$ (4)–5.2–(6)	8–10
<b>Subgenus V <i>Ligustrina</i> (Chodat) Paiva (= sect. <i>Ligustrina</i> Chodat)</b>						
<i>Polygala laureola</i> St Hil.	(74)–81.1–(87) $\times$ (46)–52.9–(56)	1.53	3	(28)–24.6–(27) $\times$ (6)–9.4–(10)	(7)–10–(12) $\times$ endocingulate	9
<i>Polygala ligustrinoides</i> A.St.Hil. & Moq.	(76)–83.6–(93) $\times$ (46)–56.3–(61)	1.48	3–3.5	(13)–13.8–(15) $\times$ (8)–9.6–(10)	(6)–6.8–(7) $\times$ endocingulate	8–9
<b>Subgenus VI <i>Brachytropis</i> (DC.) Chodat (= sect. <i>Brachytropis</i> DC.)</b>						
<i>Polygala micropophylla</i> L.	(36)–38.3–(39) $\times$ (33)–37–(40)	1.04	2.5–3	(25)–29–(32) $\times$ (4)–4.8–(6)	(5)–5.6–(6) $\times$ endocingulate	11–14
<b>Subgenus VII <i>Gymnospora</i> (Chodat) Paiva (= sect. <i>Gymnospora</i> Chodat)</b>						
<b>Subgenus VIII <i>Hebeclada</i> (Chodat) S.F. Blake (= sect. <i>Hebeclada</i> Chodat)</b>						
<i>Polygala hebeclada</i> DC.	(32)–36.1–(42) $\times$ (32)–39.9–(44)	0.90	1–2	(29)–31.8–(34) $\times$ (3)–4.4–(5)	(5)–6–(7) $\times$ endocingulate	11–13
<i>Polygala senega</i> DC.	(31)–32.8–(39) $\times$ (22)–31–(37)	1.06	1–2	(30)–31.4–(33) $\times$ (7)–8.4–(11)	2 $\times$ (8)–9.6–(12)	8–9
<b>Subgenus IX <i>Rhinotropis</i> (S.F. Blake) Paiva (= subgenus <i>Chamaebuxus</i> (DC.) Duch. sect. <i>Rhinotropis</i> S.F. Blake)</b>						
<b>Subgenus X <i>Chodatia</i> (= subgenus <i>Chamaebuxus</i> sect. <i>Artillus sensu</i> Chen)</b>						
<i>Polygala arillata</i> Buch-Ham.ex D.Don	(46)–51.4–(56) $\times$ (39)–43.6–(48)	1.18	1.5–2	(28)–30.4–(34) $\times$ (3)–3.4–(5)	(4)–6.2–(8) $\times$ endocingulate	17–18
<b>Subgenus X <i>Chodatia</i> (= subgenus <i>Pseudosemeiocardium</i> (Adema) J. Chrtrek &amp; B. Kisa sect. <i>Villosperma sensu</i> Wu &amp; Chen)</b>						
<i>Polygala wattersii</i> Hance	(30)–36.4–(42) $\times$ (53)–61.2–(65)	0.59	5	(25)–25.2–(26) $\times$ (5)–5.2–(6)	(7)–8.7–(10) $\times$ endocingulate	17–21
<b>Subgenus XI <i>Chamaebuxus</i> (DC.) Duch.</b>						
<i>Polygala chamaebuxus</i> Linn.	((50)–55.4–(62) $\times$ (48)–53.8–(60)	1.03	1–2	(37)–42.4–(45) $\times$ (5)–5.8–(6)	(5)–8–(10) $\times$ endocingulate	16–18
<b>Subgenus XII <i>Polygala</i> Duch.</b>						
<i>Polygala cruciata</i> L.	(34)–35.5–(37) $\times$ (32)–33.5–(35)	1.06	2–3	(22)–22.7–(23) $\times$ 1	(2)–2.7–(3) $\times$ endocingulate	10–12
<i>Polygala macroptera</i> DC.	(49)–52–(57) $\times$ (45)–51.3–(56)	1.01	2–3	(33)–35.6–(40) $\times$ (3)–4.4–(6)	(12)–12.6–(14) $\times$ (8)–9.2–(11)	12–15
<i>Polygala meridionalis</i> Levyns	(34)–40.6–(43) $\times$ (36)–39.7–(43)	1.02	2–3	(28)–31.6–(34) $\times$ (1.5)–3.1–(4)	(6)–10.4–(12) $\times$ endocingulate	20–21
<i>Polygala uncinata</i> C.Wright	(23)–32.1–(36) $\times$ (20)–29.1–(34)	1.10	1.5–2	(22)–24.2–(27) $\times$ (1)–3.4–(5)	(1)–2.8–(4) $\times$ 5–7 or endocingulate	10–11
<i>Polygala vulgaris</i> L.	(28)–31.8–(35) $\times$ (25)–34.4–(40)	0.92	2	(19)–23–(26) $\times$ 5	4 $\times$ endocingulate	9–12
<i>Salomonita ciliata</i> (L.) DC.	(34)–41.7–(46) $\times$ (35)–40.5–(43)	1.03	2	22 $\times$ 3	2 $\times$ endocingulate	13–14
<i>Salomonita longiciliata</i> Kurz.	(31)–38.7–(44) $\times$ (37)–41–(45)	0.94	1	(22)–23.4–(26) $\times$ (3)–4–(5)	(7)–9–(10) $\times$ endocingulate	14–16
<i>Securidaca diversifolia</i> (L.) Blake	(35)–39.4–(42) $\times$ (35)–39.3–(42)	1.00	1.5	(31)–34.4–(39) $\times$ (3)–4.4–(5)	(6)–6.4–(8) $\times$ (5)–6–(7)	11–13
<i>Securidaca longipendunculata</i> Fresen.	(32)–32.9–(35) $\times$ (32)–33.8–(35)	0.97	4–5	(23)–25.4–(27) $\times$ (2)–2.2–(3)	(2)–2.6–(4) $\times$ (5)–7.4–(8)	9–10
<i>Securidaca philippinensis</i> Chodat	(30)–33–(35) $\times$ (31)–34.8–(37)	0.95	2	(22)–25.3–(27) $\times$ 2	3 $\times$ (4)–4.6–(5)	8–9
<i>Securidaca virgata</i> Sw.	(36)–39.2–(43) $\times$ (32)–38.7–(44)	1.01	4	(28)–29.4–(31) $\times$ (3)–3.6–(4)	(3)–3.6–(4) $\times$ (5)–5.2–(6)	9–10
<i>Securidaca welwitschii</i> Oliv.	(29)–30.3–(32) $\times$ (32)–34–(36)	0.89	2.5	26 $\times$ 2	(1)–1.5–(2) $\times$ (4)–4.5–(5)	9–11
<i>Xanthophyllum affine</i> Korth.ex Mirq.	(28)–31.3–(35) $\times$ (30)–32.7–(35)	0.96	1–2	(18)–19.2–(20) $\times$ (1)–1.5–(2)	(4)–5–(6) $\times$ endocingulate	9–10
<i>Xanthophyllum ameonum</i> Chod.	(26)–25–(30) $\times$ (26)–24.7–(29)	1.01	2	(18)–20.2–(23) $\times$ (1)–1.2–(2)	3 $\times$ endocingulate	7–9
<i>Xanthophyllum fragrans</i> C.T.White	(41)–48.3–(52) $\times$ (41)–45.1–(49)	1.07	2	(24)–33.6–(40) $\times$ (2)–2.6–(3)	(8)–9–(11) $\times$ endocingulate	10–11
<i>Xanthophyllum lanceatum</i> (Mirq.) J.J.Smith	27–27.9–(29) $\times$ (23)–27–(30)	1.03	2	(17)–20–(22) $\times$ (1)–1.5–(2)	(3)–3.2–(4) $\times$ endocingulate	8–9
<i>Xanthophyllum octandrum</i> (F.Muell.) Domin	29–29.8–(31) $\times$ (28)–29.3–(31)	1.02	1.5–2	(19)–22–(24) $\times$ (2)–3–(4)	(5)–8–(10) $\times$ endocingulate	8–9
<i>Xanthophyllum papuanum</i> Meijden	(20)–22.9–(24) $\times$ (19)–20.9–(22)	1.10	1.5–2	(13)–16–(17) $\times$ 1	(4)–4.6–(6) $\times$ endocingulate	5–6
<i>Xanthophyllum vitellinum</i> D.Dietr.	(30)–37.5–(45) $\times$ (29)–30.6–(32)	1.23	2	(25)–27.9–(31) $\times$ (1)–1.6–(2)	(4)–8.6–(11) $\times$ endocingulate	9–10



**Table 3.** Summary of *Polygala* pollen literature

Species	Description	Drawing	LM	SEM	TEM	References
<i>abyssinica</i>	✓		✓			Erdtman (1952); Nair (1965); Sladkov (1967); Gupta & Sharma (1986); Kantha & Prasad (1989); Paiva (1998)
<i>africana</i>	✓		✓	✓		Paiva (1998)
<i>alba</i>	✓		✓	✓	✓	Larson & Skvarla (1961); Arreguin-Sanchez <i>et al.</i> (1988); Jones <i>et al.</i> (1995); Paiva (1998)
<i>albicans</i>	✓		✓	✓		Paiva (1998)
<i>alpestris</i>	✓		✓	✓		Furness & Stafford (1995); Paiva (1998)
<i>alpina</i>	✓		✓	✓		Villnueva & Ramos (1986); Furness & Stafford (1995); Paiva (1998)
<i>amara</i>	✓		✓	✓		Furness & Stafford (1995); Paiva (1998)
<i>amarella</i>	✓		✓	✓		Furness & Stafford (1995); Paiva (1998)
<i>ambigua</i>	✓		✓	✓		Ikuse (1956); Paiva (1998)
<i>angustifolia</i>	✓		✓	✓		Paiva (1998)
<i>apopetala</i>	✓		✓	✓		Paiva (1998)
<i>appressipilis</i>	✓		✓	✓		Arreguin-Sanchez <i>et al.</i> (1988); Paiva (1998)
<i>arcuata</i>	✓		✓	✓		Huang (1972)
<i>arillata</i>	✓	✓	✓	✓		Wang (1960); Sumithraarachchi (1982); Kantha & Prasad (1989); Chen (1991)
<i>arizonae</i>	✓		✓	✓		Paiva (1998)
<i>atacorensis</i>	✓		✓	✓		Paiva (1998)
<i>baetica</i>	✓		✓	✓		Villnueva & Ramos (1986); Ubersa & Diez (1994); Paiva (1998)
<i>baikiei</i>	✓		✓	✓		Paiva (1998)
<i>balansae</i>	✓		✓	✓		Reille (1995); Paiva (1998)
<i>barbeyana</i>	✓		✓	✓		Paiva (1998)
<i>baissieri</i>	✓		✓	✓		Villnueva & Ramos (1986); Paiva (1998)
<i>brachystachya</i>	✓		✓	✓		Kantha & Prasad (1989); Paiva (1998)
<i>bracteata</i>	✓		✓	✓		Edgeworth (1877)
<i>bulbothrix</i>	✓	✓	✓	✓		Kantha & Prasad (1989)
<i>butytacea</i>	✓		✓	✓		Paiva (1998)
<i>calcareo</i>	✓		✓	✓		Villnueva & Ramos (1986); Furness & Stafford (1995); Paiva (1998)
<i>capillaris</i>	✓		✓	✓		Paiva (1998)
<i>chamaebuxus</i>	✓	✓	✓	✓		Mohl (1835); Chodat (1896); Furness & Stafford (1995); Reille (1995); Paiva (1998)
<i>chinensis</i>	✓		✓	✓		Nair (1965); Sumithraarachchi (1982); Gupta & Sharma (1986); Kantha & Prasad (1989); Paiva (1998)
<i>comosa</i>	✓		✓	✓		Furness & Stafford (1995); Paiva (1998)
<i>compacta</i>	✓		✓	✓		Arreguin-Sanchez <i>et al.</i> (1988); Paiva (1998)
<i>cordata</i>	✓		✓	✓		Erdtman (1952)
<i>costaricensis</i>	✓		✓	✓		Paiva (1998)
<i>crisitata</i>	✓		✓	✓		Paiva (1998)
<i>crotonarioides</i>	✓		✓	✓		Nair (1965)
<i>crotonarioides</i>	✓		✓	✓		Gupta & Sharma (1986)
<i>cymosa</i>	✓		✓	✓		Jones <i>et al.</i> (1995)
<i>desertorum</i>	✓		✓	✓		Paiva (1998)
<i>elongata</i>	✓		✓	✓		Kantha & Prasad (1989); Paiva (1998)
<i>ericaefolia</i>	✓		✓	✓		Paiva (1998)
<i>erioptera</i>	✓		✓	✓		Van Campo (1958); Jain & Nanda (1966); Bonnefille & Riollet (1980); De Leonardis <i>et al.</i> (1989); El Ghazali (1989); Perveen, Ali & Qaiser (1994); Paiva (1998)
<i>fallax</i>	✓	✓	✓	✓		Chen (1991)
<i>flavescens</i>	✓		✓	✓		De Leonardis <i>et al.</i> (1989)
<i>floribunda</i>	✓		✓	✓		Paiva (1998)
<i>fruticosa</i>	✓	✓	✓	✓	✓	Graham (1963); Paiva & Santos Dias (1990); Paiva (1998)

Table 3. *Continued*

Species	Description	Drawing	LM	SEM	TEM	References
<i>furcata</i>	✓					Kantha & Prasad (1989)
<i>garcinii</i>	✓			✓		Paiva (1998)
<i>gayi</i>	✓					Paiva (1998)
<i>gazensis</i>	✓					Paiva (1998)
<i>glaucooides</i>	✓			✓		Sumithraarachchi (1982)
<i>globulifera</i>	✓	✓				Chen (1991)
<i>glomerata</i>	✓		✓	✓		Sumithraarachchi (1982); Chauhan & Bera (1990)
<i>grandiflora</i>	✓	✓				Edgeworth (1877); Nauman (1981); Paiva (1998)
<i>guineensis</i>	✓					Paiva (1998)
<i>hebantha</i>	✓					Paiva (1998)
<i>hebeclada</i>	✓					Paiva (1998)
<i>hirsutula</i>	✓			✓		Sumithraarachchi (1982)
<i>hispidula</i>	✓					Paiva (1998)
<i>hongkongensis</i>	✓					Wang (1960)
<i>incarnata</i>	✓			✓	✓	Larsen & Skvarla (1961); Jones <i>et al.</i> (1995); Paiva (1998)
<i>irregularis</i>	✓			✓		El Ghazali (1989); Perveen <i>et al.</i> (1994)
<i>irregularis</i>	✓					Paiva (1998)
<i>jamaicensis</i>	✓					Paiva (1998)
<i>japonica</i>	✓		✓			Ikuse (1956); Wang (1960); Huang (1972); Nakamura (1980); Paiva (1998)
<i>javana</i>	✓	✓		✓		Arachi (1968); Sumithraarachchi (1982); Kantha & Prasad (1989); Paiva (1998)
<i>klotzschii</i>	✓			✓		Paiva (1998)
<i>latifolia</i>	✓					Erdtman (1952); Sladkov (1967)
<i>laureola</i>	✓			✓		Paiva (1998)
<i>leptalea</i>	✓			✓		Sumithraarachchi (1982)
<i>ligustrioides</i>	✓		✓	✓		Braga (1961); Paiva (1998)
<i>limiflora</i>	✓					El Ghazali (1989)
<i>lutea</i>	✓			✓		Jones <i>et al.</i> (1995)
<i>macradenia</i>	✓			✓		Paiva (1998)
<i>macrolophos</i>	✓			✓		Sumithraarachchi (1982)
<i>macroptera</i>	✓					Paiva (1998)
<i>major</i>	✓		✓			Reille (1995)
<i>mellilotioides</i>	✓			✓		Paiva (1998)
<i>mexicana</i>	✓		✓	✓		Arreguin-Sanchez <i>et al.</i> (1988)
<i>mexicana</i>	✓			✓		Paiva (1998)
<i>microphylla</i>	✓		✓	✓	✓	Villnueva & Ramos (1986); Uberta & Diez (1994); Paiva (1998)
<i>minuta</i>	✓					Paiva (1998)
<i>monspeliaca</i>	✓		✓	✓	✓	Villnueva & Ramos (1986); De Leonardis <i>et al.</i> (1989); Uberta & Diez (1994); Reille (1995); Paiva (1998)
<i>mosii</i>	✓					Paiva (1998)
<i>munbyana</i>	✓					Paiva (1998)
<i>myrtifolia</i>	✓	✓		✓		Mohl (1835); Erdtman (1952); Paiva (1998)
<i>myrtilloides</i>	✓			✓		Arreguin-Sanchez <i>et al.</i> (1988)
<i>nana</i>	✓		✓	✓		Jones <i>et al.</i> (1995)
<i>nicaeensis</i>	✓			✓		Villnueva & Ramos (1986) (ssp.); Furness & Stafford (1995); Paiva (1998)
<i>obcordata</i>	✓					Erdtman (1952)
<i>oblongata</i>	✓					Paiva (1998)
<i>obscura</i>	✓					Paiva (1998)

<i>paniculata</i>	✓	✓	Huang (1972); Palacios-Chávez, Arreguin-Sánchez & Quiroz-García (1990); Roubik & Moreno (1991); Paiva (1998)
<i>parryi</i>	✓		Paiva (1998)
<i>perrieri</i>	✓	✓	Paiva (1998)
<i>persicariaefolia</i>	✓	✓	Kantha & Prasad (1989)
<i>persicariifolia</i>	✓		El Ghazali (1989); Paiva (1998)
<i>pilosa</i>	✓	✓	Lobreau-Callen <i>et al.</i> (1975); Straka (1975)
<i>preslii</i>	✓	✓	De Leonardis <i>et al.</i> (1989); Paiva (1998)
<i>ramosa</i>	✓	✓	Jones <i>et al.</i> (1995)
<i>reinii</i>	✓	✓	Ikuse (1956)
<i>rosmarinifolia</i>	✓	✓	Sumithraarachchi (1982); Kantha & Prasad (1989); Paiva (1998)
<i>rupestris</i>	✓	✓	Villnueva & Ramos (1986); Ubers & Diez (1994); Paiva (1998)
<i>senega</i>	✓		Ikuse (1956) (var. <i>latifolia</i> ); Paiva (1998)
<i>sepyllacea</i>	✓	✓	Erdtman (1943)
<i>serpens</i>	✓	✓	Paiva (1998)
<i>serpyllifolia</i>	✓	✓	Erdtman (1969); Blackmore & Barnes (1986); Furness & Stafford (1995); Reille (1995); Paiva (1998)
<i>shimadae</i>	✓	✓	Huang (1972)
<i>sibirica</i>	✓		Kantha & Prasad (1989)
<i>stiptata</i>	✓	✓	Paiva (1998)
<i>subalata</i>	✓	✓	Arreguin-Sanchez <i>et al.</i> (1988)
<i>sunalata</i>	✓		Paiva (1998)
<i>tatarinowii</i>	✓	✓	Nakamura (1980)
<i>telephoides</i>	✓	✓	Sumithraarachchi (1982); Kantha & Prasad (1989)
<i>timouthoides</i>	✓	✓	Braga (1961); Paiva (1998)
<i>tricornis</i>	✓	✓	Wang (1960)
<i>triflora</i>	✓	✓	Sumithraarachchi (1982)
<i>triphylla</i>	✓	✓	Huang (1972)
<i>vayreadae</i>	✓	✓	Villnueva & Ramos (1986); Paiva (1998)
<i>violoides</i>	✓	✓	Paiva (1998)
<i>virgata</i>	✓	✓	Paiva (1998)
<i>viscoides</i>	✓	✓	Paiva (1998)
<i>vulgaris</i>	✓	✓	Aldridge (1842); Edgeworth (1877); Pereira (1942, 1943); Erdtman (1952, 1969); Dimbleby (1967); Moore & Webb (1978); Simpson & Skvarla (1981); Villnueva & Ramos (1986); Moore, Webb & Collinson (1991); Furness & Stafford (1995); Reille (1995); Paiva (1998)
<i>wattersii</i>	✓		Chen (1991)
<i>webbiana</i>	✓	✓	Paiva (1998)
<i>welwitschii</i>	✓	✓	Paiva (1998)
<i>wightiana</i>	✓	✓	Kantha & Prasad (1989)
<i>youngii</i>	✓	✓	Paiva (1998)

LM, light microscopy; SEM, scanning electron microscopy; TEM, transmission electron microscopy.

Garden, Edinburgh (E). All taxa and specimens studied are listed in Table 2.

#### METHODS

Mature, unopened buds from herbarium specimens were dissected in a 1% solution of Libsorb. Pollen was acetolysed according to Erdtman (1960) and prepared for LM by mounting in glycerol jelly. Measurements were recorded using a Nikon Labophot LM. At least ten grains of each sample were measured for polar length (*P*), equatorial width (*E*), exine thickness at the pole, and aperture dimensions (Table 2). For SEM, acetolysed pollen exines in 95% ethanol were pipetted onto specimen stubs and allowed to air dry. Specimens were sputter coated with platinum and examined using a Hitachi S-2400 SEM. For TEM, acetolysed material was fixed with a 2% solution of osmium tetroxide (OsO<sub>4</sub>) in cacodylate buffer and prestained with 0.5% uranyl acetate, before embedding in Epon-araldite resin, following the method of Skvarla (1966). The pollen was then thin sectioned using a diamond knife, poststained with uranyl acetate and lead citrate, and subsequently examined in a Hitachi H-300 TEM or a Jeol JEM 1210 TEM. Palynological terminology follows Punt *et al.* (1994).

Pollen samples were databased and preparations are available for reference at the Palynology Unit, Jodrell Laboratory, Royal Botanic Gardens, Kew.

#### RESULTS

Pollen measurements are given in Table 2, and a summary of pollen characters is provided in Table 4.

##### *ATROXIMA* (FIGS 1, 2)

Pollen isopolar and prolate spheroidal in equatorial view;  $P \times E = (29)–38–(38) \times (31)–36.3–(40) \mu\text{m}$ ;  $P/E = 1.05$ . Seven to eight apertures, zonocolporate (Fig. 2); ectoapertures (colpi) measure  $(17)–21.1–(25) \times (1)–1.6–(3) \mu\text{m}$ ; endoapertures measure  $(3)–4–(6) \times 5–8 \mu\text{m}$  where endoapertures are separate, or are fused to form endocingula. Aperture apices pointed in *A. afzeliana* (Fig. 2), square in *A. liberia*,  $2.5 \mu\text{m}$  wide. Exine  $2 \mu\text{m}$  thick at poles,  $3 \mu\text{m}$  thick at equator. Surface ornamentation in *A. afzeliana* psilate (Fig. 2), punctate in *A. liberia*; aperture membrane finely granular.

##### *BADIERA*

See *Polygala*.

##### *BALGOYA* (FIGS 3–6)

Pollen isopolar and spheroidal in equatorial view (Figs 3–6);  $P \times E = (41)–45.9–(49) \times (44)–45.3–(50) \mu\text{m}$ ;  $P/E = 1.01$ . Tricolporate (Figs 4, 6). Ectoaper-

tures  $(10)–21.4–(33) \times (1)–2–(5) \mu\text{m}$ ; endoapertures  $(1)–3.6–(11) \times 3–6 \mu\text{m}$ . Exine  $(1)–1.7–(3) \mu\text{m}$  thick at poles. Surface ornamentation finely rugulate (Figs 5, 6); aperture membrane finely granular.

##### *BARNHARTIA* (FIGS 7–9)

Pollen isopolar and oblate spheroidal in equatorial view;  $P \times E = (29)–30.4–(32) \times (29)–31.8–(34) \mu\text{m}$ ;  $P/E = 0.95$ . Seven to ten apertures (Figs 7, 9), zonocolporate. Ectoapertures  $(18)–19.6–(22) \times (0.5)–2.5–(4) \mu\text{m}$ ; endoapertures  $(3)–3.2–(5) \mu\text{m}$  in length, endocingulate. Exine  $2 \mu\text{m}$  thick at poles. Surface ornamentation psilate (Figs 8, 9) with a finely granular aperture membrane.

##### *BREDEMEYERA* (FIGS 10–12)

Pollen isopolar and subprolate in equatorial view;  $P \times E = (23)–26.4–(32) \times (20)–22.5–(29) \mu\text{m}$ ;  $P/E = 1.17$ . Nine to 12 apertures (Fig. 10), zonocolporate. Ectoapertures long, nearly equal to polar length and narrow  $(18)–20.3–(23) \times (1)–1.1–(3.5) \mu\text{m}$ ; endoapertures  $(2)–2.9–(4) \times 3–5 \mu\text{m}$ , or endocingulate (Figs 10, 12). Exine  $(1.5)–1.6–(2) \mu\text{m}$  thick at poles. Surface ornamentation psilate to sparsely punctate (Fig. 11). Aperture membrane psilate.

##### *CARPOLOBIA* (FIGS 13, 14)

Pollen isopolar and spheroidal to oblate spheroidal in equatorial view;  $P \times E = (34)–41.3–(44) \times (34)–39–(45) \mu\text{m}$ ;  $P/E = 0.99$ . Ten to 15 apertures (Fig. 13), zonocolporate. Ectoapertures  $(21)–27–(32) \times (1)–2.2–(3) \mu\text{m}$ ; endoapertures  $(4)–6.7–(10) \times 3–8 \mu\text{m}$ , or endocingulate. Ectoapertures irregularly shaped in *C. alba*. Exine  $(1.5)–2.1–(3) \mu\text{m}$  thick at poles. Surface ornamentation perforate to microreticulate in *C. alba* (Figs 13, 14), and psilate and sparsely punctate in *C. goetzii*. Aperture membrane psilate (*C. alba*, Fig. 14) to finely granular (*C. goetzii*).

##### *COMESPERMA* (FIGS 15–17)

Pollen isopolar and subprolate to oblate spheroidal in equatorial view;  $P \times E = (34)–45.4–(58) \times (30)–43.3–(59) \mu\text{m}$ ;  $P/E = 1.05$ . Twelve to 18 apertures (Fig. 15), zonocolporate. Ectoapertures  $(25)–35.3–(47) \times (2)–3.2–(5) \mu\text{m}$ ; endoapertures  $(4)–7.8–(11) \mu\text{m}$  in length, endocingulate (Fig. 16). *Co. ericinum* has irregularly shaped ectoapertures. Margin of colpus membrane with granules distinctly more coarse than rest of membrane in all taxa studied, except *Co. calymega*. Exine  $(1)–2–(3) \mu\text{m}$  thick at poles. Surface ornamentation psilate (*Co. calymega*), very finely rugulate punctate (*Co. ericinum*) to punctate (*Co. virgatum*); where puncta are present, they are either

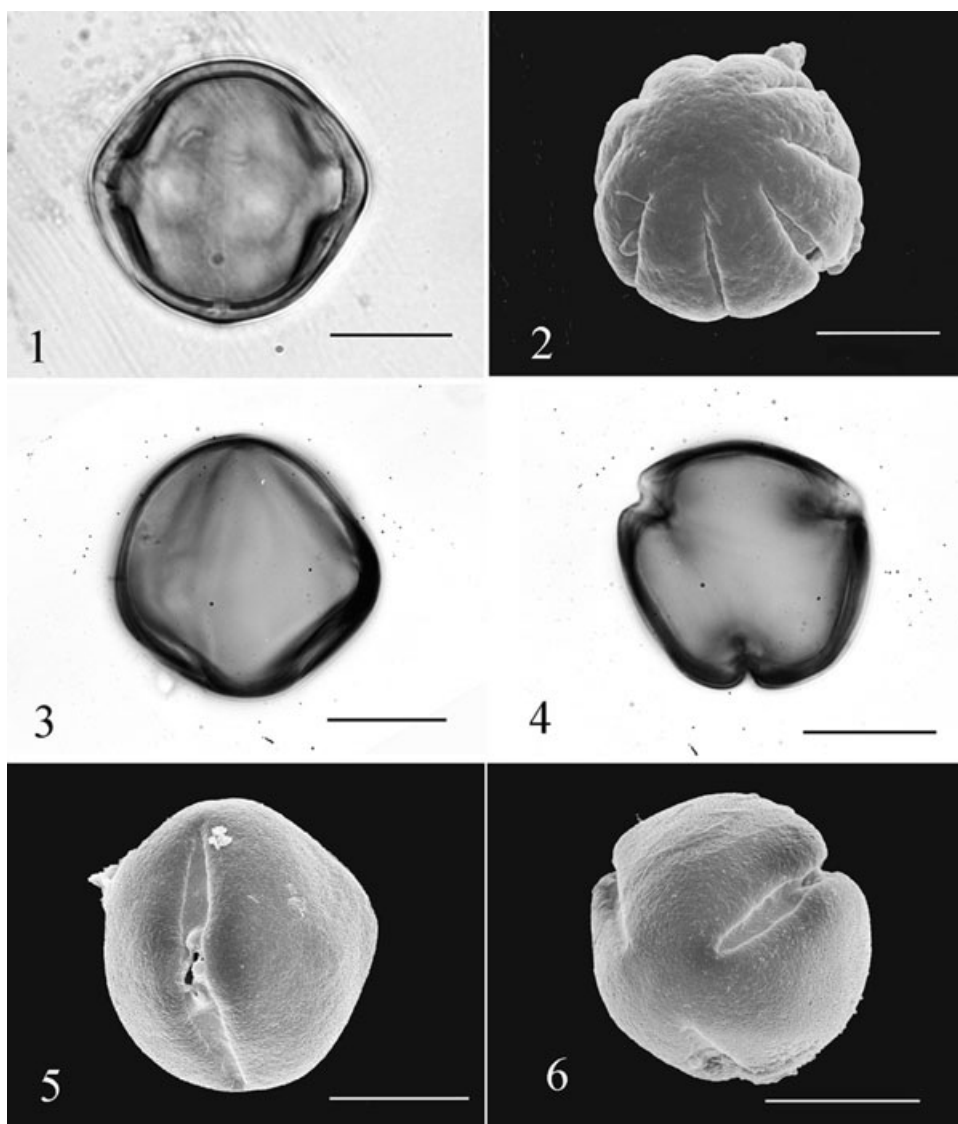
Table 4. Summary of pollen characters

Genus	Number of apertures	Average number of apertures	Endocingulum or separate endoapertures	Isopolar/heteropolar	Operculum	Larger granules around edge of aperture	Surface ornamentation
<i>Atrixima</i>	7–8	7.5	Both	Isopolar	Absent	Absent	Psilate or punctate
<i>Balgoya</i>	3	3	Separate	Isopolar	Absent	Absent	Finely rugulate
<i>Barnhartia</i>	7–10	8.5	Endocingulate	Isopolar	Absent	Absent	Psilate
<i>Bredemeyera</i>	9–12	11	Both	Isopolar	Absent	Absent	Psilate to finely punctate
<i>Carpolobia</i>	10–15	12.5	Both	Isopolar	Absent	Absent	Punctate to microreticulate, psilate to rugulate
<i>Comesperma</i>	12–18	15	Endocingulate	Isopolar	Absent	Mostly present	Punctate, psilate to finely rugulate
<i>Diclidanthera</i>	8–9	8.5	Separate	Isopolar	Absent	Absent	Psilate
<i>Epirixanthes</i>	15–18	16.5	Endocingulate	Isopolar	Sometimes present	Absent	Finely rugulate
<i>Eriandra</i>	6–8	7	Both	Isopolar	Absent	Absent	Psilate, finely punctate
<i>Heterosamara</i>	24–33	28.5	Endocingulate	Heteropolar	Absent	Present	Psilate to rugulate, punctate, lumina present
<i>Monnina</i>	12–16	14	Both	Isopolar	Absent	Absent	Psilate, perforate
<i>Moutabea</i>	11–13	12	Separate	Isopolar	Absent	Absent	Psilate to finely granular
<i>Muraltia</i>	8–16	12	Both	Isopolar	Absent	Present	Psilate, lumina present or absent
<i>Nylandtia</i>	12–14	13	Both	Isopolar	Absent	Present	Psilate, lumina present or absent
<i>Polygala</i>	8–22	15	Both	Isopolar	Absent	Sometimes present	Coarsely perforate, rugulate–fossulate
<i>Subgenus I: Phlebotaenia</i>	10–12	11	Both	Isopolar	Absent	Present	Psilate to punctate, sometimes with lumina
<i>Subgenus II: Badiera</i>	8–18	13	Both	Isopolar	Absent	Absent	Psilate–perforate
<i>Subgenus III: Hebecarpa</i>	18–22	20	Endocingulate	Isopolar	Absent	Absent	Psilate–perforate

Table 4. *Continued*

Genus	Number of apertures	Average number of apertures	Endocingulum or separate endoapertures	Isopolar/heteropolar	Operculum	Larger granules around edge of aperture	Surface ornamentation
<i>Subgenus IV:</i> <i>Acanthocladius</i>	8–10	9	Separate	Isopolar	Absent	Present	Fossulate
<i>Subgenus V: Ligustrina</i>	8–9	8.5	Endocingulate	Isopolar	Present	Absent	Psilate to granular to rugulate
<i>Subgenus VI:</i> <i>Brachytropis</i>	11–14	12.5	Endocingulate	Isopolar	Absent	Present	Finely granular with lumina
<i>Subgenus VII:</i> <i>Gymnospora</i>	No material						
<i>Subgenus VIII:</i> <i>Hebeclada</i>	8–13	10.5	Both	Isopolar	Absent	Present	Psilate
<i>Subgenus IX:</i> <i>Rhinotropis</i>	No material						
<i>Subgenus X: Chodatia,</i> <i>P. arillata</i>	17–18	17.5	Endocingulate	Isopolar	Absent	Present	Psilate with ring of depressions
<i>Subgenus X: Chodatia,</i> <i>P. arillata</i>	17–21	19	Endocingulate	Heteropolar	Absent	Absent	Psilate, punctate, perforate or rugulate, sometimes with lumina
<i>Subgenus XI:</i> <i>Chamaebuxus</i>	16–18	17	Endocingulate	Isopolar	Absent	Absent	Psilate
<i>Subgenus XII: Polygala</i>	9–21	15	Both	Isopolar	Sometimes present	Sometimes present	Psilate to finely granular, sometimes with lumina
<i>Salomonina</i>	13–14	13.5	Endocingulate	Isopolar	Absent	Absent	Rugulate to verrucate
<i>Securidaca</i>	8–13	10.5	Separate	Isopolar	Sometimes present	Present	Psilate to granular, sometimes perforate
<i>Xanthophyllum</i>	5–11	8	Endocingulate	Isopolar	Absent	Absent	Psilate, punctate



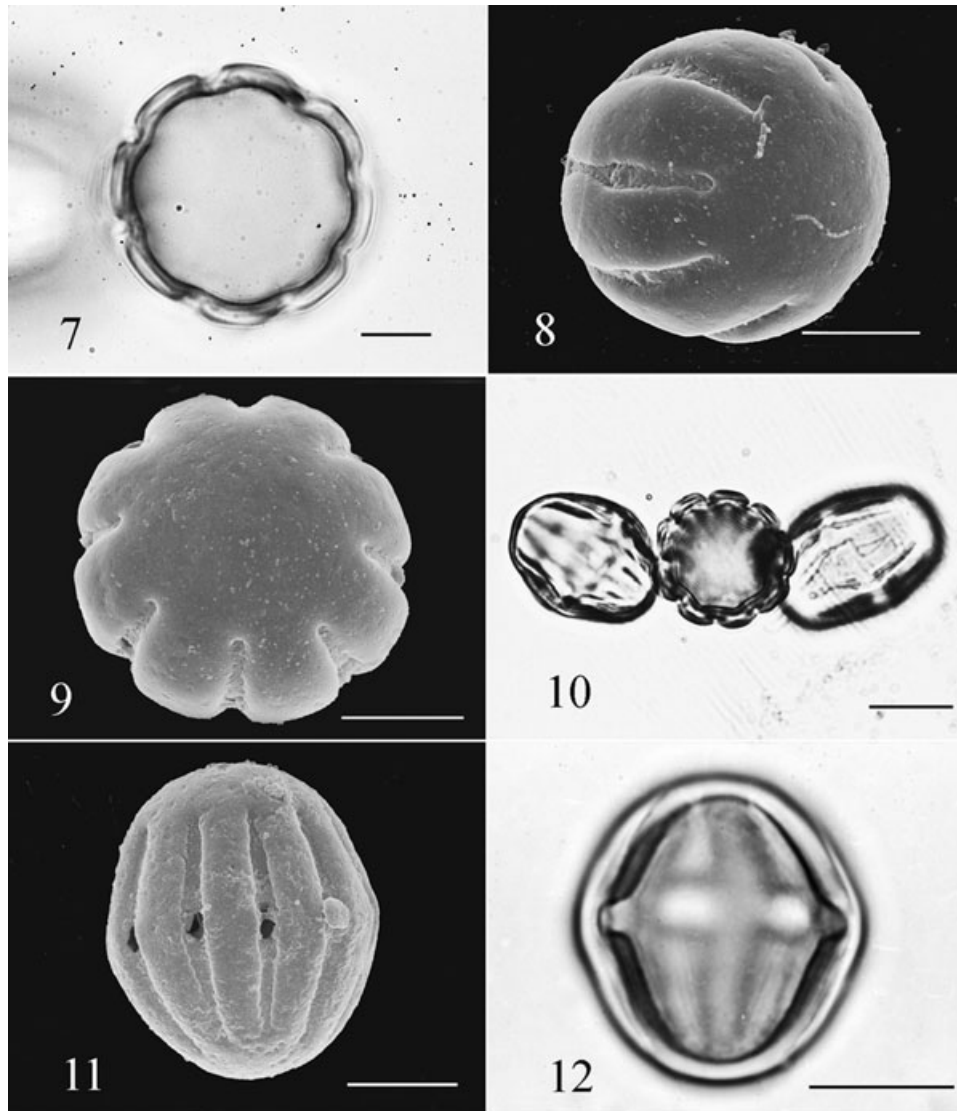


**Figures 1–6.** Fig. 1 *Atroxima liberia*, equatorial view of whole grain (light microscopy, LM). Fig. 2. *Atroxima afzeliana*, oblique polar view of whole grain showing eight apertures, pointed aperture apices, and psilate–punctate surface ornamentation (scanning electron microscopy, SEM). Fig. 3. *Balgoya pacifica*, equatorial view of whole grain (LM). Fig. 4. *Balgoya pacifica*, polar view of whole grain showing three apertures (LM). Fig. 5. *Balgoya pacifica*, equatorial view of whole grain showing colpulate aperture and finely rugulate surface ornamentation (SEM). Fig. 6. *Balgoya pacifica*, oblique polar view of whole grain showing three apertures and finely rugulate surface ornamentation (SEM). Scale bars: Figs 1, 2, 10  $\mu\text{m}$ ; Figs 3–6, 20  $\mu\text{m}$ .

small in mesocolpial regions and larger (c. 2  $\mu\text{m}$ ) in apocolpial regions (*Co. ericinum*, Fig. 15), or a uniform size (*Co. virgatum*); lumina irregularly shaped (0.5–2  $\mu\text{m}$ ) in apocolpial regions, spaced 1–2.5  $\mu\text{m}$  apart with granular lumen surface (*Co. virgatum*); aperture membrane finely granular. In thin section, columellae short and unbranched (0.2  $\mu\text{m}$ ); foot layer 0.2  $\mu\text{m}$ ; endexine 0.7  $\mu\text{m}$  with foraminae (Ferguson, 1987: Fig. 17).

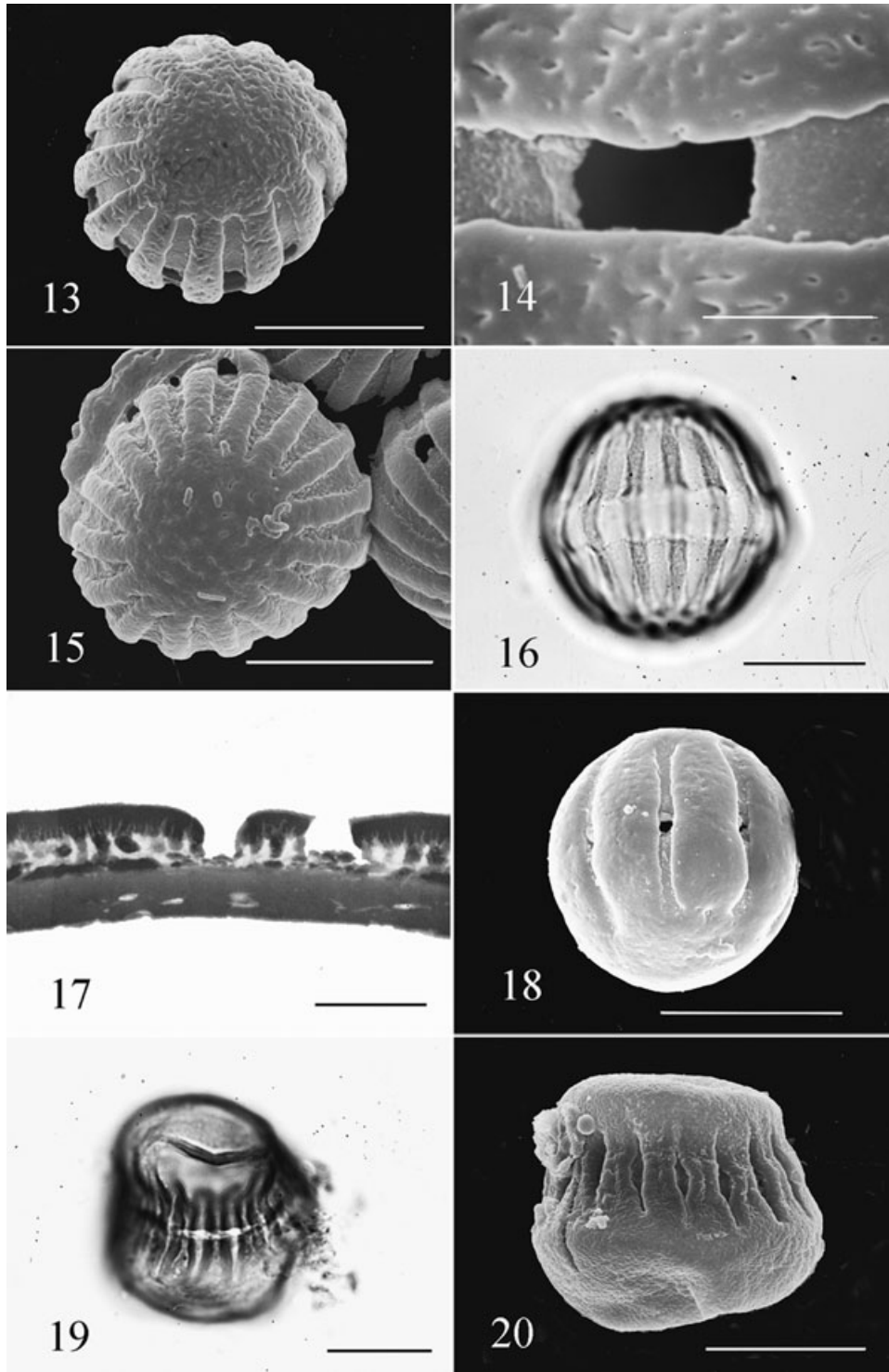
#### DICLIDANTHERA (FIG. 18)

Pollen isopolar and prolate spheroidal in equatorial view;  $P \times E = (34)–38–(40) \times (32)–36.1–(40) \mu\text{m}$ ;  $P/E = 1.05$ . Eight to nine apertures, zonocolporate. Ectoapertures (22)–24.7–(27)  $\times$  (1)–1.7–(2)  $\mu\text{m}$ ; endoapertures (2)–2.4–(3)  $\times$  (4)–5.3–(7)  $\mu\text{m}$ . Exine 2–3  $\mu\text{m}$  thick at poles. Surface ornamentation psilate with psilate aperture membrane (Fig. 18).



**Figures 7–12.** Fig. 7 *Barnhartia floribunda*, polar view of whole grain showing eight apertures (light microscopy, LM). Fig. 8 *Barnhartia floribunda*, oblique equatorial view of whole grain showing psilate surface ornamentation (scanning electron microscopy, SEM). Fig. 9 *Barnhartia floribunda*, polar view of whole grain showing eight apertures and psilate surface ornamentation (SEM). Fig. 10 *Bredemeyera microphylla*, group of three grains (LM). Fig. 11 *Bredemeyera microphylla*, equatorial view of whole grain (SEM). Fig. 12 *Bredemeyera lucida*, equatorial view of whole grain (LM). Scale bars: Figs 7–9, 11, 12, 10  $\mu\text{m}$ ; Fig. 10, 20  $\mu\text{m}$ .

**Figures 13–20.** Fig. 13 *Carpolobia alba*, polar view of whole grain showing 13 apertures (scanning electron microscopy, SEM). Fig. 14 *Carpolobia alba*, close up of aperture showing perforate surface ornamentation and psilate aperture surface (SEM). Fig. 15 *Comesperma ericinum*, polar view of whole grain showing 16 apertures and finely punctate–rugulate surface ornamentation with larger puncta in apocolpial region (SEM). Fig. 16 *Comesperma virgatum*, equatorial view of whole grain showing endocingulum (light microscopy, LM). Fig. 17 *Comesperma ericinum*, section through mesocolpial wall (transmission electron microscopy, TEM). Fig. 18 *Diclidanthera penduliflora*, equatorial view of whole grain showing psilate surface ornamentation (SEM). Fig. 19 *Epirixanthes papuana*, equatorial view of whole grain showing endocingulum and thickened aperture walls (LM). Fig. 20 *Epirixanthes papuana*, equatorial view of whole grain showing finely rugulate surface ornamentation and thickened aperture walls (SEM). Scale bars: Figs 13, 15, 16, 18–20, 20  $\mu\text{m}$ ; Fig. 14, 5  $\mu\text{m}$ ; Fig. 17, 2  $\mu\text{m}$ .



*EPIRIXANTHES* (FIGS 19, 20)

Pollen isopolar and prolate spheroidal in equatorial view;  $P \times E = (39)–39.8–(48) \times (33)–37.8–(43) \mu\text{m}$ ;  $P/E = 1.11$ . Fifteen to 18 apertures, zonocolporate.

Ectoapertures (10)–13.4–(16)  $\times$  2  $\mu\text{m}$ ; endoapertures (1)–1.4–(3)  $\mu\text{m}$  in length, endocingulate (Fig. 19). Exine 1.5  $\mu\text{m}$  thick at poles, with exine thickening (costae) around the ectoapertures. In *E. papuana*, the thinner walled areas at the poles tend to collapse

following acetolysis (Figs 19, 20). Surface ornamentation finely rugulate, smoother on exine bands covering the endocingulum (Fig. 20); aperture membrane finely granular. Exine visible over the endoaperture in *E. elongata* suggests the possible presence of opercula (requires TEM investigation).

#### ERIANDBRA (FIGS 21–23)

Pollen isopolar and oblate spheroidal in equatorial view;  $P \times E = (27)–26.2–(32) \times (25)–26.6–(30) \mu\text{m}$ ;  $P/E = 0.98$ . Six to eight apertures (Fig. 23), zonocolporate. Ectoapertures  $(17)–18.4–(20) \times (1)–1.2–(2) \mu\text{m}$ ; endoapertures  $(4)–4.4–(5) \mu\text{m}$  in length, endocingulate (Fig. 21). Exine  $2 \mu\text{m}$  thick at poles. Surface ornamentation psilate and sparsely punctate (Fig. 22); aperture membrane finely granular. In thin section, columellae short (c.  $0.1 \mu\text{m}$ ); foot layer c.  $0.1 \mu\text{m}$ ; endexine  $1 \mu\text{m}$  with foraminae (Fig. 23).

#### HETEROSAMARA (FIGS 24–28)

Pollen heteropolar, kidney-shaped, and oblate to peroblate in equatorial view (Figs 24, 26–28);  $P \times E = (9)–28.3–(47) \times (30)–54.6–(81) \mu\text{m}$ ;  $P/E = 0.5$ . Twenty-four to 33 apertures. Ectoapertures  $(11)–15.8–(27) \times (1)–1.9–(3) \mu\text{m}$ ; ectoaperture length variable depending on their position on the grain (Figs 24–26); position of endoaperture along the length of the ectoaperture not always central and variable within a sample (Figs 25, 26); endoapertures  $(1)–2.6–(6) \mu\text{m}$  in length, endocingulate. Exine  $(2)–3.8–(8) \mu\text{m}$  thick at poles. Surface ornamentation psilate in mesocolpial regions; punctate in apocolpial regions; apocolpial regions with regularly spaced circular lumina or foveolae; lumina  $(1)–1.3–(2) \mu\text{m}$ ; distance between lumina  $(0.4)–1.6–(2.5) \mu\text{m}$ ; lumen surface granular; aperture membrane granular. *Heterosamara cabrae* has circular lumina and rugulate ornamentation on its small apocolpial region, the larger apocolpial region has wide occasionally branching striations ( $1.5–2 \mu\text{m}$ ). These striations have rugulate–punctate ornamentation separated by grooves with granulate ornamentation. The ectoaper-

ture apices extend only into the small apocolpial region. The ectoaperture apices are asymmetrical in *H. cabrae* and *H. carrissoana* (Figs 24, 25); the ectoaperture apices are rounded at one end and pointed at the other. *Heterosamara umbonata* does not have punctate ornamentation in the apocolpial regions. In *H. carrissoana*, the lumina surfaces are punctate. Aperture membrane psilate to granular, with a layer of granular material around the edge of the ectoaperture margins (Figs 24, 25).

#### MONNINA (FIGS 29–31)

Pollen isopolar and prolate spheroidal to oblate spheroidal in equatorial view;  $P \times E = (29)–40.2–(49) \times (29)–29.9–(50) \mu\text{m}$ ;  $P/E = 1.00$ . Twelve to 16 apertures (Fig. 29), zonocolporate. Ectoapertures  $(19)–28.5–(40) \times (1)–2.1–(3) \mu\text{m}$ ; endoapertures  $(1)–3.2–(6) \times 3–8 \mu\text{m}$  or endocingulate (Fig. 31). Exine  $(2)–2.9–(3.5) \mu\text{m}$  thick. Surface ornamentation psilate–perforate (lumina less than  $1 \mu\text{m}$  in diameter) (Fig. 30); perforations separated by  $1–5 \mu\text{m}$ ; free-standing projecting elements from some perforations (to  $1 \mu\text{m}$  length); psilate aperture membrane (Fig. 30).

#### MOUTABEA (FIG. 32)

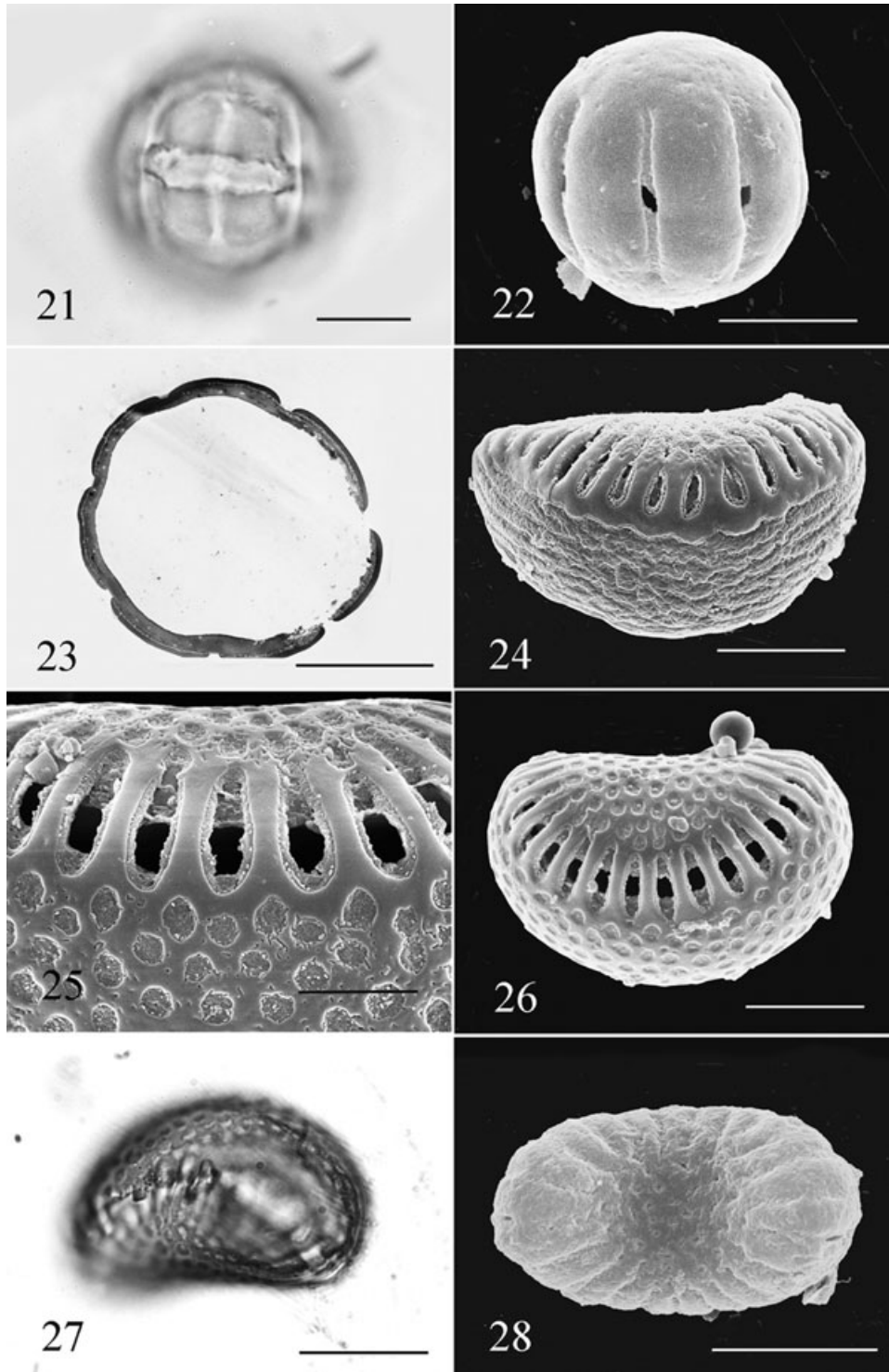
Pollen isopolar and prolate spheroidal in equatorial view;  $P \times E = (25)–29.4–(36) \times (24)–27.4–(32) \mu\text{m}$ ;  $P/E = 1.07$ . Eleven to 13 apertures, zonocolporate. Ectoapertures  $(20)–20.3–(21) \times 1 \mu\text{m}$ ; endoapertures  $(1)–1.6–(2) \times (1)–1.5–(2) \mu\text{m}$ . Exine  $4 \mu\text{m}$  thick at poles. Surface ornamentation psilate to finely granular; aperture membrane finely granular.

#### MURALTIA (FIGS 33–39)

Pollen isopolar and prolate spheroidal to suboblate in equatorial view;  $P \times E = (21)–36.9–(59) \times (21)–36.8–(52) \mu\text{m}$ ;  $P/E = 0.99$ . Eight to 16 apertures (Fig. 34), zonocolporate. Ectoapertures  $(14)–27.2–(44) \times (1)–5.3–(11) \mu\text{m}$ ; endoapertures  $(3)–4.78–(8) \times 4–13 \mu\text{m}$  or endocingulate (Figs 37, 38). *Muraltia filiformis* has a small apocolpial region (c.  $10 \mu\text{m}$  in

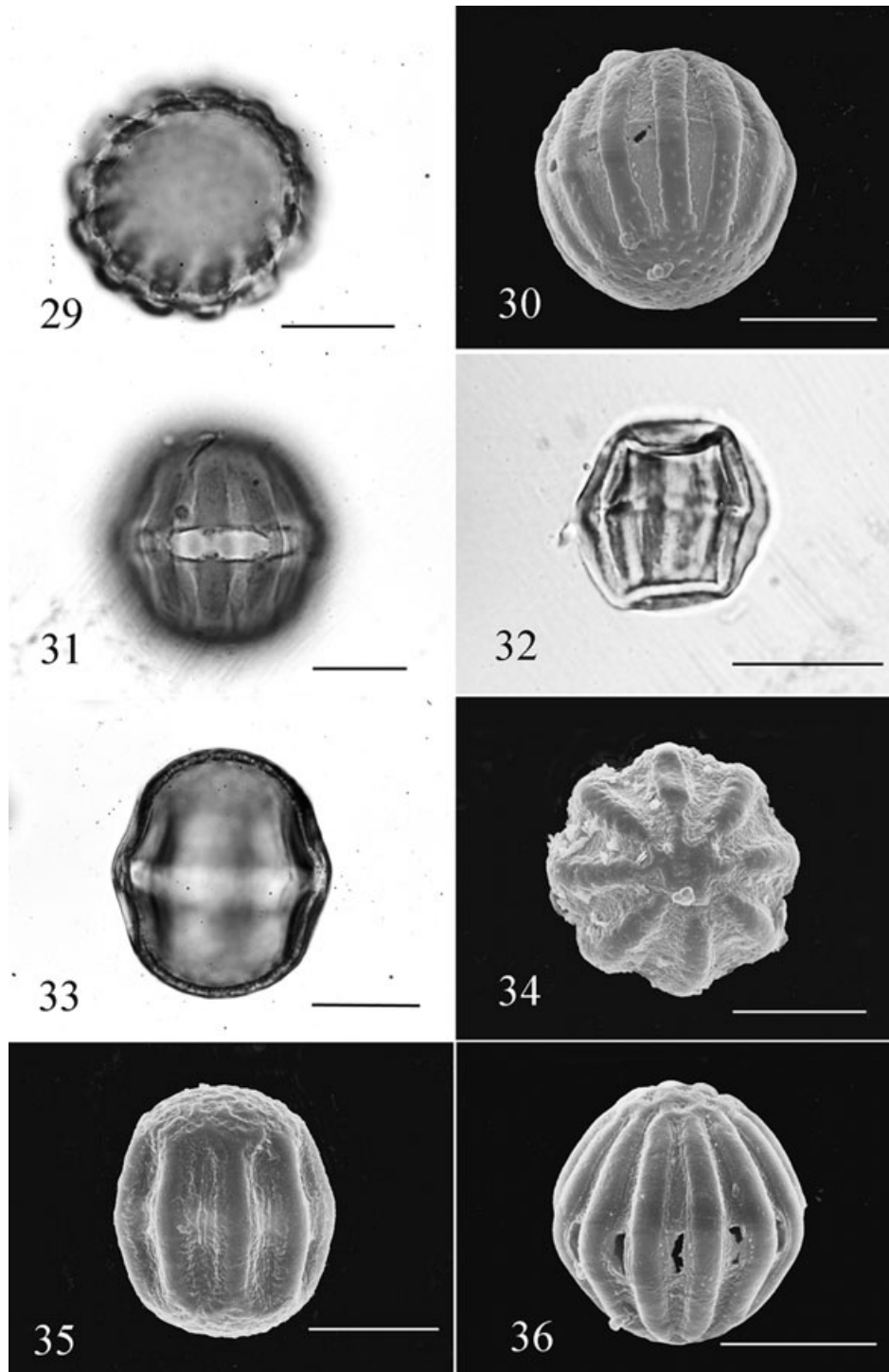
**Figures 21–28.** Fig. 21. *Eriandra fragrans*, equatorial view of whole grain showing endocingulum (light microscopy, LM). Fig. 22. *Eriandra fragrans*, equatorial view of whole grain showing psilate, sparsely punctate surface ornamentation (scanning electron microscopy, SEM). Fig. 23. *Eriandra fragrans*, transverse section (transmission electron microscopy, TEM). Fig. 24. *Heterosamara cabrae*, oblique equatorial view of whole grain showing heteropolar grain and variable size and shape of the apertures, which is related to their position on the grain. Aperture apices are rounded at one end and pointed at the opposite end (SEM). Fig. 25. *Heterosamara carrissoana*, close up of aperture showing the asymmetrical position of the endoapertures (SEM). Fig. 26. *Heterosamara carrissoana*, equatorial view of whole grain showing psilate surface ornamentation in mesocolpial regions and circular lumina in apocolpial regions (SEM). Fig. 27. *Heterosamara carrissoana*, equatorial view of whole grain (LM). Fig. 28. *Heterosamara tatarinowii*, polar view of whole grain (SEM). Scale bars: Figs 24, 26–28,  $20 \mu\text{m}$ ; Figs 21–23, 25,  $10 \mu\text{m}$ .





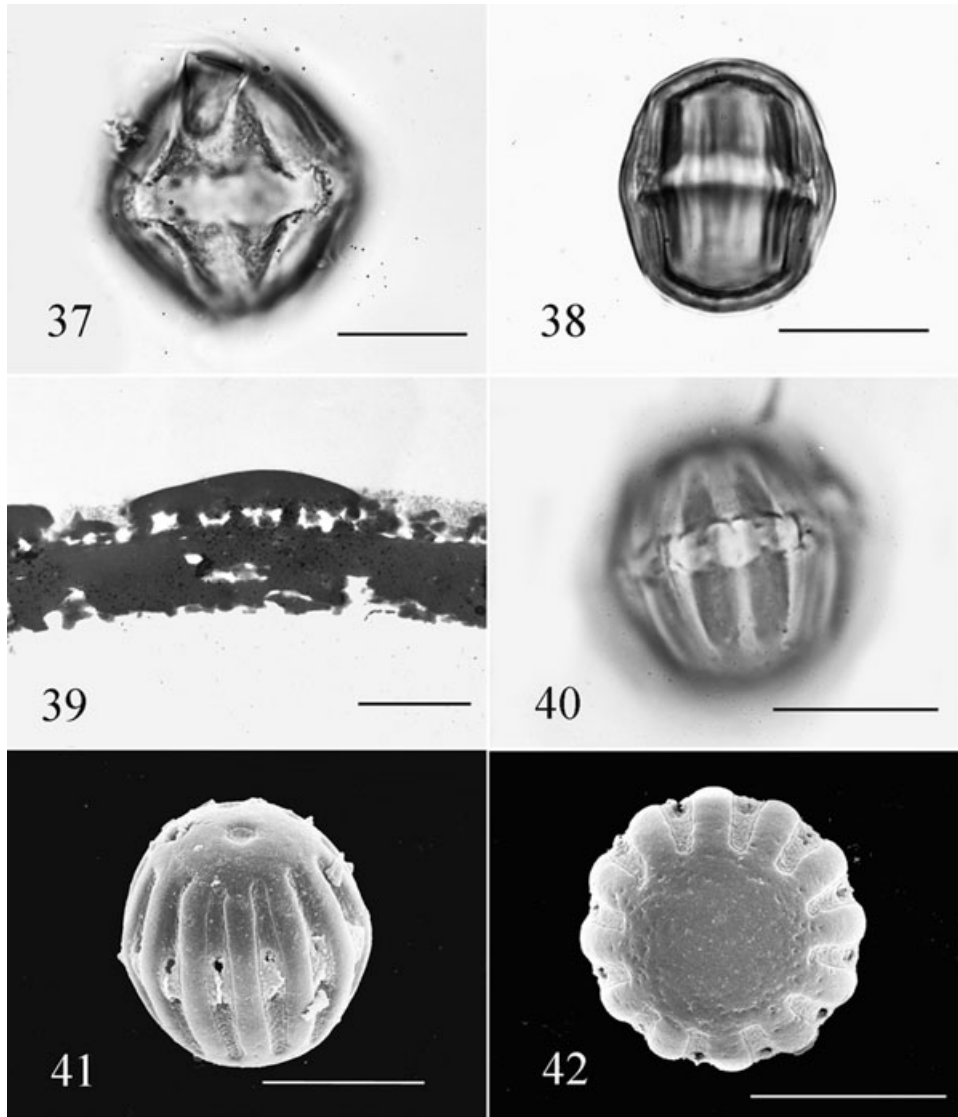
diameter). Exine (1)–2–(3)  $\mu\text{m}$  thick at poles. Surface ornamentation psilate; lumina present on apocolpia (except *M. flanaganii* and *M. mixta*) (Figs 34–36); lumina 0.5–2  $\mu\text{m}$  in diameter with coarsely granular lumen surface, lumina branching in *M. heisteria*;

aperture membrane granular (Figs 34–36); ectoaperture margin in *M. serpylloides* has distinctly larger granules. In thin section, columellae 0.2  $\mu\text{m}$  and unbranched; foot layer 0.1  $\mu\text{m}$ ; endexine 0.9  $\mu\text{m}$  thick at pole with foraminae (Fig. 39).



**Figures 29–36.** Fig. 29. *Monnina xalepensis*, polar view of whole grain showing 13 apertures (light microscopy, LM). Fig. 30. *Monnina xalepensis*, equatorial view of whole grain showing psilate–perforate surface ornamentation (scanning electron microscopy, SEM). Fig. 31. *Monnina richardiana*, equatorial view of whole grain showing endocingulum (LM). Fig. 32. *Moutabea guianensis*, equatorial view of whole grain (LM). Fig. 33. *Muraltia heisteria*, equatorial view of whole grain (LM). Fig. 34. *Muraltia filiformis*, polar view of whole grain showing eight apertures (SEM). Fig. 35. *Muraltia heisteria*, equatorial view of whole grain showing lumina present on apocolpial regions, psilate mesocolpial regions, and granular aperture membranes (SEM). Fig. 36. *Muraltia serpylloides*, equatorial view of whole grain showing similar ornamentation but more apertures when compared with Figure 35 (SEM). Scale bars, 20  $\mu$ m.





**Figures 37–42.** Fig. 37. *Muraltia filiformis*, equatorial view of whole grain showing endocingulum (light microscopy, LM). Fig. 38. *Muraltia thunbergii*, equatorial view of whole grain showing endocingulum (LM). Fig. 39. *Muraltia heisteria*, mesocolpial wall section (transmission electron microscopy, TEM). Fig. 40. *Nylandtia spinosa*, equatorial view of whole grain showing endocingulum (LM). Fig. 41. *Nylandtia spinosa*, equatorial view of whole grain showing psilate surface ornamentation with few lumina present in apocolpial region (scanning electron microscopy, SEM). Fig. 42. *Nylandtia spinosa*, polar view of whole grain showing psilate–punctate surface ornamentation in apocolpial region (SEM). Scale bars: Figs 37, 38, 40–42, 20 µm; Fig. 39, 2 µm.

*NYLANDTIA* (FIGS 40–42)

Pollen isopolar and prolate spheroidal in equatorial view;  $P \times E = (28)–34.6–(38) \times (26)–33.3–(35) \mu\text{m}$ ;  $P/E = 1.03$ . Twelve to 14 apertures (Fig. 42), zonocolporate. Ectoapertures  $(24)–24.8–(26) \times (3)–3.6–(4) \mu\text{m}$ ; endoapertures  $5 \times 5 \mu\text{m}$  or endocingulate (Fig. 40). Exine 2 µm thick at poles. Surface ornamentation psilate and punctate in apocolpial regions (Figs 41, 42); large lumina in apocolpial regions sparsely present (Fig. 41) or absent (Fig. 42); aperture

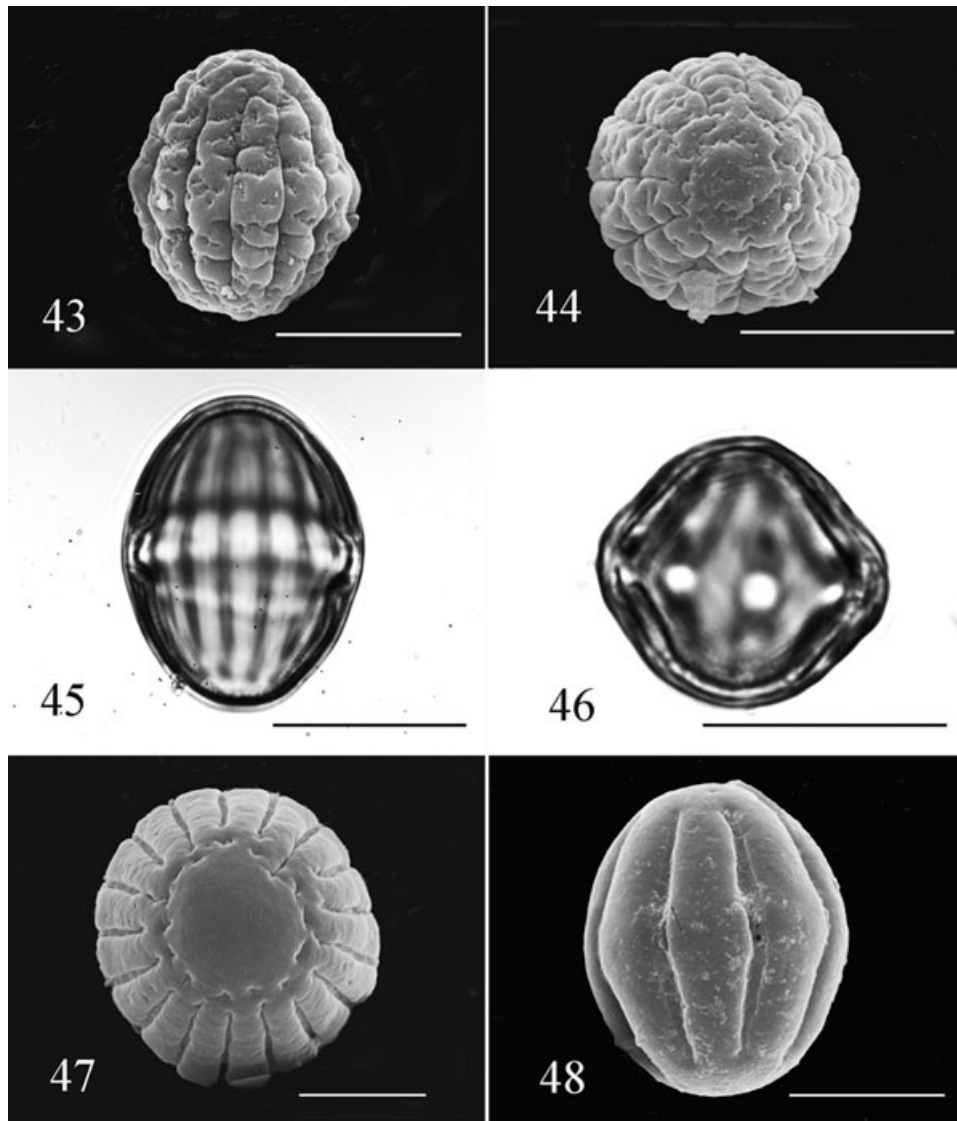
membrane granular; ectoaperture margin with distinctly larger granules.

*PHLEBOTAENIA*

See *Polygala*.

*POLYGALA* (FIGS 43–86)

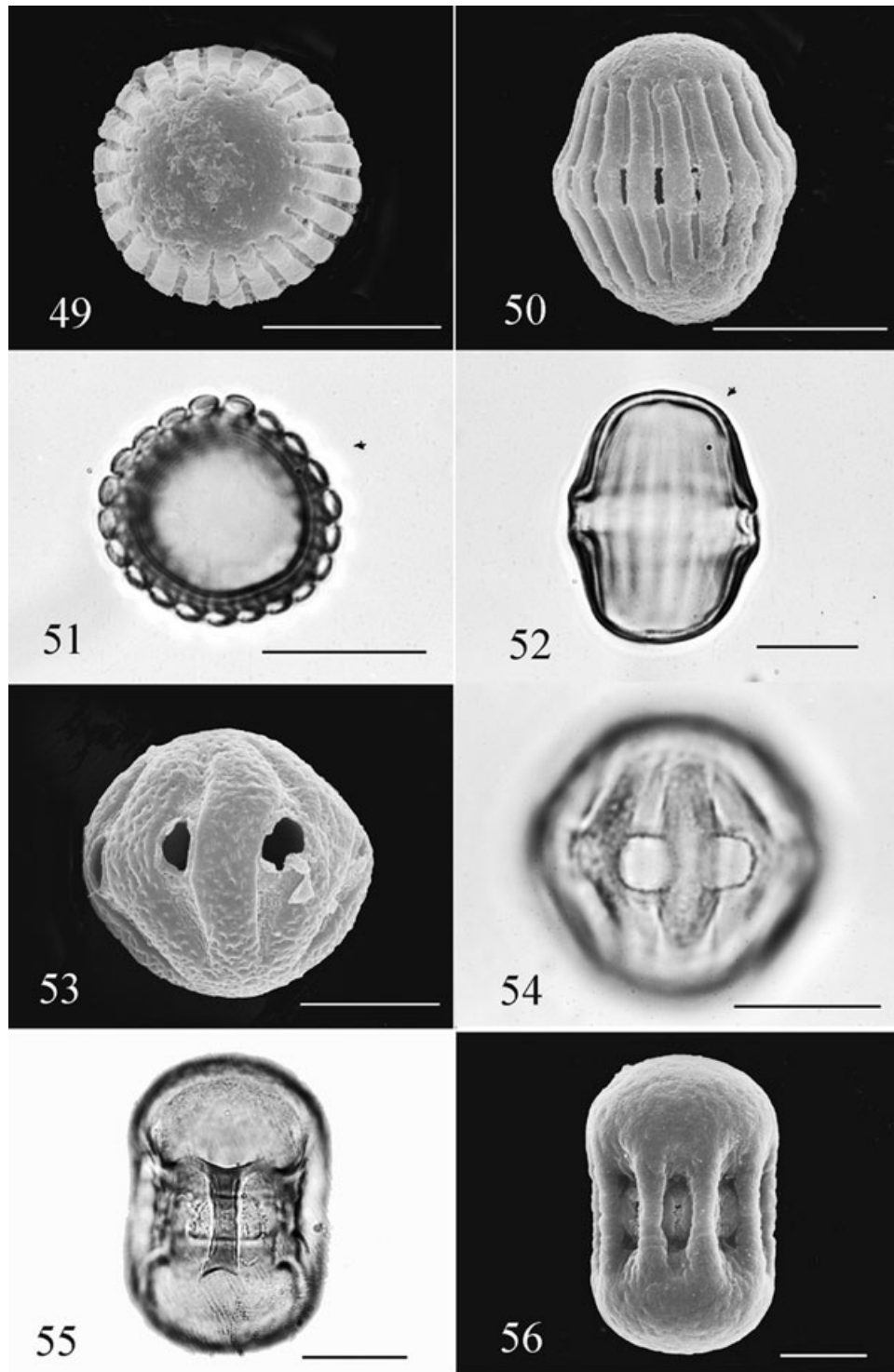
Pollen isopolar to heteropolar and prolate to oblate in equatorial view;  $P \times E = (22)–32.9–(93) \times (16)–$



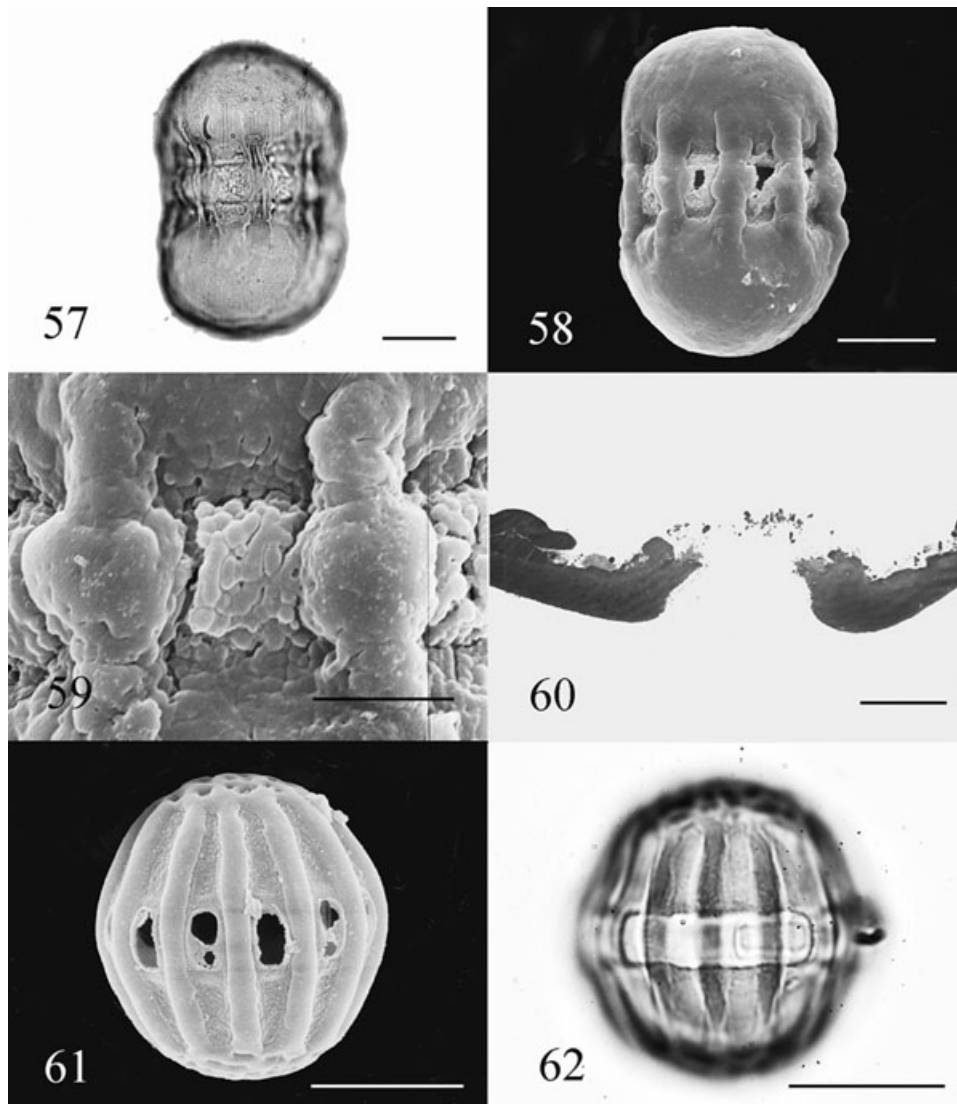
**Figures 43–48.** Fig. 43. *Phlebotaenia cowellii* (= *Polygala cowellii*), equatorial view of whole grain showing coarsely rugulate–fossulate surface ornamentation (scanning electron microscopy, SEM). Fig. 44. *Phlebotaenia cowellii* (= *Polygala cowellii*), polar view of whole grain showing 11 apertures (SEM). Fig. 45. *Badiera caracasana* (= *Polygala caracasana*), equatorial view of whole grain showing endocingulum (light microscopy, LM). Fig. 46. *Badiera oblongata* (= *Polygala oblongata*), equatorial view of whole grain showing discrete endoapertures (LM). Fig. 47. *Badiera panaea* (= *Polygala panaea*), polar view of whole grain showing a ring of depressions above aperture apices, psilate apocolpium, and 17 apertures (LM). Fig. 48. *Badiera panaea* (= *Polygala panaea*), equatorial view of whole grain showing psilate surface ornamentation (SEM). Scale bars, 20  $\mu\text{m}$ .

28.4–(65)  $\mu\text{m}$ ;  $P/E = 1.16$ . Eight to 22 apertures, zonocolporate. Ectoapertures (13)–21–(45)  $\times$  (1)–1.9–(11)  $\mu\text{m}$ ; endoapertures (1)–3.8–(14)  $\times$  3–12  $\mu\text{m}$  or endocingulate. Exine (1)–1.8–(5)  $\mu\text{m}$  thick at poles. Surface ornamentation psilate to granular; lumina absent or present; lumina, where present, sometimes restricted to apocolpial regions, sometimes also present in mesocolpial regions; lumen surface granular; aperture membrane finely to coarsely granular.

*Subgenus I Phlebotaenia* (Griseb.) S.F. Blake (= genus *Phlebotaenia* sensu Griseb.) (Figs 43, 44)  
Species examined: *Phlebotaenia cowellii*, *Ph. cuneata*. Pollen isopolar and subprolate to prolate spheroidal in equatorial view;  $P \times E = (26)$ –31.6–(40)  $\times$  (21)–27.1–(30)  $\mu\text{m}$ ;  $P/E = 1.16$ . Ten to 12 apertures, zonocolporate. Ectoapertures long and narrow (17)–23.6–(31)  $\times$  1  $\mu\text{m}$ ; endoapertures (1)–3.1–(4)  $\times$  4–7  $\mu\text{m}$  (endocingulate in *Ph. cowellii*). Exine 2  $\mu\text{m}$



**Figures 49–56.** Fig. 49. *Polygala obscura*, polar view of whole grain showing 22 apertures (scanning electron microscopy, SEM). Fig. 50. *Polygala obscura*, equatorial view of whole grain (SEM). Fig. 51. *Polygala obscura*, polar view of whole grain showing 21 apertures (light microscopy, LM). Fig. 52. *Polygala obscura*, equatorial view of whole grain showing endocingulum (LM). Fig. 53. *Polygala klotzschii*, equatorial view of whole grain showing fossulate surface ornamentation (SEM). Fig. 54. *Polygala klotzschii*, equatorial view of whole grain showing discrete endoapertures (LM). Fig. 55. *Polygala laureola*, equatorial view of whole grain (LM). Fig. 56. *Polygala laureola*, equatorial view of whole grain (SEM). Scale bars, 20  $\mu\text{m}$ .



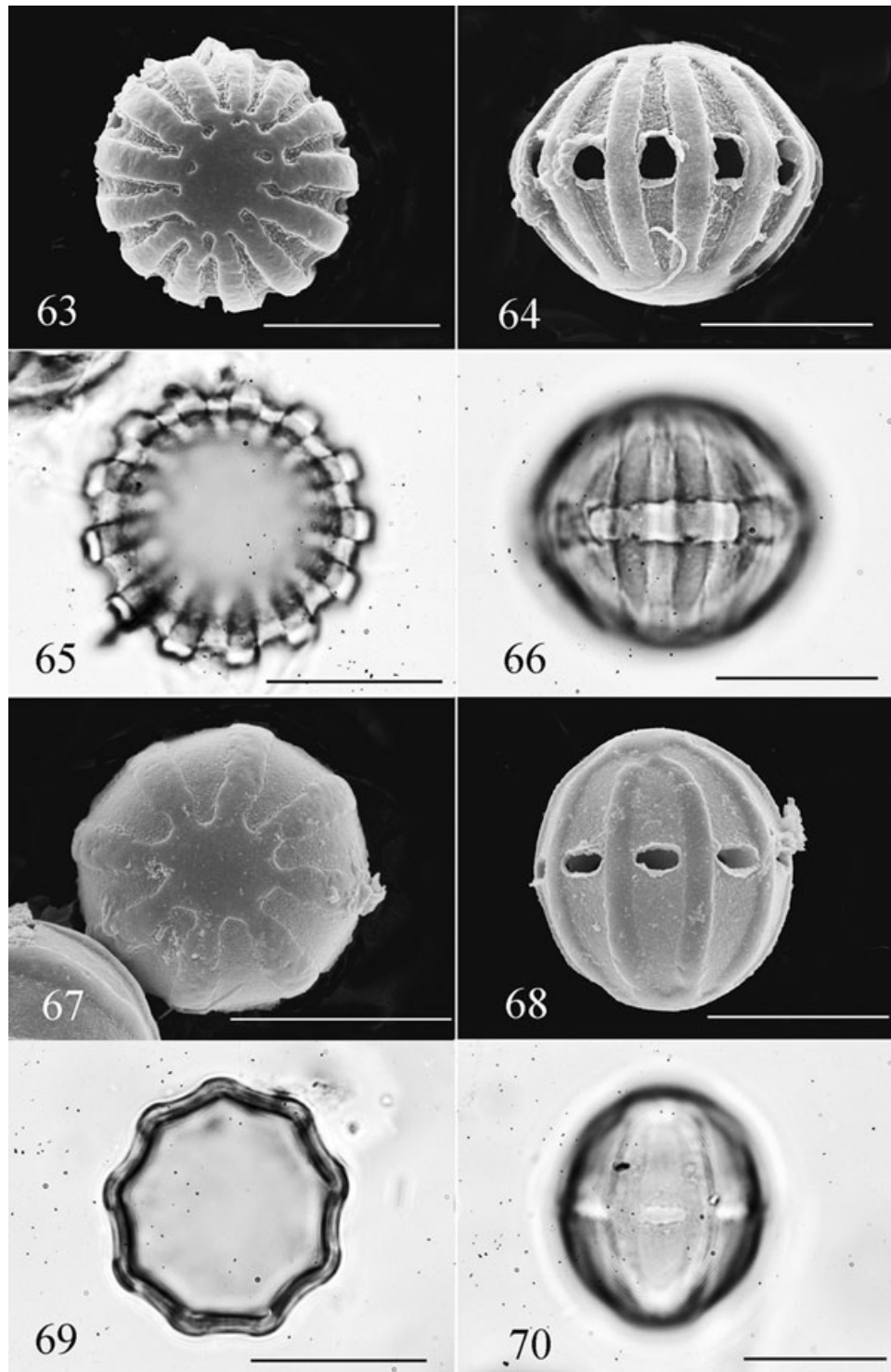
**Figures 57–62.** Fig. 57. *Polygala ligustrioides*, equatorial view of whole grain (light microscopy, LM). Fig. 58. *Polygala ligustrioides*, equatorial view of whole grain showing psilate surface ornamentation (scanning electron microscopy, SEM). Fig. 59. *Polygala ligustrioides*, detail of aperture showing operculum (SEM). Fig. 60. *Polygala ligustrioides*, section through endoaperture area (transmission electron microscopy, TEM). Fig. 61. *Polygala microphylla*, equatorial view of whole grain showing finely granular mesocolpial surface ornamentation and lumina visible in apocolpial regions (SEM). Fig. 62. *Polygala microphylla*, equatorial view of whole grain showing endocingulum (LM). Scale bars: Figs 57, 58, 61, 62, 20  $\mu\text{m}$ ; Fig. 59, 5  $\mu\text{m}$ ; Fig. 60, 2  $\mu\text{m}$ .

thick at poles. Surface ornamentation coarsely perforate, or coarsely perforate and coarsely rugulate-fossulate (Figs 43, 44); lumina 0.5  $\mu\text{m}$  wide separated by 0.5–2.5  $\mu\text{m}$ ; lumina surfaces coarsely granular and lumina branching in *Ph. cowellii*; aperture membrane granular, although ectoapertures are too narrow to observe the detail of the membrane in *Ph. cowellii*. In *Ph. cunneata*, the ectoaperture margins have distinctly larger granules.

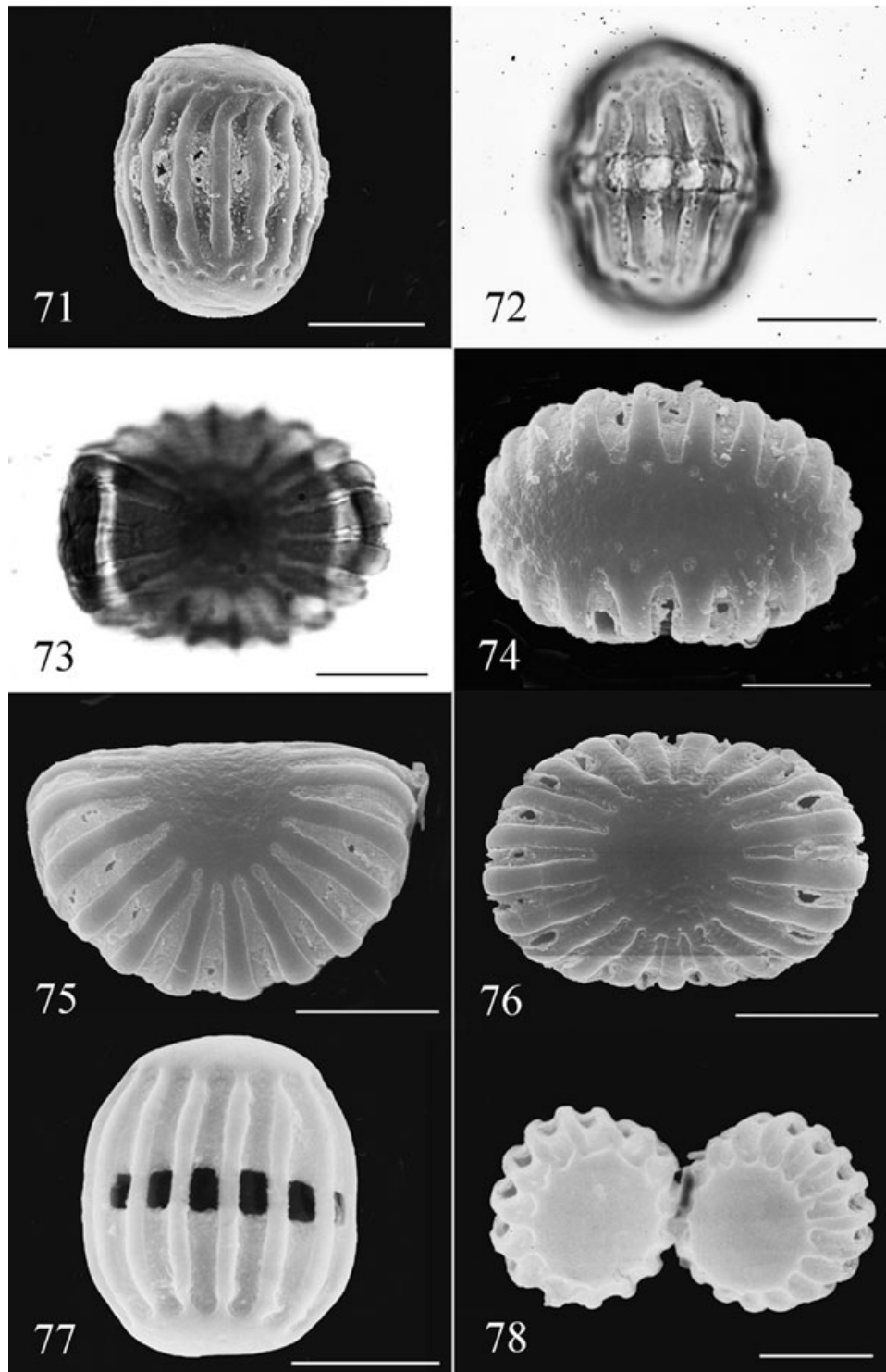
*Subgenus II Badiera* (DC.) S.F. Blake (=genus *Badiera sensu DC.*) (Figs 45–48)

Species examined: *Badiera acuminata*, *B. caracasana*, *B. diversifolia*, *B. fuertesii*, *B. oblongata*, *B. penaea*. Pollen isopolar and subprolate to oblate spheroidal in equatorial view;  $P \times E = (20)–29.5–(49) \times (16)–31.2–(38) \mu\text{m}$ ;  $P/E = 1.1$ . Eight to 18 apertures (generally eight to 12, with exception of *B. caracasana*, Fig. 45, which has 17–18), zonocolporate. Ectoapertures  $(10)–21.4–(33) \times (1)–2–(5) \mu\text{m}$ ;



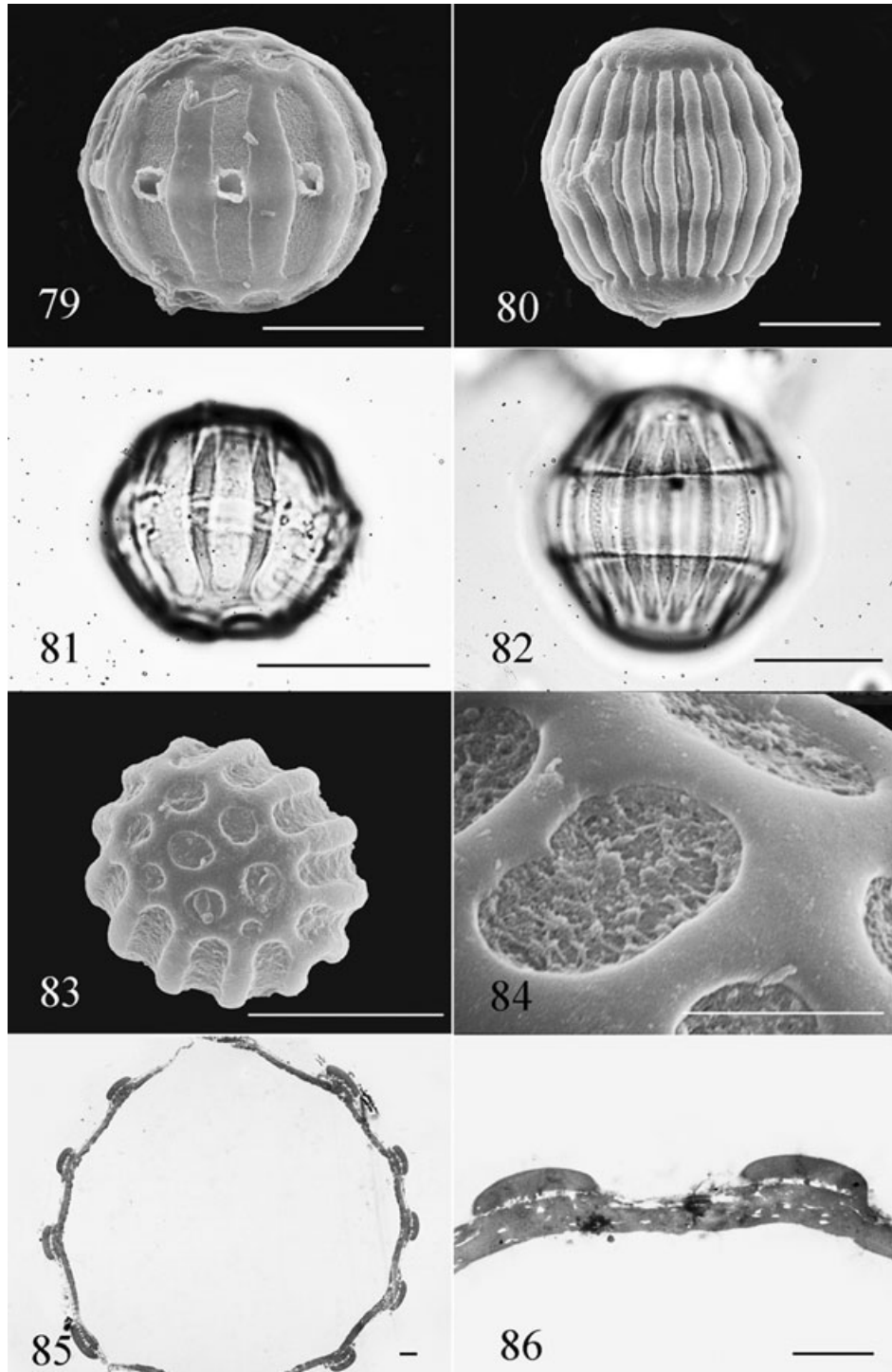


**Figures 63–70.** Fig. 63. *Polygala hebeclada*, polar view of whole grain showing 13 apertures (scanning electron microscopy, SEM). Fig. 64. *Polygala hebeclada*, equatorial view of whole grain (SEM). Fig. 65. *Polygala hebeclada*, polar view of whole grain showing 13 apertures (light microscopy, LM). Fig. 66. *Polygala hebeclada*, equatorial view of whole grain showing endocingulum (LM). Fig. 67. *Polygala senega*, polar view of whole grain showing eight apertures (SEM). Fig. 68. *Polygala senega*, equatorial view of whole grain (SEM). Fig. 69. *Polygala senega*, polar view of whole grain showing nine apertures (LM). Fig. 70. *Polygala senega*, equatorial view of whole grain showing discrete endoapertures (LM). Scale bars, 20  $\mu\text{m}$ .



**Figures 71–78.** Fig. 71. *Polygala arillata*, equatorial view of whole grain (scanning electron microscopy, SEM). Fig. 72. *Polygala arillata*, equatorial view of whole grain showing endocingulum (light microscopy, LM). Fig. 73. *Polygala wattersii*, polar view of whole grain; endocingula can be seen on the left and right (LM). Fig. 74. *Polygala wattersii*, opposite polar view of whole grain compared with Figure 73 (SEM). Fig. 75. *Polygala wattersii*, oblique polar view of whole grain (SEM). Fig. 76. *Polygala wattersii*, polar view of whole grain showing 21 apertures (cf. Fig. 73) (SEM). Fig. 77. *Polygala chamaebuxus*, equatorial view of whole grain (SEM). Fig. 78. *Polygala chamaebuxus*, polar view of two grains (SEM). Scale bars, 20  $\mu$ m.





**Figures 79–86.** Fig. 79. *Polygala cruciata*, equatorial view of whole grain (scanning electron microscopy, SEM). Fig. 80. *Polygala meridionalis*, equatorial view of whole grain showing psilate surface ornamentation without lumina in apocolpial regions and opercula over endoapertures (SEM). Fig. 81. *Polygala vulgaris*, equatorial view of whole grain showing endocingulum (light microscopy, LM). Fig. 82. *Polygala meridionalis*, equatorial view of whole grain (LM). Fig. 83. *Polygala vulgaris*, polar view of whole grain showing lumina on apocolpial area and 11 apertures (SEM). Fig. 84. *Polygala vulgaris*, close-up of surface detail showing large lumina (SEM). Fig. 85. *Polygala vulgaris*, transverse section through whole grain (transmission electron microscopy, TEM). Fig. 86. *Polygala vulgaris*, transverse section through mesocolpial wall (TEM). Scale bars: Figs 79–83, 20  $\mu\text{m}$ ; Fig. 84, 5  $\mu\text{m}$ ; Figs 85, 86, 2  $\mu\text{m}$ .

endoapertures  $(1)–3.6–(11) \times 3–6 \mu\text{m}$  (Fig. 46 shows endoapertures that are not joined), or endocingulate (Fig. 45). Exine  $(1)–1.7–(3) \mu\text{m}$  thick at poles. Surface ornamentation psilate, or, in *B. fuertesii*, sparsely punctate; aperture membrane finely granular, or, in *B. acuminata*, coarsely granular. The margins of the colpus membranes in *B. acuminata* and *B. fuertesii* are edged with coarser granules. In *B. caracasana* and *B. penaea* (Fig. 47), the apocolpia often have a ring of depressions independent of, or joined to, the ectoaperture apices. In thin section (*B. fuertesii*), columellae short and unbranched ( $0.1 \mu\text{m}$ ); foot layer  $0.1 \mu\text{m}$  in mesocolpial regions; endexine  $1 \mu\text{m}$  with foraminae.

*Subgenus III Hebecarpa* (Chodat) S.F. Blake (= sect. *Hebecarpa* Chodat) (Figs 49–52)

Species examined: *P. obscura*. Pollen isopolar and subprolate–spheroidal in equatorial view;  $P \times E = (36)–38.2–(41) \times (27)–33.7–(35) \mu\text{m}$ ;  $P/E = 1.13$ . Eighteen to 22 apertures, zonocolporate. Ectoapertures  $(26)–26.8–(28) \times (1)–1.2–(2) \mu\text{m}$ ; endoapertures  $(4)–4.8–(5) \mu\text{m}$  in length and endocingulate (Fig. 52). Exine  $1.5 \mu\text{m}$  thick at poles. Surface ornamentation psilate–perforate, with lumina up to  $1 \mu\text{m}$  in diameter. In *P. obscura* (Figs 49, 50), the number of lumina present in the apocolpial region varies in one sample from two to numerous. Aperture membrane granular.

*Subgenus IV Acanthocladus* (Klotzsch ex Hassk.) Paiva (= genus *Acanthocladus* Klotzsch ex Hassk.) (Figs 53, 54)

Species examined: *P. klotzschii*. Pollen isopolar and spheroidal in equatorial view;  $P \times E = (24)–26–(27) \times (23)–25.5–(28) \mu\text{m}$ ;  $P/E = 1.02$ . Eight to ten apertures, zonocolporate. Ectoapertures  $(18)–19.2–(20) \times (2)–2.2–(3) \mu\text{m}$ ; endoapertures  $(4)–4.2–(5) \times (4)–5.2–(6) \mu\text{m}$ , endoapertures are not joined (Fig. 54). Exine  $2 \mu\text{m}$  thick at poles. Surface ornamentation is fossulate in apocolpial and mesocolpial regions (Fig. 53). Aperture membrane granular, the ectoaperture margin has distinctly larger granules.

*Subgenus V Ligustrina* (Chodat) Paiva (= sect. *Ligustrina* Chodat) (Figs 55–60)

Species examined: *P. laureola*, *P. ligustrioides*. Pollen isopolar and prolate in equatorial view;  $P \times E = (74)–82.4–(93) \times (46)–54.6–(61) \mu\text{m}$ ;  $P/E = 1.51$ . Eight to nine apertures, zonocolporate. Ectoapertures  $(13)–19.2–(27) \times (6)–9.5–(10) \mu\text{m}$ ; endoapertures  $(6)–8.5–(12) \mu\text{m}$  in length and endocingulate. Exine  $3–3.5 \mu\text{m}$  thick at poles. Surface ornamentation variable: psilate, granular, rugulate, or occasionally microperforate. Aperture membrane coarsely granular (Fig. 59). Opercula may be present (Fig. 59),

although they may be lost during acetolysis. In thin section, infratectum  $0.1 \mu\text{m}$  thick at pole,  $0.9 \mu\text{m}$  thick at equator (*P. ligustrioides*); foot layer  $1.3 \mu\text{m}$  thick (pole) and  $2.2 \mu\text{m}$  thick (equator) and coarsely granular; endexine  $0.4 \mu\text{m}$  at pole with foraminae; endexine at equator sometimes separates behind mesocolpial regions with  $0.3 \mu\text{m}$  of endexine attached to the foot layer and large ( $8 \mu\text{m}$ ) endexinous protrusions on either side of the endocingulum; foraminae absent in protrusions.

*Subgenus VI Brachytropis* (DC.) Chodat (= sect. *Brachytropis* DC.) (Figs 61, 62)

Species examined: *P. microphylla*. Pollen isopolar and spheroidal in equatorial view;  $P \times E = (36)–38.3–(39) \times (33)–37–(40) \mu\text{m}$ ;  $P/E = 1.03$ . Eleven to 14 apertures, zonocolporate. Ectoapertures  $(25)–29–(32) \times (4)–4.8–(6) \mu\text{m}$ ; endoapertures  $(5)–5.6–(6) \mu\text{m}$  in length and endocingulate (Fig. 62). Exine  $2.5–3 \mu\text{m}$  thick at poles. Surface ornamentation finely granular, the lumina that are present in apocolpial areas are either round and less than  $1 \mu\text{m}$  in diameter or elongated forming a reticulate pattern. Aperture membrane granular, larger granules on ectoaperture margin.

*Subgenus VII Gymnospora* (Chodat) Paiva (= sect. *Gymnospora* Chodat)

No material available.

*Subgenus VIII Hebeclada* (Chodat) S.F. Blake (= sect. *Hebeclada* Chodat) (Figs 63–70)

Species examined: *P. hebeclada*, *P. senega*. Pollen isopolar spheroidal in equatorial view;  $P \times E = (31)–34.5–(42) \times (22)–35.5–(44) \mu\text{m}$ ;  $P/E = 0.98$ . Eight to 13 apertures, zonocolporate. Ectoapertures  $(29)–31.6–(34) \times (3)–6.4–(11) \mu\text{m}$  (*P. senega* has very wide ectoapertures, Figs 67–70); endoapertures  $(2)–4–(7) \times (8)–9.6–(12) \mu\text{m}$  (*P. senega*, Fig. 70) or endocingulate (*P. hebeclada*, Fig. 66). Exine  $1–2 \mu\text{m}$  thick at poles. Surface ornamentation psilate (Figs 63, 64, 67, 68). Aperture membranes finely granular, ectoaperture margins edged with a line of differing ornamentation.

*Subgenus IX Rhinotropis* (S.F. Blake) Paiva [= subgenus *Chamaebuxus* (DC.) Duch. sect. *Rhinotropis* S.F. Blake]

No material available.

*Subgenus X Chodatia* (= subgenus *Chamaebuxus* sect. *Arillus sensu Chen*) (Figs 71, 72)

Species examined: *P. arillata*. Pollen isopolar and subprolate in equatorial view;  $P \times E = (46)–51.4–(56) \times (39)–43.6–(48) \mu\text{m}$ ;  $P/E = 1.18$ . Seventeen to 18 apertures, zonocolporate. Ectoapertures  $(28)–30.4–$

(34) × (3)–3.4–(5) μm; endoapertures (4)–6.2–(8) μm in length and endocingulate (Fig. 72). Exine 2 μm thick at poles. Surface ornamentation psilate with a ring of depressions present at edge of apocolpial area above ectoaperture apices (Fig. 71). Aperture membrane margins have distinctly larger granules.

*Subgenus X Chodatia continued*

[= subgenus *Pseudosemeiocardium* (Adema)

*J. Chrtek & B. Kisa sect. Villosperma sensu*

*Wu & Chen*] (Figs 73–76)

Species examined: *P. wattersii*. Pollen heteropolar with one larger and one smaller apocolpial region, with one axis shorter than the other, producing a kidney-shaped grain. Oblate in equatorial view;  $P \times E = (30)–36.4–(42) \times (53)–61.2–(65)$  μm;  $P/E = 0.59$ . Seventeen to 21 apertures (Figs 74, 76). Ectoapertures (25)–25.2–(26) × (5)–5.2–(6) μm; endoapertures (7)–8.7–(10) μm and endocingulate. Exine 5 μm thick at poles. *Polygala wattersii* is heteropolar in shape, size, and ornamentation of the apocolpia, as in *Heterosamara*. Small apocolpium has psilate to perforate ornamentation (Figs 75, 76). Large apocolpium has punctate (Fig. 74) to rugulate ornamentation, occasionally with circular regularly spaced lumina around the edge of the apocolpial area above the ectoaperture apices (Fig. 74).

*Subgenus XI Chamaebuxus* (DC.) Duch. (Figs 77, 78)

Species examined: *P. chamaebuxus*. Pollen isopolar and spheroidal in equatorial view;  $P \times E = (50)–55.4–(62) \times (48)–53.8–(60)$  μm;  $P/E = 1.03$ . Sixteen to 18 apertures, zonocolporate. Ectoapertures (37)–42.2–(45) × (5)–5.8–(6) μm; endoapertures (5)–8–(10) μm in length and endocingulate. Exine 1–2 μm thick at poles. Surface ornamentation psilate, aperture membrane granular (Figs 77, 78).

*Subgenus XII Polygala* Duch. (Figs 79–86)

Species examined: *P. cruciata*, *P. macroptera*, *P. meridionalis*, *P. uncinata*, *P. vulgaris*. Pollen isopolar and spheroidal in equatorial view;  $P \times E = (23)–38.4–(57) \times (20)–37.6–(56)$  μm;  $P/E = 1.02$ . Nine to 21 apertures, zonocolporate. Ectoapertures (19)–27.4–(40) × (1)–3.4–(6) μm; endoapertures (1)–6.5–(14) × 5–11 μm or endocingulate. Pollen of *P. macroptera* consistently lacks an endocingulum, the endoapertures appear to be separate [endoaperture width (4)–8–(12) μm]. Some apertures within the sample of *P. uncinata* are also not endocingulate. Exine 1.5–3 μm thick at poles. Surface ornamentation psilate to finely granular, either without [*P. meridionalis* (Fig. 80), *P. uncinata*] or with lumina in apocolpial areas that are small (less than 1 μm in *P. macroptera*) or large [up to 7 μm in *P. cruciata* (Fig. 79) and *P. vul-*

*garis* (Figs 83, 84)]. Aperture membrane variable: psilate in *P. meridionalis*, punctate in *P. uncinata* and *P. cruciata*, finely granular in *P. macroptera*, and coarsely granular in *P. vulgaris*. Ectoaperture margins in *P. macroptera* and *P. uncinata* are edged with distinctly larger granules; in *P. uncinata*, the ectoaperture membranes are psilate in the centre, punctate in the outer areas, and coarsely granular at the edges. Possible presence of opercula in *P. macroptera* and *P. meridionalis* (Fig. 80). In thin section, *P. vulgaris* has short and unbranched (0.1 μm) columellae; the foot layer is indistinct or absent; endexine 0.5–1 μm with foraminae (Fig. 86).

*SALOMONIA* (FIGS 87–90)

Pollen isopolar and prolate spheroidal in equatorial view;  $P \times E = (34)–41.7–(46) \times (35)–40.5–(43)$  μm;  $P/E = 1.03$ . Thirteen or 14 apertures, zonocolporate. Ectoapertures (22)–22.7–(26) × (3)–4.5–(5) μm; endoapertures (2)–5.5–(10) μm and endocingulate (Fig. 87). Exine (1)–1.5–(2) μm thick at poles. Surface ornamentation rugulate (Fig. 88) to verrucate in apocolpial regions; aperture membrane granular. In thin section, columellae c. 0.1 μm; infratectal layer undulating and varying in thickness (Figs 89, 90); foot layer variable in thickness (up to 0.1 μm); endexine 0.6 μm.

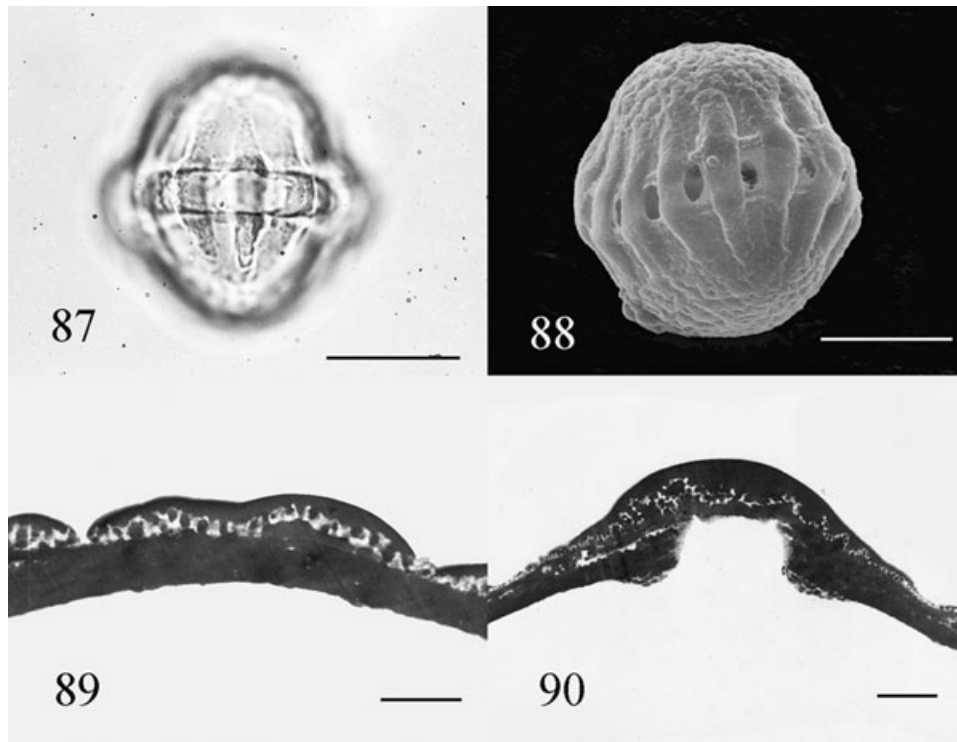
*SECURIDACA* (FIGS 91–98)

Pollen isopolar and prolate spheroidal to oblate spheroidal in equatorial view;  $P \times E = (29)–35–(43) \times (31)–36.1–(44)$  μm;  $P/E = 0.95$ . Eight to 13 apertures (Figs 93, 96), zonocolporate. Ectoapertures (22)–28.1–(39) × (2)–2.4–(5) μm; endoapertures (22)–22.7–(26) × (3)–3.5–(5) μm, endoapertures not joined (Figs 91, 97). *Securidaca longipedunculata* is parasyncolporate, with an apocolpial region that is isolated by a groove linking the ectoaperture apices (Fig. 93). The ectoaperture margins have large granules, and these continue to be present in the groove delimiting the apocolpial region. Exine (1.5)–2.7–(5) μm thick at poles. Surface ornamentation psilate (Fig. 93) to granular (Fig. 92), *S. virgata* is perforate in apocolpial and mesocolpial regions; aperture membrane psilate to granular, operculum present in some samples of *S. longipedunculata* (Figs 93, 94), *S. virgata*, and *S. welwitschii*. In thin section, columellae 0.2 μm; foot layer variable (to 0.5 μm); endexine 1.8 μm with foraminae (Figs 96, 98).

*XANTHOPHYLLUM* (FIGS 99–102)

Pollen isopolar and subprolate to oblate spheroidal in equatorial view;  $P \times E = (20)–31.8–(52) \times (19)–30–(49)$  μm;  $P/E = 1.04$  (*X. vitellinum* is unusual within





**Figures 87–90.** Fig. 87. *Salomonium ciliata*, equatorial view of whole grain showing endocingulum (light microscopy, LM). Fig. 88. *Salomonium longiciliata*, equatorial view of whole grain showing rugulate apocolpial regions and psilate mesocolpial region (scanning electron microscopy, SEM). Fig. 89. *Salomonium ciliata*, transverse section through polar wall (transmission electron microscopy, TEM). Fig. 90. *Salomonium ciliata*, longitudinal section through mesocolpial wall that overlies endocingulum; note undulating foot layer and infratectal layer (TEM). Scale bars: Figs 87, 88, 20  $\mu\text{m}$ ; Figs 89, 90, 2  $\mu\text{m}$ .

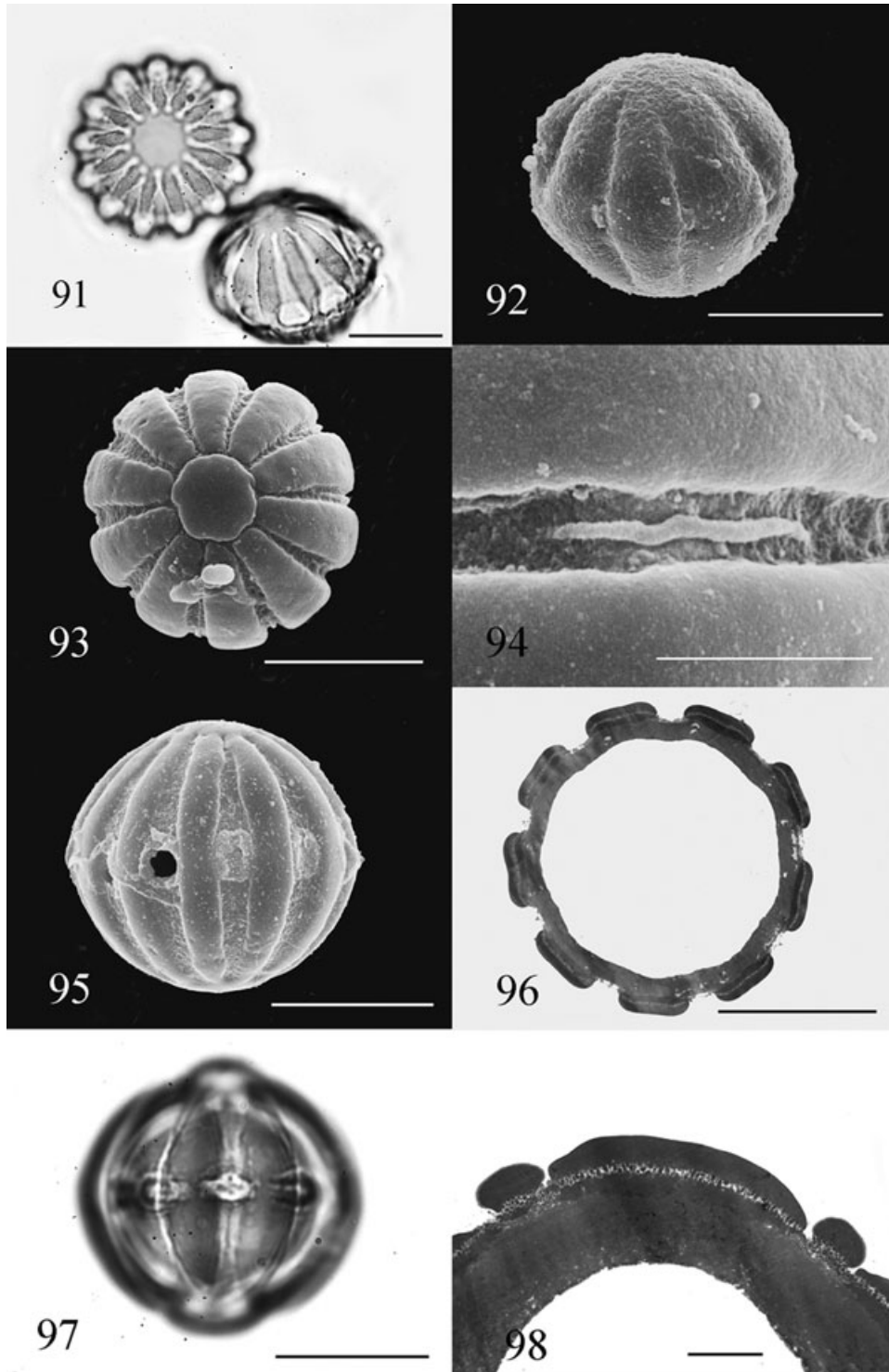
the genus having a subprolate shape). Five to 11 apertures (Fig. 102), *X. papuanam* has the lowest aperture number in Polygalaceae apart from *Balgoya*. Zonocolporate. Ectoapertures (13)–22.7–(40)  $\times$  (1)–1.8–(4)  $\mu\text{m}$ ; endoapertures (3)–5.9–(11)  $\mu\text{m}$  and endocingulate (Figs 100, 101). Exine (1.5)–1.9–(2)  $\mu\text{m}$  thick. Surface ornamentation psilate–punctate (Fig. 99), *X. amoenum* has lumina (less than 1  $\mu\text{m}$  in diameter) with coarsely granular surfaces; aperture membrane granular. In thin section (*X. octandrum*), columellae short and unbranched (0.1  $\mu\text{m}$ ); foot layer thin and discontinuous (less

than 0.05  $\mu\text{m}$ ); polar endexine 0.4  $\mu\text{m}$  with foraminae; equatorial endexine lamellate at endocingulum (1  $\mu\text{m}$  thick), thicker with foraminae adjacent to endocingulum (3  $\mu\text{m}$ ).

## DISCUSSION

The pollen of Quillajaceae and Surianaceae has more in common with that of Leguminosae than with Polygalaceae (Claxton *et al.*, 2005), and the phylogeny resulting from molecular analyses based on three plastid DNA regions (*rbcL*, *trnL* intron, and *trnL-F*

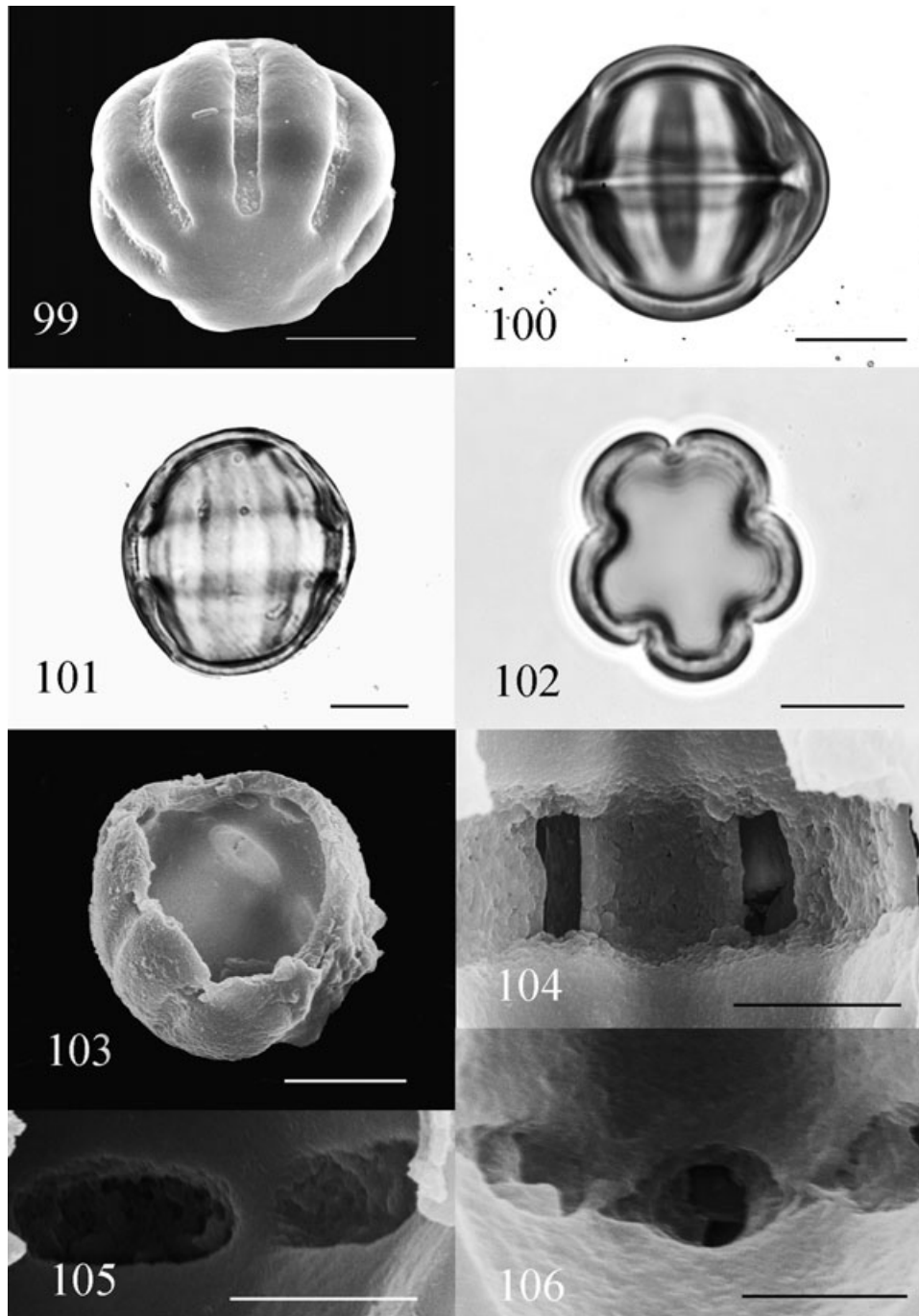
**Figures 91–98.** Fig. 91. *Securidaca diversifolia*, two grains showing polar and equatorial views (light microscopy, LM). Fig. 92. *Securidaca philippinensis*, equatorial view of whole grain showing granular surface ornamentation (scanning electron microscopy, SEM). Fig. 93. *Securidaca longipedunculata*, polar view of whole grain showing ten apertures with opercula visible over some endoapertures, psilate surface ornamentation, and parasyncolpory (SEM). Fig. 94. *Securidaca longipedunculata*, close up of aperture showing operculum present over endoaperture area (SEM). Fig. 95. *Securidaca paniculata*, equatorial view of whole grain (SEM). Fig. 96. *Securidaca longipedunculata*, transverse section showing nine apertures, thick endexine with foraminae, and relatively thin infratectum (TEM). Fig. 97. *Securidaca longipedunculata*, equatorial view of whole grain showing discrete endoapertures (LM). Fig. 98. *Securidaca longipedunculata*, transverse section through wall showing opercula (transmission electron microscopy, TEM). Scale bars: Figs 91–93, 95–97, 20  $\mu\text{m}$ ; Fig. 94, 5  $\mu\text{m}$ ; Fig. 98, 2  $\mu\text{m}$ .



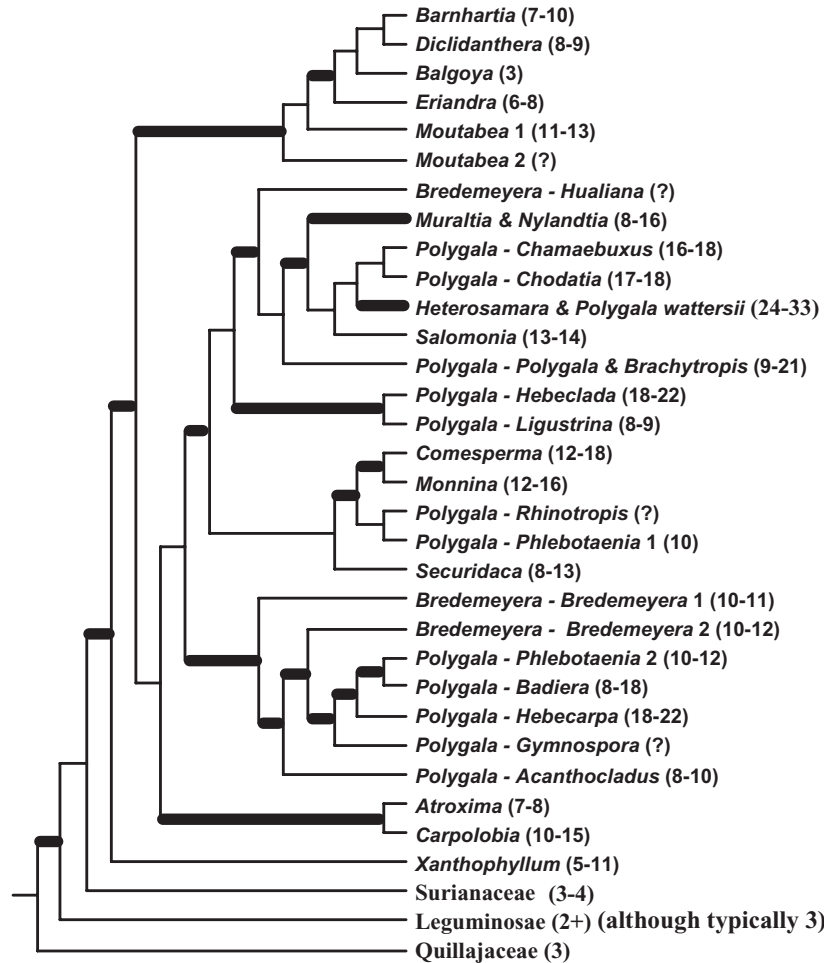
spacer) (Fig. 107) also suggests that the polycolpate condition is characteristic of the Polygalaceae. Within the family, the aperture number shows a high degree of variability within and amongst genera, species, and individual flowers, with ectoapertures (colpi) numbering between five and 33 (Tables 2 and 4) (numbering

three only in *Balgoya*). Labouriau & Morphy (1969) examined colpi number relative to pollen grain size in *Bredemeyera floribunda*, and concluded that there was no relationship (see also Arreguin-Sanchez *et al.*, 1988). This is also the case in our data. Aperture number does, however, broadly correlate with the





**Figures 99–106.** Fig. 99. *Xanthophyllum octandrum*, oblique polar view of whole grain showing psilate surface ornamentation (scanning electron microscopy, SEM). Fig. 100. *Xanthophyllum affine*, equatorial view of whole grain showing narrow endocingulum (light microscopy, LM). Fig. 101. *Xanthophyllum fragrans*, equatorial view of whole grain showing endocingulum (LM). Fig. 102. *Xanthophyllum papuanum*, polar view of whole grain showing five apertures (LM). Fig. 103. *Securidaca philippinensis*, image of half a pollen grain showing both external and internal surfaces. The internal surface shows lalongate endoapertures that are not joined (SEM). Fig. 104. *Xanthophyllum fragrans*, internal surface of the grain showing endocingulum forming a latitudinal band. The longitudinal spaces occur where the ectoapertures (colpi) pass over the endocingulum (SEM). Fig. 105. *Xanthophyllum amoenum*, internal pollen wall surface showing lalongate endoapertures (SEM). Fig. 106. *Badiera diversifolia* (= *Polygala diversifolia*), internal pollen wall surface showing lalongate endoapertures that are sometimes joined and sometimes not quite joined to each other (SEM). Scale bars: Figs 99–103, 10  $\mu\text{m}$ ; Figs 104–106, 5  $\mu\text{m}$ .



**Figure 107.** Schematic representation of the phylogenetic tree of the Fabales with emphasis on the family Polygalaceae, based on three plastid DNA regions (*rbcL*, *trnL* intron, and *trnL-F* spacer) adapted from Forest *et al.* (2007). Branches which receive bootstrap support greater than 90% are marked in bold. Aperture numbers are indicated in parentheses. Some nonmonophyletic genera are indicated with numerals: *Moutabea* 1, *Mo. guianensis*; *Moutabea* 2, *Mo. acueata* and *Mo. excoriata*; *Phlebotaenia* 1, *Ph. cuneata*; *Phlebotaenia* 2, *Ph. cowelli*; *Bredemeyera* 1, *Br. floribunda*, *Br. altissima*, and *Br. lucida*; *Bredemeyera* 2, *Br. microphylla*.

phylogenetic relationships in Polygalaceae (Persson, 2001; Forest *et al.*, 2007; Fig 107). Early diverging clades in the family have lower aperture numbers than later branching ones. The pollen of Quillajaceae has three apertures, and this family is sister to the rest of the Fabales clade. The next branching family, Leguminosae, has predominantly three-apertured pollen, but there is some variability within the group, with the pollen of some taxa having between one and nine apertures (Banks *et al.*, 2003). In Surianaceae, the genus *Stylobasium* has pollen with three to four apertures (Claxton *et al.*, 2005). In Polygalaceae, pollen of the first branching genus *Xanthophyllum* has between five and 11 apertures. The next branching clade, comprising the genera *Moutabea*, *Eriandra*, *Balgoya*, *Diclidanthera*, and *Barnhartia* (tribe Mouta-

beae), has pollen with three to 13 apertures. *Atroxima* and *Carpolobia* (tribe Carpolobieae) form the next clade, and have seven to 15 apertures. The remaining genera form tribe Polygaleae and comprise the polyphyletic *Polygala* plus *Bredemeyera*, *Comesperma*, *Heterosamara*, *Monnina*, *Muraltia* (including *Nylandtia*), *Salomonina*, and *Securidaca*; they have eight to 33 apertures. An increase in aperture number is characteristic of the whole family. It appears that, in a comparable manner to the successiform trend in Caryophyllaceae, recognized by Van Campo (1976), there has been a pattern of repeated increase in aperture number. In this connection, *Balgoya* merits special attention, being the only genus in the Polygalaceae that has tricolporate pollen. We have included images of the pollen obtained in our study despite the

paucity of material; as a rare monotypic endemic from New Caledonia, few herbarium specimens exist. All available material was examined by us or for us. The genus was first described by Morat & van der Meijden (1991), and pollen has not been described previously because flowers with anthers containing pollen are rarely found. This has led to the conclusion that the species is either dioecious or apomictic (Morat & van der Meijden, 1991). Recent molecular analyses suggest that *Balgoya* is an early branching lineage in the tribe Moutabeae. Its position within the tribe, and as part of a clade that also includes *Barnhartia*, *Diclidanthera*, and *Eriandra*, is secure; however, because of missing sequence data, the precise placement of this genus remains uncertain (Persson, 2001; Forest, 2004; Forest *et al.*, 2007; F. Forest, pers. observ.). Notwithstanding this uncertainty, its position in the phylogeny of Polygalaceae further underlines the repeated trend in other members of the family towards an increase in aperture number.

Within the tribe Moutabeae, the pollen morphology of *Barnhartia* and *Diclidanthera* is very similar (Figs 7–9, 18), and a sister relationship of these two genera is also suggested by molecular analyses (Fig. 107; Persson, 2001).

*Polygala* has a high degree of pollen morphological variation amongst the subgenera, and molecular phylogenetic analyses also suggest that the genus is polyphyletic (Fig. 107; Persson, 2001; Forest, 2004; Forest *et al.*, 2007). The species examined here show some correlation between pollen morphology, the taxonomy of Paiva (1998), and the groups delimited by recent molecular analyses. For example, *P. laureola* and *P. ligustrioides* in subgenus *Ligustrina* have distinctive and very similar pollen morphology (Figs 55–60). However, kidney-shaped pollen, which has previously been thought to be confined to the genus *Heterosamara*, occurs outside the genus as delimited by Paiva (1998), for example in *P. wattersii* (Figs 73–76), *P. arucata*, and *P. triphylla* (Huang, 1968, 1972). Molecular analyses also support a close relationship between *Heterosamara* and *P. wattersii* (F. Forest, pers. observ.). *Polygala wattersii* has previously been placed in different *Polygala* subgenera in various taxonomic treatments (Chen, 1991; Paiva, 1998). The pollen data obtained in this study suggest that *P. wattersii* may be better placed in *Heterosamara*.

The phylogenetic analysis of Forest & Manning (2006) shows that species of genus *Nylandtia* are nested within subgenus *Psiloclada* of genus *Muraltia*, and pollen morphological data also support this result (Figs 33–42).

*Balgoya*, *Diclidanthera*, *Moutabea*, and *Securidaca* have pollen with separate endoapertures. In other taxa, the degree of endoaperture fusion to form endocingula is variable at an infraspecific level

(Figs 103–106; Table 4). The occurrence of lalongate endoapertures, combined with the increased aperture number found in Polygalaceae pollen, would logically lead to an overlap of the endoaperture areas to form endocingula. How this increased area of thin pollen wall around the equator of the grain affects the structural integrity of the pollen, and its function, is at present unknown. Lalongate endoapertures are also present in the pollen of all genera in families Quillajaceae and Surianaceae (Claxton *et al.*, 2005), and in pollen of a few genera of Leguminosae (Ferguson & Skvarla, 1981; Banks & Klitgaard, 2000).

The length of the ectoapertures is variable, particularly within *Polygala*. Relatively short ectoapertures occur in *Epirixanthes*, *Heterosamara*, *P. wattersii*, *P. ligustrioides*, and *P. laureola* (this study), and have been reported in *P. leptalea* (Sumithraarachchi, 1982). Opercula have been found in *Securidaca virgata*, *S. longipedunculata* (Fig. 94), and *S. welwitschii*, and possibly also in *Epirixanthes elongata*, *P. macroptera*, and *P. meridionalis* (Table 4). In the literature, opercula have been found in *S. longipedunculata* (Coetzee & Robbertse, 1985), *P. reinii* (Ikuse, 1956), *P. microphylla* (Villneuva & Ramos, 1986), and *P. alba*, *P. appressipilis*, and *P. mexicana* (Arreguin-Sanchez *et al.*, 1988). It is possible that opercula may be more widespread than is currently documented. Loss of these structures during acetolysis may make them difficult to recognize once specimens have been prepared. The presence of opercula in unacetolysed Polygalaceae pollen may make an interesting topic for further study.

A margin of differing ornamentation around the ectoapertures occurs in *Comesperma ericinum*, *Co. hispidulim*, *Co. virgatum*, *Co. volubile*, *Heterosamara cabrae*, *H. carrssoana*, *H. tatarinowii*, *Muraltia serpyllodes*, *Nylandtia spinosa*, *Badiera fuertesii*, *P. acuminata*, *P. cunneata*, *P. klotzschii*, *P. microphylla*, *P. hebeclada*, *P. senega*, *P. arillata*, *P. macroptera*, *P. uncinata*, and *S. longipedunculata* (Table 4). Other taxa with larger granules around the margin of the aperture membrane are *P. cymosa* and *P. ramosa* (the ornamentation around the margin was described as verrucate by Jones *et al.*, 1995). In some instances, this margin appears to be formed from a different layer of the pollen wall (Figs 24, 25).

*Securidaca longipedunculata* is the only species in Polygalaceae known to have parasyncolpate pollen (Fig. 93), although some species of *Polygala* examined in this study have indentations or other sculptural patterns in or around the apocolpial area (Figs 47, 49, 63, 71, 80). Pollen of the genera *Tetraberlinia*, *Tamarindus*, and *Aphanocalyx* (Banks & Klitgaard, 2000) of the legume subfamily Caesalpinioideae has been documented to be parasyncolporate. Syncolporate pollen has not been found in Polygalaceae, Surianaceae, or Quillajaceae (Claxton *et al.*, 2005). It is,

however, present in the two legume subfamilies Caesalpinioideae (Graham & Barker, 1981; Banks & Klitgaard, 2000; Banks *et al.*, 2003) and Papilionoideae (Ferguson & Skvarla, 1981), where this character has been found to be polymorphic at both the infrageneric and infraspecific level (Banks *et al.*, 2003).

It is primarily the large number of apertures in Polygalaceae that makes the pollen of this family distinct from that of the other closely related families Leguminosae, Surianaceae, and Quillajaceae. This presents an interesting phenomenon, very comparable with the successiform trend identified by Van Campo (1976) in the pollen of Caryophyllales. How this pattern of increasing aperture number is mediated developmentally, and what are the implications for harmomegathic or germination processes, deserves further study.

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