

## MORPHOLOGY AND EVOLUTION OF ARYTERA POLLEN (SAPINDACEAE–CUPANIEAE)

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### SUMMARY

A description of *Arytera* pollen based on light and scanning electron microscopic observations is presented. Four aperture types and two ornamentation types (one divided into two subtypes) can be distinguished. The commonest aperture types are colporate and parasyncolporate; each of the other two types occurs in a single species. The main ornamentation types are rugulate and striate-rugulate; the latter has small or large lumina. Polymorphism occurs in both characters in several species. A cladistic analysis of *Arytera* shows two distinct evolutionary trends in the pollen: 1) aperture system from parasyncolporate to colporate, and 2) ornamentation from striate-rugulate with small lumina to striate-rugulate with large lumina. The plesiomorphic state of the character ornamentation remains uncertain. The result obtained contributes to the doubt whether primitively colporate pollen occurs within the subfamily Sapindoideae. In contrast to the general view of evolution in Sapindaceae pollen, the aperture system of *Arytera* pollen did not appear to be more conservative than the ornamentation. The evolutionary changes in the aperture system and ornamentation do not 'coincide', which suggests them to be functionally relatively independent.

### INTRODUCTION

*Arytera* is a sapindaceous genus of 28 species, of which one (*A. littoralis*) is found from NE India throughout SE Asia and Malesia to the Solomon Islands, while the others occur in New Guinea, Australia and the Pacific. The genus has recently been revised, and the present pollen study was undertaken in order to enlarge the data matrix for a cladistic analysis of the infrageneric relationships (Turner, in prep.). In addition, such an analysis would offer a good opportunity to evaluate the hypothesis of the colporate pollen type being derived from the (para)syncolporate type in the subfamily Sapindoideae (Van der Ham, 1990).

*Arytera* pollen has been poorly known to date. The colporate pollen of the widespread *A. littoralis* was briefly described and illustrated with light micrographs by Wang & Chien (1956), Chang (1982), and Liu (1986). Muller & Leenhouts (1976) reported the occurrence of the (para)syncolporate type in *Arytera*. Van der Ham (1977a) listed the distribution of both aperture types in 13 species, and provided the first scanning electron micrographs (see also Van der Ham, 1990). Cookson & Pike (1954) and Taylor (1989) studied the pollen of *A. littoralis* and *A. foveolata* in relation to the fossil, (para)syncolporate pollen genus *Cupanieidites*, which is considered to represent ancestral Sapindaceae pollen.

## MATERIAL AND METHODS

Twenty-five of the 28 *Arytera* species were available for pollen sampling. A few widespread or pollen morphologically variable species were sampled more extensively than the others. The collections are listed below in alphabetical order. They are kept in the Rijksherbarium, Leiden (L), unless indicated otherwise. The pollen slides and micrographs are all kept in the Rijksherbarium.

*Arytera* Blume

- arcuata* Radlk. — New Caledonia: *MacKee* 25149, 41368.  
*bifoliolata* S.T. Reynolds — Australia: *Godwin* s.n. (BRI); *Hyland* 10854 (BRI); *Persietz* 87 (MEL); *Sharpe* 4171 (CANB), 4184 (CANB); *Smith* 10638; *Webb & Tracey* 13247.  
*brackenridgei* (Gray) Radlk. — Solomon Islands: *BSIP* 5645, 5726, 14968 — New Hebrides: *Cabalion* 1520 — Fiji: *Greenwood* 478 (K); *Smith* 4562 — Tonga: *Crosby* 32 (K).  
*bullata* H. Turner — New Guinea: *Hartley* 12077 (K).  
*chartacea* Radlk. — New Caledonia: *MacKee* 41134, 42449; *Vieillard* 2381.  
*collina* (Pancher & Sebert) Radlk. — New Caledonia: *MacKee* 22074, 33563; *McMillan* 5049.  
*aff. collina* H. Turner — New Caledonia: *Veillon* 7380 (P).  
*densiflora* Radlk. — New Guinea: *Jacobs* 9509; *Ledermann* 9555 (M); *Schodde* 2438.  
*distylis* (F. Muell.) Radlk. — Australia: *Jessup* 266 (BRI); *Schodde* 5594 (K).  
*divaricata* F. Muell. — Australia: *Brass* 19157; *Hyland* 1353.  
*foveolata* F. Muell. — Australia: *Lam* 7631, 7673; *Williams* s.n. (BRI).  
*gracilipes* Radlk. — New Caledonia: *MacKee* 20384, 38028; *Vieillard* 2403 (M).  
*lautereriana* (Bailey) Radlk. — Australia: *Bailey* s.n. (M); *Gray* 4850 (BRI); *Hyland* 4168, 4218; *McDonald et al.* 3183; *Pearson* s.n. (BRI); *Schodde* 3255 (CANB).  
*lepidota* Radlk. — New Caledonia: *McPherson* 4252, 5667.  
*lineosquamulata* H. Turner — New Guinea: *Carr* 14969 — Australia: *Webb & Tracey* 13258.  
*litoralis* Blume — Vietnam: *D'Alleizette* 1458, s.n. — Thailand: *van Beusekom & Santisuk* 2929 — Philippines: *PNH* 15708 — Borneo: *SAN* 35056 — Java: *Backer* 74, s.n. — New Guinea: *NGF* 15490.  
*macrobotrys* (Merr. & L.M. Perry) R.W. Ham — New Guinea: *Brass* 7464 (A) — Australia: *Dockrill* 467 (BRI).  
*microphylla* (Benth.) Radlk. — Australia: *Michael* 3029 (K).  
*morobeana* H. Turner — New Guinea: *LAE* 74816.  
*multijuga* H. Turner — New Guinea: *Flenley* ANU 2846.  
*musca* H. Turner — New Guinea: *Brass* 7620, 7743; *Pullen* 7229.  
*neobudensis* (Guillaumin) H. Turner — New Hebrides: *Bernardi* 13030, 13367 — New Caledonia: *MacKee* 18973.  
*novaebritanniae* H. Turner — New Guinea: *NGF* 26789, 26856.  
*pauciflora* S.T. Reynolds — Australia: *Brass* 20251; *Graham* 2488 (BRI); *Sankowsky & Sankowsky* 594 (BRI).  
*pseudofoveolata* H. Turner — New Guinea: *Brass* 5560 (A).

No pollen samples were available of *Arytera brachyphylla* Radlk., *A. dictyoneura* S.T. Reynolds and *A. miniata* H. Turner.

All samples were studied with light microscopy, and most of them with scanning electron microscopy as well, applying the techniques described by Van der Ham (1990). The terminology used follows the 'Glossary' of Punt et al. (1994).

## DESCRIPTION

*Arytera* pollen grains are small or rarely medium-sized ( $P = 13.0$  (17.4)  $20.7 \mu\text{m}$ ,  $E = 19.7$  (23.3)  $28.4 \mu\text{m}$ ). Pollen grain shape is oblate to oblate spheroidal ( $P/E = 0.57$  (0.77)  $0.96$ ). The equatorial outline (= polar view) is triangular to subcircular; triangular outlines have convex to slightly concave sides. The meridional outline (= equatorial view) is elliptic (sometimes with  $\pm$  acuminate ends) in oblate grains, and subcircular in oblate spheroidal grains.

*Arytera* pollen is (2–)3(–4) aperturate, and usually colporate (type A; e.g. Plate 3: 1) or (para)syncolporate (type B; e.g. Plate 1: 1). Several intermediate forms between type A and type B have been observed: pollen grains with apocolpial fields largely (A\*; Plate 3: 4) to slightly (B\*; Plate 1: 3) connected to the mesocolpia. Several collections of *A. lautereriana* have colporate pollen with wide, sunken colpi (type C; Plate 1: 2). One collection of *A. pauciflora* shows syncolporate pollen grains in which the colpi are bridged halfway between the poles and the apertures (type D; Plate 3: 6). The size (A) of the apocolpium or apocolpial field is up to  $12 \mu\text{m}$  ( $A/E = 0$  (0.21)  $0.39$ ). The pollen grains are usually (sub)isopolar with respect to this feature; heteropolar grains were found in a few parasyncolporate samples.

The endoapertures are circular to lologate pori, measuring  $1\text{--}3 \mu\text{m}$  meridionally and  $1\text{--}2 \mu\text{m}$  equatorially, and are often indistinct (especially at the lateral sides).

Total exine thickness (SEM) is  $1\text{--}1.7 \mu\text{m}$  in the centre of a mesocolpium. Nexine  $0.35\text{--}0.7 \mu\text{m}$ . Infratectum  $0.15\text{--}0.35 \mu\text{m}$ , columellate. Tectum  $0.4\text{--}0.8 \mu\text{m}$ .

The ornamentation is essentially either rugulate (type 1) or striate-rugulate (type 2). Both types are rather diverse. Rugulate ornamentation shows a dense criss-cross pattern of short, straight muri enclosing small (usually  $< 0.5 \mu\text{m}$ ) lumina (Plate 1: 1–6). The muri may be less prominent or hardly distinct, which results in rugulate-perforate or nearly perforate to microreticulate forms (Plate 1: 3, 5). Striate-rugulate ornamentation shows longer, curving muri in a more or less dense network or sub-parallel pattern (Plates 2, 3). The lumina may be small ( $< 0.5 \mu\text{m}$ ; subtype 2a; Plate 2: 1–4, 6) or relatively large ( $0.5\text{--}1.5 \mu\text{m}$ ; (micro)reticulate forms: subtype 2b; Plates 2: 5 & 3: 1–6).

Table 1 lists the values/states of a number of the above mentioned characters for the individual species studied. Below several of these characters are discussed in more detail.

*Aperture system*

The aperture system in *Arytera* pollen shows a complete series from the colporate to the parasyncolporate state. The extremes of this series have been described in the Sapindaceae as type A and type B respectively (Muller & Leenhouts, 1976). The intermediate forms demonstrate varying degrees of coherence between the apocolpia and mesocolpia. In a study of *Alectryon* pollen (Van der Ham, 1990) such forms were labeled as type A\* and type B\*, representing pollen grains with apocolpial fields being largely (A\*) or slightly (B\*) connected to the mesocolpia (Fig. 1).

Most *Arytera* species have either type A or type B pollen. In a few other species varying proportions of either type A and A\* or type B and B\* were found (see Table 1). *Arytera bifoliolata* (Plate 2: 3, 4) shows both type A (*Hyland 10854*, *Persietz 87*,

Table 1. Infrageneric variation of pollen characters in *Arytera*.

<i>Arytera</i>	P	E	P/E	A/E	aperture type	ornamentation type
<i>arcuata</i>	13 (16.3) 18	17 (25.0) 27	0.52 (0.65) 1.06	0 (0.16) 0.20	B	1
<i>bifoliolata</i> A	17 (19.3) 26	13 (19.7) 25	0.79 (0.98) 1.53	0.10 (0.20) 0.33	A	2a
<i>bifoliolata</i> B	15 (16.1) 20	17 (20.8) 26	0.65 (0.77) 1.06	0.18 (0.31) 0.47	B	2a
<i>brackenridgei</i>	12 (15.4) 21	19 (24.2) 29	0.52 (0.64) 0.90	0.08 (0.15) 0.25	B	1
<i>bullata</i>	12 (13.0) 14	21 (22.8) 24	0.50 (0.75) 0.67	0.18 (0.22) 0.26	B, (B*)	1
<i>chartacea</i>	15 (18.3) 20	23 (25.6) 28	0.54 (0.71) 0.87	0.16 (0.20) 0.28	B	2a
<i>collina</i>	14 (17.6) 20	22 (25.3) 29	0.54 (0.70) 0.87	0.11 (0.21) 0.33	B	2a
<i>aff. collina</i>	16 (19.4) 22	25 (28.4) 32	0.59 (0.68) 0.84	0.19 (0.20) 0.21	B	2a
<i>densiflora</i>	15 (18.1) 21	17 (20.1) 23	0.70 (0.90) 1.11	0.26 (0.32) 0.38	A	2b
<i>disyllis</i>	16 (18.1) 21	17 (21.8) 25	0.74 (0.83) 1.24	0.19 (0.32) 0.55	B	2a, b
<i>divaricata</i>	15 (18.1) 22	18 (21.6) 27	0.73 (0.84) 0.91	0.09 (0.19) 0.30	A	2a, b
<i>foveolata</i>	16 (20.1) 25	21 (25.5) 30	0.69 (0.97) 0.88	0.12 (0.17) 0.20	B*, (B)	2b
<i>gracilipes</i>	13 (15.2) 21	21 (24.5) 28	0.50 (0.62) 0.88	0 (0.16) 0.20	B	1
<i>lautereriiana</i> B	10 (14.6) 17	20 (23.9) 30	0.42 (0.61) 0.85	0.16 (0.22) 0.25	B	1
<i>lautereriiana</i> C	15 (17.3) 21	18 (19.8) 23	0.75 (0.88) 1.10	0.24 (0.39) 0.51	C	1
<i>lepidota</i>	12 (13.7) 16	21 (22.9) 27	0.52 (0.60) 0.68	0.15	B	1
<i>lineosquamulata</i>	10 (18.7) 23	17 (20.8) 23	0.59 (0.89) 1.17	0.15 (0.22) 0.28	A	2a
<i>litoralis</i>	16 (20.7) 24	18 (21.7) 25	0.76 (0.95) 1.17	0.18 (0.27) 0.34	A	2a, b
<i>macrobotrys</i>	12 (14.2) 16	21 (24.1) 28	0.50 (0.59) 0.68	0.17 (0.24) 0.32	B	1
<i>microphylla</i>	15 (16.2) 18	18 (19.7) 21	0.75 (0.82) 0.95	0.15 (0.20) 0.25	B*	2a
<i>morbeana</i>	18 (20.2) 23	19 (21.3) 24	0.82 (0.95) 1.21	0.23	A	2b
<i>multijuga</i>	19 (20.1) 21	26 (27.0) 28	0.68 (0.74) 0.81	0.11 (0.15) 0.19	B, (B*)	2a
<i>musca</i>	18 (20.7) 23	18 (21.6) 24	0.87 (0.96) 1.15	0.29 (0.30) 0.31	A, A*	2b
<i>neoebudensis</i>	16 (17.9) 21	20 (27.4) 31	0.75 (0.65) 0.80	0.24 (0.29) 0.34	B	2a
<i>novaebritanniae</i>	15 (18.7) 22	20 (22.8) 26	0.72 (0.82) 1.00	0.04 (0.09) 0.13	A, (A*)	2a
<i>pauciflora</i> A	13 (17.2) 21	17 (22.3) 25	0.65 (0.77) 1.00	0 (0.04) 0.09	A	2a
<i>pauciflora</i> D	16 (17.6) 21	20 (22.8) 26	0.69 (0.77) 0.85	0	D	2b
<i>pseudofoveolata</i>	18 (20.6) 24	20 (22.7) 26	0.76 (0.91) 1.00	0.18	A	2a

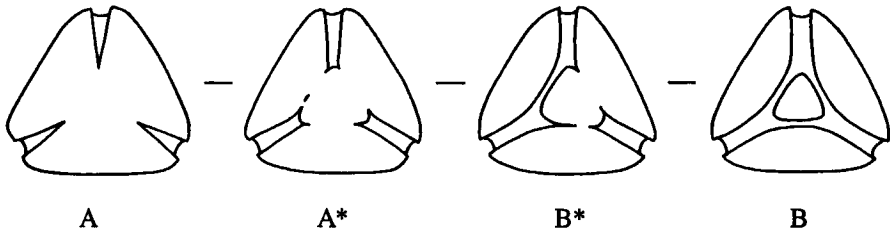


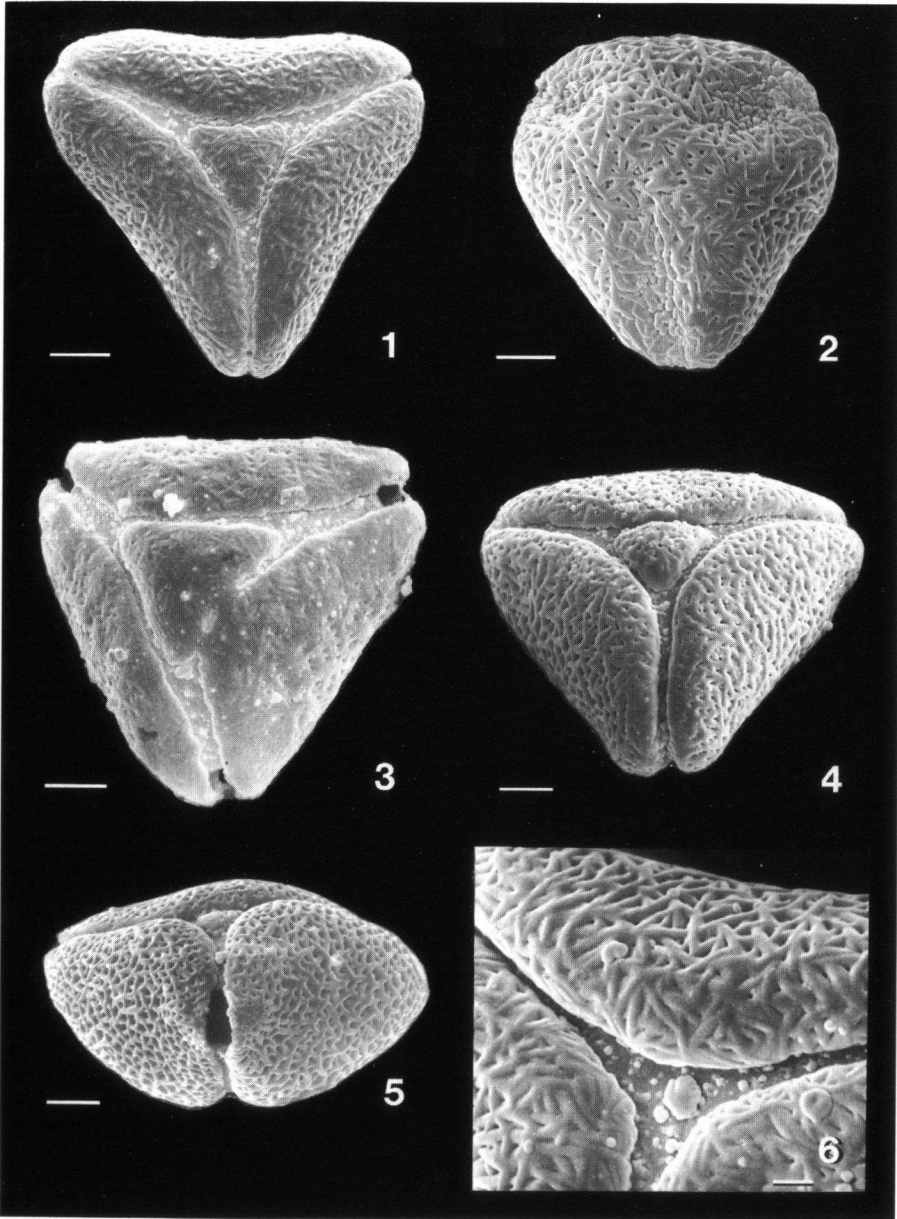
Fig. 1. Colporate pollen (type A), parasyncolporate pollen (type B), and two intermediate forms: with apocolpial field largely (A\*) and slightly (B\*) connected to the mesocolpia.

*Smith 10638, Webb & Tracey 13247*) and type B (*Godwin s.n., Sharpe 4171, 4184*). Also in *A. lautereriana* (Plate 1: 1, 2) the samples yielded either colporate (*Bailey s.n., Hyland 4168, 4218, McDonald et al. 3183, Pearson s.n.*) or parasyncolporate (*Gray 4850, Schodde 3255*) pollen (type B). However, the colporate type in this species deviates from type A in having rather indistinct, wide, short (av. A/E = 0.39), sunken colpi, and it is distinguished here as type C. *Arytera lautereriana* is distributed along the eastern coast of Queensland (Australia). The collections with type B come from the northernmost localities (17° 18' and 17° 27' S), while those with type C derive from more southern regions (20° 10' to 26° 44' S).

*Arytera pauciflora* (Plate 3: 5, 6) has colporate pollen with relatively long, sometimes fused colpi (*Sankowsky & Sankowsky 594, Brass 20251*), and syncolporate pollen with mesocolpial bridges halfway between the poles and the equatorial plane (*Graham 2488*). The latter is separated here as type D. Similar mesocolpial bridges were observed in two species of (para)syncolporate genera also belonging to the tribe Cupanieae: in *Cnesmocarpon discoloroides* (*Adema & Van der Ham, 1993*) and in *Pentascyphus thyrsoiflorus* (*Leprieur 335, French Guiana*). Syncolporate pollen grains without mesocolpial bridges were observed in small percentages (< 10%) in a few parasyncolporate *Arytera* samples (see Table 1); as in Muller & Leenhouts (1976) they are included in type B.

#### *Aperture system and pollen grain shape*

As in *Alectryon* pollen (Van der Ham, 1990) the type of aperture system in *Arytera* pollen appeared to be correlated with the shape of the pollen grain. Figure 2 displays the relation between aperture system (A+A\*, B+B\*, C or D) and P/E value: in general, colporate pollen is less oblate than parasyncolporate pollen (compare Plate 1: 5 with Plate 2: 6). As in *Alectryon*, the 'turning point' between colporate and parasyncolporate is an average P/E value of approximately 0.82. The relation between aperture system and P/E value is clearly demonstrated by the pollen of *A. bifoliolata*. The parasyncolporate pollen has an average P/E of 0.77, while the colporate, though further similar pollen has an average P/E of 0.98. A mechanical explanation of this relation was given by Van der Ham (1990).



**Plate 1** — *Azytera*, SEM photographs; bar = 3  $\mu\text{m}$  (except in 6: 1  $\mu\text{m}$ ).

- 1, 2: *A. lautereriana*. 1: polar view of aperture type B (Schodde 3255); 2: polar view of aperture type C (Hyland 4168).
- 3 : *A. bullata* (Hartley 12077), polar view of aperture type B\*.
- 4 : *A. arcuata* (MacKee 41368), oblique polar view of aperture type B.
- 5 : *A. brackenridgei* (Greenwood 478), oblique equatorial view of aperture type B.
- 6 : *A. gracilipes* (MacKee 20384), detail polar area of  $\pm$  syncolporate grain.

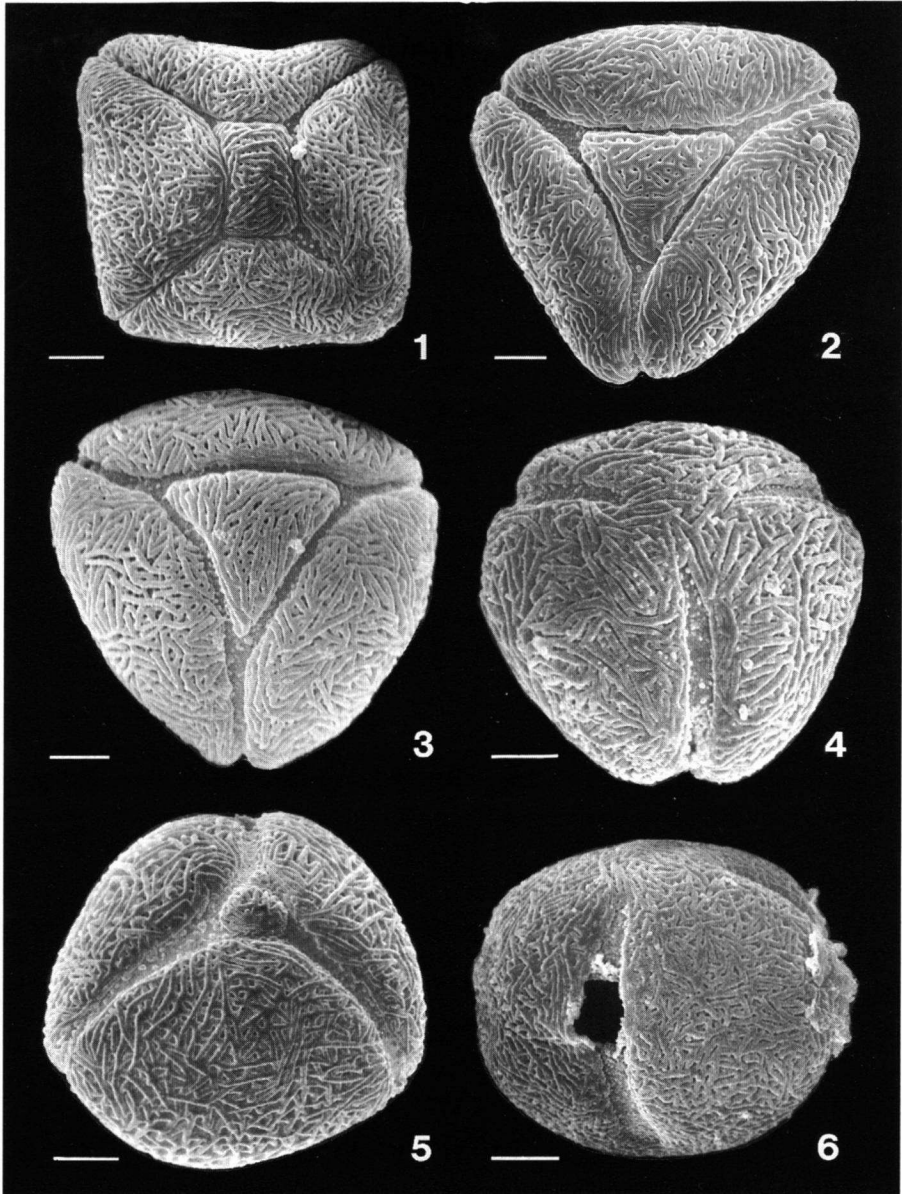
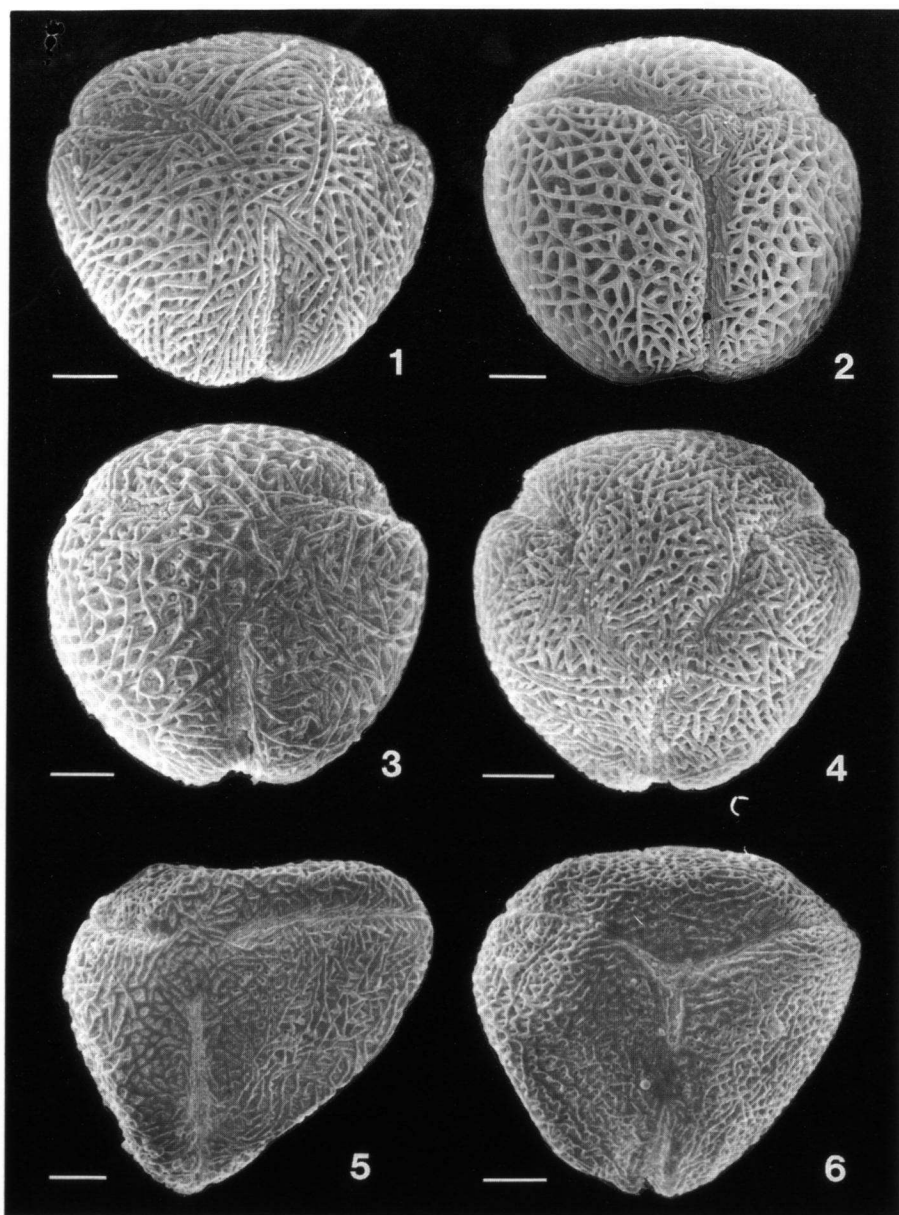


Plate 2 — *Arytera*, SEM photographs; bar = 3 µm.

- 1 : *A. multijuga* (Flenley ANU 2846), polar view of aperture type B (4-parasyncolporate).
- 2 : *A. chartacea* (Vieillard 2381), polar view of aperture type B.
- 3, 4: *A. bifoliolata*. 3: polar view of aperture type B (Sharpe 4184); 4: oblique polar view of aperture type A (Smith 10638).
- 5 : *A. distylis* (Schodde 5594), oblique polar view of aperture type B.
- 6 : *A. pseudofoveolata* (Brass 5560), equatorial view of aperture type A.



**Plate 3** — *Arytera*, SEM photographs; bar = 3  $\mu\text{m}$ .

- 1 : *A. densiflora* (Jacobs 9509), polar view of aperture type A.
- 2 : *A. foveolata* (Williams s.n.), oblique polar view of aperture type B\*.
- 3, 4: *A. musca*. 3: polar view of aperture type A (Brass 7620); 4: polar view of aperture type A\* (Pullen 7229).
- 5, 6: *A. pauciflora*. 5: polar view of aperture type A (Sankowsky & Sankowsky 594); 6: polar view of aperture type D (Graham 2488).



In addition to being most oblate, the pollen of the species *A. bullata* to *A. arcuata* in Figure 2 generally has an equatorial outline with straight to slightly concave sides, while that with higher P/E values has equatorial outlines with convex sides (compare Plate 1: 1 with Plate 2: 3).

In contrast to *Alectryon* pollen there is no relation between aperture system and the size of the apocolpial field (A) in *Arytera* pollen. In *Alectryon* pollen the average A/E is < 0.40 in colporate pollen and > 0.40 in parasyncolporate pollen, while in *Arytera* pollen it is < 0.40 in both colporate and parasyncolporate pollen.

#### *Ornamentation and pollen grain shape*

Two main ornamentation types can be distinguished in *Arytera* pollen (see also Description):

1. rugulate patterns, showing short, straight muri (Plate 1)
2. striate-rugulate patterns, showing long, curving muri (Plates 2, 3)

In type 2 the muri may enclose small or large lumina. Therefore, this type is subdivided into two intergrading subtypes:

- 2a. patterns with lumina < 0.5  $\mu\text{m}$  (Plate 2: 2)
- 2b. patterns with lumina between 0.5 and 1.5  $\mu\text{m}$  (Plate 3: 2)

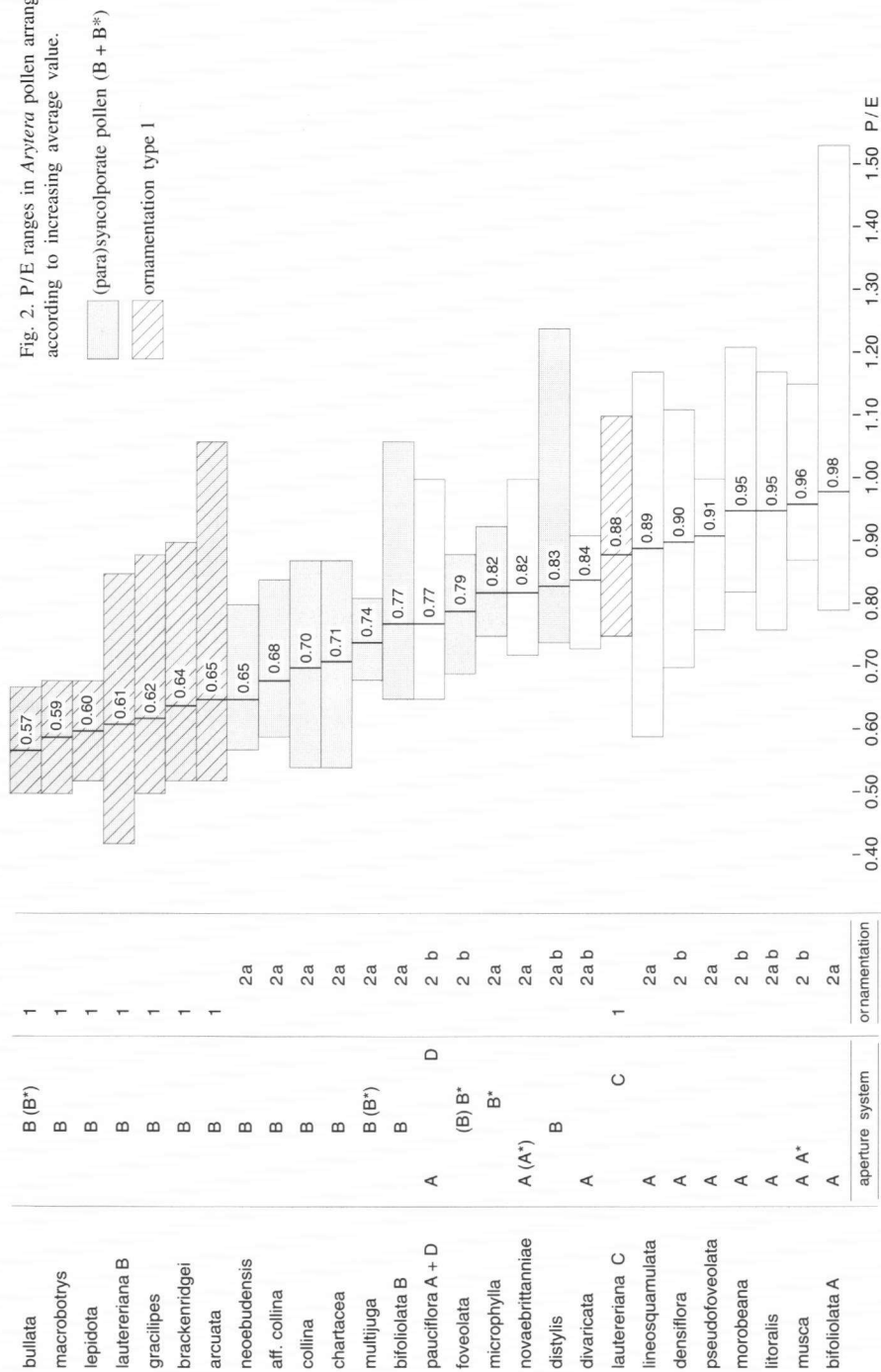
Type 1 appeared to be present only in the species with the lowest P/E values: parasyncolporate species with straight to slightly concave equatorial outlines (*A. bullata* to *A. arcuata* in Fig. 2), and in the samples of *A. lautereriana* belonging to aperture system type C (av. P/E = 0.88). Type 2 occurs in both colporate and parasyncolporate species, although subtype 2b is absent in parasyncolporate pollen with relatively low P/E values (*A. neoebudensis* to *A. bifoliolata* B in Fig. 2).

#### POLLEN MORPHOLOGICAL SUBDIVISION OF ARYTERA

According to pollen morphology, *Arytera* can be subdivided into two more or less distinct groups (Fig. 2):

- I. Species with pollen showing rugulate ornamentation, low P/E values ( $\leq 0.65$ ) and straight to slightly concave equatorial outlines. The aperture system is usually parasyncolporate; part of *A. lautereriana* has pollen with deviating colporate apertures (and consequently a high P/E value), but the ornamentation is rugulate.  
Species included: *A. arcuata*, *A. brackenridgei*, *A. bullata*, *A. gracilipes*, *A. lautereriana*, *A. lepidota*, *A. macrobotrys*.
- II. Species with pollen showing striate-rugulate ornamentation, higher P/E values ( $\geq 0.65$ ), and convex equatorial outlines. The aperture system is colporate to parasyncolporate, and may vary within a species; part of *A. pauciflora* has pollen with deviating syncolporate apertures. The group can be further subdivided into colporate and parasyncolporate species, but, in view of the variability of the aperture system in some species (*A. bifoliolata* has both types), this distinction seems to be of minor importance.

Fig. 2. P/E ranges in *Arytera* pollen arranged according to increasing average value.



Species with parasyncolporate pollen: *A. bifoliolata*, *A. chartacea*, *A. collina*, *A. aff. collina*, *A. distylis*, *A. foveolata*, *A. microphylla*, *A. multijuga*, *A. neoebudensis*.

Species with colporate pollen: *A. bifoliolata*, *A. densiflora*, *A. divaricata*, *A. lineosquamulata*, *A. litoralis*, *A. morobeana*, *A. musca*, *A. novaebritanniae*, *A. pauciflora*, *A. pseudofoveolata*.

A subdivision of group II based on ornamentation is still less feasible, because the subtypes 2a and 2b occur together in 3 species (Fig. 2). Subgroups of group II based on the ornamentation subtypes do not correspond with those based on aperture system type, though the parasyncolporate species in group II with lowest P/E values (*A. neoebudensis* to *A. bifoliolata* B in Fig. 2) always have subtype 2a.

#### PHYLOGENETIC ANALYSIS

Turner (in prep.) performed a cladistic analysis of *Arytera*. *Cupaniopsis anacardioides* and several *Mischocarpus* species were used as outgroups. The data matrix contained 78 informative characters from macromorphology and leaf anatomy, plus one pollen morphological character, namely the aperture system (type B or B\* versus type A or A\*). Because the coding of this character was based on preliminary data, the results differed slightly from those presented here. Using Hennig86 (Farris, 1988), coding polymorphism as unknown data, the analysis resulted in 17 different cladograms (Turner, in prep.).

Because the present study showed a second character (ornamentation type) to be promising, and the aperture types were interpreted slightly differently here, the analysis was repeated including the new data but using the same methodology. Both characters were treated as unordered.

*Mischocarpus* pollen has aperture type B or B\* and ornamentation type 1 or subtype 2b (Van der Ham, 1977b). Pollen of *Cupaniopsis anacardioides* has aperture type B and ornamentation subtype 2b (Adema, 1991). Analysis with Hennig86 resulted in 32 most parsimonious cladograms (l = 341 steps, CI = 0.30, RI = 0.59). Among these cladograms, three were chosen as the best on the basis of their highest average unit retention index (see Turner, in prep. for a full discussion of the rationale behind using this measure). Figure 3 shows the strict consensus tree of these three cladograms, which has the same number of steps. The only differences with the result obtained by Turner (in prep.) are that in that study *A. foveolata* is the sister species of *A. novaebritanniae*, *A. divaricata* is placed in a trichotomy with *A. litoralis* and its present sister group, and that the trichotomy in the *bifoliolata* group is resolved with *A. distylis* at the base. There are four possibilities to fill in the required steps in the pollen characters (see below).

Figure 3 shows that four *Arytera* species are not included in the ingroup: *A. bulata*, *A. lautereriana*, *A. macrobotrys*, and *A. multijuga*. The latter is incompletely known macromorphologically (only two specimens with very young flowers), and is most appropriately placed as species *incertae sedis* within *Arytera* (Turner, in prep.); *A. brachyphylla*, still more incompletely known, was excluded from the analysis.

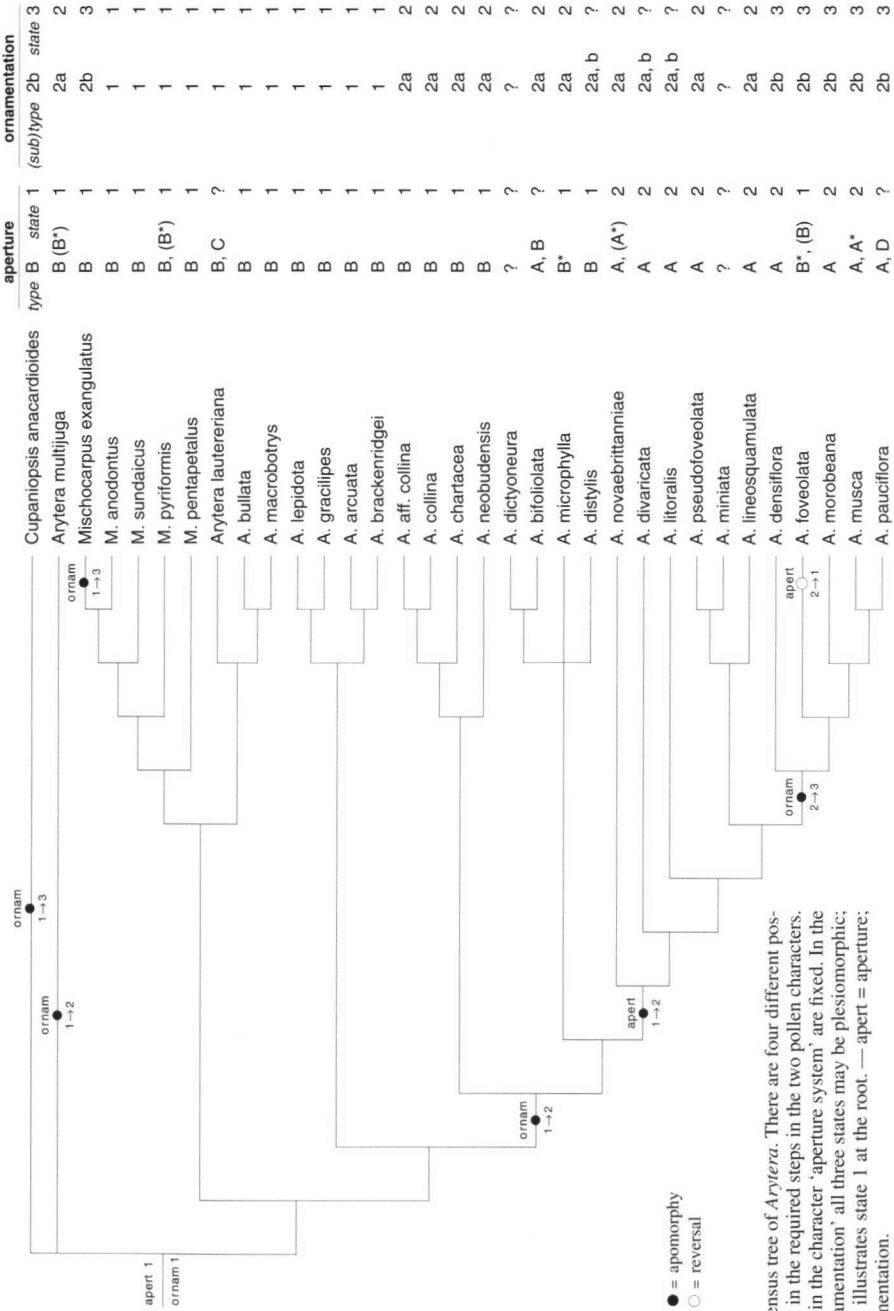


Fig. 3. A consensus tree of *Arytera*. There are four different possibilities to fill in the required steps in the two pollen characters. The two steps in the character 'aperture system' are fixed. In the character 'ornamentation' all three states may be plesiomorphic; the above tree illustrates state 1 at the root. — apert = aperture; ornam = ornamentation.

The other three species form a monophyletic group (the *lautereriana* group), which is probably best treated as a separate genus (Turner, in prep.; see also Van der Ham 1977a, 1990).

The (para)syncolporate type B is the plesiomorphic character state within *Arytera*. This character takes two steps in the ingroup. The colporate type (A + A\*) is a synapomorphy for the clade consisting of *A. densiflora*, *A. divaricata*, *A. lineosquamulata*, *A. litoralis*, *A. morobeana*, *A. musca*, *A. novaebritanniae*, *A. pauciflora*, *A. pseudofoveolata*, and *A. foveolata*. The parasyncolporate (B\* + B) pollen of the latter is found to be a reversal.

The plesiomorphic state for the ornamentation type cannot be reconstructed unambiguously. Each of the three (sub)types can be placed at the root. Even within *Arytera sensu stricto*, the plesiomorphic state cannot be determined with certainty. Either rugulate ornamentation (type 1) is plesiomorphic (in that case forming a synapomorphy for *Arytera* plus *Mischocarpus*), then striate-rugulate ornamentation with relatively small lumina (subtype 2a) is a synapomorphy within *Arytera*; or subtype 2a is plesiomorphic, in which case type 1 forms a synapomorphy for *A. arcuata*, *A. brackenridgei*, *A. gracilipes*, and *A. lepidota*, with a parallel in the clade consisting of *Mischocarpus* plus the *lautereriana* group, and striate-rugulate ornamentation with relatively large lumina (subtype 2b) is an autapomorphy for *Cupaniopsis anacardioides*. Adema (1991) suggested that *C. anacardioides* is not the most basal species in *Cupaniopsis*. Therefore, optimising the ornamentation type on the cladogram for that genus might allow a choice for one of the possible reconstructions. Unfortunately, however, the ancestral character state for *Cupaniopsis* is also ambiguous. Figure 3 illustrates the tree in which ornamentation type 1 is at the root of the tree, and, consequently, at the root of *Arytera sensu stricto*. Subtype 2b is a certain synapomorphy for the clade consisting of *A. densiflora*, *A. foveolata*, *A. lineosquamulata*, *A. miniata*, *A. morobeana*, *A. musca*, *A. pauciflora*, and *A. pseudofoveolata*. Polymorphism (subtypes 2a and 2b) is found in *A. distylis*, *A. divaricata*, and *A. litoralis*. The occurrence of ornamentation type 2a in *A. multijuga* lends slight support to the hypothesis that this species actually does belong to *Arytera sensu stricto*. Within *Arytera sensu stricto*, the ornamentation type in all cases takes two steps, without reversals.

#### DISCUSSION AND CONCLUSION

Muller & Leenhouts (1976) distinguished 12 pollen types within the Sapindaceae. The colporate type A, present in all 13 tribes, was regarded as the basic type, and the (para)syncolporate type B, known from 4 tribes, as derived from type A. Type B is only found in the subfamily Sapindoideae. It is especially common in the tribe Cupanieae (known in 32 out of the 47 genera), and occurs in a few genera in the Melioccoceae (3/5), Nephelieae (1/12: *Alectryon*) and Schleichereae (1/13: *Schleichera*).

Van der Ham (1977a, 1977b), studying pollen of *Arytera* and *Mischocarpus*, accepted this evolutionary trend. In contrast, Van der Ham & Van Heuven (1989) considered the colporate condition in *Guioa* pollen as derived from the parasyncolporate type, being the result of complete coalescence of the apocolpial fields and the adjacent parts of the mesocolpia. They doubted whether primitively colporate pollen

exists within the Cupanieae. On the basis of fossil evidence, palaeo-ecological and macromorphological data and a functional interpretation Van der Ham (1990) hypothesised that type B is plesiomorphic within the subfamily Sapindoideae, and frequently changed into type A. Cladistic analysis of genera possessing both types was suggested to elaborate this hypothesis. Adema (1991), analysing *Cupaniopsis*, demonstrated type A to be largely apomorphic; one reversal to the plesiomorphic type B was found.

Also the cladistic analysis of *Arytera* demonstrated the (para)syncolporate pollen type B to be plesiomorphic, although the presence of the types B\* and B in *A. foveolata* shows that, as in *Cupaniopsis*, reversals may arise. The occurrence of both type A and type B in *A. bifoliolata* and intermediate forms in six other species shows that the character states are not always fully fixed. The result obtained contributes to the doubt whether primitively colporate pollen occurs within the subfamily Sapindoideae. The pollen types C and D, found in a part of the samples of *A. lautereriana* and *A. pauciflora*, respectively, may be considered as autapomorphies that are not fully fixed. The polymorphism found in the aperture system (types A+B, B+C, or A+D) does not correlate with variation in other characters, neither in the pollen, nor in the macromorphology.

Within *Arytera*, ornamentation shows a trend from rugulate (type 1) to striate-rugulate (subtype 2a) to striate-rugulate with large lumina (subtype 2b), or from striate-rugulate (subtype 2a) to rugulate (type 1) on the one hand, and to striate-rugulate with large lumina (subtype 2b) on the other. Muller (1979) assumed a functional relationship between a colporate aperture system and meridionally striate ornamentation, the latter being well-adapted to the harmomegathic system of colporate pollen grains. Such a relation was found in *Alectryon* (Van der Ham, 1990), where colporate pollen is usually striate or striate-rugulate, and parasyncolporate pollen striate-rugulate or rugulate. Remarkably, striate ornamentation is very rare in *Arytera*; it was observed only as a minor form in one sample of *A. novaebritanniae*, and may be considered as a form of striate-rugulate ornamentation in which the lumina are 'compressed' between subparallel muri. Instead, a change towards patterns with relatively large lumina can be noted in *Arytera* pollen.

In conclusion, *Arytera* pollen shows two distinct evolutionary trends: 1) aperture system from parasyncolporate to colporate, and 2) ornamentation from striate-rugulate with small lumina to striate-rugulate with large lumina. The plesiomorphic state for the latter character remains uncertain. Polymorphism occurs in both characters in several species. The evolutionary changes in the aperture system and ornamentation do not 'coincide', which suggests them to be functionally relatively independent. In contrast to the general conclusion of Muller & Leenhouts (1976) regarding evolution of Sapindaceae pollen, the aperture system of *Arytera* pollen does not appear to be more conservative than the ornamentation.

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