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RESEARCH ARTICLE

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Pollen morphology of Philippine species of *Phyllanthus* (*Phyllanthaceae*, *Euphorbiaceae* s.l.)

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Key words

Euphorbiaceae
Philippines
Phyllanthaceae
Phyllanthus
pollen morphology
SEM
taxonomy

Abstract The pollen morphology of 21 Philippine *Phyllanthus* species belonging to five subgenera and eleven sections was studied using scanning electron microscopy. Eleven pollen types were recognized, of which seven were previously reported and four are newly described, i.e., the *Phyllanthus erythrotrichus* type, the *P. glochidioides* type, the *P. securinegoides* type and the *Pilate* type. The pollen morphology of the Philippine *Phyllanthus* species included in this study provides insight into the taxonomy as well as the phylogeny of these species.

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INTRODUCTION

Phyllanthus is the largest genus of the *Phyllanthaceae* (*Euphorbiaceae* s.l.). It contains about 830 species (Govaert et al. 2000). On the basis of a large molecular analysis of *Phyllanthus* and its relatives, Kathriarachchi et al. (2006) recommended the inclusion of *Breynia*, *Glochidion*, *Reverchonia* and *Sauropus* to form a large monophyletic genus *Phyllanthus* s.l. This genus would then comprise c. 1 269 species (Govaert et al. 2000). They found that the subgenera *Conami*, *Emblica*, *Eriococcus*, *Gomphidium* (sensu Schmid 1991) and *Xylophylla* (except for *P. sellowianus*) are monophyletic, whereas the subgenera *Isocladus*, *Kirganelia* and *Phyllanthus* appeared to be not monophyletic. Most clades obtained in their analyses were supported by palynological characters.

In the study of the West Indian species of *Phyllanthus*, Webster (1956) discovered the extraordinary diversity of pollen morphology within the species using light microscope (LM). Punt (1967) showed two series of *Phyllanthus* pollen types and proposed their evolutionary trends. The precise usage of pollen characters in taxonomy for the small pollen size, usually around 20–30 µm diam is difficult, therefore the aid of scanning electronic microscope (SEM) in the observation of the exine ornamentation is necessary. At least 30 pollen types were reported in 220 species of *Phyllanthus* studied using LM and/or SEM (Erdtman 1952, Webster 1956, 1986, Köhler 1965, 1967, Punt 1967, 1972, 1980, 1987, Punt & Rentrop 1973, Bor 1979, Meewis & Punt 1983, Long & Yu 1984, Rossignol et al. 1987, Lobreau-Callen et al. 1988, Chen & Wu 1997, Webster & Carpenter 2002, Wei et al. 2002, Sagun & Van der Ham 2003, Santiago et al. 2004).

In the Philippines, more than 30 species of *Phyllanthus* have been reported previously and can be classified into five subgenera and eleven sections (Elmer 1908, 1910, 1911, Robinson 1909, 1911, Merrill 1912, 1914, 1920, 1923, Quisumbing & Merrill 1928, Airy Shaw 1983, Hoffmann et al. 2003). The minute unisexual flowers and the variable leaf morphology caused the classification of some species to remain in doubt. In order to provide new evidence for the species classification, we undertook the present pollen morphological study of Philippine *Phyllanthus* species.

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MATERIAL AND METHODS

Pollen samples were collected from specimens deposited in the following herbaria: L, NHU, PUH (Table 1).

Per sample, anthers of 1–3 flowers were placed in 1.5 ml centrifuge tubes, immersed in acetic acid for 30 min until soft, crushed by a glass bar to release the pollen grains, and then acetolyzed (Erdtman 1952). The acetolyzed pollen was then dehydrated in a series of 70 %, 90 % and 100 % ethanol and pipeted onto a filter membrane to be air dried. Under a thin layer of gold coating, the pollen grains were examined and photographed using a Hitachi S-800 Scanning Electron Microscope. Pollen size was based on measuring 2–4 pollen grains per sample. The terminology used in this paper follows Huang (1972) and Punt et al. (2007).

RESULTS

Eleven pollen types were recognized in the Philippine *Phyllanthus* species studied (Table 2), seven of which have been reported previously and four (*P. erythrotrichus* type, *P. glochidioides* type, *P. securinegoides* type, *Pilate* type) might be reported here for the first time. A key to the pollen types is presented below.

Key to the pollen types

1. Pollen grain pantoporate . . . . . *P. buxifolius* type
1. Pollen grain colporate, syncolporate or areolate (i.e. pantosyncolpate). 2
2. Pollen grain syncolporate or areolate (i.e. pantosyncolpate) 3
2. Pollen grain colporate 5
3. Pollen grain areolate (i.e. pantosyncolpate), with 16–26 colpi . . . . . *P. virgatus* type
3. Pollen grain syncolporate, with three colpi 4

4. Lumina of the reticulum with granules . . *P. maritimus* type
4. Lumina of the reticulum without granules *P. casticum* type
5. Pollen grain 3-colporate 6
5. Pollen grain 4- or 5-colporate 8
6. Colpi nearly confluent at the poles, exine ornamentation rugulate-reticulate . . . . . *P. acidus* type
6. Colpi not confluent at the poles, exine ornamentation bi-reticulate or striate-reticulate 7
7. Exine ornamentation bi-reticulate, pollen grain subprolate to prolate . . . . . *P. amarus* type
7. Exine ornamentation striate-reticulate, pollen grain prolate . . . . . *P. erythrotrichus* type
8. Exine ornamentation pilate, colpi obscure . . . . *Pilate* type
8. Exine ornamentation reticulate or bi-reticulate, colpi distinct 9
9. Exine ornamentation bi-reticulate, pollen grain 4- or 5-colporate . . . . . *P. urinaria* type
9. Exine ornamentation reticulate, pollen grain 4-colporate. 10
10. Colpus margins smooth, muri round verrucate . . . . . *P. securinegoides* type
10. Colpus margins ragged, muri coniculate . . . . . *P. glochidioides* type

Table1 Locality and voucher specimens of the Philippine *Phyllanthus* species sampled in this study.

Species	Location	Voucher
P. acidus (L.) Skeels	Santa, Luzon	Gaerlan, F.J.M. et al. PPI 10249 (L)
P. amarus Schumach. & Thonn.	Palawan	Wu, M.-J. 2951 (NHU)
P. benguetensis C.B.Rob.	Luzon	Merrill, E.D. 9684 (L)
P. buxifolius (Blume) Müll.Arg.	Bohol	Ramos, M. BS 43248 (L)
P. erythrotrichus C.B.Rob.	Susong-Dalaga, Luzon	Robinson, C.B. BS 29333 (L)
P. glochidioides Elmer	Paraiso, Luzon	Edaño, G.E. PNH 40177 (L)
P. kinabaluicus Airy Shaw	Beaufort Mountain, Palawan	Ridsdale, C.E. SMHI 241 (L)
P. lamprophyllus Müll.Arg.	Palawan	Gaerlan, F.J.M. PPI 13214 (L)
P. lanceifolius Merr.	Catanduanes	Ramos, M. & G. Edano BS 75281 (PUH)
P. megalanthus C.B.Rob.	Luzon	Curran, H.M. FB 17243 (L)
P. mindorensis C.B.Rob.	Lobo, Luzon	Sulit, M.D. PNH 15718 (L)
P. ramosii Quisumb. & Merr.	Luzon	Mabesa, C. 853 (L)
P. reticulatus Poir.	Los Baños, Luzon	Hallier, J.G. 4117 (L)
P. samarensis Müll.Arg.	Paranas, Samar	Reynoso, E.J. PPI 7550 (L)
P. securinegoides Merr.	Panacan, Palawan	Sulit, M.D. PNH 16268 (L)
P. sibuyanensis Elmer	Magallanes, Sibuyan	Elmer, A.D.E. 12113 (L)
P. urinaria ssp. *nudicarpus* Rossignol & Haicour	Palawan	Wu, M.-J. 2952 (NHU)
P. urinaria ssp. *urinaria* L.	Palawan	Wu, M.-J. 2954 (NHU)
P. virgatus G.Forst.	Palawan	Wu, M.-J. 2953 (NHU)
P. aff. *glochidioides*	Tagkawayan, Luzon	Lagrimas, M.Q. PNH 39954 (L)
P. aff. *samarensis*	Santa Cruz, Luzon	Ridsdale, C.E.1479 (L)
Phyllanthus sp. A	Bohol	Ramos, M. BS 43203 (L)

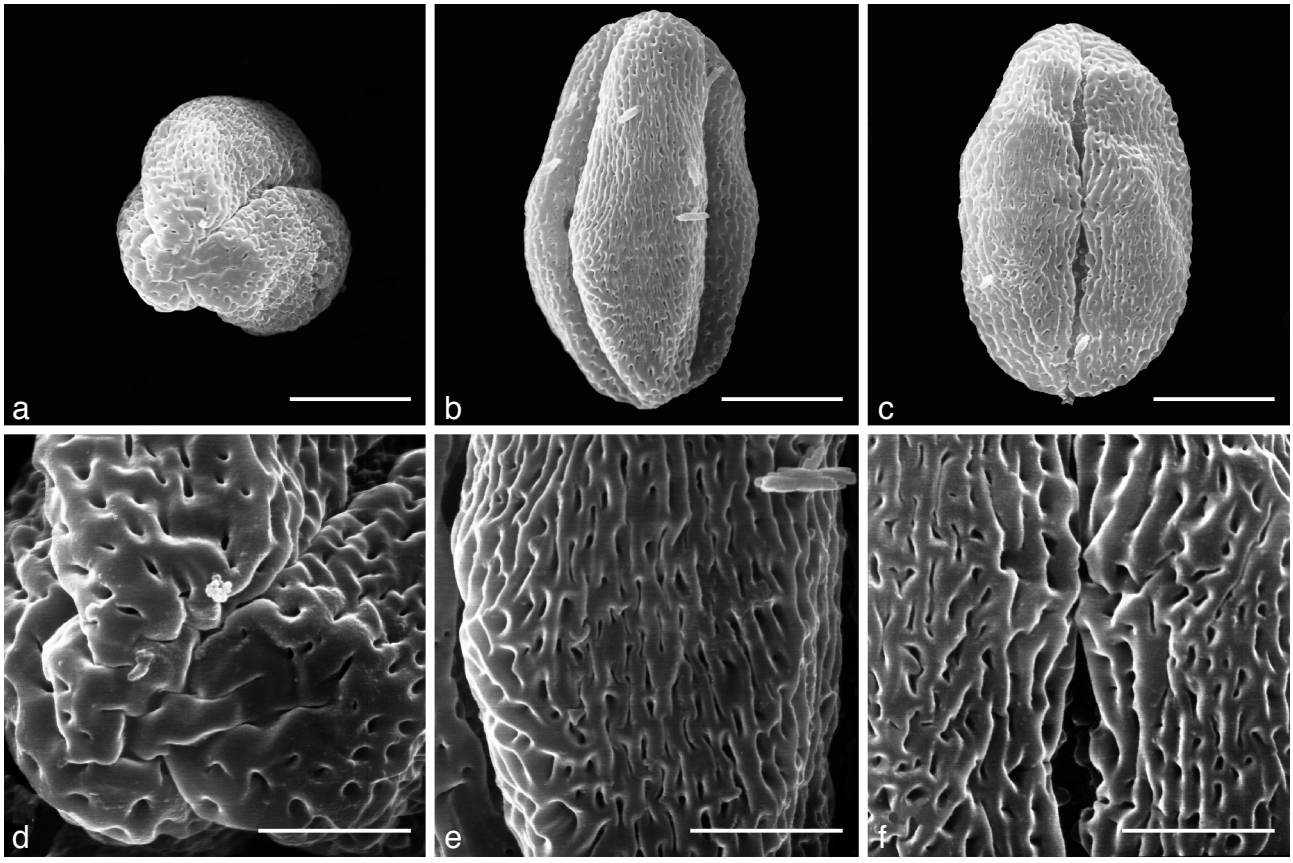

Fig. 1 Scanning electron micrographs of the *Phyllanthus erythrotrichus* type. a–f. *P. erythrotrichus*. — Scale bars: a–c = 5 µm, d–f = 2 µm.

Table 2 Pollen types of Philippine *Phyllanthus* species.

Subgenus	Section	Pollen type	Taxa	Aperture	Equatorial shape	Size P by E (µm)	P/E	Ornamentation
Eriococcus	*Scepasma*	*P. buxifolius* type	*P. buxifolius*	numerous	spheroidal to ellipsoidal	22.2–22.4 by 24.4–25.6	–	reticulate
	Emblicastrum	*P. buxifolius* type	*P. lamprophyllus*	numerous	spheroidal to ellipsoidal	22.9–24.6 by 21.3–22.9	–	reticulate
	Eriococcus	*P. buxifolius* type	*P. kinabaluicus*	numerous	spheroidal to ellipsoidal	20.0–20.4 by 20.0–20.4	–	reticulate
			P. megalanthus	numerous	spheroidal to ellipsoidal	25.0 by 24.4–26.1	–	reticulate
			P. mindorensis	numerous	spheroidal to ellipsoidal	17.5–18.0 by 18.0	–	reticulate
			P. sibuyanensis	numerous	spheroidal to ellipsoidal	18.0–20.0 by 18.3–19.6	–	reticulate
Gomphidium	*Adenoglochidion*	*P. maritimus* type	*P. ramosii*	3-syncolporate	oblate spheroidal	15.8–16.7 by 17.1	0.92–0.98	reticulate
	Gomphidium	*P. glochidioides* type	*P. glochidioides*	4-colporate	subprolate	21.7–22.1 by 17.5–18.8	1.15–1.26	reticulate
			P. aff. *glochidioides*	4-colporate	subprolate	19.1–20.8 by 15.8–17.5	1.19–1.21	reticulate
		P. securinegoides type	*P. securinegoides*	4-colprolate	prolate spheroidal	22.9–24.3 by 21.9–22.9	1.00–1.11	reticulate
Isocladus	*Paraphyllanthus*	*P. erythrotrichus* type	*P. erythrotrichus*	3-colporate	prolate to perprolate	15.3–19.3 by 9.3–10.0	1.58–2.08	striated reticulate
	Paraphyllanthus	*P. virgatus* type	*P. lanceifolius*	areolate	spheroidal to ellipsoidal	17.5–22.5 by 17.5–19.6	–	coarsely reticulate
	Macraea	*P. virgatus* type	*P. samarensis*	areolate	spheroidal to ellipsoidal	15.3–16.7 by 15.0–16.3	–	coarsely reticulate
			P. virgatus	areolate	spheroidal to ellipsoidal	16.7–18.8 by 15.8–18.8	–	reticulate
			P. aff. *samarensis*	areolate	spheroidal to ellipsoidal	18.3–19.6 by 19.2–20.0	–	reticulate
Kirganelia	*Anisonema*	*P. casticum* type	*P. reticulatus*	3-syncolporate	oblate spheroidal	11.1–11.7 by 11.7–12.5	0.91–0.96	reticulate
	Cicca	*P. acidus* type	*P. acidus*	3-colporate	oblate spheroidal	12.3–13.3 by 13.3–15.0	0.89–0.95	rugulate reticulate
Phyllanthus	*Phyllanthus*	*P. amarus* type	*P. amarus*	3-colporate	prolate speroidal to subprolate	15.3–17.0 by 13.0–15.7	1.06–1.31	bireticulate
	Urinaria	*P. urinaria* type	*P. benguetensis*	4-colprolate	prolate	20.0–22.1 by 12.1–13.3	1.63–1.76	bireticulate
			P. urinaria ssp. *nudicarpus*	4-colprolate	prolate	22.5–23.8 by 12.9–14.6	1.63–1.74	bireticulate
			P. urinaria ssp. *urinaria*	4-colprolate	prolate	16.0–16.3 by 11–12	1.36–1.45	bireticulate
not assigned	not assigned	*Pilate* type	*Phyllanthus* sp. A	4-colporate	subprolate	14.3 by 11–12.3	1.16–1.30	pilate

DESCRIPTION OF THE POLLEN TYPES

I. ***Phyllanthus erythrotrichus*** type — Fig. 1

Pollen grains prolate to perprolate. P = 15.3–19.3 µm, E = 9.3–10.0 µm, P/E = 1.58–2.08.

Aperture system — 3-colporate.

Ornamentation — Striate-reticulate, lumina small and narrow.

Species included — *P. erythrotrichus*.

Note — The ornamentation is similar to that of the *P. urinaria* type, but the lumina are narrower.

II. ***Phyllanthus virgatus*** type — Fig. 2, 3

Pollen grains spheroidal to ellipsoidal. Polarity unknown. Size = 15.3–22.5 by 15.0–20.0 µm.

Aperture system — Areolate (i.e. pantosyncolpate).

Ornamentation — Reticulate to coarsely reticulate.

Species included — *P. lanceifolius*, *P. samarensis, P. virgatus*, *P.* aff. *samarensis*.

Note — The number of lumina per areola varies: *P. lanceifolius* and *P. samarensis*: ± 30, *P. virgatus*: ± 60, and *Phyllanthus* aff. *samarensis*: ± 70. *Phyllanthus* aff. *samarensis* differs from the other species of the *P. virgatus* type by its colpus margins consisting of two parallel muri rather than four.

References — Punt 1980, 1987, Long & Yu 1984, Webster 1986, Lobreau-Callen et al.1988, Chen & Wu 1997.

III. ***Phyllanthus casticum*** type — Fig. 4

Pollen grains oblate spheroidal. P = 11.1–11.7 µm, E = 11.7–12.5 µm, P/E = 0.91–0.96.

Aperture system — 3-syncolporate.

Ornamentation — Reticulate.

Species included — *P. reticulatus*.

Note — This type is similar to the *P. acidus* type, but differs by its confluent colpi.

References — Köhler 1965, Punt 1967, 1980, Bor 1979, Long & Yu 1984, Lobreau-Callen et al. 1988.

IV. ***Phyllanthus acidus*** type — Fig. 5

Pollen grains oblate spheroidal. P = 12.3–13.3 µm, E = 13.3–15.0 µm, P/E = 0.89–0.95.

Aperture system — 3-colporate, colpi nearly confluent at the poles.

Ornamentation — Rugulate-reticulate.

Species included — *P. acidus.*

References — Köhler 1965, 1967, Punt 1967.

V. ***Phyllanthus amarus*** type

Pollen grains prolate spheroidal to subprolate. P = 15.3–17.0 µm, E = 13.0–15.7 µm, P/E = 1.06–1.31.

Aperture system — 3-colporate.

Ornamentation — Bi-reticulate.

Species included — *P. amarus.*

Note — This type and the *P. urinaria* type have both bireticulate ornamentation, but they differ in the number of colpi.

References — Punt & Rentrop 1973, Bor 1979, Punt 1980, Long & Yu 1984, Chen & Wu 1997.

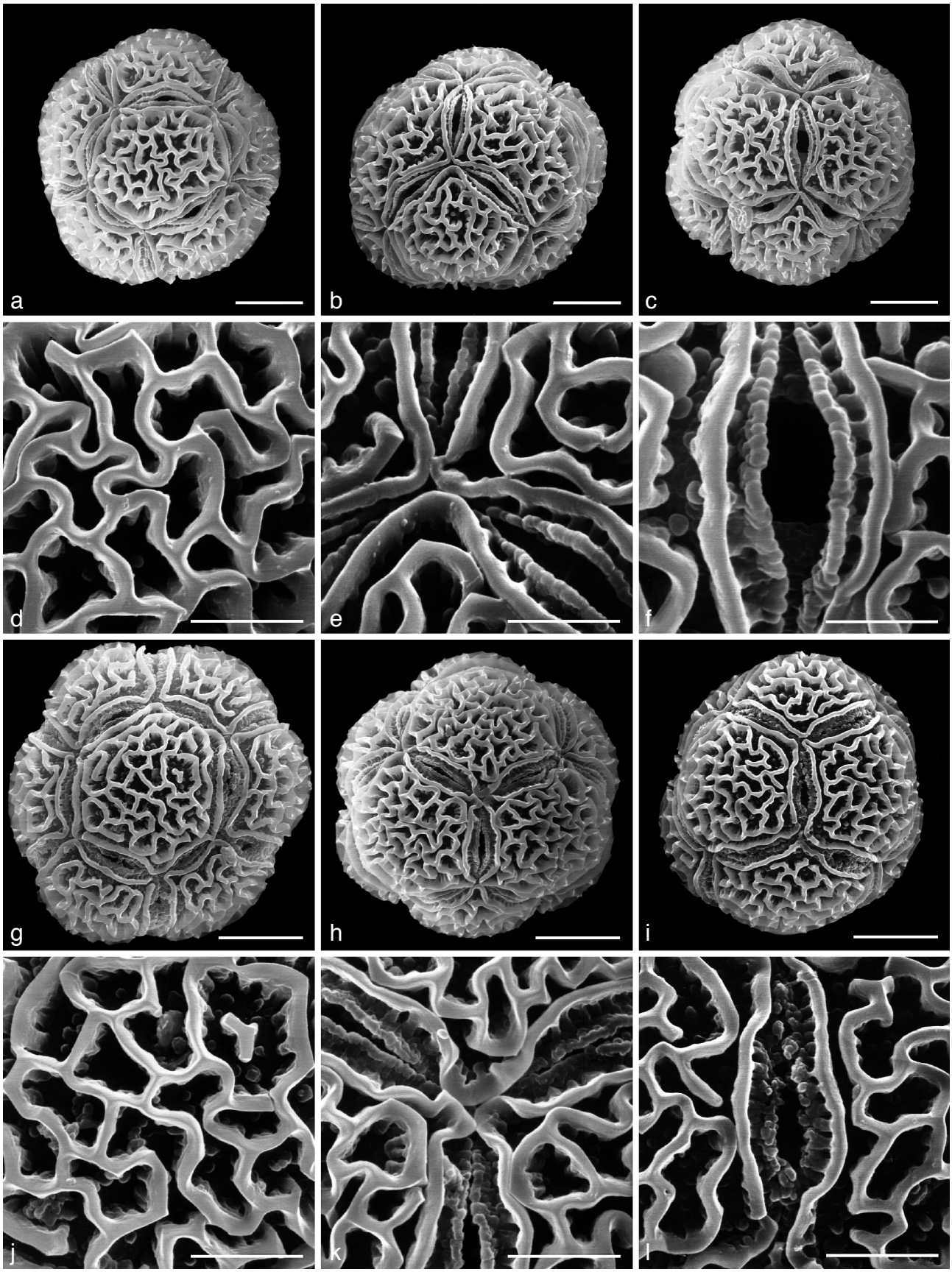

Fig. 2 Scanning electron micrographs of the *Phyllanthus virgatus* type. a–f. *P. lanceifolius*; g–l. *P. samarensis*. — Scale bars: a–c, g–i = 5 µm, d–f, j–l = 2 µm.

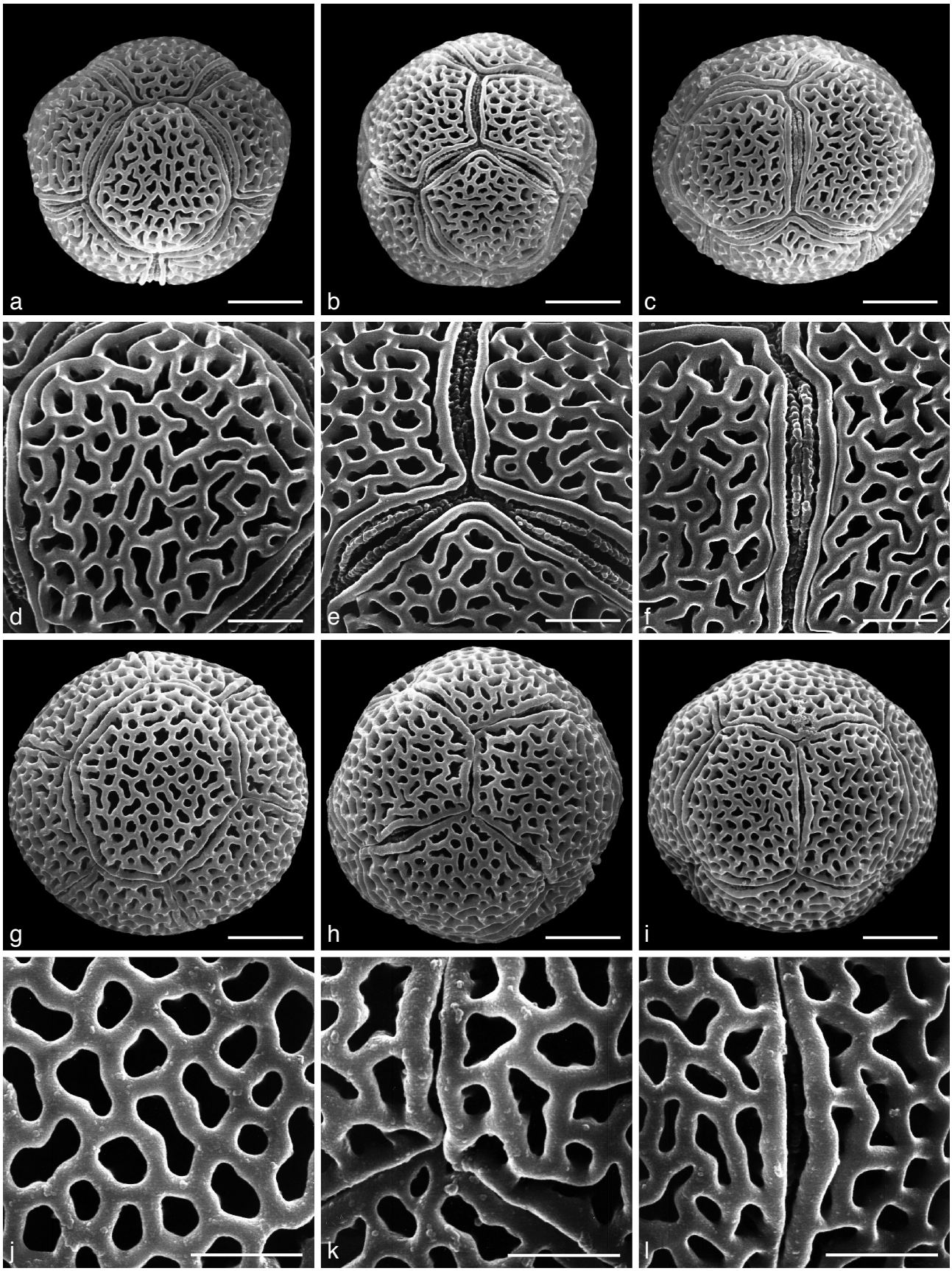

Fig. 3 Scanning electron micrographs of the *Phyllanthus virgatus* type. a–f. *P. virgatus*; g–l. *P.* aff. *samarensis*. — Scale bars: a–c, g–i = 5 µm; d–f, j–l = 2 µm.

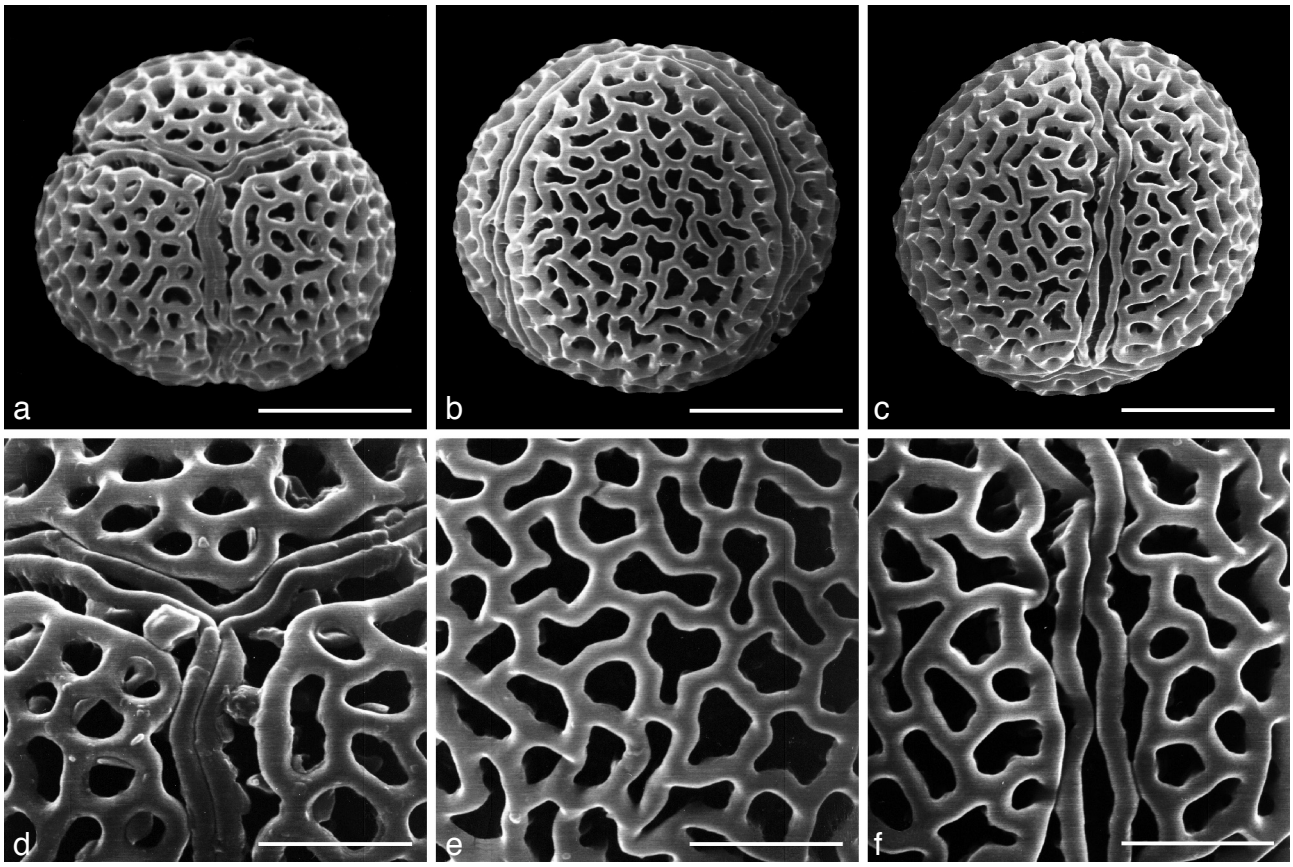

Fig. 4 Scanning electron micrographs of the *Phyllanthus casticum* type. a–f. *P. reticulatus*. — Scale bars: a–c = 5 µm, d–f = 2 µm.

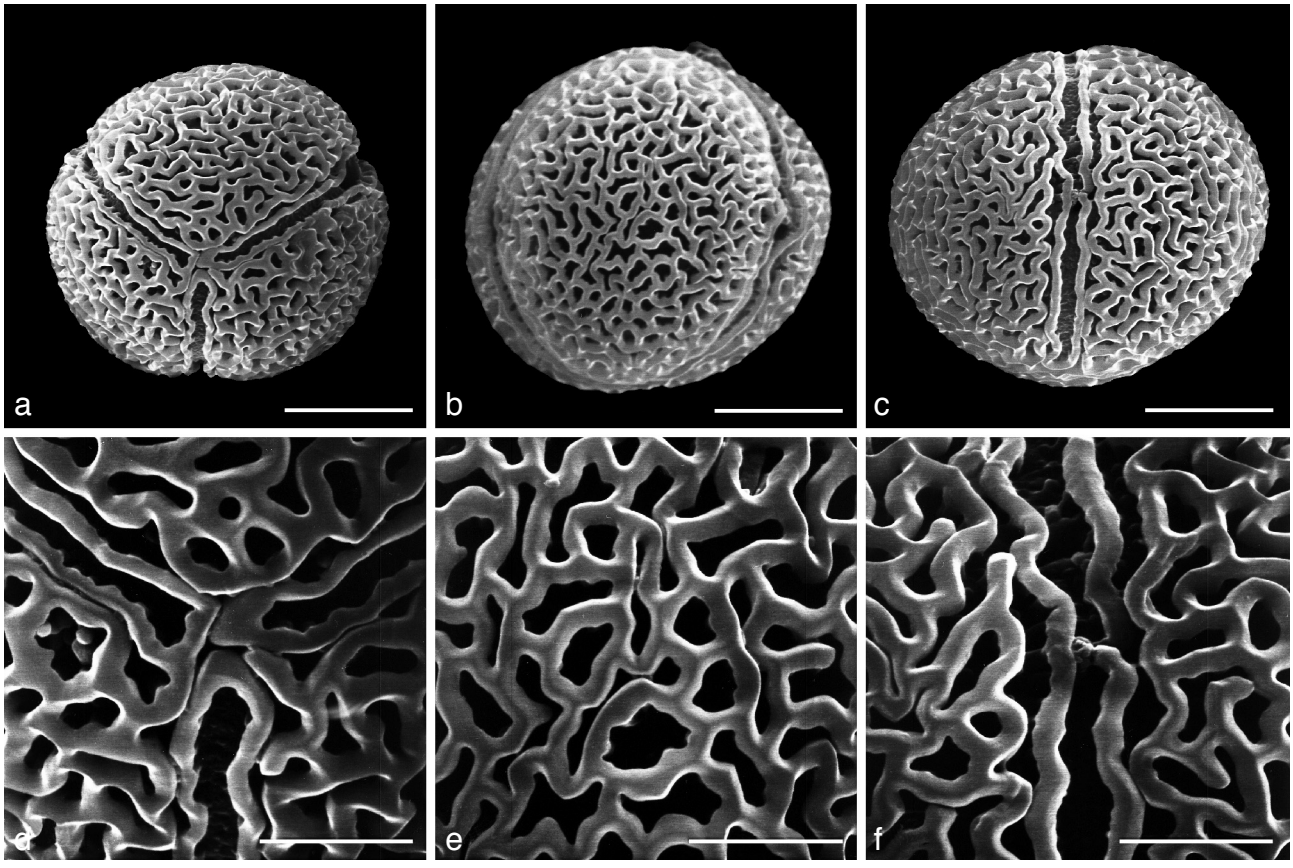

Fig. 5 Scanning electron micrographs of the *Phyllanthus acidus* type. a–f. *P. acidus*. — Scale bars: a–c = 5 µm, d–f = 2 µm.

VI. ***Phyllanthus urinaria*** type — Fig. 6

Pollen grains prolate. P = 16.0–23.8 µm, E = 11.05–14.6 µm, P/E = 1.36–1.76.

Aperture system — 4- or 5-colporate, colpi narrow.

Ornamentation — Bi-reticulate.

Species included — *P. benguetensis*, *P. urinaria* (both subspecies).

Note — Rossignol et al. (1987) found that species in sect. *Urinaria* with chromosome number 2n = 50 have 4-colporate pollen, while species with chromosome number 2n = 100 have 5-colporate pollen.

References — Punt & Rentrop 1973, Bor 1979, Long & Yu 1984, Rossignol et al. 1987, Chen & Wu 1997.

VII. ***Phyllanthus buxifolius*** type — Fig. 7

Pollen grains spheroidal to ellipsoidal. Polarity unknown. Size = 17.5–25.3 by 18.0–26.1 µm.

Aperture system — Pantoporate.

Ornamentation — Coarsely reticulate, less than 10 granules per lumen.

Species included — *P. buxifolius, P. kinabaluicus, P. lamprophyllus, P. megalanthus, P. mindorensis, P. sibuyanensis.*

References — Punt 1980, 1987, Long & Yu 1984, Wei et al. 2002.

VIII. ***Phyllanthus maritimus*** type — Fig. 8

Pollen grains oblate spheroidal. P = 15.8–16.7 µm, E = 17.1 µm, P/E = 0.92–0.98.

Aperture system — 3-syncolporate.

Ornamentation — Reticulate, lumina with small granules.

Species included — *P. ramosii*.

Note — The *P. maritimus* type is similar to the *P. casticum* type, but differs by the presence of granules in the lumina.

References — Punt 1980, Meewis & Punt 1983.

IX. ***Phyllanthus glochidioides*** type — Fig. 9

Pollen grains subprolate. P = 17.1–22.1 µm, E = 15.8–18.8 µm, P/E = 1.15–1.26.

Aperture system — 4-colporate, colpi slit-like, with ragged margins.

Ornamentation — Coarsely reticulate.

Species included — *P. glochidioides, Phyllanthus* aff. *glochidioides.*

X. ***Phyllanthus securinegoides*** type — Fig. 10

Pollen grains prolate spheroidal. P = 22.9–24.3 µm, E = 21.9–22.9 µm, P/E = 1.00–1.11.

Aperture system — 4-colporate, colpi with smooth margins.

Ornamentation — Reticulate.

Species included — *P. securinegoides.*

XI. ***Pilate*** type — Fig. 11

Pollen grains subprolate. P = 14.3 µm, E = 11.0–12.3 µm, P/E = 1.16–1.30.

Aperture system — 4-colporate, colpi obscure using SEM.

Ornamentation — Pilate, pila mostly with rounded capita.

Note — This type is similar to the inaperturate pollen grains of *P. attenuatus* (subg. *Conami*, sect. *Hylaeanthus*; Webster & Carpenter 2002), but differs by the presence of colpi.

Species included — *Phyllanthus* sp. A.

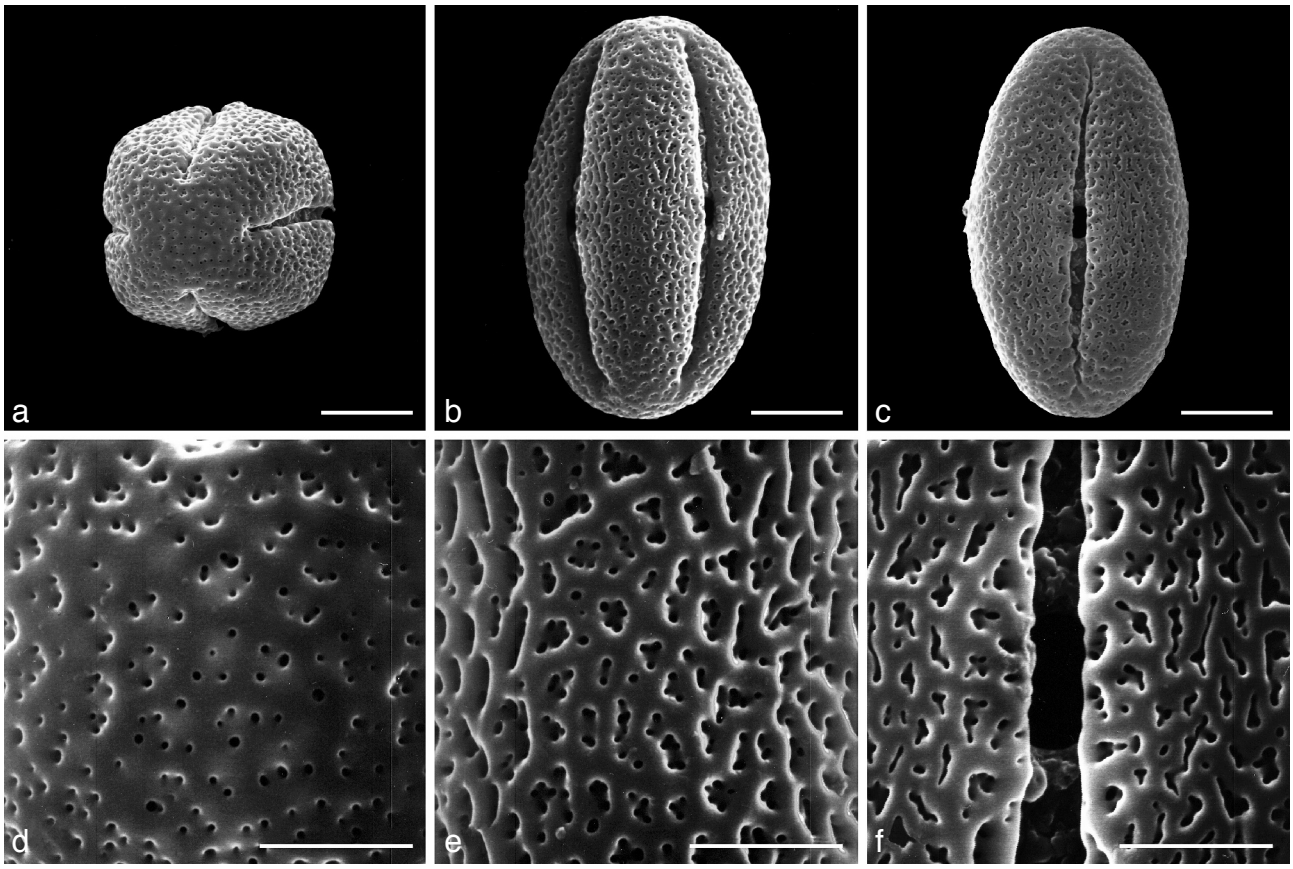

Fig. 6 Scanning electron micrographs of the *Phyllanthus urinaria* type. a–f. *P. benguetensis*. — Scale bars: a–c = 5 µm, d–f = 2 µm.

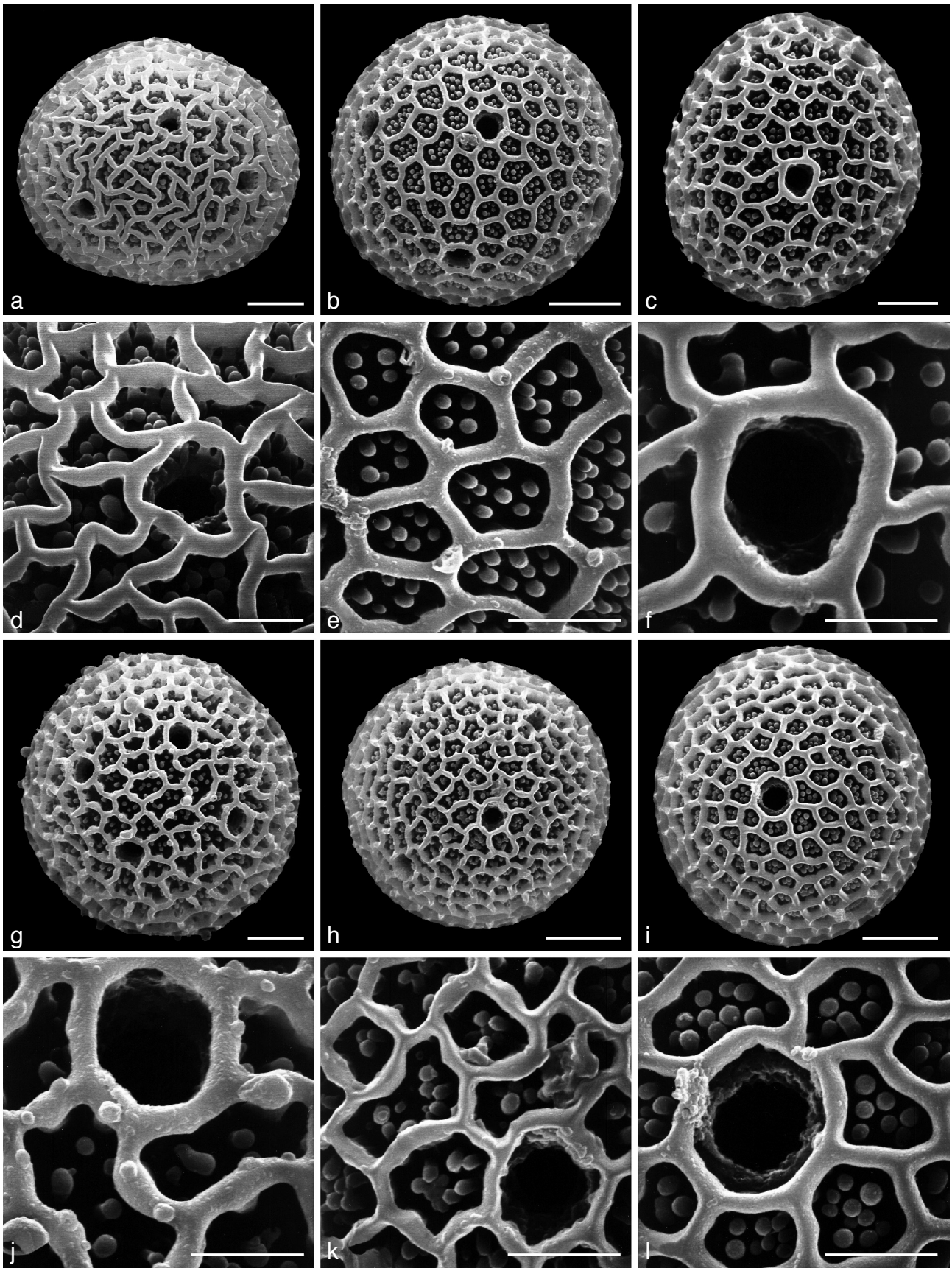

Fig. 7 Scanning electron micrographs of the *Phyllanthus buxifolius* type. a, d. *P. buxifolius*; b, e. *P. kinabaluicous*; c, f. *P. lamprophyllus*; g, j. *P. megalanthus*; h, k. *P. mindorensis*; i, l. *P. sibuyanensis*. — Scale bars: a–c, g–i = 5 µm; d–f, j–l = 2 µm.

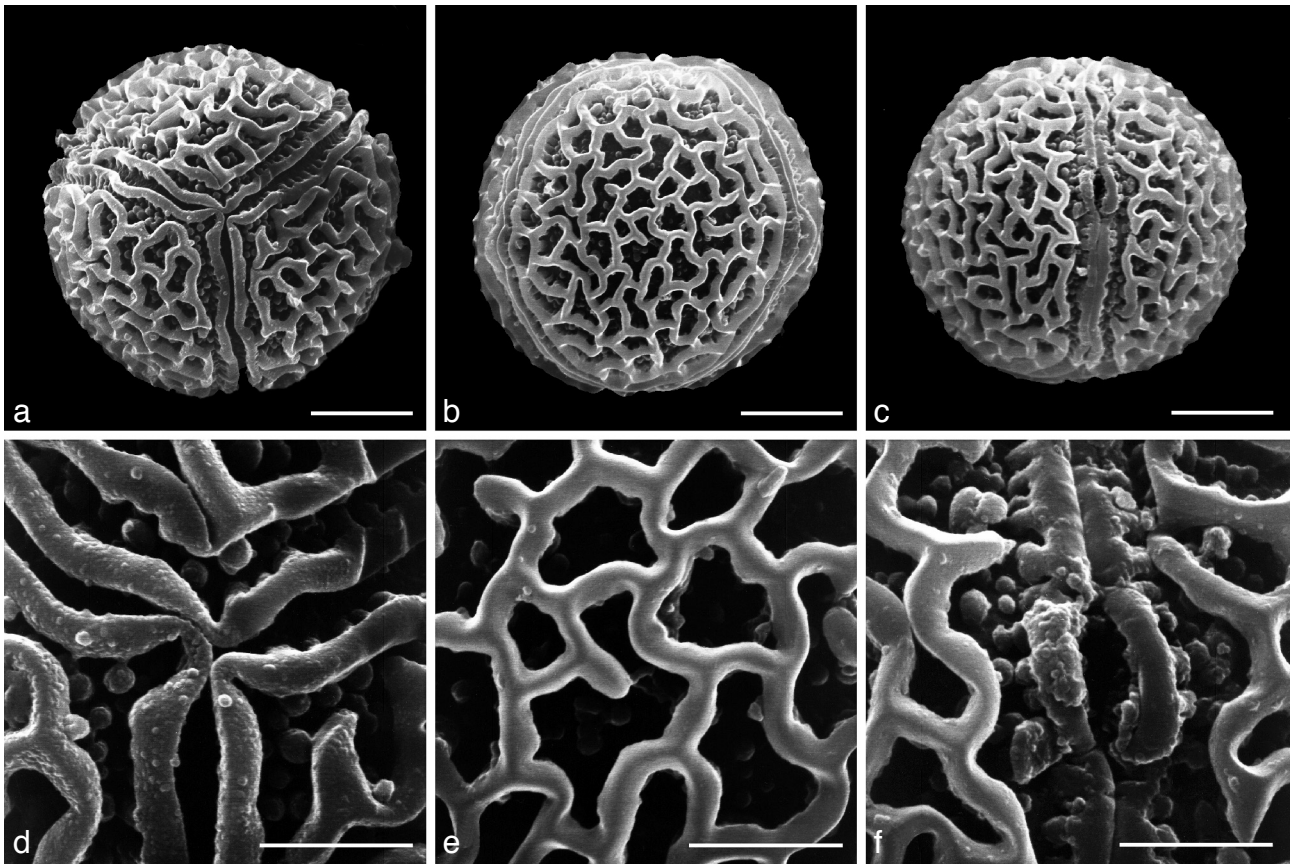

Fig. 8 Scanning electron micrographs of the *Phyllanthus maritimus* type. a–f. *P. ramosii*. — Scale bars: a–c = 5 µm, d–f = 2 µm.

DISCUSSION

Pollen types and infrageneric classification

Five of the 11 pollen types in Philippine *Phyllanthus* each occur in a single section (Table 2). The *P. amarus* type and *P. urinaria* type, both belonging to subg. *Phyllanthus*, have the same bireticulate ornamentation, but differ in the number of colpi. The *P. acidus* type, *P. casticum* type and *P. maritimus* type share reticulate exine ornamentation. However, the *P. maritimus* type has granules in the lumina. The *P. acidus* type and *P. casticum* type (both subg. *Kirganelia*) can be distinguished by the length of their colpi.

Two pollen types occur in more than one section: the *P. virgatus* type in the two sections of subg. *Isocladus*, the *P. buxifolius* type in the three sections of subg. *Eriococcus*. The *P. buxifolius* type, found in six species, is homogeneous. The *P. virgatus* type, found in four species, varies in the morphology of the colpus margins. *Phyllanthus* aff. *samarensis* has colpus margins consisting of a single murus, while the other species have colpus margins comprising two muri. Therefore, it might be appropriate to describe a different subtype for *P.* aff. *samarensis*. Evidently, the areolate pollen of *P. lanceifolius* (sect. *Paraphyllanthus*; Merrill 1914) is closer to that of sect. *Macraea* than to the 3-colporate pollen of *P. erythrotrichus* (sect. *Paraphyllanthus*; Punt 1967, 1987). Transferring *P. lanceifolius* to sect. *Macraea* should therefore be considered.

Pollen morphologically, subg. *Gomphidium*, including three pollen types, is most heterogeneous in Philippine *Phyllanthus*. The *P. maritimus* type (sect. *Adenoglochidion*) is 3-syncolporate. The *P. glochidioides* type and *P. securinegoides* type (both sect. *Gomphidium*) have 4-colporate pollen. They differ by their exine ornamentation and the morphology of the colpus margins.

Merrill (1914) found *P. securinegoides* hard to classify. He noticed that *P. securinegoides* did not fit in sect. *Gomphidium*, because the scarce styles are united, spreading and prominently cleft. Hence, he suggested that a new section should be described. Pollen morphology confirms Merrill's opinion.

Phyllanthus sp. A has not been assigned to a section and subgenus yet. Its pollen (*Pilate* type), is similar to the pilate pollen of *P. attennutus* (subg. *Conami*, sect. *Hylaeanthus*; Webster & Carpenter 2002), but has a 4-colporate apertural system.

Pollen types and phylogenetic relationships

Subgenera *Isocladus*, *Kirganelia* and *Phyllanthus* are not monophyletic, based on ITS and matK DNA sequence analyses (Kathriarachchi et al. 2006). According to these data, sect. *Paraphyllanthus* is more primitive than sect. *Macraea* (subg. *Isocladus*), sect. *Anisonema* more primitive than sect. *Cicca* (subg. *Kirganelia*) and *P. amarus* more primitive than sect. *Urinaria* (subg. *Phyllanthus*). Punt (1967) considered an increased number of colpi as a derived feature. Thus, the *P. erythrotrichus* type of sect. *Paraphyllanthus* would be more primitive than the *P. virgatus* type of sect. *Macraea*, and the *P. amarus* type of sect. *Phyllanthus* is more primitive than the *P. urinaria* type of sect. *Urinaria*. In these cases the pollen morphological trend proposed by Punt is concordant with the DNA sequence data. According to Punt (1967), the colporate *P. acidus* type of sect. *Cicca* is more primitive than the syncolporate *P. casticum* type of sect. *Anisonema*. This conflicts with the DNA sequence data. However, comparing the ornamentation in detail, the *P. casticum* type of sect. *Anisonema* has a primitive reticulate ornamentation and the *P. acidus* type of sect. *Cicca* has an advanced rugulate-reticulate ornamentation. This result tells us that the ornamentation trend is concordant with the DNA sequence data of Kathriarachchi et al. (2006).

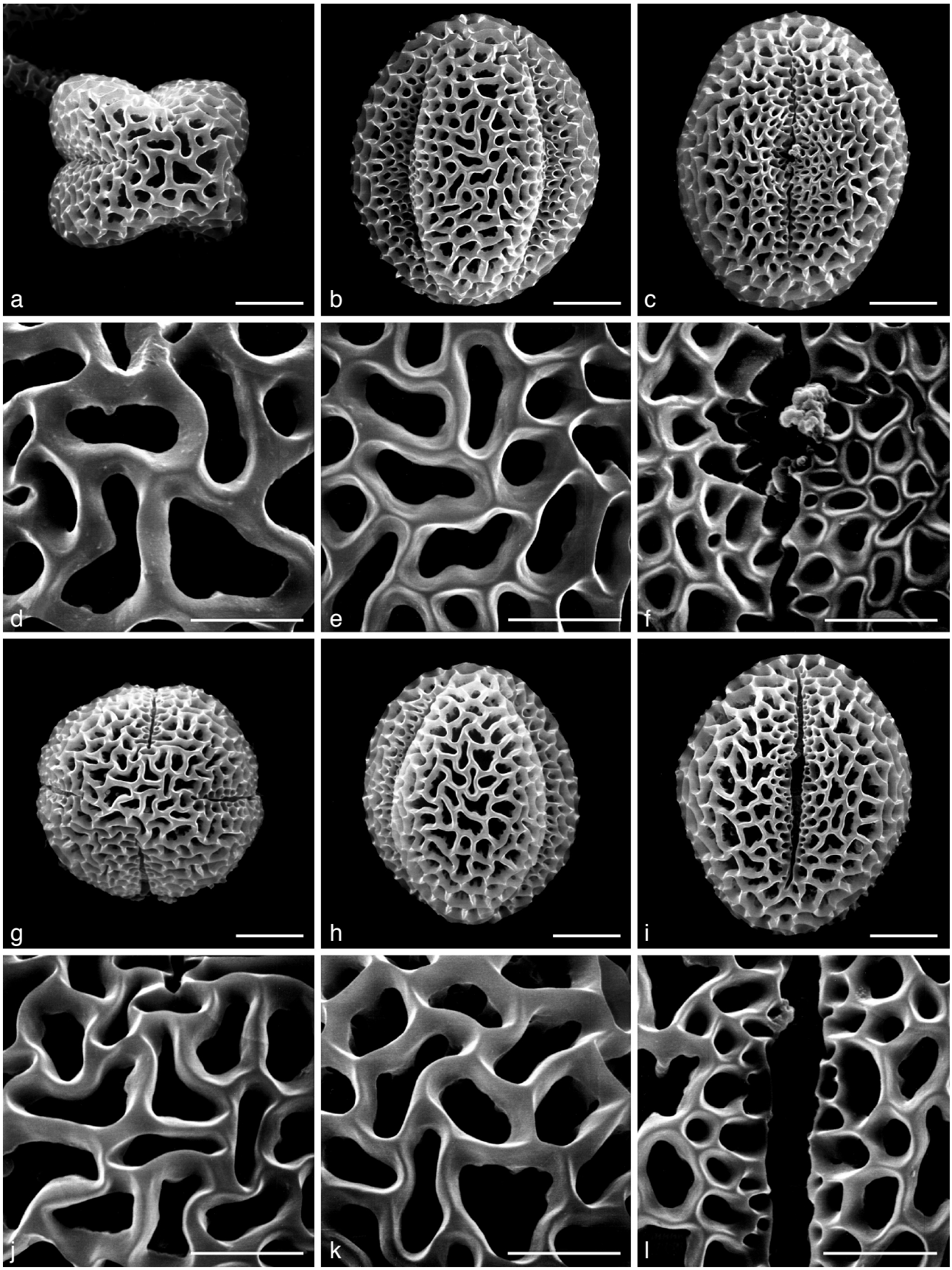

Fig. 9 Scanning electron micrographs of the *Phyllanthus glochidioides* type. a–f. *P. glochidioides*; g–l. *Phyllanthus* aff. *glochidioides*. — Scale bars: a–c, g–i = 5 µm; d–f, j–l = 2 µm.

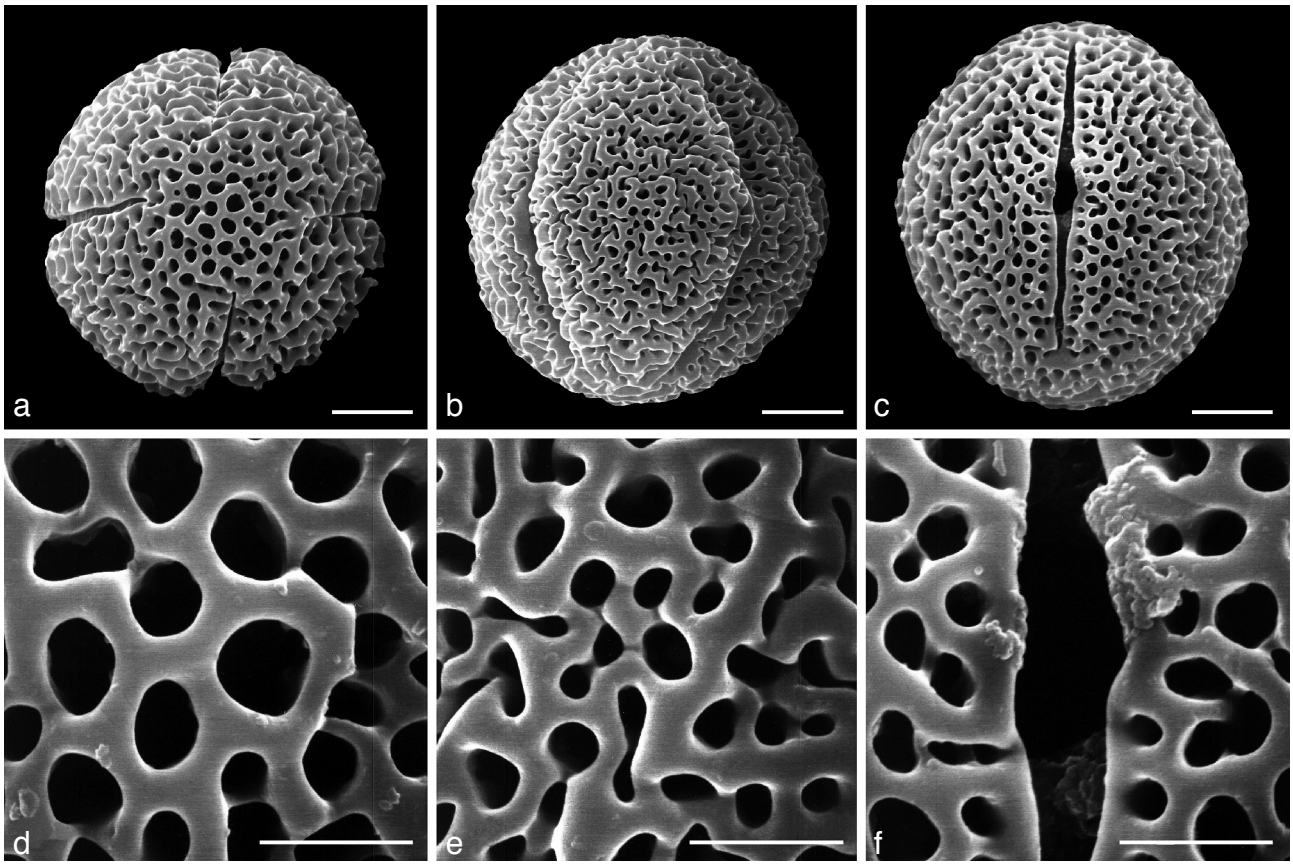

Fig. 10 Scanning electron micrographs of the *Phyllanthus securinegoides* type. a–f. *P. securinegoides*. — Scale bars: a–c = 5 µm, d–f = 2 µm.

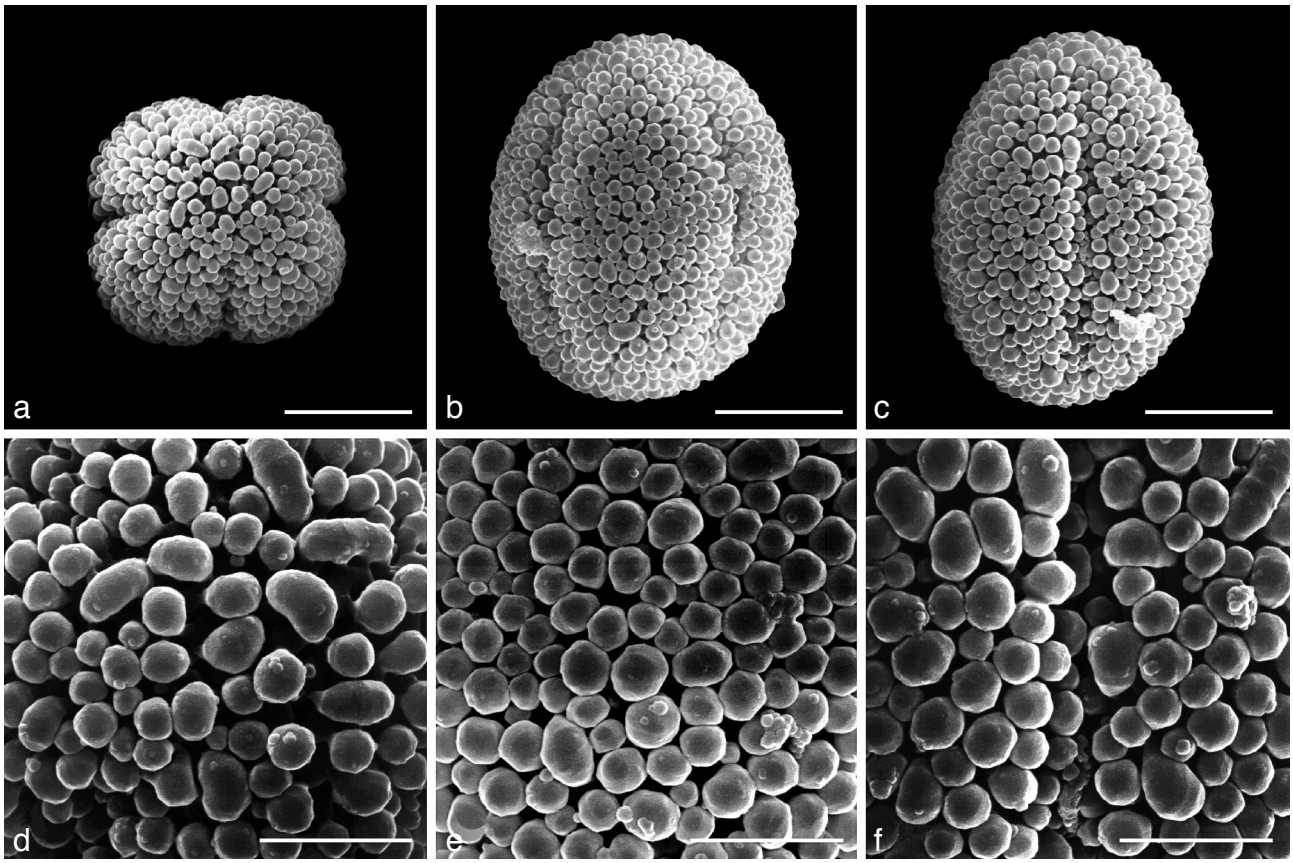

Fig. 11 Scanning electron micrographs of the *Pilate* type. a–f. *Phyllanthus* sp. A. — Scale bars: a–c = 5 µm, d–f = 2 µm.

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