

Pollen morphology and systematics of palaeotropical *Phyllanthus* and related genera of subtribe Phyllanthinae (Euphorbiaceae)

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Received 6 July 2007; accepted for publication 25 September 2007

The observations of pollen from 27 species of subtribe Phyllanthinae using scanning electron microscopy reveal considerable morphological diversity in palaeotropical *Phyllanthus* and the related palaeotropical genera *Breynia*, *Glochidion*, and *Sauropus*. The tribe appears to be monophyletic, but the pollen morphology does not support the monophyly of *Phyllanthus* or *Sauropus*. Within *Phyllanthus*, the pollen characters suggest a close relationship between the subgenera *Emblica* and *Phyllanthodendron*. They also reveal a surprising morphological congruence between the pollen grains of section *Ceramanthus* (subgenus *Isocladus*) and those of subgenus *Eriococcus*, although it is not clear whether this similarity is homoplastic. The presence of diploporate colpi is a synapomorphy uniting *Breynia* and *Sauropus*, but may be homoplastic in *Phyllanthus*. The affinities suggested by the morphological features of the pollen in the Phyllanthinae are concordant with recent molecular phylogenies. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 157, 591–608.

ADDITIONAL KEYWORDS: *Breynia* – *Emblica* – Flueggeinae – *Glochidion* – *Sauropus* – scanning electron microscopy.

INTRODUCTION

Pollen morphological studies have made important contributions to the classification of the Euphorbiaceae since the seminal works of Erdtman (1952) and Punt (1962). The pollen of *Phyllanthus*, the third largest genus in the family, has received considerable attention as an important character in inferring systematic relationships (Webster, 1956–1958; Punt, 1962, 1967, 1987; Köhler, 1965; Lobreau-Callen, Punt & Schmid, 1988; Lobreau-Callen, 1991; other works cited later). Webster & Carpenter (2002) examined 22 species of neotropical *Phyllanthus* using scanning electron microscopy (SEM), with particular attention paid to the subgenera *Conami* and *Emblica*. It was concluded that the neotropical taxa of *Phyllanthus* may have arisen from a double colonization, originat-

ing in Africa (subgenus *Kirganelia*) and Asia (subgenus *Emblica*). A study by Sagun & Van der Ham (2003), using both light microscopy (LM) and SEM, included all of the genera of the subtribe Flueggeinae (as defined by Webster, 1994): *Breynia*, *Flueggea*, *Glochidion*, *Margaritaria*, *Phyllanthus*, *Reverchonnia*, *Richeriella*, and *Sauropus*. The species of *Phyllanthus* studied by Sagun & Van der Ham (2003) were selected for having pollen grains with diploporate colpi, in order to assess the relationships within the generic group of *Breynia*, *Sauropus*, and *Phyllanthus*. In this study, we cover the ‘higher’ Flueggeinae (treated here as subtribe Phyllanthinae by G. L. Webster, unpubl. data) – *Breynia*, *Glochidion*, *Phyllanthus*, and *Sauropus* – thus complementing the work of Sagun & Van der Ham (2003).

To complement our work on the pollen of the neotropical taxa of *Phyllanthus* (Webster & Carpenter, 2002), in this study, our attention is focused on the

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palaeotropical taxa of *Phyllanthus* and the related palaeotropical genera of subtribe Phyllanthinae (Table 1). The pollen of *Phyllanthus* subgenus *Emblica* is of particular interest because it is the only neotropical subgenus of woody species well represented in America as well as the palaeotropics, although some species of subgenus *Conami* are suggestively similar (in pollen and gross morphology) to African species of subgenus *Kirganelia* (Brunel & Roux, 1977; Meewis & Punt, 1983). By contrast with the taxa of subgenus *Kirganelia*, which are largely concentrated in Africa/Madagascar (with a few species extending to Australasia), the Old World species of subgenus *Emblica* are strictly Asiatic. Furthermore, the palaeotropical sections of subgenus *Emblica* are all different from the American sections (Table 1). The genera lacking a floral disc – *Breynia*, *Glochidion*, and *Sauropus* – are Asiatic and partially sympatric with taxa of the subgenera *Kirganelia* and *Emblica*, but the phylogenetic relationships between these taxa are not entirely clear. In this study, our observations of palaeotropical species of *Phyllanthus* and related Phyllanthinae (*Breynia*, *Glochidion*, and *Sauropus*) are compared with those of earlier palynologists and with recent phylogenies based on molecular data by Wurdack *et al.* (2004), Kathriarachchi *et al.* (2005), and Samuel *et al.* (2005).

MATERIAL AND METHODS

Pollen was prepared for SEM using a modification of the procedure described in Lynch & Webster (1975) and Webster & Carpenter (2002). Staminate flowers were selected from herbarium specimens and immersed in 0.5% Aerosol OT for at least 24 h. The flowers were dissected whilst immersed in Aerosol and the anthers were removed under a dissecting microscope. Pollen was removed from the anthers by squeezing with forceps and the pollen grains were pipetted into 1500- μ L plastic reaction tubes. (The tubes were centrifuged at 150 *g* for 45 s prior to each change of solution.) The pollen was then rinsed with deionized water, immersed in 50% acetone, and placed in a water bath sonicator for 15 min to remove pollenkitt. The acetone was removed, replaced with fresh 50% acetone, and sonicated for an additional 15 min. The pollen was then rinsed in deionized water and dehydrated in ethanol (50%, and two changes of 100%). After centrifugation, pollen was pipetted onto aluminium SEM stubs without adhesive; the ethanol was then allowed to evaporate for 30 min. The stubs were coated with gold in a Denton Desk II Sputter Coater for approximately 120 s, and examined with a Hitachi 3500N scanning electron microscope at 5 kV. The terminology for the description of pollen grains is based on Punt *et al.* (1994).

RESULTS

DESCRIPTIONS OF POLLEN GRAINS

(ARRANGED BY TAXA, TABLE 1)

ANDRACHNEAE SUBTRIBE ANDRACHNINAE

Leptopus

Pollen grains prolate, three-colporate, colpi monoporate, unbordered; pores lalongate, pointed or diffuse at ends; exine tectate, reticulate, or tectate-perforate.

Leptopus (Andrachne) phyllanthoides (Nutt.) Müll. Arg. (Fig. 1). Arkansas, Demaree 36808 (DAV). Grains $22 \times 17 \mu\text{m}$; colpi narrow, unbordered, *c.* $19 \mu\text{m}$ long; exine tectate-perforate, lumina *c.* $0.5 \mu\text{m}$ in diameter. LM observations by Köhler (1965) indicate lalongate pointed ora.

PHYLLANTHEAE SUBTRIBE PHYLLANTHINAE

Phyllanthus

Pollen grains prolate to spheroidal, mostly three- to six-colporate or pantoporate, colpi monoporate or diploporate, bordered or unbordered; pores circular to lalongate; exine tectate-reticulate to pilate or clypeate.

Subgenus Isocladus: Pollen grains subprolate to spheroidal, three- or four-colporate or pantoporate, colpi monoporate; pores lalongate to circular; exine tectate-reticulate to tectate-perforate or clypeate.

Section Antipodanthus: Pollen grains subprolate to spheroidal, three- or four-colporate; colpi monoporate; exine tectate-reticulate to tectate-perforate.

Phyllanthus hirtellus. F. Muell. ex Müll. Arg. (Figs 17, 18). Grains subspheroidal, *c.* $20 \mu\text{m}$ in diameter; colpi 3, $12\text{--}13 \mu\text{m}$ long; exine tectate-reticulate; muri fenestrate, *c.* $0.3\text{--}0.4 \mu\text{m}$ across, $1\text{--}1.2 \mu\text{m}$ high, enclosing deep lumina with granules.

Section Diandri (see Appendix): Phyllanthus diandrus Pax (Fig. 5). Gabon, de Wilde 4534 (MO). Grains subprolate, $18\text{--}19 \mu\text{m}$ in diameter; colpi 3, narrow, monoporate, curving and almost meeting at poles; exine tectate-reticulate, brochi regular, roundish, *c.* $0.4\text{--}0.5 \mu\text{m}$ in diameter.

Subgenus Kirganelia: Pollen grains spheroidal to oblate, three-colporate, sometimes syncolporate; colpi monoporate or diploporate, bordered or nonbordered; pores mostly circular; exine reticulate to vermiculate.

Section Anisonema: Pollen grains spheroidal or subspheroidal, three-colporate; colpi monoporate, bordered or unbordered; exine tectate-reticulate to vermiculate.

Table 1. Systematic arrangement of taxa discussed in the text (new taxa indicated by an asterisk given in Appendix)

SUBTRIBE *Andrachninae* Müll. Arg.
Leptopus Decne.: *Leptopus phyllanthoides* (Nutt.) G. L. Webster (*Andrachne phyllanthoides* Nutt.)

SUBTRIBE *Flueggeinae* Müll. Arg.
Flueggea Willd.: *Flueggea jullienii* (Beille) G. L. Webster

SUBTRIBE *Phyllanthinae* Pax
Phyllanthus L.

SUBGENUS *Isocladus* G. L. Webster
 Section *Antipodanthus* G. L. Webster: *Phyllanthus hirtellus* (F. Muell.) Müll. Arg.
 Section *Ceramanthus* (Hassk.) Baill.: *Phyllanthus cochinchinensis* Spreng. [= *Cathetus fasciculatus* Lour.];
P. welwitschianus Müll. [= *Cathetus welwitschianus* (Müll. Arg.) G. L. Webster] Arg.
 Section *Diandri* G. L. Webster*: *Phyllanthus diandrus* Pax

SUBGENUS *Kirganelia* (Juss.) Kurz
 Section *Anisonema* (A. Juss.) Griseb.: *Phyllanthus archboldianus* Airy Shaw & G. L. Webster; *P. casticum* Willemet;
P. ciccoides Müll. Arg.; *P. deplanchei* Müll. Arg.
 Section *Brazzeani* Brunel & Roux: *Phyllanthus dinklagei* Pax
 Section *Chorisandra* (Wight) Müll. Arg.: *Phyllanthus pinnatus* (Wight) G. L. Webster
 Section *Cicca* (L.) Müll. Arg.: *Phyllanthus acidus* (L.) Skeels; *P. delpyanus* Hutch.; *P. wildemanii* Beille
 Section *Floribundi* Pax & K. Hoffm.: *Phyllanthus muellerianus* (Kuntze) Exell
 Section *Menarda* (Comm. ex A. Juss.) Müll. Arg.: *Phyllanthus cryptophilus* (Comm. ex A. Juss.) Müll. Arg.;
P. purpureus Müll. Arg.

SUBGENUS *Gomphidium* (Baill.) G. L. Webster
 Section *Adenoglochidion* (Müll. Arg.) Müll. Arg.: *Phyllanthus aeneus* Baill.; *P. brassii* C. T. White; *P. caesius* Airy Shaw
 & G. L. Webster; *P. maritimus* J. J. Sm.
 Section *Calodictyon* G. L. Webster: *Phyllanthus tuerckheimii* G. L. Webster
 Section *Eleutherogynium* Müll. Arg.: *Phyllanthus loranthoides* Baill.; *P. myrianthus* Müll. Arg.
 Section *Gomphidium* Baill.: *Phyllanthus acinacifolius* Airy Shaw & G. L. Webster; *P. amicorum* G. L. Webster;
P. bourgeoisii Baill.; *P. rupi-insularis* Hosok.

SUBGENUS *Emblica* (Gaertn.) Kurz
 Section *Emblica* (Gaertn.) Baill.: *Phyllanthus emblica* L.
 Section *Microglochidion* Müll. Arg.: *Phyllanthus maguirei* Jabl.; *P. myrsinites* Kunth in H. B. K.; *P. subapicalis* Jabl.;
P. vacciniifolius (Müll. Arg.) Müll. Arg.
 Section *Pityrocladus* G. L. Webster: *Phyllanthus ruscifolius* Müll. Arg.; *P. symphoricarpoides* Kunth in H. B. K.
 Section *incertae sedis*: *Phyllanthus annamensis* Beille; *P. hasskarlianus* Müll. Arg.

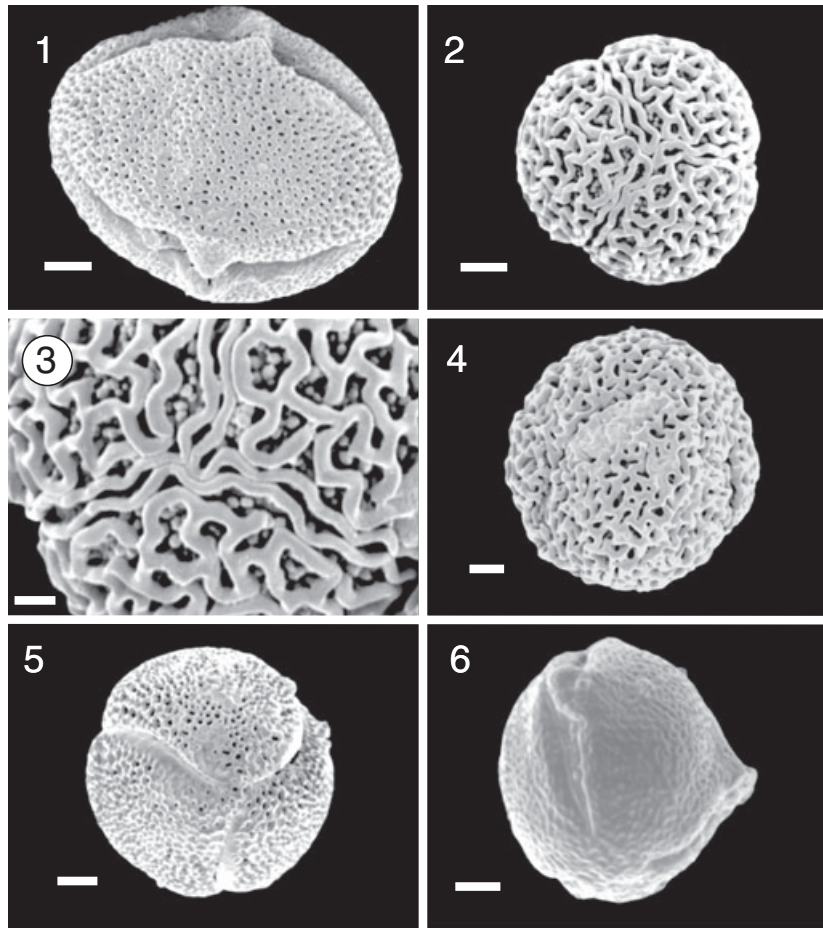
SUBGENUS *Phyllanthodendron* (Hemsl.) G. L. Webster*
 Section *Phyllanthodendron* (Hemsl.) Beille: *Phyllanthus mirabilis* Müll. Arg.; *P. roseus* (Craib & Hutch.) Beille
 Section *Pseudactephila* Croizat: *Phyllanthus anthopotamicus* Hand.-Mazz.

SUBGENUS *Phyllanthus*
 Section *Phyllanthus*: *Phyllanthus lokohensis* Leandri; *P. virgulatus* Pax
 Section *incertae sedis*: *Phyllanthus myrtaceus* Sond.

SUBGENUS *Eriococcus* (Hassk.) Croizat & Metc.
 Section *Eriococcus* (Hassk.) Müll. Arg.: *Phyllanthus kinabaluicus* Airy Shaw; *P. palauensis* Hosok.; *P. rubescens* Beille;
P. sikkimensis Müll. Arg.; *P. sootepensis* Craib
 Section *Eriococcodes* Müll. Arg.: *Phyllanthus acutissimus* Miq.; *P. ruber* (Lour.) Spreng.

SUBGENUS *INCERTAE SEDIS*: *Phyllanthus albiflorus* (F. Muell.) Müll. Arg.
Glochidion J. R. & G. Foster: *Glochidion billardieri* Baill.; *G. hylandii* Airy Shaw; *G. philippicum* (Cav.) C. B. Rob.;
G. sericeum (Blume) Zoll. & Moritzi

Sauropus Blume
 Section *Ceratogynum* (Wight) Müll. Arg.: *Sauropus amoebiflorus* Airy Shaw; *S. quadrangularis* (Willd.) Müll. Arg.;
S. rigidus Thwaites; *S. spatulifolius* Beille
 Section *Breyniopsis* (Beille) Croizat: *Sauropus perrieri* (Beille) Croizat
 Section *Sauropus*: *Sauropus androgynus* (L.) Merr.; *S. bacciformis* (L.) Airy Shaw; *S. lissocarpus* Airy Shaw
Breynia J. R. & G. Forster: *Breynia cernua* (Poir.) Müll. Arg.



Figures 1–6. Pollen grains of *Leptopus* and *Phyllanthus*. Fig. 1. *Leptopus phyllanthoides*, equatorial view. Scale bar, 3 μm . Figs 2–6. *Phyllanthus*. Figs 2 and 3. Subgenus *Kirganelia*: *Phyllanthus muellerianus*, polar view. Scale bars, 2 μm and 1 μm , respectively. Figs 4–6. Subgenus *Phyllanthus*. Fig. 4. *Phyllanthus virgulatus*. Fig. 5. *Phyllanthus diandrus*. Fig. 6. *Phyllanthus myrtaceus*. Scale bars, 3 μm .

Phyllanthus casticum. Wilemet. Aldabra, Fosberg 49162 (DAV). Grains oblate-spheroidal, three-lobed, 11–12 μm in diameter; colpi 3, narrow; monoporate; exine semitectate-reticulate, somewhat heterobrochate (brochi mostly 0.5–1 μm across).

Phyllanthus muellerianus (Kuntze) Exell (Figs 2, 3). Central African Republic, Fangouda 273 (DAV). Grains three-lobed, c. 12 μm in diameter; colpi irregular, meeting at poles, muri thickish (0.3–0.4 μm), somewhat vermiculate, enclosing central granules.

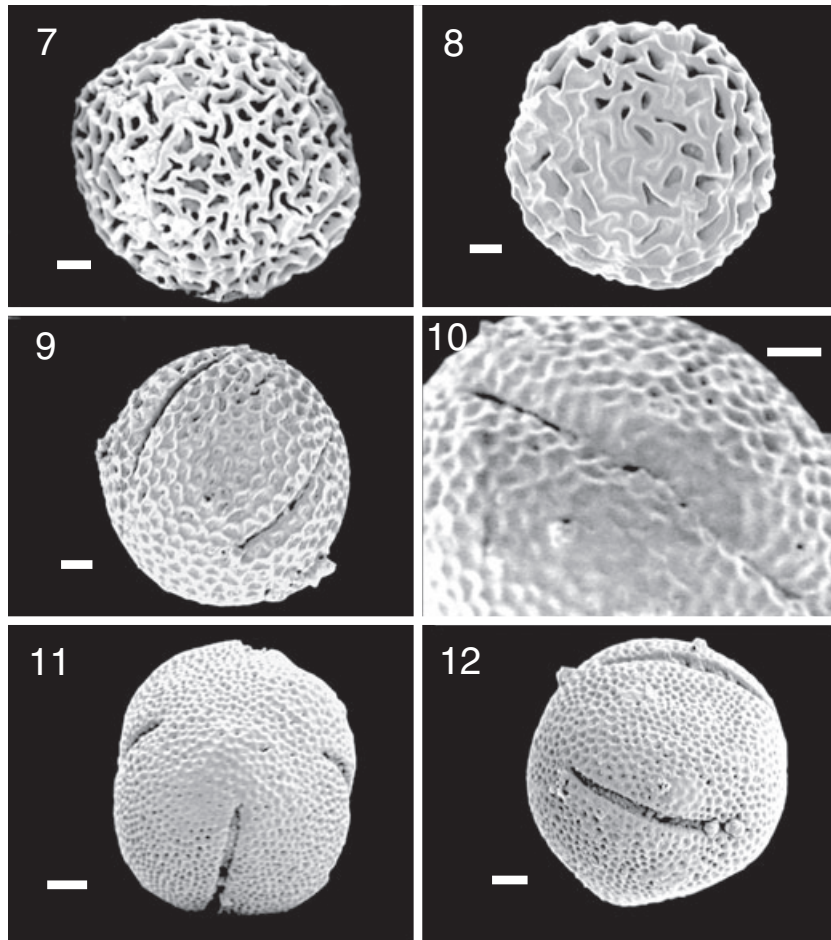
Subgenus Phyllanthus: Pollen grains spheroidal to prolate, three to four-colporate; colpi monoporate, usually unbordered; pores lalongate; exine tectate-reticulate to tectate-perforate.

Section Phyllanthus: *Phyllanthus lokohensis* Leandri. Madagascar, Miller & Randrianasolo 4633 (MO).

Grains subprolate, obtuse at poles, c. 24 \times 18 μm , three-colporate, colpi narrow, c. 16 μm long, monoporate; exine tectate-reticulate, brochi roundish, c. 1 μm in diameter.

Phyllanthus virgulatus Müll. Arg. Zambia, Angus 594 (MO). Grains nearly spheroidal, slightly three-lobed in polar view, 21–22 μm in diameter; colpi 3, narrow, monoporate; exine tectate-reticulate, heterobrochate, brochi, 0.7–1.5 μm in diameter.

Section incertae sedis: *Phyllanthus myrtaceus* Sond. (Fig. 6). South Africa, Van Wyk 729 (MO). Grains subprolate, obtuse at poles, 18–21 \times 14–16 μm , three-colporate; colpi long (c. 15 μm), straight, c. 1.5 μm broad, granular, monoporate, protruding at pole; exine tectate-reticulate, lumina regular, slightly angular, c. 0.3–0.4 μm in diameter.



Figures 7–12. Pollen grains of palaeotropical *Phyllanthus* species. Figs 7 and 8. Subgenus *Emblica*. Fig. 7. *Phyllanthus annamensis*. Fig. 8. *Phyllanthus hasskarlianus*. Scale bars, 2 μm . Figs 9 and 10. Subgenus *Phyllanthodendron*. Fig. 9. *Phyllanthus mirabilis*, near-equatorial view. Fig. 10. *Phyllanthus anthopotamicus*. Scale bars, 3 μm and 2 μm , respectively. Figs 11 and 12. Subgenus *Eriococcus*. *Phyllanthus roseus*, polar and equatorial views, respectively. Scale bars, 3 μm .

Subgenus Emblica: Pollen grains spheroidal to subprolate, four- to ten-colporate, apocolpia prominent, colpi monoporate or diploporate; pores \pm circular; exine reticulum mostly tectate-reticulate.

Section Emblica: *Phyllanthus emblica* L., not pictured here, has been illustrated with LM by Köhler (1965) and with SEM by Punt (1987); they describe the grains as subprolate, four- or five-colporate, monoporate, with circular endopores and finely reticulate exine. The two following species, although similar in vegetative and floral morphology, have very divergent pollen grains and may not belong in section *Emblica*.

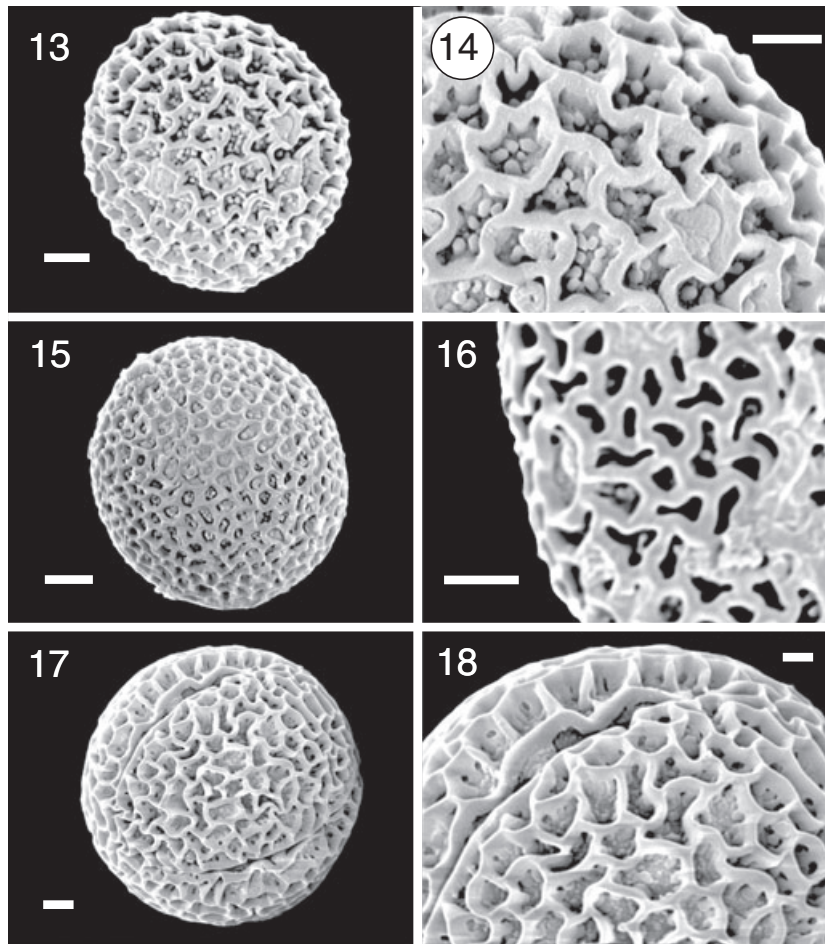
Phyllanthus annamensis Beille (Fig. 7). Annam, Clemens 4096 (MO). Grains spheroidal, 16–17 μm in diameter, three-brevicolporate; colpi narrow, unbordered, c. 5 μm long; exine vermiculate-reticulate.

Phyllanthus hasskarlianus Müll. Arg. (Fig. 8). Java, Soejarto 94 (DAV). Grains subspheroidal, 8–9 μm in

diameter; pantoporate or brevicolporate, up to 2 μm long; exine coarsely reticulate (\pm vermiculate), muri c. 0.5 μm broad, lumina irregular, 0.5–2 μm in diameter, without granules.

Subgenus Phyllanthodendron: (Some details after W. Punt, unpubl. data) Pollen grains suboblate to subprolate, often flattened at poles, three- to five-stephanocolporate, colpi monoporate; pores lalongate; exine tectate-reticulate or tectate-perforate.

Section Phyllanthodendron: *Phyllanthus mirabilis* Müll. Arg. (Fig. 9). Thailand, Smitinand 1096 (UC). Grains oblate spheroidal, flattened at poles, c. 20 μm in diameter, three- or four-colporate, colpi narrow and short (c. 8 μm long), monoporate; brochi regular, \pm pentagonal or hexagonal, c. 1.5 μm across, lumina indistinctly granular.



Figures 13–18. Pollen grains of *Phyllanthus* subgenera *Eriococcus* and *Isocladius*. Figs 13–16. Subgenus *Eriococcus*. Figs 13 and 14. *Phyllanthus palauensis*. Scale bars, 3 μm and 2 μm , respectively. Fig. 15. *Phyllanthus kinabaluicus*. Scale bar, 3 μm . Fig. 16. *Phyllanthus ruber*. Scale bar, 2 μm . Figs 17 and 18. Subgenus *Isocladius*. *Phyllanthus hirtellus*. Scale bars, 2 μm and 1 μm , respectively.

Section Pseudactephila: Phyllanthus anthopotamicus Hand.-Mazz. (Fig. 10). China, Li Zhiyou 28622 (MO). Grains subprolate, c. $20 \times 17 \mu\text{m}$, five-colporate, colpi straight and narrow; exine tectate-reticulate, brochi regular, somewhat angled, lumina c. $0.5 \mu\text{m}$ in diameter.

Phyllanthus roseus (Craib & Hutch.) Beille (Figs 11, 12). Thailand, van Beusekom 1779 (MO). Grains subprolate, four-colporate, colpi straight, with granular membrane; exine finely tectate-reticulate.

Subgenus Eriococcus: (Some details after W. Punt, unpubl. data). Pollen grains spheroidal to subprolate, pantoporate, pores c. $12\text{--}16$, circular; exine \pm coarsely reticulate.

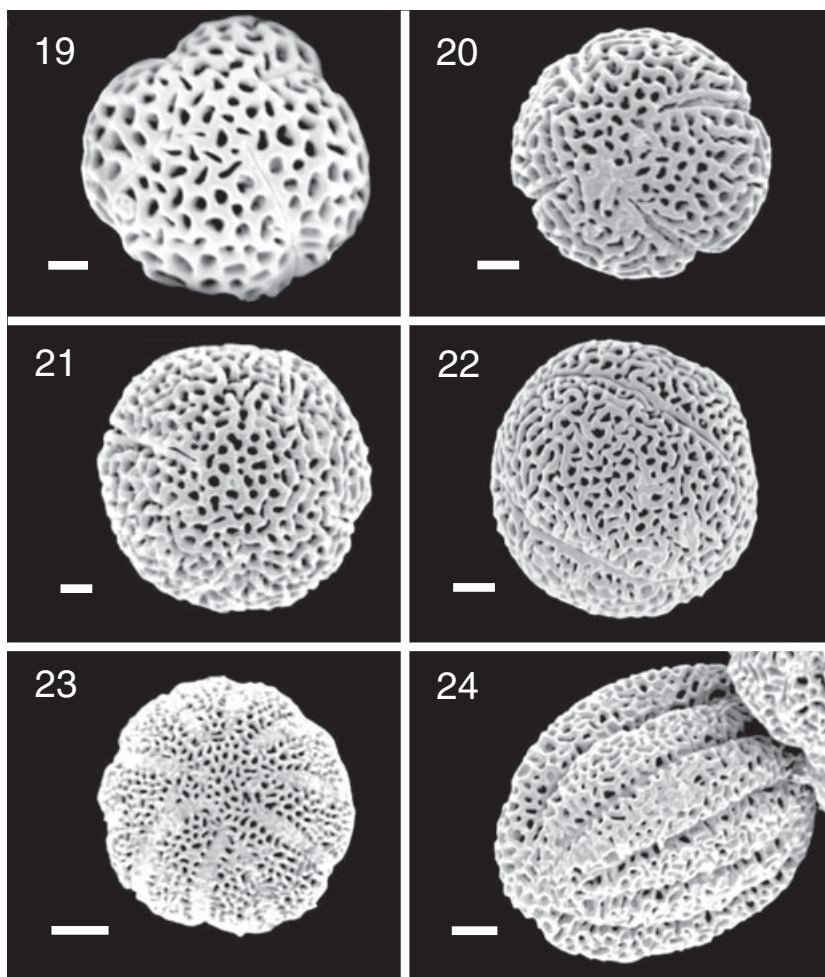
Section Eriococcus: Phyllanthus palauensis Hosok. (Figs 13, 14). Palau, Cheatham 190 (DAV). Grains spheroidal, c. $18 \mu\text{m}$ in diameter, pantoporate, pores

c. $1\text{--}1.3 \mu\text{m}$ in diameter; exine vermiculate-reticulate, muri c. $0.3\text{--}4.5 \mu\text{m}$ in diameter; lumina $1\text{--}2 \mu\text{m}$ across, each with three to eight granules.

Phyllanthus kinabaluicus Airy Shaw (Fig. 15). Kalimantan, Beaman *et al.* 7782 (DAV). Grains spheroidal, $16\text{--}17 \mu\text{m}$ in diameter; pantoporate, pores c. $1.5 \mu\text{m}$ in diameter; exine evenly reticulate, muri c. $0.5 \mu\text{m}$ in diameter, lumina c. $0.7\text{--}1 \mu\text{m}$ in diameter, enclosing granules.

Phyllanthus rubescens Beille. Annam, Poilane 6912 (UC). Grains spheroidal, $22\text{--}24 \mu\text{m}$ in diameter; pantoporate, pores not clearly distinguishable; reticulum very coarse, muri c. $1\text{--}1.5 \mu\text{m}$ in diameter, \pm vermiculate; lumina $2\text{--}5 \mu\text{m}$ along longest axis, enclosing granules.

Phyllanthus sikkimensis Müll. Arg. Thailand, Maxwell 86–600 (MO). Grains subspheroidal, $16\text{--}18 \mu\text{m}$ in diameter; pantoporate, pores round to angular, $1\text{--}2 \mu\text{m}$ in diameter; exine tectate-reticulate,



Figures 19–24. Pollen grains of *Glochidion* and *Sauropus*. Figs 19–22. *Glochidion*. Fig. 19. *Glochidion billardieri*. Scale bar, 2 μm . Fig. 20. *Glochidion hylandii*. Scale bar, 3 μm . Fig. 21. *Glochidion philippicum*. Scale bar, 2 μm . Fig. 22. *Glochidion sericeum*. Scale bar, 3 μm . Figs 23 and 24. *Sauropus*. Fig. 23. *Sauropus rigidus*. Fig. 24. *Sauropus spatulifolius*. Scale bars, 4 μm and 3 μm , respectively.

brochi slightly irregular, muri 0.2–0.3 μm in diameter, lumina c. 0.5–1 μm in diameter, mostly with a solitary granule.

Section Eriococcodes: Phyllanthus ruber (Lour.) Spreng. (Fig. 16). China, East Hainan Team 26 (MO). Grains spheroidal, 22–23 μm in diameter; pantoporate, pores c. 2 μm in diameter; exine coarsely reticulate, muri \pm vermiculate, muri c. 0.5 μm broad, lumina irregular, 1–2 μm in diameter, indistinctly granular.

Glochidion

Pollen grains suboblate to prolate spheroidal, four- to six-colporate, colpi monoporate, bordered; pores circular; exine tectate-reticulate (sometimes coarse).

Glochidion billardieri Baill. (Fig. 19). New Caledonia, Webster 18380 (DAV). Grains suboblate, four-lobed in polar view, 14–15 μm in diameter; colpi 4, narrow; exine tectate-reticulate, evenly brochate, muri thick (1–1.5 μm thick), lumina round or slightly angled, 1–1.5 μm in diameter. Also illustrated (SEM) by Lobreau-Callen (1991).

Glochidion hylandii Airy Shaw (Fig. 20). Queensland, Webster & Hyland 18880 (DAV). Grains prolate spheroidal, slightly four-lobed, 18–19 μm in diameter; colpi 4, narrow, distinctly marginate, c. 13 μm long; exine tectate-reticulate, slightly heterobrochate along colpus; muri c. 0.5 μm in diameter.

Glochidion philippicum (Cav.) C. B. Rob. (Fig. 21). Australia, Webster & Tracey 18973 (DAV). Grains subspheroidal or prolate spheroidal, 18–19 μm in diameter; colpi 4, bordered, sometimes interrupted

medianly; exine tectate-reticulate, brochi somewhat irregular.

Glochidion sericeum (Blume) Zoll. & Moritzi (Fig. 22). Sumatra, Burley 1451 (DAV). Grains subspheroidal, slightly four- or five-lobed, *c.* 20 µm in diameter; colpi 4 or 5, narrow, indistinctly marginate, 15–16 µm long; exine tectate-reticulate, somewhat vermiculate.

LM illustration by Punt (1962). LM descriptions of *G. zeylanicum* (Gaertn.) A. Juss. and *G. puberum* (L.) Hutch. by Erdtman (1952), and of *G. concolor* Müll. Arg., *G. littorale* Blume, *G. obscurum* (Willd.) Blume, *G. ramiflorum* J. R. & G. Forster, and *G. superbum* Baillon by Punt (1962), indicate that all are four-colporate. However, Köhler (1965) reported five-colporate grains in *G. fagifolium* (Müll. Arg.) Miq. ex Bedd. [= *G. hohenackeri* (Müll. Arg.) Bedd.] and *G. moonii* Thwaites.

Sauropus

Pollen grains oblate spheroidal to oblate, 6–12-colporate; colpi diploporate (at least in part), bordered or unbordered; pores circular; exine finely tectate-reticulate to tectate-perforate.

Section Ceratogynum: Sauropus rigidus Thwaites (Fig. 23). Sri Lanka. Wheeler 12609 A (DAV). Grains oblate, 18–19 µm in diameter, eight- to ten-colporate; colpi distinctly bordered; exine evenly tectate-reticulate, lumina 0.3–0.5 µm in diameter. In the related species *S. quadrangularis* (Willd.) Müll. Arg., Köhler (1965) reported six- or seven-diploporate colpi and lumina up to 1.3 µm in diameter.

Sauropus spatulifolius Beille (Fig. 24). Hawaii (cult.), Staples 1140 (BISH). Grains subprolate, *c.* 20–21 × 17–20 µm; colpi 9 or 10, *c.* 15 µm long, narrow, unbordered; exine tectate-reticulate, somewhat heterobrochate and vermiculate, lumina mostly 0.7–1 µm in diameter.

Section Sauropus: Sauropus androgynus (L.) Merr. Florida (cult.), Unander 1463 (DAV). Grains misshapen, ± oblate, 32–36 µm in diameter; exine coarsely furrowed and pitted, ± tectate-perforate, lumina *c.* 0.2–0.3 µm in diameter. Punt (1962; LM) reported oblate spheroidal normal grains 25.5 × 28 µm, with eight or nine colpi.

Section Breyniopsis: Sauropus pierreii (Beille) Croizat was not examined by SEM. However, LM descriptions and illustrations by Punt (1962) and Köhler (1965) indicate subprolate pollen grains with six or seven colpi, consistently diploporate. Except for the shape, the pollen grains appear to be consistent with other species of *Sauropus*.

Section incertae sedis: Sauropus albiflorus (F. Muell. ex Müll. Arg.) Airy Shaw (Fig. 25). Queensland, 15.x.1948, Clemens s.n. (DAV). Grains spheroidal, 15–17 µm in diameter; apertures indistinct; exine reticulate, slightly vermiculate, muri 0.3–0.4 µm in diameter, lumina *c.* 1.5–2 µm in diameter, with copious granules.

Sauropus amoebiflorus Airy Shaw (Fig. 26). Thailand, Maxwell 89–764 (MO). Grains oblate spheroidal, 24 µm in diameter; colpi 10 or 11, narrow and incised; exine tectate-perforate, lumina 0.3–0.6 µm in diameter.

Sauropus bacciformis (L.) Airy Shaw (Fig. 27). Philippines, Bicknell 1210 (DAV). Grains oblate spheroidal, 20–21 µm in diameter; colpi 5 or 6, incised, very narrow and without distinct margins; exine tectate-perforate, lumina rounded, mostly 0.4–0.6 µm in diameter. Described from LM by Punt (1962) as having oblate pollen grains, 27.5 × 32.5 µm, with consistently diploporate colpi.

Sauropus lissocarpus Airy Shaw (Figs 28 and 29), Australia, Evans M3402 (MO). Grains prolate spheroidal, *c.* 17 µm long, 12 µm in diameter, with eight narrow colpi; exine tectate-perforate, lumina 0.3–0.6 µm in diameter.

Breynia

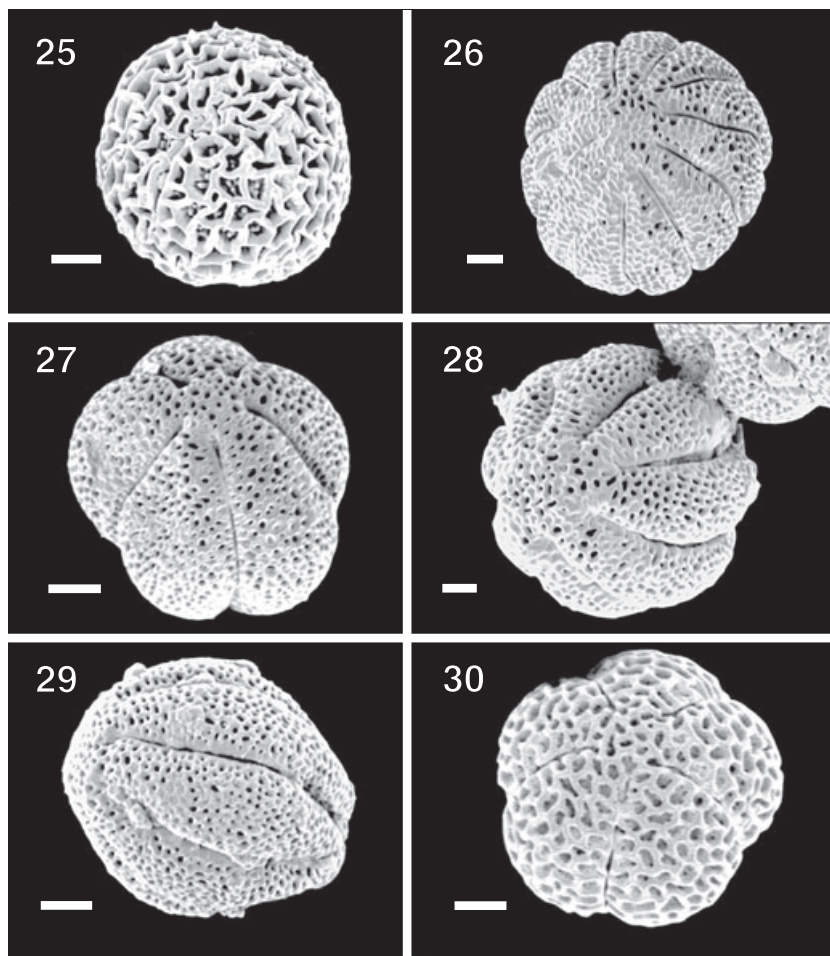
Pollen grains mostly oblate, five- to ten-colporate, sometimes syncolporate; colpi (at least in part) diploporate, narrow, incised, indistinctly bordered; pores circular; exine coarsely tectate-reticulate or transitional to tectate-perforate.

Breynia cernua (Poir.) Müll. Arg. (Fig. 30). Kalimantan, Jarvie & Ruskandi 5038 (DAV). Grains oblate, 19–20 µm in diameter, five-colporate; exine tectate-perforate, somewhat heterobrochate, rounded lumina 0.5–1 µm in diameter. Köhler (1965; LM) described *B. cernua* and *B. disticha* J. R. & G. Forster as having five to ten colpi, and Lobreau-Callen (1991) provided an SEM illustration of *B. disticha*.

Breynia oblongifolia (Müll. Arg.) Müll. Arg. New Caledonia, Webster 18788 (DAV). Grains oblate, 20–21 µm in diameter; colpi 5 or 6, narrow, irregular; exine tectate-reticulate, evenly brochate, lumina 0.3–0.5 µm in diameter. LM illustrations of *B. fruticosa* (L.) Hook. (Erdtman, 1952) and *B. disticha* J. R. & G. Forst. (Köhler, 1965) indicate six to eight colpi.

RESUMÉ OF POLLEN MORPHOLOGY IN PALAEO-TROPICAL PHYLLANTHINAE

This pollen morphological survey of approximately 30 taxa of subtribe Phyllanthinae (subtribe Flueggeinae ex. p., *sensu* Webster, 1994) indicates a striking palynological diversity in *Phyllanthus*, a moderate spread of aperture and exine sculpturing diversity in



Figures 25–30. Pollen grains of *Sauropus* and *Breynia*. Figs 25–29. *Sauropus*. Fig. 25. *Sauropus albiflorus*. Scale bar, 3 μm . Fig. 26. *Sauropus amoebiflorus*. Scale bar, 3 μm . Fig. 27. *Sauropus bacciformis*. Scale bar, 4 μm . Figs 28 and 29. *Sauropus lissocarpus*. Scale bars, 2 μm and 3 μm respectively. Fig. 30. *Breynia cernua*. Scale bar, 3 μm .

Sauropus and *Glochidion*, and considerable uniformity in *Breynia*. Observations on species of *Phyllanthus* include 15 species in six subgenera: *Kirganelia*, *Emblica*, *Gomphidium*, *Phyllanthodendron*, *Phyllanthus*, and *Eriococcus*. The pollen morphology of *Leptopus (Andrachne) phyllanthoides* (Nutt.) Müll. Arg. is included (Fig. 1) to illustrate the apparently plesiomorphic condition in the clade that includes tribe Phyllantheae: grains \pm prolate, three-colporate, colpi monoporate, and exine tectate-perforate or tectate-reticulate.

The present study includes observations on seven subgenera and 13 sections of *Phyllanthus*; however, several species cannot be definitively located in a section. No typical species of subgenus *Isocladus* are illustrated here, as both *P. hirtellus* (F. Muell.) Mull. Arg. and *P. diandrus* Pax are of uncertain affinity. The curious twisted colpi of the pollen grains of *P. diandrus* are unique amongst all the taxa observed

in this study. The vegetative characters (narrowly winged branches and auriculate stipules) of *P. diandrus* suggest a possible affinity with two sections of subgenus *Isocladus*, but its unique pollen sets it apart, and it is referred to a new section, *Diandri*, in the Appendix.

In subgenus *Kirganelia*, which may prove to be the sister group of the subgenera other than *Isocladus*, the pollen grains are mainly spheroidal to oblate, the colpi is usually bordered, and the exinous sculpturing is often coarse. Our observations of the pollen of *P. casticum* P. Willemet (section *Anisonema*) and *P. muellerianus* (Kuntze) Exell (section *Floribundi*) match the descriptions of Punt (1980) and Meewis & Punt (1983). The pollen in *P. casticum* resembles that of certain other African/Madagascan taxa, such as *P. pinnatus* (Wight) G. L. Webster (section *Chorisandra*), in its three-colporate grains with narrow unbordered colpi and a semitectate-reticulate exine (Punt,

1987). This appears to be the ancestral morphological condition in the palaeotropical taxa of *Phyllanthus*. The pollen in subgenus *Gomphidium* is typically more like that of *P. muellerianus* in its tendency to syncolpy and its vermiculate exine ornamentation, as indicated in the studies of Australasian species by Punt (1980), Lobreau-Callen *et al.* (1988), and Webster (1988).

The pollen of subgenus *Emblica* has been less thoroughly studied than that of subgenus *Gomphidium*. Köhler (1965), in describing (LM) the pollen of *P. emblica* L., noted that the four- to six-monoporate colpi have circular ora that are not always equatorially positioned. The pollen grains of *P. emblica*, illustrated (SEM) by Punt (1987), are typical for the subgenus in their slightly prolate shape, four narrow colpi, and tectate-reticulate exine. The species reported here, *P. annamensis* Beille (Fig. 7) and *P. hasskarlianus* Müll. Arg. (Fig. 8), are anomalous in having brevicolporate (apparently monoporate) grains with vermiculate exine. The pollen grains of *P. annamensis*, in particular, resemble those of species in subgenus *Eriococcus*; however, Punt (unpubl. data) associated the pollen of *P. annamensis* and *P. hasskarlianus* with other species (for example, *P. baeobotryoides* Müll. Arg. and *P. geoffrayi* Beille that clearly belong in subgenus *Emblica*).

The pollen grains of the neotropical taxa of subgenus *Emblica*, such as *P. symphoricarpoides* Kunth and *P. ruscifolius* Müll. Arg., in the neotropical section *Pityrocladus* (Webster, 2002), are similar, with four or five monoporate colpi (Webster & Carpenter, 2002). However, in some species of section *Microglochidion*, the five to eight colpi are diploporate (Punt, 1967; Sagun & Van der Ham, 2003), and diploporate colpi have also been observed in the neotropical subgenus *Conami* (Webster & Carpenter, 2002).

Subgenus *Phyllanthodendron* is a very distinctive Asiatic group that was recognized as a separate genus by Croizat (1942). The pollen grains of the three species examined – *P. anthopotamicus* Hand.-Mazz., *P. mirabilis* Müll. Arg., and *P. roseus* (Craib & Hutch.) Beille – with three to five monoporate colpi, are rather similar to those of *P. emblica* in size and sculpturing (Figs 9–12). This suggests the possibility of a close relationship between subgenera *Emblica* and *Phyllanthodendron*, which have roughly sympatric ranges in south-eastern Asia.

Subgenus *Eriococcus*, with over 50 species in several sections, is the most palynologically diverse of the palaeotropical subgenera of *Phyllanthus* (G. L. Webster, unpubl. data). The seven species studied from sections *Eriococcus* and *Eriococcodes* are all pantoporate instead of colporate, a feature that separates subgenus *Eriococcus* from other palaeotropical groups of *Phyllanthus*. The species within section *Eriococcus* show significant differences in exine sculpturing,

which is relatively fine in *P. kinabaluicus* (Fig. 15) and *P. sikkimensis* Müll. Arg., but extremely coarse in *P. ruber* (Lour.) Spreng (Fig. 16). Together with other morphological characters, this suggests that a number of subsections may need to be created within section *Eriococcus*.

The species in subgenus *Phyllanthus* are mostly listed under section *Phyllanthus*, although infrasubgeneric relationships are still less satisfactorily delineated in the palaeotropical taxa than in those in the neotropics (G. L. Webster, unpubl. data). The pollen grains of species such as *P. lokohensis* Leandri, from Madagascar, are rather typical for section *Phyllanthus*, especially subsection *Swartziani*. Species such as *P. virgulatus* Müll. Arg. (Fig. 4) clearly differ from American species of subsection *Swartziani* (Punt & Rentrop, 1974) in their spheroidal pollen grains with a coarse, somewhat irregular, reticulum; they also may be referable to a separate subsection. By contrast, the pollen of *P. myrtaceus* Sond. (Fig. 6), from South Africa, is very distinctive in its large colpi that are distended at the pore; it probably belongs to a separate subsection from the other African species.

The genera of subtribe Phyllanthinae show different degrees of pollen morphological divergence. The mainly four-colporate pollen grains of *Glochidion* (Figs 19–22), a large genus of Asia and Australasia, appear to be quite similar to those of some species of *Phyllanthus* subgenus *Emblica*, except for their coarser exine ornamentation. By contrast, the grains of *Breynia* and *Sauropus* are divergent in their mostly oblate shape and larger number of diorate colpi. There is a considerable resemblance between the grains of *Breynia* and *Sauropus* and the South American species of section *Microglochidion* (in which diorate colpi also occur). However, as pointed out below, this is probably an instance of convergent evolution.

DISCUSSION

Our results offer some insight into the phylogenetic relationships amongst the subgenera of *Phyllanthus*, and also between *Phyllanthus* and related genera of the subtribe Phyllanthinae. Fortunately, a number of critical studies of the pollen of palaeotropical taxa of *Phyllanthus* are available, especially by Punt (1962, 1967, 1972, 1980, 1986, 1987), but also by Bor (1979), Lobreau-Callen *et al.* (1988), and Meewis & Punt (1983). In the recent palynological study of the neotropical taxa of *Phyllanthus* (Webster & Carpenter, 2002), it was noted that most of the woody American species belong to endemic American subgenera (*Conami* and *Xylophylla*), and that subgenus *Emblica* is the only woody subgenus with significant representation in both the Old World and New World.

The interpretation of the results of palynological studies of Old World taxa of *Phyllanthus* is complicated because of the incomplete coverage by modern taxonomic revisions since the treatment of tropical African species by Hutchinson (1912), although the east African species have been thoroughly reviewed by Radcliffe-Smith (1987, 1996). The pioneering work on Philippine species by Robinson (1909) was followed by a comprehensive treatment of the species in Indochina by Beille (1927), and by the extensive publications of Airy Shaw, who contributed a number of useful treatments of Euphorbiaceae for Thailand (Airy Shaw, 1971), Borneo (Airy Shaw, 1975), New Guinea (Airy Shaw, 1980a), Australia (Airy Shaw, 1980b), and Sumatra (Airy Shaw, 1981). More recently, Schmid (1991) published a revision of the more than 100 New Caledonian species, and Florence (1997) provided a treatment of most of the Polynesian species. However, these works do not consider in detail the phylogenetic relationships between the subgenera and sections of palaeotropical *Phyllanthus*.

A critical baseline for comparative studies of pollen morphology in *Phyllanthus* was provided by Meewis & Punt (1983) in their study of the African species of subgenus *Kirganelia*. Punt (1967) had earlier pointed out the palynological similarities between *Phyllanthus*, *Flueggea*, and *Margaritaria*. Webster (1984) noted that the pollen structure in some eastern Asiatic species (for example, *Flueggea jullienii* Beille) is similar to that in *P. pinnatus* (Wight) G. L. Webster, in subgenus *Kirganelia* (section *Chorisandra*). It appears possible that section *Chorisandra* may be the sister group of the other sections in subgenus *Kirganelia*, and perhaps the sister group to all the other woody subgenera of *Phyllanthus*.

Brunel (1975) and Meewis & Punt (1983) described trends in the evolution of pollen morphology in subgenus *Kirganelia*, and made a number of suggestions about the applicability of pollen data in emending the classification of sections. Brunel proposed several groups within section *Floribundi*, some of which (for example, *Chorisandra*) should probably be treated as separate sections. Within subgenus *Kirganelia*, Brunel circumscribed *Kirganelia* to include the *P. casticum* complex and restricted section *Anisonema* to *P. reticulatus* Poir. and related species. This seems to be a reasonable proposal, and is reflected in the revised classification in Table 1. Meewis & Punt (1983), studying a larger number of species in greater detail, concurred with many of Brunel's proposals (although noting that his proposed new names were not validly published). They also provided an interesting phyletic tree of pollen types, with *P. pinnatus* as the 'sister group' of the pollen clade which terminates in the '*P. archboldianus*' pollen type that links African species of subgenus *Kirganelia* with those in

Australasia. The classification of the African species of subgenus *Kirganelia* remains difficult because pollen types in some instances do not correlate well with fruit and flower characters.

The status of subgenus *Cicca* now appears to be resolved, partially by reference to pollen characters. In the original concept of Webster (1957), it included four sections (*Ciccopsis*, *Cicca*, *Aporosella*, and *Emblia*). That classification placed too much emphasis on fruit morphology, and the subgenus has been successively dismembered. A separate subgenus *Emblia* was recognized by Webster (1967b), following the earlier disposition of Kurz (1874). However, further scrutiny of the remaining taxa in subgenus *Cicca* has shown that the pollen grains are very similar to those in subgenus *Kirganelia*. Brunel (1975) made a breakthrough with his discovery that the West African species he identified as *P. delpyamis* Hutch belongs to section *Cicca*. Although this plant appears to be *P. wildemanii* Beille [represented by *Chevalier* 12721, 13305 (P)], which was incorrectly synonymized with *P. profusus* N. E. Br. by Govaerts, Frodin & Radcliffe-Smith (2000), it appears virtually certain that the commonly cultivated 'grosella' (*P. acidus* [L.] Skeels) is a domesticated form of a West African species. Consequently, *Cicca* has now been downgraded from subgenus to section (Webster, 2001), coordinate with the Cuban section *Ciccopsis* (whose relationships remain uncertain).

The pollen of subgenus *Gomphidium* has been reviewed by Punt (1980) for New Guinea, Lobreau-Callen *et al.* (1988) and Lobreau-Callen (1991) for New Caledonia, and Webster (1988) for eastern Melanesia. In the circumscription of Webster & Airy Shaw (1971), as modified by Webster (unpubl. data), subgenus *Gomphidium* is an entirely palaeotropical group, except for a single isolated species (*P. tuerckheimii* G. L. Webster) endemic to Central America (Webster, 1967a). Punt recognized five pollen types within the New Guinea species, based on exine ornamentation, presence of granules in the lumina, and degree of polar syncolpy. Notably, he also recognized two pollen types from Australasian species of subgenus *Kirganelia*: one for *P. archboldianus* Airy Shaw & G. L. Webster (section *Anisonema*), and the other for *P. ciccoides*, *P. novae-hollandiae*, and *P. reticulatus*. However, this pollen evidence does not always match the classification of Webster and Airy Shaw: *P. caesius* Airy Shaw & G. L. Webster had been assigned to section *Anisonema* (in subgenus *Kirganelia*), but was placed by Punt (1980) into the same pollen type as *P. maritimus* J. J. Sm. (section *Adenoglochidion* in subgenus *Gomphidium*).

The pollen morphological studies of the New Caledonian species of *Phyllanthus* by Lobreau-Callen *et al.* (1988) and Lobreau-Callen (1991) were based on

the examination of nearly 50 species, almost half of those described by Schmid (1991). In New Caledonia, there is only one species of subgenus *Kirganelia*, *P. deplanchei* Müll. Arg., which has the pollen type of the Malagasian *P. casticum*. In subgenus *Gomphidium*, there is only one species, *P. bourgeosii* Baill., with the 'basic' *P. acinacifolius* type that is so prevalent in New Guinea. Lobreau-Callen *et al.* (1988) concluded that from pollen of the *P. acinacifolius* type, with colpi having undifferentiated margins and not meeting the poles, there have arisen successively the more 'advanced' *P. loranthoides* and *P. aeneus* pollen types in other species of section *Gomphidium* and in all species of sections *Adenoglochidion* and *Pentaglochidion* (according to the classification of Schmid, 1991). Their diagram indicates the morphological (and, by implication, phylogenetic) relationships between the pollen types and taxa in New Guinea and New Caledonia. It is somewhat disconcerting that the *P. aeneus* pollen type, found in both New Caledonia and New Guinea, appears to be independently derived (at least twice) from the *P. acinacifolius* and *P. loranthoides* pollen types. The authors noted above candidly state that the correspondence between pollen type and current classifications is far from satisfactory. However, the rarity of the *P. acinacifolius* type and the absence of the *P. loranthoides* type in New Caledonia suggest that the centre of diversification of subgenus *Gomphidium* was probably in New Guinea (or adjacent areas), whence it later spread to tropical Australia and to New Caledonia and further into Melanesia.

The more limited study of the eastern Melanesian species by Webster (1988) accords with the findings of Punt (1980) and Lobreau-Callen *et al.* (1988). In addition to one widespread species (*P. ciccooides* Müll. Arg.) of subgenus *Kirganelia* that has reached the Santa Cruz Islands and Vanuatu, and an endemic species of section *Eleutherogyinium* in Vanuatu, there are four species of section *Gomphidium* in Fiji that all have the *P. aeneus* pollen type. The sixth Melanesian species of section *Gomphidium*, *P. amicorum* G. L. Webster from the island of Eua in Tonga, is both the easternmost species of the section and one of the most enigmatic: morphologically, it is most similar to *P. rupi-insularis* Hosok., of the Balau group in the Caroline Islands. As in New Guinea, so in Micronesia and eastern Melanesia, inferences from comparisons of pollen type with floral morphology do not lead to entirely convincing results.

The most aberrant of all the taxa of subgenus *Gomphidium* is undoubtedly the monotypic section *Calodictyon*, which is restricted to Central America (Guatemala to Honduras). As noted by Webster (1967b), the floral morphology – with three free stamens and three duplex staminate disc segments –

is similar to that of species of section *Gomphidium* in New Guinea. The leaves, in size and texture, are somewhat similar to those of *P. brassii* C. T. White in Queensland. The pollen grains of *P. tuerckheimii* G. L. Webster (the only species of section *Calodictyon*) differ from those described from New Guinea (Punt, 1980) and New Caledonia (Lobreau-Callen *et al.*, 1988) in their very coarse per-reticulate tectum and unbordered colpi; therefore, it is possible that section *Calodictyon* is misplaced in subgenus *Gomphidium*. However, none of the American species of subgenera *Emblia* and *Conami*, examined by Webster & Carpenter (2002), show any meaningful similarities to section *Calodictyon*. The evidence at present still (rather weakly) supports placement of the section into subgenus *Gomphidium*.

In previous surveys of pollen morphology in *Phyllanthus*, subgenus *Emblia* has been somewhat neglected. Köhler (1965) and Punt (1987) illustrated the pollen of *P. emblica* L. and noted that the grains are oblate spheroidal, four- or five-colporate, with narrow colpi, circular endoporus, and a tectate-reticulate exine. In a manuscript based on his LM studies, W. Punt (pers. comm.) described his *P. emblica* type as 'spheroidal, stephanocolporate, with narrow nonbordered slightly sunken monorate colpi, costate mostly circular pores, and reticulate exine with capita thicker and broader than columellae'. The pollen grains of *P. ruscifolius* Müll. Arg. and *P. symphoricarpoides* Kunth, from the recently described South American section *Pityrocladus* (Webster, 2002), closely resemble those of section *Emblia* (Webster & Carpenter, 2002). Although Pax & Hoffmann (1931) transferred *P. symphoricarpoides* to *Glochidion* because of its more or less unlobed styles, the pollen evidence is persuasive in confirming its placement in subgenus *Emblia*. The pollen of section *Microglochidion*, the other American section of subgenus *Emblia*, is discussed below in relation to the pollen of *Glochidion* and *Sauropus*.

A group that exhibits some interesting similarities to subgenus *Emblia* is subgenus *Phyllanthodendron*, which was accepted by Croizat (1942) as a distinct genus. *Phyllanthodendron* has very distinctive staminate flowers with more or less caudate sepals and an androecium of three connate stamens with long apiculate anthers. The seeds are different from those in subgenus *Emblia* (and in most taxa of *Phyllanthus*) in having a ventral excavation somewhat reminiscent of that in *Flueggea* or *Glochidion*. The pollen grains of *P. anthopotamicus* Hand.-Mazz. (Fig. 10) and *P. mirabilis* Müll. Arg. (Fig. 9), of section *Phyllanthodendron*, are similar to those of *P. emblica* in their subprolate shape, short narrow colpi, and evenly brochate exine reticulum; however, they differ in having lalongate rather than circular pores (W. Punt, unpubl. data).

Further study is needed to determine whether *Phyllanthodendron* should be treated as a distinct subgenus, an independent genus, or subsumed into subgenus *Emblica*.

Subgenus *Eriococcus*, like subgenera *Emblica* and *Phyllanthodendron*, is centred in eastern Asia and does not extend beyond New Guinea and Australia, with the single exception of *P. palauensis* Hosok. (Figs 13, 14) in the Caroline Islands. *Eriococcus* differs from all other palaeotropical woody taxa of *Phyllanthus*, except for section *Ceramanthus* (in subgenus *Isocladus*), in its pantoporate pollen grains. There is considerable variation in exine structure within the sections of subgenus *Eriococcus*, especially in section *Eriococcus*. The pollen of a Bornean species, *P. kinabaluicus* Airy Shaw (Fig. 15), is typical in its perfectly spherical shape with an evenly brochate tectate-reticulum exine that has granules in the lumina. The grains of *P. sikkimensis* Müll. Arg. are similar, except for a slightly more irregular reticulum. In contrast, *P. rubescens* Beille is distinguished by an extremely coarse reticulum.

The pollen grains of subgenus *Eriococcus* bear some similarity to those of section *Ceramanthus*, which have been studied in detail by Punt (1972). Although the apertures of the species studied in section *Ceramanthus* differ from those in subgenus *Eriococcus* by their more elongate shape, the reticulum is similar. The question arises therefore as to whether there is a close relationship between section *Ceramanthus* and subgenus *Eriococcus*. In favour of such a supposition is a similarity of the androecium in both groups: stamens few (three in *Ceramanthus*, two to four in *Eriococcus*) with filaments connate. However, in other vegetative and reproductive characters, the groups are very different: the species in subgenus *Eriococcus* are monoecious, with typical phyllanthoid branching, four often lacerate sepals in staminate flowers, and smooth seeds, whereas the species in section *Ceramanthus* are dioecious, lack phyllanthoid branching, have six entire sepals in the staminate flowers, and punctulate seeds.

An even more challenging problem than the affinities of subgenus *Eriococcus* is the nature of the relationship between *Phyllanthus* and its 'satellite' genera of subtribe Phyllanthinae: *Breynia*, *Glochidion*, and *Sauropus*. Pax & Hoffmann (1931) recognized five genera in their subtribe Glochidiinae: *Glochidion*, *Breynia*, *Breyniopsis*, *Putranjiva*, and *Leptonema*. However, the last two genera do not even belong in the Phyllanthaceae (Webster, 1994), and *Putranjiva*, according to recent molecular studies (Wurdack *et al.*, 2004; Samuel *et al.*, 2005), is not even euphorbiaceous.

In their extensive palynological survey of the genera of Flueggeinae, Sagun & Van der Ham (2003)

supplemented SEM with LM preparations that illustrated the features of colpi and endoapertures. They placed considerable emphasis on the distribution of monoporate and diploporate colpi in interpreting morphological evolution and in evaluating generic relationships and delimitations in the Phyllanthinae. Their survey of pollen in *Phyllanthus* was restricted to species with diploporate colpi: subgenus *Conami* (section *Nothoclema*) and section *Microglochidion* from the neotropics, and palaeotropical species of subgenus *Kirganelia* (section *Menarda*).

Sagun & Van der Ham (2003) suggested the possibility that diploporate colpi may be a homoplastic character, as their seven pollen types occur in various subgenera and sections of *Phyllanthus*, *Breynia*, and *Sauropus*, but not in *Glochidion*. As the pantoporate condition in *Phyllanthus* appears to have originated independently in subgenera *Isocladus*, *Conami*, *Eriococcus*, and *Xylophylla*, it is not unreasonable to assume that the diploporate (and stephanocolporate) condition has also arisen more than once. In subgenus *Emblica* sections *Emblica* and *Pityrocladus*, only pollen grains with monoporate colpi have been reported (Webster & Carpenter, 2002). Sagun & Van der Ham (2003) illustrated diploporate (or triploporate) colpi in three species of section *Microglochidion* – *P. subapicalis* Jabl., *P. vacciniifolius* (Müll. Arg.) Müll. Arg., and *P. websterianus* Steyererm. – as well as enumerating several others. However, they did not mention that strictly monoporate colpi occur in some species of section *Microglochidion*, such as *P. maguirei* Jabl. and *P. myrsinites* Kunth in H.B.K. (W. Punt, unpubl. data). Their scanning electron micrographs of pollen of *P. websterianus* Steyererm. confirmed the tentative placement of this species in section *Microglochidion* by Webster & Carpenter (2002). Although additional sampling in section *Microglochidion* would be desirable, the present evidence suggests that section *Microglochidion* may indeed belong to subgenus *Emblica*, and has acquired diploporate and oligoporate colpi independently of the taxa in subgenus *Conami*. It appears probable that the clypeate (synrugoidorate) pollen grains of *Phyllanthus* subgenus *Xylophylla* originated from a South American progenitor with diploporate colpi.

A possible phylogenetic hypothesis reflecting these various trends in palynological diversity would be to postulate two main clades within subtribes Flueggeinae and Phyllanthinae. The strictly 'monoporate' clade includes *Margaritaria*, *Flueggea*, *Glochidion*, and *Phyllanthus* subgenera *Isocladus*, *Kirganelia* (most taxa), *Gomphidium*, *Emblica* (sections *Emblica*, *Pityrocladus*), and *Phyllanthus* in both the palaeotropics and neotropics, and *Phyllanthodendron* in Asia. The 'diploporate' clade (including some monoporate taxa) includes *Phyllanthus* subgenera *Kirganelia*

(section *Menarda*), *Emblica* (section *Microglochidion* in part), *Conami*, *Cyclanthera*, and *Xylophylla*, plus the genera *Breynia* and *Sauropus*. It is most parsimonious to assume that diploporate colpi arose in a single episode within African/Madagascan taxa and, following the classic phytogeographical model ('out of Africa') proposed for the Euphorbiaceae by Bentham (1878), dispersed westwards to South America, giving rise to section *Microglochidion*, and eastwards to Asia and Australasia, providing the source for *Breynia* and *Sauropus*. This scenario seems plausible biogeographically for the palaeotropics, but questionable for the neotropics, where diploporate colpi seem to have arisen independently within subgenera *Emblica* and *Conami*.

Of the genera of Phyllanthinae lacking a floral disc, *Glochidion* seems closest to *Phyllanthus* in both floral and pollen morphology. The status of *Glochidion* as a genus separate from *Phyllanthus* has fluctuated considerably during the last two centuries. Müller (1863) was the first to recognize *Glochidion* as distinct, but, by the time the treatment of the Euphorbiaceae was published in the *Prodromus* only 3 years later (Müller, 1866), he had changed his mind and transferred all species of *Glochidion* to *Phyllanthus*. Bentham (1880) accepted Müller's conservative inclusion of *Glochidion* within *Phyllanthus*, but Hooker (1887), in the *Flora of British India*, argued for generic separation, and was followed by Pax (1890) and most 20th century writers. The characters recently used to distinguish *Glochidion* – lack of a floral disc, unlobed styles, and invaginated seeds with fleshy testa – are not diagnostic, except for the seed character.

The pollen grains of *Glochidion* appear quite similar to some of those in *Phyllanthus* subgenus *Emblica*. For example, the grains of Indonesian species, such as *G. philippicum* (Cav.) C. B. Rob. (Fig. 21) and *G. sericeum* (Blume) Hook. f. (Fig. 22), and the types of the segregate genera *Coccoglochidion* and *Glochidionopsis*, are close to *P. emblica* in their flattened poles, short colpi, and tectate-reticulate exine. Other species, such as *G. billiardieri* Baill. (Fig. 19) and *G. hylandii* Airy Shaw (Fig. 20), from New Caledonia and Queensland, have more finely reticulate (almost tectate-perforate) exine ornamentation and bordered colpi. It is clear that pollen evidence alone provides no support for the generic recognition of *Glochidion*, and raises the possibility that *Glochidion* was derived from the clade including *Phyllanthus* subgenus *Emblica*. However, Sagun & Van der Ham (2003) inferred a different possible phylogenetic pattern by pointing out the palynological similarity between *Glochidion* and *Flueggea*.

Van Welzen (2003), in a revisional study of *Sauropus*, provided a phylogeny of the genera of Phyllan-

thinae, suggesting that the *Phyllanthus* taxa with monoporate colpi are the sister group to the other Phyllanthinae. In Van Welzen's diagram, *Glochidion* is indicated as the sister group to *Breynia*, *Sauropus*, and the taxa of *Phyllanthus* with diploporate colpi. This result is approximately equivalent to the molecular-based phylogenies of Wurdack *et al.* (2004) and Samuel *et al.* (2005), except that the diploporate taxa of *Phyllanthus* are not included in those analyses. The suggested relationship between the genera *Glochidion*, *Breynia*, and *Sauropus* appears reasonable, but it does not seem likely that the neotropical diploporate taxa of *Phyllanthus* (for example, section *Microglochidion*) are the sister group to *Sauropus*. In fact, Sagun & Van der Ham (2003) pointed to significant commonalities between the pollen grains of *Breynia* and *Sauropus*, and suggested that the two genera may not be distinct. Furthermore, they noted the possibility that the character of diploporate colpi may be homoplastic, arising independently within different taxa of *Phyllanthus*.

The genus *Breynia* has nearly always been recognized as distinct from *Phyllanthus* since the authoritative treatment by Müller (1866) in the *Prodromus*. The staminate flowers in *Breynia* are more highly modified than in *Glochidion*, with the sepals fused into a turbinate-truncate cup. The pollen grains, illustrated by *B. cernua* (Poir.) Müll. Arg. (Fig. 30) and *B. oblongifolia* (Müll. Arg.) Müll. Arg., are similar to those of *G. philippicum* (Fig. 21) in exine ornamentation, but have five to seven colpi instead of four. Punt (1962) reported eight to ten colpi in *B. fruticosa* (L.) Hook. f. Both *Breynia* and *Sauropus* differ from *Glochidion* in having diploporate colpi.

Sauropus appears to be the sister genus of *Breynia*, and has even more highly derived staminate flowers with the calyx flattened and often produced in curious lobes. Most species of *Sauropus*, such as *S. amoebiflorus* Airy Shaw (Fig. 26) and *S. rigidus* Thwaites (Fig. 23), have distinctive oblate pollen grains with 10–12 bordered colpi and a fine reticulum with small brochi. The pollen grains of *S. spatulifolius* Beille (Fig. 24) are similar to those of *S. amoebiflorus* and *S. rigidus*, but have unbordered colpi. Much more divergent, however, are the pollen grains of *S. bacciformis* (L.) Airy Shaw (Fig. 27), which have only five or six colpi and a very fine reticulum (\pm tectate-perforate), suggestive of *Glochidion*. *Sauropus pierrei* (Beille) Croizat, which was placed in a separate genus *Breyniopsis* by Pierre, has pollen grains even more elongated than those of *S. bacciformis*; the two species possibly could be grouped together in a separate section. *Sauropus* is much more heterogeneous than *Breynia* or *Glochidion*, and its infrageneric relationships appear to be complex; Van Welzen (2003)

found it impractical to recognize the sections of Pax & Hoffmann (1922).

The pollen data indicate that two species transferred from *Phyllanthus* to *Sauropus* by Airy Shaw (1980b) and Govaerts *et al.* (2000) appear to be misplaced in their new position. *Phyllanthus hirtellus* F. Muell. ex Müll. Arg. (Figs 17, 18) and *P. albiflorus* F. Muell. ex Müll. Arg. (Fig. 25) agree in lacking a floral disc, and were placed in *Phyllanthus* section *Glochidion* by Bentham (1873). Airy Shaw (1980b) transferred them to *Sauropus* apparently on the basis of this floral character. However, the pollen of both species is dissimilar to that of *Sauropus*, because of its nearly spheroidal shape, three colpi, and distinctive exine sculpturing. *Phyllanthus hirtellus* deviates strongly from *Sauropus* in its nonphyllanthoid branching, and possibly could be placed within subgenus *Isocladus*, although the lack of a floral disc does not agree with any section of that subgenus. *Phyllanthus albiflorus* has the phyllanthoid branching habit of many of the species transferred to *Sauropus* by Airy Shaw (1980b), but its spheroidal pollen grains have indistinct apertures and somewhat vermiculate exine sculpturing. It is tentatively placed as species *incertae sedis* following the other sections of *Sauropus*, as its true assignment remains uncertain.

CONCLUSIONS

A number of models of the evolution of pollen grains in the Phyllanthoideae have been published, including those of Köhler (1967) and Punt (1967). Köhler emphasized the correlation between advancing levels of polyploidy and increases in the number of colpi and pores, culminating in the clypeate ('synrugoidorate') pollen grains of high-polyploid species of *Phyllanthus* subgenus *Xylophylla*. Punt emphasized changes in the shape of pollen grains and pores, colpal margins, and exine sculpturing. Both models are useful in phylogenetic analyses of the subtribe Phyllanthinae. Köhler (1967) suggested that the plesiomorphic state in pollen morphology would include a prolate shape, tectate-porate exine, elongated monoporate colpi, and lalongate elliptical pores. This is consistent with the model of Punt (1967, 1986), which postulates a number of morphological changes in shape (prolate to oblate), colpal length (elongated to porate), endoaperture (elliptic to circular), number of pores (monoporate to diploporate), and exine sculpturing (reticulate to vermiculate or inordinate). These hypothetical changes are exemplified by the study of Sagun & Van der Ham (2003).

The conclusions of Köhler (1967) and Punt (1967) that the genera of subtribe Flueggeinae (s.s.) – *Flueggea*, *Margaritaria*, and *Richeriella* – display the plesiomorphic condition of prolate grains, elongated

bordered monoporate colpi, and perforate-tectate to reticulate exine are consistent with Sagun & Van der Ham (2003). However, there is some difference in the pores of *Margaritaria*, which are circular to broadly elliptical with rounded ends, and the distinctly lalongate pores with pointed ends found in *Flueggea* and *Richeriella*. The phylogenies of Kathriarachchi *et al.* (2005) placed *Margaritaria* as the sister to the other genera of the Flueggeinae (s.s.) and the Phyllanthinae. The study of Samuel *et al.* (2005) unequivocally placed *P. calycinus* at the base of the *Phyllanthus* clade; data from W. Punt (unpubl. data) show a more or less circular endoporus in *P. calycinus* similar to that of *Margaritaria*. It appears that there are two basic pollen types within *Phyllanthus* subgenus *Isocladus*: prolate or subprolate grains with elongated colpi and lalongate elliptical or oblong pores with diffuse to pointed tips (section *Paraphyllanthus*), and more or less spheroidal grains with shorter colpi and circular or slightly lalongate pores (section *Antipodanthus*). Köhler (1965) presented a diagram of pollen types, in which *Andrachne*, with the strictly monoporate *Paraphyllanthus* type, is basal and also found in *Phyllanthus* subgenus *Phyllanthus*, whereas the *Antipodanthus* type leads to *Embllica*, *Phyllanthodendron*, and the diploporate types found in *Phyllanthus* subgenus *Xylophylla*, *Breynia*, and *Glochidion*. Punt (1967) illustrated these trends in a similar fashion, with the citation of individual species.

The interpretation of pollen characters in the phylogeny of subtribe Phyllanthinae must now take into account the recent discovery of a remarkable obligate pollination mutualism between a Gracillariid moth (*Epicephala*) and three genera of Phyllanthinae: *Glochidion* (Kato, Takimura & Kawakita, 2003), *Phyllanthus* (Kawakita & Kato, 2004a), and *Breynia* (Kawakita & Kato, 2004b). This relationship, analogous to the well-known *Yucca/Pronuba* mutualism, involves concurrent pollination and ovipositing by the moth, with apparently a different moth species for each plant species. Although this kind of pollination has not yet been reported in *Sauropus*, it seems highly probable that *Sauropus* follows the same pattern. The extraordinary diversification of species in *Phyllanthus* and *Glochidion* (> 1200 species) presumably reflects the competitive advantage of this pollination system. The distinctive stylar apparatus of *Glochidion* appears to be directly related to the particular pollination behaviour of the moth (Kato *et al.*, 2003) when compared with *Phyllanthus* (Kawakita & Kato, 2004a). However, it is not yet clear what influence, if any, this mutualistic system bears on the diversification of pollen structure in the Phyllanthinae.

Wurdack *et al.* (2004) and Samuel *et al.* (2005) have shown that Flueggeinae is a monophyletic sister

group of the Phyllanthinae, and their data support the monophyly of the *Glochidion/Breynia-Sauropus* clade, with *Phyllanthus* as a sister group. Most of these studies indicate *Flueggea* to be the sister group of *Phyllanthus*, as tentatively suggested by Webster (1984). It is also consistent with the suggestion of Sagun & Van der Ham (2003) that *Breynia* and *Sauropus* may not be separable at the generic level. *Glochidion*, *Breynia*, and *Sauropus* comprise a clade that may have originated from an ancestral group within or coordinate with *Phyllanthus* subgenus *Emblica*. It has been noted above that *Phyllanthodendron* could also have arisen from an *Emblica*-like ancestor. Nevertheless, the floral structure of *Phyllanthodendron* is very different from that of the glochidiine genera, and its origin has probably been independent. These conclusions derived from comparative pollen morphology and analyses of molecular data obviously pose some difficulties for generic circumscriptions in the subtribe Phyllanthinae. Although the character of diploporate colpi is potentially useful for determining phylogeny, its resolving power in classification is limited by indications of homoplasy.

There are two almost equally distasteful solutions to these problems in classification: (1) a circumscription more conservative than that of Müller (1866), in which *Glochidion*, *Breynia*, and *Sauropus* are incorporated into *Phyllanthus* as subgenera; or (2) the splitter's solution of maintaining these three genera but breaking up *Phyllanthus* into a number of smaller genera. This would not entirely solve the dilemma, because there would still remain the problem of whether to achieve monophyly by including *Glochidion*, *Breynia*, and *Sauropus* in a vastly expanded genus *Emblica*. Thus, although pollen evidence strongly suggests that *Phyllanthus* in the traditional circumscription is paraphyletic, the solution to the redefinition of generic boundaries in the subtribe Phyllanthinae still requires more intensive analysis.

ACKNOWLEDGEMENTS

This study was supported by a Faculty Research Grant from the University of California, Davis. We wish to thank Dr Ellen Dean (Director of the Davis Herbarium) and Rick Harris (Director of the Microscopy and Imaging Facility at Davis) for assistance. We also wish to thank the curators of the herbaria of the Bishop Museum, Missouri Botanical Garden, and University of California, Berkeley for making material available for study. Dr Kenneth Wurdack (Smithsonian Institution) was helpful in sharing the results of his molecular studies. Dr Atsushi Kawakita (Kyoto University) discussed the implications of the pollination system in the Phyllanthinae. Extremely valuable

assistance was provided by Dr Willem Punt (Institute of Systematic Botany, State University of Utrecht, Netherlands) who generously provided critical advice and access to his unpublished manuscripts.

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APPENDIX

NEW TAXA

****Phyllanthus* section *Diandri* G. L. Webster, *sect. nov.***

Frutex (vel arbuscula) dioicus, ramis ancipitibus, foliis alternis distichis, stipulis auriculatis; floribus

axillaribus glomerulatis; sepalis 6; staminibus 2 discretis; pollinibus granis colpibus spiralis; stylis bifidis. Typus: *Phyllanthus diandrus* Pax.

Dioecious shrubs or small trees, branches narrowly winged or angled; leaves alternate, distichous, cuspidate; stipules auriculate; flowers in axillary glomerules; sepals 6; stamens 2, filaments free or nearly so; pollen grains with twisted colpi connivent at poles, exine tectate-reticulate; ovary three-locular, styles bifid.

This monotypic West African section apparently belongs in subgenus *Isocladus*; it shares some vegetative characters with species of sections *Ceramanthus* and *Macraea*. However, the three-colporate pollen of *P. diandrus* is very different from the pantoporate pollen of those two sections.

****Phyllanthus* subgenus *Phyllanthodendron* (Hemsl.) G. L. Webster, *stat. nov.***

Phyllanthodendron Hemsl. Ic. Pl. 26: t. 2563, 2564, 1898. Type: *Phyllanthus mirabilis* Müll. Arg.

Croizat (1942) made some good arguments, based on the distinctive floral and seed morphology, for treating *Phyllanthodendron* as a distinct genus. It can be considered a group coordinate with subgenus *Emblia*, and clearly merits subgeneric status. Possibly both *Emblia* and *Phyllanthodendron* could be treated as genera distinct from *Phyllanthus* when further evidence becomes available.