Pollen morphology and phylogenetic relationships in neotropical *Phyllanthus* (Euphorbiaceae)

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In order to provide new insights into phylogenetic relationships among the neotropical taxa of *Phyllanthus*, 28 illustrations are provided of the pollen grains of 22 selected species studied from 11 sections of the subgenera represented in the neotropics. Special attention has been given to subgenus *Conami* because of its variability in pollen morphology: of eight species illustrated, the apertures are diploporate colpi in three species and pores in five species; exine ornamentation is vermiculate in two species and pilate in the other six species. The six species in the neotropical sections *Pityrocladus* and *Microglochidion* (subgenus *Emblica*) are characterized by prolate grains with an increased number of colpi (4–8). Of particular interest are species in which the pollen exine is clypeate (with exine shields); clypeate pollen grains are illustrated in two species of subgenus *Xylophylla* and in one species of section *Cyclanthera* that has unique exine shields with single central pila. The pollen of the one Brazilian phylloclade-bearing species illustrated (in section *Choretropsis*) has 3-colporate grains with reticulate exine, typical for subgenus *Phyllanthus*, and very different from the clypeate grains of the West Indian phylloclade-bearing species in section *Xylophylla*. This pollen evidence clearly demonstrates homoplasy in the origin of phylloclades in *Phyllanthus*. Pollen morphological data suggest that the neotropical taxa of *Phyllanthus* have arisen following colonization from Africa (subgenus *Kirganelia*) and Asia (subgenus *Emblica*). © 2002 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2002, **138**, 325–338.

ADDITIONAL KEYWORDS: clypeate – diploporate colpi – exine shields – homoplasy – phylloclades – pilate exine – SEM – vermiculate exine.

INTRODUCTION

The genus *Phyllanthus*, with over 800 described species (Govaerts *et al.*, 2000), is the largest and morphologically most diverse genus in the subfamily Phyllanthoideae. Currently, the species are assigned to ten subgenera (Webster, ined.) and a large number of sections, many of them described by Müller (1863, 1866, 1873), and summarized by Pax & Hoffmann (1931). The enumeration by Govaerts *et al.* (2000) lists all species of the genus but does not include supraspecific taxa. The importance of pollen morphology in indicating lines of relationship within the genus was pointed out by Erdtman (1952) and later by Webster (1956–58), Punt (1962, 1967), and Köhler (1965, 1967). Pollen characters (originally observed by light microscopy) have been shown by Webster (1956–58, 1967a) to be highly diagnostic for delimiting supraspecific taxa in *Phyllanthus*. In a long sequence of studies, Punt (1967, 1972, 1980, 1986, 1987; Punt & Rentrop, 1974; Meewis & Punt, 1983) has reviewed pollen structure using light microscopy (LM) and scanning electron microscopy (SEM) for a wide sampling of species of *Phyllanthus*, especially from Africa and Asia. Punt (1987) provided the first general review of the subgenera of *Phyllanthus* that illustrated the pollen morphological variation as seen with SEM. However, because of the lack of detailed monographic studies of the subgenera and sections, the trends of morphological evolution in pollen, and their relevance to the infrageneric taxonomy of the genus, remain only partially elucidated.

The present work focuses on the pollen diversity in some neotropical taxa of *Phyllanthus*, with particular attention to those that are assigned to subgenus *Conami* (or that have been associated with it). In its original circumscription (Webster, 1956–58), subgenus *Conami* was characterized by the production of

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compound (bipinnatiform) deciduous branchlets, 3- or 6-merous flowers, connate stamens with horizontally dehiscing anthers, and ± spheroidal pollen grains with short colpi or pores and 'echinulose' (echinate) exine sculpturing. Punt (1987) illustrated the pollen of sections *Apolepis* and *Nothoclema*, and described it as having pilate exine ornamentation and lacking ectoapertures in both sections. Punt (1986) also compared the pilate grains of *P. orbiculatus* Rich. (sect. *Apolepis*) with those of *P. dinklagei* Pax, an African species of subgenus *Kirganelia*, but suggested that the similarity might be due to convergence. This seems a reasonable conclusion, since *P. dinklagei* is very different from the neotropical taxa of subgenus *Conami* in its simply pinnatiform branchlets, 5-merous perianth, staminate disk of five segments, and androecium of five free stamens with longitudinally (vertically) dehiscent anthers.

Since it appears that further analysis of the possible palynological relationships between African and tropical American species of *Phyllanthus* requires better sampling of species in subgenus *Conami*, we have examined several additional species of section *Nothoclema*. In a study of the eastern Melanesian species of *Phyllanthus*, Webster (1988) illustrated the pollen of some species of section *Gomphidium*. The pollen of these species is characteristically oblate, 3-colporate (often syncolporate), monorate (with single pores), and with ± vermiculate exine sculpturing similar to western Melanesian species of subgenus *Gomphidium* studied by Punt (1980) and by Lobreau-Callen *et al.* (1988). Furthermore, Webster (1988) pointed out that the species of subgenus *Gomphidium* from Fiji and Tonga have bipinnatiform branchlets and floral characteristics similar to species of the neotropical section *Nothoclema*. In addition to exploring possible relationships of subgenus *Conami* with other neotropical taxa, we wish to evaluate possible links with Melanesian as well as African species.

Also examined was pollen of some species in sections *Microglochidion* and *Pityrocladus* (subgenus *Emblica*), and species in subgenera *Phyllanthus* and *Xylophylla*, as well as aberrant groups such as section *Cyclanthera*. The species in section *Microglochidion*, which are conspicuous in the shrubby vegetation on top of the *tepuis* in the Guayana highlands, are morphologically different from section *Nothoclema* in their coriaceous leaves on unramified branchlets and floral features such as the common occurrence of apiculate anthers and unbranched styles.

MATERIAL AND METHODS

A total of 22 neotropical species of *Phyllanthus* was selected for study and illustration with SEM. Pollen

material was taken from herbarium sheets, mostly in the herbarium at the University of California, Davis (DAV). Treatment followed the method of Lynch & Webster (1975), which was developed for observation by scanning electron microscopy (SEM) without submitting the pollen grains to acetolysis. Several of the steps in the protocol of Lynch and Webster were omitted in order to minimize the loss of pollen during processing. Where appropriate, SEM observations were checked by LM, using a Zeiss compound microscope with oil immersion.

Staminate flowers selected from herbarium sheets were immersed in a solution of detergent (Aerosol OT) for a minimum of 24 h. Pollen was then extracted from the anthers under a dissecting scope and pipetted into plastic 1500 μL reaction tubes. The pollen, immersed in Aerosol OT, was held in the tubes for an additional 24 h to ensure full expansion of the grains. The tubes were centrifuged for 45 s at 1000 rpm to concentrate pollen and facilitate changing of solutions. The Aerosol OT was then pipetted off and the pollen rinsed with distilled water. After 10 min, the distilled water was removed, and 50% acetone added. The tubes were then sonicated in a water-bath sonicator for 5 min to remove pollenkitt. The pollen was then immersed in another change of acetone for 10 min, followed by a 10 min rinse in distilled water. Pollen was then dehydrated in a series of 50% and 100% ethanol (each for 5 min), and then in a second change of 100% ethanol for 1 h.

After dehydration was complete, the tubes were centrifuged again, and the pollen pipetted onto aluminium SEM stubs. The ethanol was allowed to evaporate for *c*. 30–45 min When dry, the stubs were inserted into a Denton Desk II Cold Sputter Coater and coated with gold for 70 s. The pollen was then examined and photographed using a Hitachi S-3500 N Scanning Electron Microscope. The terminology used in descriptions of the pollen mainly follows the glossary of Punt *et al.* (1994).

DESCRIPTIONS OF THE POLLEN GRAINS

(Specimens cited without designation of herbarium acronym are all from DAV; nomenclature follows Govaerts *et al.*, 2000).

SUBGENUS *ISOCLADUS*

Section *Antipodanthus*: Pollen grains prolate or subglobose, 3-colporate, colpi monoporate; exine tectate.
Phyllanthus dawsonii Steyerm. (Fig. 19). (Brazil, *Hatschbach 36339*). Grains *c*. 38–39 × 26–27 μm; colpar margins unthickened; exine tectate-perforate.

SUBGENUS *CONAMI*

Pollen grains ± spheroidal, 3-colporate to porate, exine vermiculate or pilate.

Section *Nothoclema*. Pollen grains small and ± spheroidal, 3-colporate or porate, colpi (where developed) diploporate; exine vermiculate or pilate. The species of this section show considerable pollen morphological differences.

Type 1. *Phyllanthus anisolobus* Müll. Arg. (Fig. 1) (Costa Rica, *Webster 16823*). *Phyllanthus graveolens* Kunth (Fig. 2) (Peru, *Woytkowski 6780*, MO). Diam 12–13 µm; colpi diploporate (pores terminal), margin slightly thickened (0.2–0.25 µm diam); exine vermiculate, muri *c*. 0.25–0.4 µm diam. *P. caymanensis* G. L. Webster and G. R. Proctor and *P. mocinianus* Baill., with similar exine sculpturing, are illustrated (SEM) in Webster & Proctor (1984) and *P. mocinianus* (LM) in Webster (1966). The colpi in *P. anisolobus* appear obscure in SEM.

Type 2. *Phyllanthus acuminatus* Vahl (Figs 3, 4) (Panama, *Webster & Breckon 16522*). Diam. *c*. 18 µm; colpi 8–9 µm long, with prominent borders 0.7–1 µm diam., diploporate (pores 2 per colpus, terminal, diam. *c*. 1.5 µm); exine pilate, pila rounded or polygonal, 1–2 µm diam., mixed with smaller pila 0.5–1 µm diam., occasionally elongated (to 3 µm). Also illustrated (LM) by Punt (1962). *P. mcvaughii* G. L. Webster (Guatemala, *Webster et al. 11698*), illustrated (SEM) in Webster & Proctor (1984) and (LM) by Webster (1966), is similar but with longer colpi having less hypertrophied margins (*c*. 0.2–0.25 µm diam.).

Type 3. *Phyllanthus pavonianus* Baill. (Fig. 5) (Peru, *Weberbauer 7664*, US). Diam. 18–19 µm; colpi not evident; pantoporate but pores obscure in SEM; exine pilate as in *P. acuminatus*; pila rounded, diam. 0.6–1 µm. *Phyllanthus brasiliensis* (Aubl.) Poir. (Fig. 6) (Brazil, *Ehringhaus et al. 378*) is similar but grains are ± malformed; pantoporate (as seen with LM), but pores sunken (Punt, 1987) and scarcely visible with SEM; also illustrated (LM, as *P. subglomeratus*) by Köhler (1967) and (SEM) by Brunel (1975; as *P. subglomeratus*) and by Meewis & Punt (1983) and (as *P. acuminatus*) by Punt (1987).

Section Apolepis. Grains subspheroidal, exine sculpturing similar to type 3 of sect. *Nothoclema*.

Phyllanthus orbiculatus Rich. (Fig. 7) (Paraguay, *Arbo et al. 1599*). Diam. 16–17 µm; colpi absent; zonoporate, pores 4 (5) (Punt, pers. comm.); exine pilate, pila rounded, diam. 0.7–1 µm. Also illustrated (LM) by Bancilhon (1971) and (SEM) by Punt (1986, 1987).

Section *Hylaeanthus*. Grains subspheroidal, ectocolpi obsolete, pores not evident in SEM; exine pilate.

Phyllanthus attenuatus Miq. (Fig. 8) (Suriname, *Irwin et al. 55435*). Diam. 18–19 µm; colpi absent, pores obscure in SEM; exine pilate, pila rounded, heterogeneous in size, diam. 0.3–1 µm. *Phyllanthus skutchii* Standl. (Figs 9, 10) (Costa Rica, *Skutch 5491*). Grains smaller, diam. 12–13 µm, pila more irregular, some elongated or S-shaped, often perforate.

SUBGENUS *EMBLICA*

Pollen grains prolate or subprolate to subspheroidal, colpi 4–7, elongated, monoporate or diploporate, often with terminal or subterminal pores; exine semitectate, reticulate.

Section *Pityrocladus*.

Phyllanthus symphoricarpoides Kunth (Fig. 11) (Colombia, *Soejarto 3110*, HUA); *P. ruscifolius* Müll. Arg. (Fig. 12) (Colombia, *Dodson et al. 1562*). Grains subspheroidal, diam. 15–16 µm; colpi 4 or 5, emarginate, short (*c*. 5 µm long), monoporate (pore central); exine semitectate-reticulate, heterobrochate (brochi 0.2–0.7 µm diam.).

Section *Microglochidion*.

Type 1. *Phyllanthus duidae* Gleason (Figs 13, 14) (Venezuela, *Huber 13231*) Grains subprolate, 24 × 22 µm; colpi 7 or 8, narrow, not marginate, diploporate (pores subterminal); exine semitectate-reticulate, less heterobrochate than *P. symphoricarpoides*. *P. myrsinites* Kunth (Fig. 15) (Brazil, *Prance et al. P24765*). Grains very similar, 18–19 × 17 µm, colpi 5 or 6. The diploporate colpi of *P. pycnophyllus* Mûll. Arg. are illustrated (LM) by Punt (1986).

Type 2. *Phyllanthus vacciniifolius* (Müll. Arg.) Müll. Arg. (Fig. 16) (Venezuela, *Prance & Huber 28343*). Grains prolate, *c*. 24 × 18–20 µm; colpi 8, marginate, diploporate; exine semitectate-reticulate (transitional to vermiculate). Also illustrated by Punt (1987).

Type 3. *Phyllanthus websterianus* Steyerm. (Figs 23, 24) (Brazil, *Allem & Werneck 3653*). Grains spheroidal, diam. 18–19 µm; colpi marginate, partly anastomosing, diploporate; exine vermiculate, transitional to semitectate-reticulate. Illustrated (LM) by Punt (1967).

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Section *Lysiandra*. Pollen grains spheroidal, colpi 3, narrow (margins not thickened), monoporate; pori central, round; exine semitectate-reticulate (pattern transitional to vermiculate).

Phyllanthus harrimanii G. L. Webster (Figs 25, 26) (Mexico, *Nesom 5987*). Diam. 15–16 µm; colpi 3 (?), irregular in distribution, partly connected in loops, margins not thickened; pores not evident in SEM; exine semitectate-reticulate, somewhat heterobrochate, brochi 0.3–1 µm across.
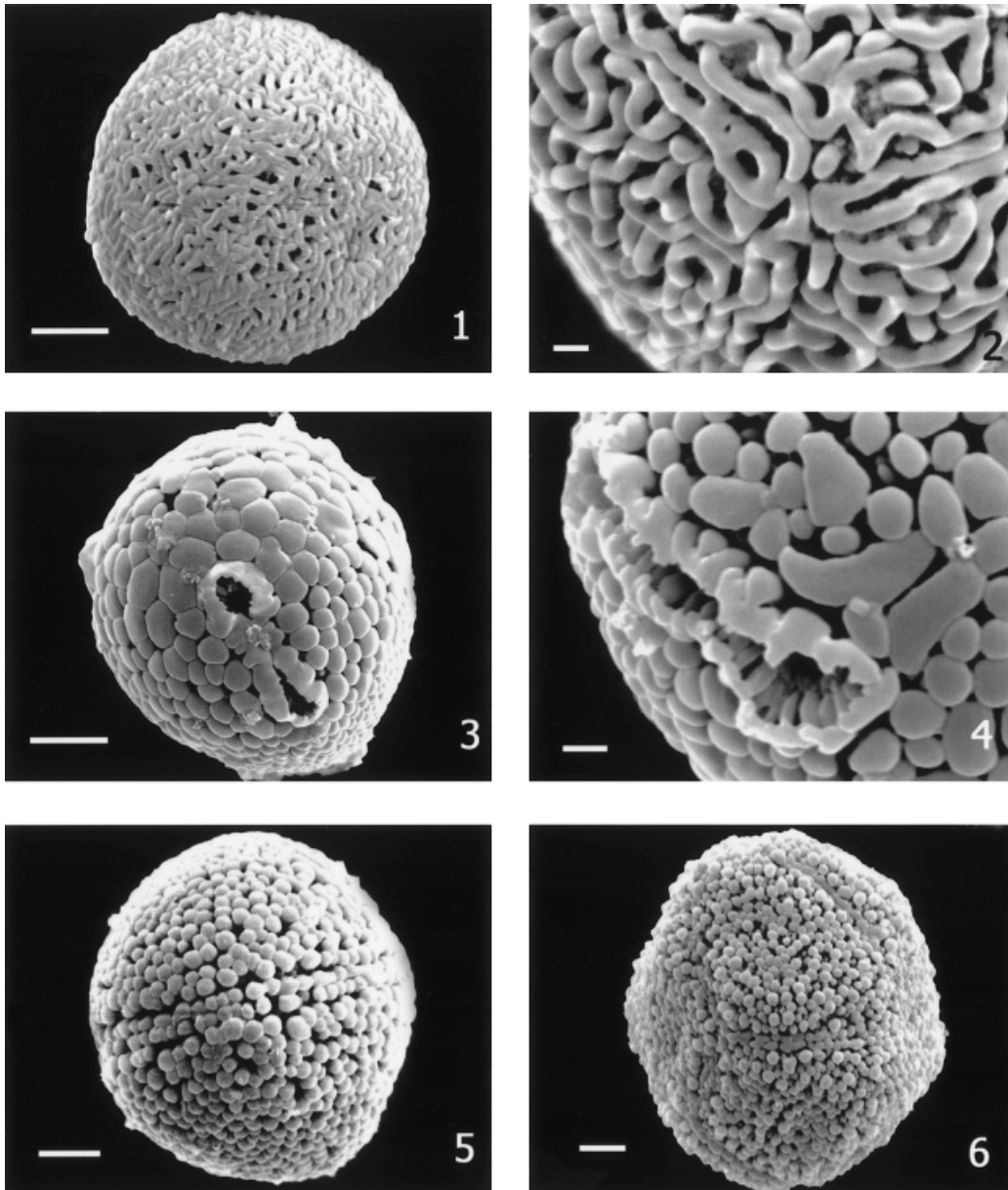
Figures 1–6. SEMs of species in subgenus *Conami* section *Nothoclema*. Fig. 1. *P. anisolobus*. Scale bar = 3 μm. Fig. 2. *P. graveolens* (polar view). Scale bar = 1 μm. Figs 3, 4. *Phyllanthus acuminatus*, showing whole grain and enlargement of colpar area. Scale bars = 4 μm, 1 μm respectively. Fig. 5. *P. pavonianus*. Scale bar = 3 μm. Fig. 6. *P. brasiliensis*. Scale bar = 3 μm.

SUBGENUS *CYCLANTHERA*

Section *Cyclanthera*. Pollen grains spheroidal, pantoporate (not evident in SEM); exine shields ± circular, muri thin-walled, each areole enclosing a central rounded incrassate pilum.

Phyllanthus lindenianus Baill. (Figs 27, 28) (Hispaniola, *Mejía et al. 1288*). Diam. 16–20 μm; areoles *c*. 3 μm diam; muri 0.2–0.3 μm thick; each enclosing a solitary central pilum 1–1.3 μm diam.; pila sometimes with central pits. A LM view of *P. berteroanus* Mûll. Arg. illustrated by Webster (1956–58)

SUBGENUS *XYLOPHYLLA*

Sections *Elutanthos* and *Brachycladus*. Pollen grains spheroidal; clypeate, colpi anastamosing, enclosing
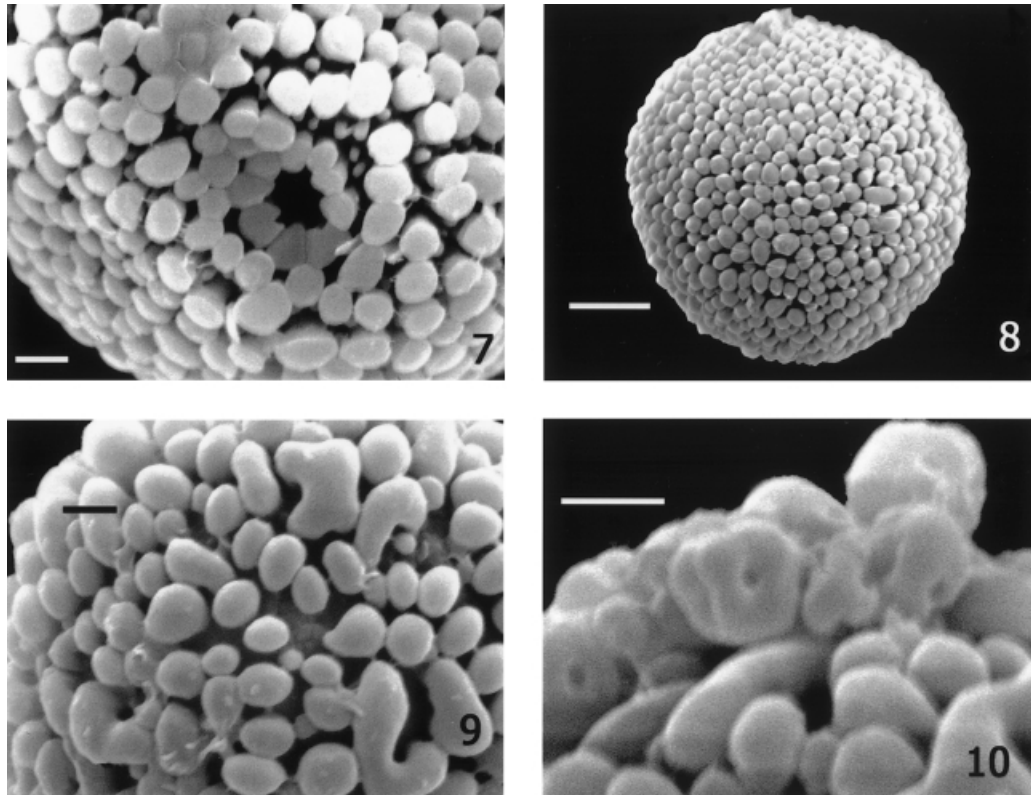
Figures 7–10. SEMs of species in other sections of subgenus *Conami*. Sect. *Apolepis*. Fig. 7. *P. orbiculatus* (view showing pore). Sect. *Hylaeanthus*. Fig. 8. *Phyllanthus attenuatus*; Figs 9, 10. *P. skutchii* (enlarged views). Scale bars = 1μm.

large areolate exine shields; pantoporate, pores circular (most distinct in LM), at intersections of colpi; exine semitectate-reticulate.

Phyllanthus poeppigianus (Müll. Arg.) Müll. Arg. (section *Elutanthos;* Fig. 17) (Brazil, *Cordeiro 135*); *P. spruceanus* Müll. Arg. (section *Brachycladus*; Fig. 18) (Brazil, *Maas et al. 474*, UC). Diam. *c*. 15μm; colpi (rugae) with thickened margins, pores scarcely evident in SEM; exine semitectate-vermiculate. This is the characteristic kind of pollen with exine shields in subgenus *Xylophylla*, designated as 'clypeate' by Halbritter & Hesse (1995); illustrated by Punt (1986, 1987) for *P. latifolius,* and (LM) by Webster (1956–58) for *P. maleolens* Urb. & Ekm., and (LM) by Köhler (1967) for *P. mimosoides* Sw.

SUBGENUS *PHYLLANTHUS*

Section *Phyllanthus*. Pollen grains prolate; colpi 3 or 4, monoporate, margins usually not thickened; pores central, elliptic (lalongate) to round; exine semitectate to tectate-perforate.

Phyllanthus almadensis Müll. Arg. (Fig. 20) (Brazil, *dos Santos 3614*). Grains *c*. 25 × 15μm; colpi *c*. 18μm long; pore central, prominent; exine finely tectate-perforate (pores 0.1–0.2μm diam.). *Phyllanthus subemarginatus* Müll. Arg. (Fig. 21). (Brazil, *Carauta 2582*). Grains *c*. 17–18 × 13μm; colpi *c*. 14μm long; exine semitectate-reticulate, somewhat heterobrochate.

Section *Choretropsis*. Pollen grains subspheroidal to subprolate, colpi 3, monoporate, margins not thickened; pores central, round; exine semitectate-reticulate.

Phyllanthus flagelliformis Müll. Arg. (Fig. 22) (Brazil, *Mori & Boom 14406*). Grains subspheroidal to subprolate, diam. 18–20μm; colpi narrow, not bordered; exine coarsely reticulate (brochi *c*. 1–2μm diam.), lumina of brochi with conspicuous granules.

DISCUSSION

The species illustrated in this study provide a selection of nearly all the major pollen morphological types that have been observed in the neotropical species of *Phyllanthus*. There are several species, notably *Phyllanthus lindenianus, P. harrimanii,* and *P. websterianus*, that are anomalous, and indeed the extraordinary grains of *P. lindenianus* (Figs 27, 28) appear to have no counterpart within the Euphorbiaceae, nor within any other angiosperm family.
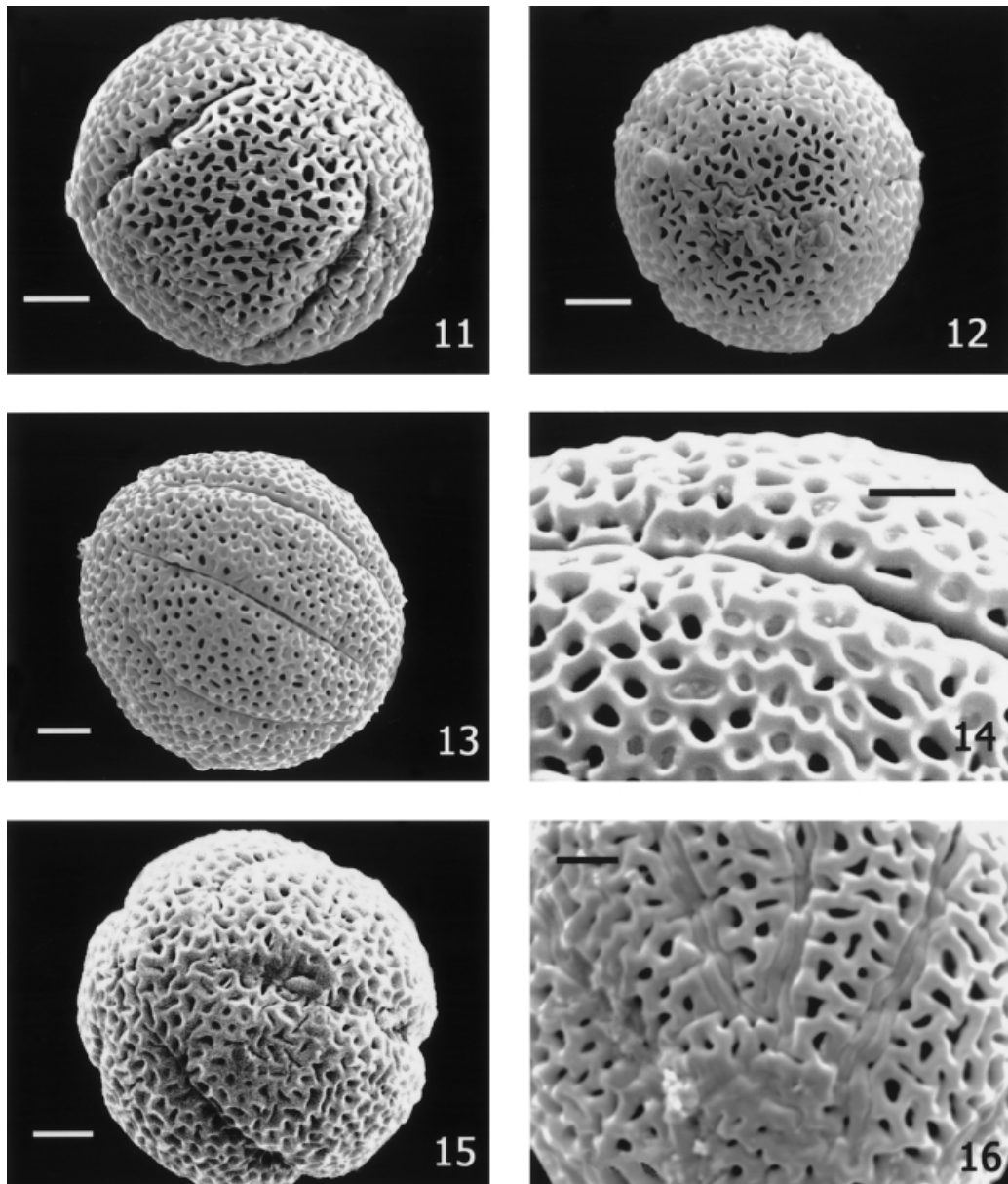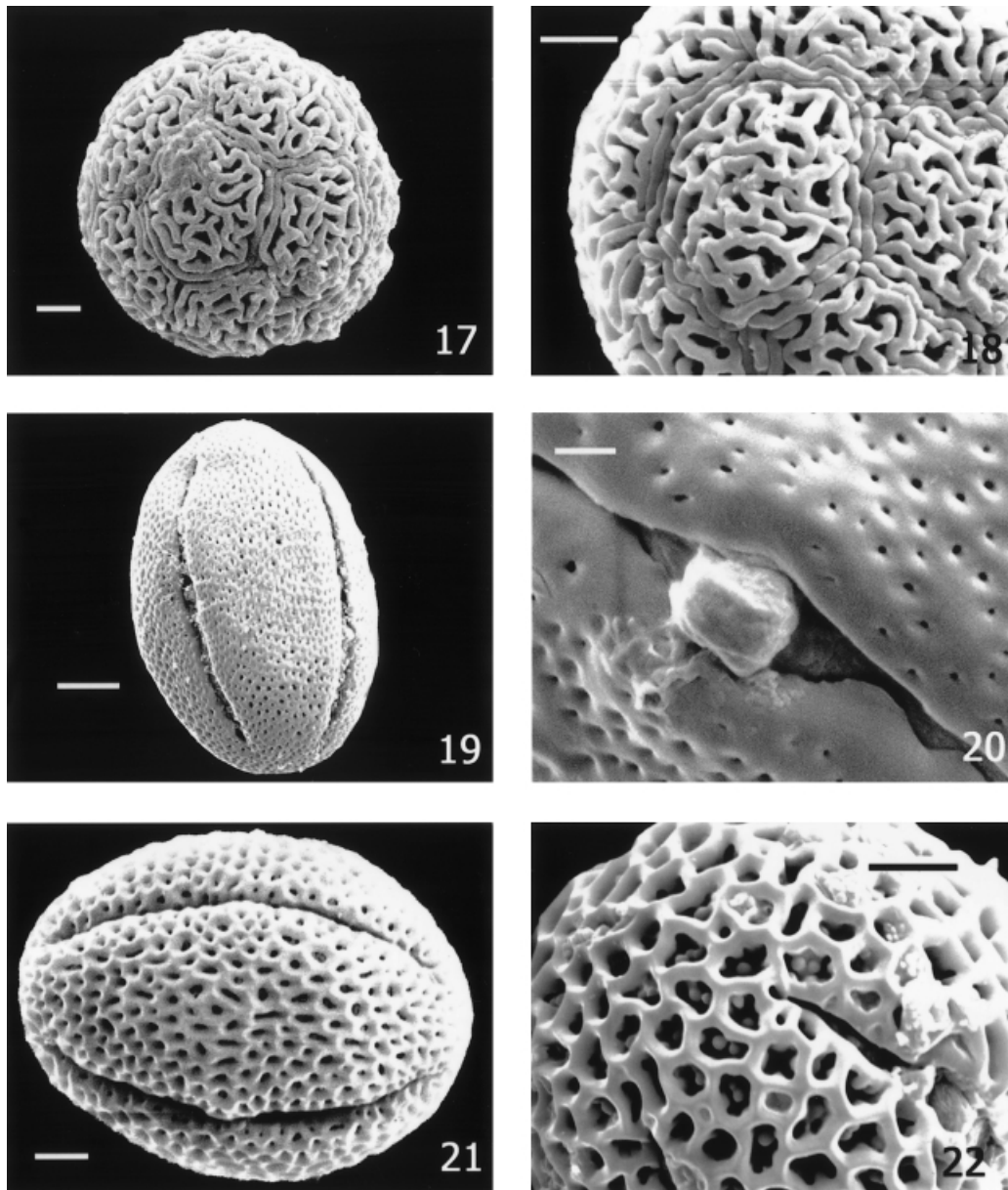
Figures 11–16. SEMs of species in subgenus *Emblica*. Figs 11, 12. Section *Pityrocladus*. Scale bars = 3 μm. Fig. 11. *Phyllanthus symphoricarpoides* (oblique equatorial view). Fig. 12. *P. ruscifolius* (polar view). Figs 13–16. Section *Microglochidion*. Figs 13, 14. *P. duidae*; Fig. 13. Equatorial view. Scale bar = 4 μm. Fig. 14. Detail of tectum. Scale bar = 2 μm. Fig. 15. *P. myrsinites* (oblique polar view). Scale bar = 3 μm. Fig. 16. *P. vacciniifolius* (polar view). Scale bar = 2 μm.

However, the significance of our observations is that they provide useful guideposts for assigning species to subgenera and sections in a way that better reflects the probable phylogeny.

Phyletic diagrams illustrating trends of specialization in the morphology of *Phyllanthus* pollen grains have been provided earlier by Punt (1967) and Köhler (1967). Punt, using taxa such as *Andrachne phyllan-* *thoides* (Nutt.) Müll. Arg. as an 'outgroup', postulated several characters as 'apomorphies': oblate shape; syncolpy, pluricolpy (4+), and porate apertures; thickened colpar margins; circular pores and doubling of pores (endoapertures); and vermiculate or 'inordinate' exine sculpturing. Köhler, independently adopting some of these same criteria, emphasized the association of apomorphic characters with increasing levels of polyploidy

Figures 17–22. SEMs of species in subgenus *Xylophylla* and subgenus *Phyllanthus*. Figs 17, 18. Subgenus *Xylophylla*, Section *Brachycladus*. Scale bars = 2 µm. Fig. 17. *Phyllanthus poeppigianus*. Fig. 18. *P. spruceanus*. Figs 19–22. Sect. *Phyllanthus*. Figs 19, 20. *P. almadensis*. Fig. 19. Equatorial view. Scale bar = 5 µm. Fig. 20. View of colpus with pore. Scale bar = 1 µm. Fig. 21. *P. subemarginatus* (equatorial view). Scale bar = 2 µm. Fig. 22. *P. flagelliformis* (oblique polar view). Scale bar = 3 µm.

(from 2*x* to 12*x*). These observations are of obvious relevance to the problems of identifying clades within *Phyllanthus*, but still have not provided sufficient evidence for the decoding of phylogenetic relationships. The large size of the genus, complexity of morphological variation, and apparent homoplasy in some characters create formidable difficulties to proposing phylogenies based on pollen characters alone.

Following Punt (1967), the pollen in subgenus *Isocladus*, exemplified by *Phyllanthus dawsonii* Steyrm. (Fig. 19), would be regarded as approximating the plesiomorphic state in *Phyllanthus*. However, this may be questioned on the basis of a particularly significant study by Meewis & Punt (1983) on the African taxa of subgenus *Kirganelia*. It appears from both palynological and other morphological data (much of it provided
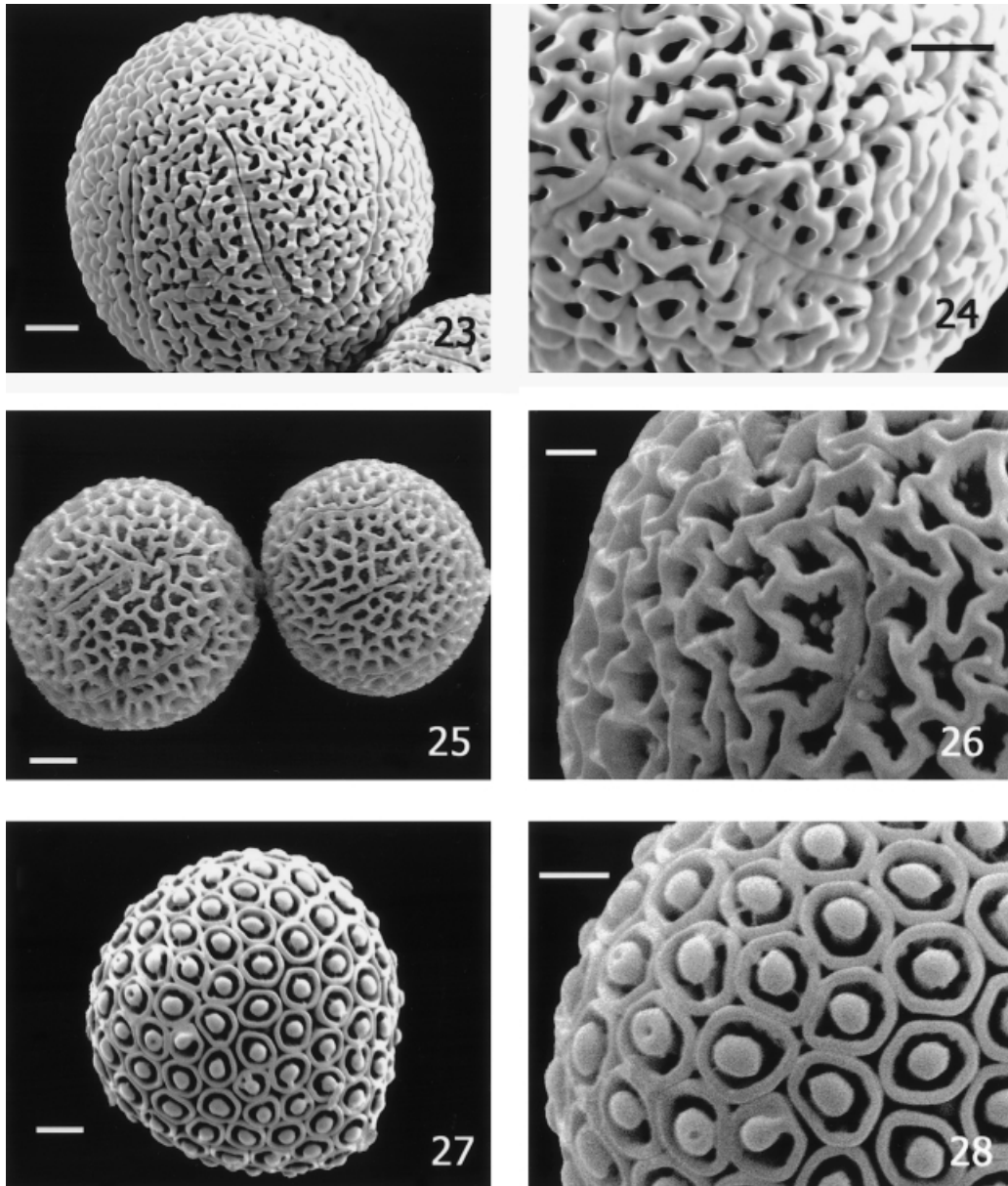
Figures 23–28. SEMs of species in sections of unresolved taxonomic position. Figs 23–26. Section *Microglochidion* (vel aff.). Figs 23, 24. *Phyllanthus websterianus*. Scale bars = 3μm, 2μm respectively. Section *Lysiandra:* Figs 25, 26. *P. harrimanii*. Scale bars = 3μm, 1μm respectively. Sect. *Cyclanthera*. Figs 27, 28. *P.lindenianus*. Scale bars = 3μm, 2μm respectively.

by Brunel 1975) that subgenus *Kirganelia* is the 'keystone' (sister) group in *Phyllanthus* from which most (or all) of the other subgenera and sections with phyllanthoid branching have evolved. This suggests that there appear to be two very different pollen 'archetypes' (plesiomorphic states) within *Phyllanthus*: the prolate grains with elongated endocolpus and reticulate exine in subgenus *Isocladus*, and the subprolate to spheroidal, often syncolporate grains with reticulate to vermiculate exines and roundish endocolpus in subgenus *Kirganelia* and related taxa. The systematic significance of this basic dichotomy in pollen characters between the herbaceous and woody phylads remains to be elucidated.

For purposes of comparison, descriptions of species in this study have been arranged in the classification of Webster (1956–58), as later modified in Webster (1967a, 1967b, 1988) and Webster & Airy Shaw (1971).

In these studies, no species of subgenus *Kirganelia* (with the exception of three species in sections *Cicca* and *Ciccopsis*) have been recognized as native to the Americas, and no species of subgenus *Conami* as native to Africa. However, because of the palynological relationships discussed below, the neotropical subgenus *Conami* would appear to be an appropriate starting point because of considerable similarities to subgenus *Kirganelia*.

In the original circumscription of Webster (1956–58), the American subgenus *Conami* included two sections: *Nothoclema* and *Apolepis*. Within section *Nothoclema*, which includes ten species that are often difficult to distinguish in the herbarium, pollen morphology is surprisingly diverse. Three pollen types are recognizable: (1) grains with three colpi and vermiculate exine sculpturing (Figs 1, 2; *Phyllanthus anisolobus, P. mocinianus*); (2) grains with three colpi and pilate sculpturing (Figs 3, 4; *P. acuminatus, P. mcvaughii*); and (3) porate grains with no functional colpi, and pilate sculpturing (Figs 5, 6; *P. brasiliensis, P. pavonianus*). The single species of section *Apolepis*, *P. orbiculatus* (Fig. 7)*,* and the species of section *Hylaeanthus* (Figs 8–10), have pollen grains similar in shape and sculpturing to those of *P. pavonianus*. Thus within subgenus *Conami* there appears to be a sequential modification of pollen morphology from the plesiomorphic state of grains with three long bordered colpi and vermiculate exine (*P. anisolobus*) through those with long bordered colpi and pilate exine (*P. mcvaughii*) and short colpi with pilate exine (*P. acuminatus*) to porate grains with pilate exine (*P. pavonianus* and section *Apolepis*). There are other woody neotropical species that differ in vegetative morphology (larger leaves and unramified branchlets) but appear to be close to sect. *Nothoclema* in floral and pollen characters. In species of the newly described section *Hylaeanthus* G. L. Webster (Webster, in press) such as *Phyllanthus attenuatus* Miq. (Fig. 8) and *P. skutchii* Standl. (Figs 9, 10), the spheroidal pollen grains have pilate exine sculpturing as in *P. acuminatus, P. pavonianus*, and *P. brasiliensis*. In *P. skutchii*, the coarse irregular pilate exine sculpturing is strikingly similar to that of *P. acuminatus*. The pollen evidence supports a placement of sect. *Hylaeanthus* within subgenus *Conami,* even though species of sect. *Hylaeanthus*, with short unramified branchlets, are so similar in aspect to species of sections *Brachycladus* and *Elutanthos* (in subgenus *Xylophylla*) that they have often been confused in herbaria. However, the pollen grains of *P. poeppigianus* (Müll. Arg.) Müll. Arg. (Fig. 17) and *P. spruceanus* (Fig. 18) are completely different in their clypeate exine pattern characteristic of subgenus *Xylophylla* (Webster 1956–8; Halbritter & Hesse 1995). This pollen evidence suggests that there has been remarkable convergence

in habit between Amazonian species of three rather distant sections in different subgenera.

It is notable that the vermiculate exine sculpturing of *Phyllanthus anisolobus* Müll. Arg. (Fig. 1) and *P. graveolens* Kunth (Fig. 2) strikingly resembles that of some of the African species of subgenus *Kirganelia* illustrated by Meewis & Punt (1983, e.g. *P. polyanthus* Pax, *P. profusus* N. E. Br.). In this regard, it appears signficant that Brunel & Roux (1977) reported from West Africa a species, *P. dinklagei* Pax, in subgenus *Kirganelia* (section *Brazzaeani*) with pilate pollen grains that they compared to the pollen of the South American *P. orbiculatus* in subgenus *Conami*. Brunel and Roux therefore suggested that section *Brazzaeani* should be included in subgenus *Conami*, which would consequently become an American/African disjunct rather than an endemic American taxon.

The survey of pollen in African species of subgenus *Kirganelia* by Meewis & Punt (1983) suggests a morphological sequence strikingly similar to that shown in subgenus *Conami*, except that it begins one step 'earlier', with 3-colporate grains that have a reticulate exine (e.g. *Phyllanthus pinnatus* (Wight) G. L. Webster, *P. reticulatus* Poir.), followed by 3-colporate grains with vermiculate exine (*P. polyanthus* Pax, *P. tessmannii* Hutch.), 3-colporate grains with exine transitional to pilate (*P. klainei* Hutch. [synonymized with *P. polyanthus* by Govaerts *et al.*, 2000]), and finally 3-porate grains with pilate exine (*P. dinklagei*). Since similar pilate exine ornamentation is otherwise unknown in *Phyllanthus*, this remarkable parallelism between subgenus *Conami* and some of the West African species of subgenus *Kirganelia* suggests possible derivation from a common ancestor. Additional evidence for a possible relationship is the presence of pollen grains with diploporate colpi in at least two African species of subgenus *Kirganelia* (*P. polyanthus, P. purpureus* Müll. Arg (Punt) (W. Punt, pers. comm.).

However, the parallelism in pollen characters between the American subgenus *Conami* and the African taxa of subgenus *Kirganelia* is not unique, for a somewhat similar sequence can be detected in taxa of subgenus *Gomphidium* in eastern Asia and Melanesia (Punt 1980; Webster 1988; Lobreau-Callen *et al.* 1988). Three-colporate grains with reticulate exine are known from New Guinea (*Phyllanthus acinacifolius* Airy Shaw & Webster) and New Caledonia (*P. bourgeoisii* Baill.); and 3-colporate grains with vermiculate exine in New Guinea (*P. warburgii* K. Schum.), New Caledonia (*P. chamaecerasus* Baill.), Micronesia (*P. rupi-insularis* Hosok.), New Hebrides (*P. myrianthus* Müll. Arg.), and Tonga (*P. amicorum* G. L. Webster). Webster (1988) noted that some Fijian species, such as *P. pergracilis* Gillespie and *P. heterodoxus* Müll. Arg., not only have similar pollen but also share vegetative characters (bipinnatiform

branchlets) with species of subgenus *Conami*. However, the oblate shape and consistently monoporate colpi of species in subgenus *Gomphidium* are divergent from the pollen characters observed in subgenus *Conami*, so that the similarity in exine sculpturing may not indicate a close systematic relationship. Among the woody neotropical taxa of *Phyllanthus*, there are a significant number of species that belong neither to subgenus *Conami* nor to subgenus *Xylophylla*; most of these show relationships to subgenus *Emblica*. The majority of the American species of subgenus *Emblica,* such as *P. duidae* Gleason (Figs 13, 14). *P. myrsinites* Kunth (Fig. 15) and *P. vacciniifolius* (Müll. Arg.) Müll. Arg. (Fig. 16), are referable to section *Microglochidion*, in which the pollen grains are characteristically prolate, with multiple (4–8) diploporate colpi (Punt, 1986), and reticulate (semitectate) exine sculpturing. However, it should be noted that at least one species of sect. *Microglochidion*, *P. strobilaceus* Jabl., has monoporate colpi (Punt, pers. comm.), so that the presence of diploporate colpi is not a synapomorphy defining sect. *Microglochidion*.

In *P. websterianus* Steyerm. (Figs 23, 24), a Brazilian species of somewhat uncertain position (but probably to be referred to section *Microglochidion*), the pollen grains are aberrant in their colpar morphology, but the colpi are diploporate (W. Punt, pers. comm.). The pollen of *P. harrimanii* G. L. Webster (Figs 25, 26), a Mexican species of sect. *Lysiandra*, is strikingly similar, but the two species are very different in floral morphology, and do not appear to belong to the same section. The anastomosing colpi and vermiculate exine seen in pollen grains of *P. websterianus* and *P. harrimanii* suggest a possible affinity with subgenus *Xylophylla*, and indeed a possible sister group relationship between that subgenus and subgenus *Emblica*.

Variation within section *Microglochidion,* with many species represented on the *tepuis* of the Guayana shield (Jablonski, 1967; Webster, 1999) needs to be further explored. Some South American species of subgenus *Emblica* cannot easily be accommodated within sect. *Microglochidion* and appear best referred to a newly described section *Pityrocladus* (Webster, in press); examples are provided by *P. symphoricarpoides* Kunth (Fig. 11) and *P. ruscifolius* Müll. Arg. (Fig. 12; also Punt 1967). In these species the pollen grains are subprolate with usually only four or five colpi instead of 5–8, the colpi are monoporate, and the exine is more or less heterobrochate. The pollen grains of *P. symphoricarpoides* have a distinct resemblance to pollen of Asiatic species of sect. *Emblica*.

Sampling within subgenus *Phyllanthus* has been limited to a few characteristic or unusual species of two sections (*Phyllanthus* and *Choretropsis*). *Phyllanthus almadensis* Müll. Arg., a species endemic to Bahia in Brazil, was separated from other species by

Müller 1873) by its remarkable habit, a subshrub whose branchlets have opposite large leaves and racemoid inflorescences. This habit is unique and unlike any other Brazilian species of subgenus *Phyllanthus*; but the prolate pollen grains with three long nonmarginate colpi and tectate-perforate exine (Fig. 20) are comparable to those of other species of section *Phyllanthus* (Punt 1962, 1967; Punt & Rentrop, 1974; Bor, 1979). Similar pollen grains are also found in species of subgenus *Isocladus* such as the Brazilian *P. dawsonii* Steyerm. (Fig. 19), of section *Antipodanthus*. In contrast, other South American species of section *Phyllanthus* such as as *P. subemarginatus* Müll. Arg. (Fig. 21) have subspheroidal grains with a coarse reticulum. The phylloclade-bearing Brazilian species of sect. *Choretropsis* such as *P. flagelliformis* Müll. Arg. (Fig. 22), have pollen grains very similar to those of *P. subemarginatus* and relatives, but quite different from the pollen of the West Indian phyllocladebearing species of sect. *Xylophylla* (Webster, 1956–58); it appears evident that superficially similar phylloclades have evolved independently in subgenus *Phyllanthus* and in subgenus *Xylophylla*.

The most extraordinary pollen exine ornamentation observed in this study is that of *Phyllanthus lindenianus* Baill. (Figs 27, 28) of section *Cyclanthera*, in which the clypeate exine sculpturing suggests a honeycomb. Each 'cell' (areole) consists of a single central 'pilum' encircled by a murus. The central element is similar to the exinous knobs (pila) seen in species of subgenus *Conami* (cf. Figs 4, 5, 6), but none of those species have pila encircled by muri. The pollen grains of sect. *Cyclanthera* do not resemble any of the clypeate pollen grains illustrated by Halbritter & Hesse (1995).

In the orginal study of Webster (1956–58), *Phyllanthus lindenianus* Baill. and other species of sect. *Cyclanthera* were referred to subgenus *Phyllanthus,* largely because of their herbaceous habit and reduced androecium. However, section *Cyclanthera* differs from all other American taxa of subgenus *Phyllanthus* in the unique androecium (synandrium), strictly solitary flowers, and purplish floral pigments. The only similar taxon is section *Callitrichoides*, which includes the single rare endemic Cuban species *P. carnosulus* Müll. Arg.; the two sections are now associated in subgenus *Cyclanthera* (Webster, in press). Pollen material of *P. carnosulus* was not available for SEM studies, but the LM illustration of pollen of *P. carnosulus* (Webster, 1956–8) shows a unique banded pattern interpreted as ribbon-shaped areoles. Because of the resemblance in floral morphology in the two sections, it appears most parsimonius to derive the 'foveolate' exines of sect. *Cyclanthera* from the 'banded' exine of sect. *Callitrichoides*, but it must be admitted that the morphological gap seems very large.

There is a rather striking resemblance between the pollen exine of section *Callitrichoides* with that of *Phyllanthus subapicalis* Jabl. in section *Microglochidion* (Webster, SEM ined.). However, in section *Cyclanthera* there are also some suggestive characters indicating possible affinity with subgenus *Conami*. The resemblance of the pila in section *Cyclanthera* to those of some species of sect. *Nothoclema* were noted above, and the production of ramified (bipinnatiform) branchlets in some species of sect. *Cyclanthera* seems suggestive. However, *P. orbiculatus* of section *Apolepis* is even more similar in its herbaceous habit, dissected pistillate disk, and verruculose seeds (as well as the pilate exine ornamentation). Therefore, despite the divergence in pollen morphology, the totality of characters suggests the possibility that sections *Callitrichoides* and *Cyclanthera* could be regarded as a highly specialized and aberrant clade associated with subgenus *Conami*. On the other hand, an alternative hypothesis of the possible origin of the *Cyclanthera* pollen type could be based on the interpretation that the unique 'areoles' are highly reduced from the exine shields of the well-known clypeate grains of subgenus *Xylophylla*. The illustrations of the clypeate pollen grains of *Phyllanthus* × *elongatus* (Jacq.) Steud. illustrated by Halbritter & Hesse (1995) show exine shields with a well-defined murus surrounding a central field of heterobrochate reticulum. The topological relationship suggests that the exine shield of the *Cyclanthera* type of pollen grain could be derived by reduction of the central reticulum-field to a single pilum. Nevertheless, the evidently close relationship of section *Cyclanthera* with section *Callitrichoides*, and the great vegetative and floral differences from subgenus *Xylophylla,* argue against this alternative explanation. Overall, it has to be concluded that while section *Callitrichoides* is most similar in pollen morphology to section *Microglochidion* (in subgenus *Emblica*), section *Cyclanthera* in many respects is closest to section *Apolepis* (in subgenus *Conami*). Since sections *Callitrichoides* and *Cyclanthera* clearly belong to the same subgenus, the pollen evidence available at present yields exasperatingly contradictory conclusions.

Punt (1967) suggested that the primitive (most plesiomorphic) pollen morphology in *Phyllanthus* is that found in species such as *P. maderaspatensis* L. (subgenus *Isocladus*) and *P. pinnatus* (Wight) Webster (subgenus *Kirganelia*). As noted by Punt, the putatively basal pollen morphological type, prolate, 3-colporate, colpi with single pores, and exine semi-tectate-reticulate, occurs in other genera of the tribe Phyllantheae, such as *Flueggea* and *Margaritaria*, that have less specialized floral characteristics. Although there is considerable morphological variability in the pollen of *Flueggea* (Webster, 1984), the

grains of some Asiatic species (*F. acicularis* (Croizat) G. L. Webster and *F. jullienii* (Beille) G. L. Webster) are particularly similar to those of *P. pinnatus* (in subgenus *Kirganelia*).

In the study of the West Indian species of *Phyllanthus* (Webster, 1956–8), it was suggested that possible phylogenetic connections between the Old World subgenus *Kirganelia* and the New World subgenus *Cicca* (now included within subgenus *Kirganelia*; Webster, ined.) may be inferred from the similarity of the Cuban species *P. pseudocicca* Griseb. (sect. *Ciccopsis*) to African species of subgenus *Kirganelia* such as *P. physocarpus* Müll. Arg. This raises the possibility of an ancient African/West Indian connection that may have involved the colonization of the Americas by taxa of subgenus *Kirganelia*. On the other hand, the affinities of sections *Pityrocladus* and *Microglochidion* (in subgenus *Emblica*) point towards an Asiatic connection. The palynological evidence suggests that most of the indigenous woody neotropical species of *Phyllanthus* belong to two major clades: one with stephanocolporate pollen, including section *Microglochidion* (subgenus *Emblica*), and the other with clypeate pollen, in a dozen sections of subgenus *Xylophylla*. The cytological data provided by Mangenot *et al.* (1977), which show high levels of polyploidy in subgenus *Xylophylla*, lend some support to the hypothesis of Köhler (1967) that polyploidy (amphiploidy) has been involved in the orgin of the clypeate ('synrugoidorate') pollen of subgenus *Xylophylla*.

CONCLUSIONS

The results of this study reinforce the earlier assertions of Webster (1956–58), Punt (1967, 1987) and Köhler (1965) that pollen morphological data provide extremely valuable clues to phylogenetic relationships within *Phyllanthus*. They also suggest new concepts of relationship that will require taxonomic changes to better reflect phylogeny. Brunel (1975) was correct in suggesting that the sections of subgenus *Kirganelia* need to be critically revised. Accumulating studies during the past 40 years indicate that pollen evidence has not only been crucial in clarifying relationships between species groups, but has also provided striking demonstrations that taxa misleadingly convergent in vegetative structure (e.g. sections *Hylaeanthus*/*Brachycladus*; *Choretropsis*/*Xylophylla*) can readily be separated by pollen morphology.

Nevertheless, the demonstrated utility of pollen characters as indicators of systematic affinity is somewhat limited by widespread parallelism and homoplasy. Striking instances of problems in homology include vermiculate exine sculpturing (subgenus *Kirganelia* section *Floribundi* and subgenus

Gomphidium/subgenus *Conami* section *Nothoclema*/ subgenus *Xylophylla*); pilate exine sculpturing (subgenus *Kirganelia section Brazzaeani*/subgenus *Conami*); diploporate colpi (subgenus *Kirganelia* sections *Floribundi* and *Pseudomenarda*/subgenus *Conami*/subgenus *Emblica* section *Microglochidion*).

Among the neotropical taxa of *Phyllanthus*, it now appears that most of the woody species (apart from subgenus *Conami*) may belong to a single clade rooted in subgenus *Emblica*. Section *Microglochidion*, represented by many striking endemic species in the *tepuis* of the Guayana highlands, appears to be a monophyletic group even though diploporate colpi are not a synapomorphy for the entire section. Müller (1863) originally described *Microglochidion* as a section of the Old World genus *Glochidion* because of the unlobed styles, which are common but not invariant in the group. Some other characters, such as the apiculate anthers, are also shared by section *Microglochidion* and *Glochidion*, but the well-developed floral disk and especially the diploporate colpi provide arguments against any affiliation with that genus.

The systematic affinities of subgenus *Conami* remain in question. Although the diploporate colpi might appear to suggest a possible affiliation with sect. *Microglochidion*, the pollen grains of sect. *Nothoclema* differ in their subspheroidal shape, fewer colpi, and vermiculate to pilate exine ornamentation. In these characteristics, subgenus *Conami* appears closer to Old World taxa of subgenera *Kirganelia* and *Gomphidium*. Additional evidence, perhaps from molecular studies, will have to be obtained in order to clarify these subgeneric relationships.

The comparisons of species studied in this investigation yield some new perspectives on the origin of the clypeate ('areolate' or 'synrugoidorate') pollen grains of the neotropical subgenus *Xylophylla*. It was suggested by Webster (1956–58) that the pollen of *Phyllanthus subcarnosus* Wright ex Müll. Arg. in the West Indian section *Omphacodes*, with very large pollen shields, might represent the basal stage from which the pollen of other taxa (with smaller pollen shields) was derived. However, this does not provide a straightforward explanation of the origin of the clypeate pollen of subgenus *Xylophylla* because the pollen of the putative sister species in subgenus *Kirganelia*, *P. pseudocicca* Griseb. (section *Ciccopsis*) is 3-colporate, monoporate, and angulaperturate (Webster, 1956–58). As noted above, the origin of the distinctive clypeate pollen grains of subgenus *Cyclanthera* also remains unclear.

There have been two earlier suggestions that go part of the way to explaining the origin of clypeate pollen in subgenus *Xylophylla*. Köhler (1967) pointed out that increase in number of apertures in *Phyllanthus* is correlated with polyploidy; clypeate grains occur in species with chromosome complements at the tetraploid level or higher (Webster & Ellis, 1962; Mangenot *et al.*, 1977). Punt (1986) made the crucial observation that the clypeate grains of subgenus *Xylophylla* must have arisen from an ancestral type with diploporate colpi and a tendency to syncolpy. In terms of this model, the ancestral forms should have had the spheroidal syncolporate grains (with vermiculate exine) of Old World species of subgenus *Kirganelia* (and subgenus *Gomphidium*), and the diploporate grains of South American species of section *Microglochidion*. Unfortunately, the subprolate multicolporate grains with reticulate exine of species of section *Microglochidion* do not provide an ideal set of putative ancestral characters. This could be accounted for by a very speculative hypothesis of hybridization between a species of sect. *Ciccopsis* and a species of sect. *Microglochidion*, with the multiplication of colpi leading to the characteristic clypeate exine ornamentation of subgenus *Xylophylla*. The task lying ahead is to attempt to falsify this hypothesis, or to provide a more plausible one on the basis of a more complete data base (especially for section *Microglochidion*) than is now available.

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APPENDIX

CLASSIFICATION OF THE SPECIES OF *PHYLLANTHUS* DISCUSSED IN THE TEXT

Subgenus I. *Isocladus*
  Section 1. *Paraphyllanthus*: *Phyllanthus maderaspatensis* L.
  Section 2. *Antipodanthus*: *Phyllanthus dawsonii* Steyerm.
Subgenus II. *Kirganelia*
  Section 1. *Chorisandra*: *Phyllanthus pinnatus* (Wight) G. L. Webster
  Section 2. *Floribundi*: *Phyllanthus klainei* Hutch., *P. physocarpus* Müll. Arg*., P. polyanthus* Pax, *P. profusus* N. E. Br., *P. tessmannii* Hutch.
  Section 3. *Anisonema*: *Phyllanthus reticulatus* Poir.
  Section 4. *Pseudomenarda*: *Phyllanthus purpureus* Müll. Arg.
  Section 5. *Brazzeani*: *Phyllanthus dinklagei* Pax
  Section 6. *Cicca*: *Phyllanthus chacoensis* Morong

Section 7. *Ciccopsis*: *Phyllanthus pseudocicca* Griseb.
Subgenus III. Gomphidium

Section 1. *Ardisianthus*: *Phyllanthus acinacifolius* Airy Shaw & G. L. Webster, *P. bourgeoisii* Baillon.

Section 2. *Gomphidium*: *Phyllanthus amicorum* G. L. Webster, *P. chamaecerasus* Baillon, *P. heterodoxus* Müll. Arg., *P. pergracilis* Gillespie, *P. rupi-insularis* Hosok.

Section 3. *Adenoglochidion*: *Phyllanthus myrianthus* Müll. Arg.

Section 4. *Nymania*: *Phyllanthus warburgii* K. Schum.
Subgenus IV. *Conami*

Section 1. *Nothoclema*: *Phyllanthus acuminatus* Vahl, *P. anisolobus* Müll. Arg., *P. brasiliensis* (Aubl.) Poir. (including *P. subglomeratus* Poir.), *P. caymanensis* G. L. Webster & Proctor, *P. graveolens* Kunth, *P. mcvaughii* G. L. Webster, *P. mocinianus* Baillon, *P. pavonianus* Baillon.

Section 2. *Hylaeanthus*: *P. attenuatus* Miq., *P. skutchii* Standl.

Section 3. *Apolepis*: *Phyllanthus orbiculatus* Rich.
Subgenus V. Emblica

Section 1. *Pityrocladus*: *Phyllanthus ruscifolius* Müll. Arg., *P. symphoricarpoides* Kunth

Section 2. *Microglochidion*: *Phyllanthus duidae* Gleason, *P. myrsinites* Kunth, *P. pycnophyllus* Müll.

Arg., *P. strobilaceus* Jabl., *P. vacciniifolius* (Müll. Arg.) Müll. Arg.; *P. websterianus* Steyerm.
Incertae sedis

Phyllanthus harrimanii G. L. Webster (referred to section *Lysiandra* by Webster 1978)
Subgenus VI. Cyclanthera

Section *Callitrichoides*: *Phyllanthus carnosulus* Müll. Arg.

Section *Cyclanthera*: *Phyllanthus berteroanus* Müll. Arg., *P. lindenianus* Baillon
Subgenus VII. *Xylophylla*

Section 1. *Omphacodes*: *Phyllanthus subcarnosus* C. Wright ex Müll. Arg.

Section 2. *Brachycladus*: *Phyllanthus spruceanus* Müll. Arg.

Section 3. *Hemiphyllanthus*: *Phyllanthus maleolens* Urb. & Ekm., *P. mimosoides* Sw.

Section 4. *Xylophylla*: *Phyllanthus latifolius* (L.) Sw.

Section 5. *Elutanthos*: *Phyllanthus poeppigianus* (Müll. Arg.) Müll. Arg.
Subgenus VII. *Phyllanthus*

Section 1. *Phyllanthus*: *Phyllanthus almadensis* Müll. Arg., *P. subemarginatus* Müll. Arg.

Section 2. *Choretropsis*: *Phyllanthus flagelliformis* Müll. Arg., *P. goianensis* L. J. M. Santiago, *P. sarothamnoides* Govaerts & Racl.-Sm.