

The pollen morphology of *Phyllanthus* (Euphorbiaceae) section *Choretropsis*

LAURA JANE MOREIRA SANTIAGO^{1*}, RICARDO PEREIRA LOURO²,
MARGARETE EMMERICH³ and ORTRUD MONIKA BARTH⁴

¹Laboratório de Biotecnologia, Centro de Biociências e Biotecnologia, Universidade Estadual do Norte Fluminense, Rua Alberto Lamego 2000, Horto, Campos dos Goytacazes, 28015–620 Rio de Janeiro, Brazil

²Laboratório de Ultraestrutura Vegetal, Departamento de Botânica, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

³Departamento de Botânica, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

⁴Laboratório de Palinologia, Departamento de Botânica, Instituto de Biologia; Departamento de Geologia, Instituto de Geociências, Universidade Federal do Rio de Janeiro; Departamento de Virologia, Instituto Oswaldo Cruz / Fiocruz, Rio de Janeiro, Brazil

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The pollen grain morphology of the eight South American species of the genus *Phyllanthus*, subgenus *Phyllanthus*, section *Choretropsis*, endemic to Brazil, was investigated using light and scanning electron microscopy. The high homogeneity in pollen shape, as well as aperture number and configuration, allowed the definition of a basic pollen type for this section, viz. prolate spheroidal or subprolate, zonocolporate with 4–5 invaginated colpi, sexine reticulate. Two subtypes have been observed, based on pollen grain apertures and exine sculpture. The first subtype is characterized by straight and narrow colpi provided with costae, lalongate endoapertures and a reticulum of rectilinear muri as in *P. choretroides* and *P. spartioides*. The second subtype has wider colpi without costae, circular endoapertures and a reticulum with curvilinear muri as in *P. flagelliformis*, *P. goianensis* and *P. scoparius*, or curvilinear-rectilinear muri as in *P. angustissimus*, *P. gladius* and *P. klotzschianus*. It was demonstrated that the pollen shape and the number of colpi varied within and between some of the species. The results suggest that pollen grain morphology, in association with plant architecture and the presence of phylloclades, constitute additional evidence to delimit the species of the section *Choretropsis* and to further understand their evolutionary origin within the genus *Phyllanthus*. © 2004 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2004, 144, 243–250.

ADDITIONAL KEYWORDS: Brazilian plants – light microscopy – scanning electron microscopy – taxonomy.

INTRODUCTION

The genus *Phyllanthus* is represented by 750–800 species comprising terrestrial herbs, shrubs, small trees or floating aquatic plants dispersed predominantly in the Old World and with about 200 species in America (Webster, 1956, 1994a,b; Webster & Carpenter, 2002). It has been suggested that the West Indies and Brazil are the main centres of *Phyllanthus* speciation in the New World (Webster, 1956, 1967).

The heterogeneity in plant architecture in association with pollen grain ornamentation were proposed as the main taxonomic characters to establish the sections within the genus (Webster, 1956, 1957, 1958, 1988, 1994a, 1999, 2002; Webster & Airy Shaw, 1971; Webster & Proctor, 1984). These structures were shown to be an important tool in understanding the evolution of *Phyllanthus* species at section and subsection levels. The presence of modified branchlets, called phylloclades, was considered to be the most derived condition within *Phyllanthus* species architecture (Webster, 1956, 1957, 1958). It was proposed that these structures developed in xerophytic plants, with

*Corresponding author. E-mail: laura@uenf.br

reduction and sometimes loss of leaf blades to avoid excessive plant transpiration (Dingler, 1885; von Troll, 1967). The taxa are distributed in two main taxonomic groups: the section *Choretropsis*, characterized by reticulate pollen grains and pinnatifid branchlets, and the section *Xylophylla*, whose species have areolate pollen grains and bipinnatifid branchlets (Webster, 1958). The species of the sections *Choretropsis* and *Xylophylla* are endemic to the West Indies and South America, respectively (Mueller Argoviensis, 1863, 1866, 1873; Benthams, 1878; Benthams & Hooker, 1880; Pax, 1890; Pax & Hoffmann, 1923, 1931; Webster, 1956, 1958; Santiago, 1988a,b).

The section *Choretropsis* is represented by nine species, eight of which are endemic to Brazil, with the main distribution in cerrado, sand dunes and highlands (Santiago, 1988a,b). Plant architecture, as well as the morphology and internal arrangement of *Phyllanthus* species branchlets, led to the subdivision of this section into the subsection *Choretropsis*, represented by *P. choretroides*, *P. goianensis* and *P. spartioides*, and characterized mainly by cylindrical branchlets which developed palisade-like cells, and the subsection *Applanata*, comprising *P. angustissimus*, *P. edmundoi*, *P. flagelliformis*, *P. gladius*, *P. klotzschianus* and *P. scoparius*, characterized mainly by flattened branchlets which developed palisade-like cells (Santiago, 1988a,b). Pollen morphology and evolutionary characteristics in the genus *Phyllanthus* have been extensively studied (Punt, 1962, 1972, 1980; Punt & Rentrop, 1974; Bor, 1979; Meewis & Punt, 1983; Lobreau-Callen, Punt & Schmid, 1988; Webster, 1994a,b).

The structure of pollen grains of some species of the section *Choretropsis* was investigated by Webster & Carpenter (2002). However, the palynological analysis of the other *Choretropsis* taxa may provide valuable information in further understanding the evolutionary relationship between these uncommon Brazilian plants and other *Phyllanthus* species. The pollen grain morphology of Brazilian species of the section *Choretropsis*, using light and scanning electron microscopy, was analysed in the present study with the aim of providing additional information on their taxonomy.

MATERIAL AND METHODS

Pollen grains were obtained from herbarium specimens deposited at Museu Nacional do Rio de Janeiro, UFRJ (R); Herbarium Bradeanum (HB); Centro de

Pesquisas da Lavoura Cacaueira (CEPEC); Universidade de Campinas (UEC); Instituto de Biociências, Departamento de Botânica, Universidade de São Paulo (SPF).

MATERIAL EXAMINED

Phyllanthus angustissimus – Hensold *et al.* s/n°, Proc. Santana do Riacho – R; Mello Barreto e Brade n° 1.194, Serra do Cipó, Minas Gerais – R; *P. choretroides* – M.C.E. Amaral *et al.* Proc. Santana do Riacho – R; B. Stannard *et al.* s/n°, Serra da Bocaina, Minas Gerais – SPF; *P. flagelliformis* – S. Pinheiro 1.966, Proc. Jaguaquara – CEPEC; E. Pereira e A.P. Duarte n° 10.026, Morro do Chapéu, Bahia – HB; *P. gladius* – T.S. Santos 2915, Proc. Nilo Peçanha, Bahia – CEPEC; B. Weimberg s/n°, Vila Velha, Espírito Santo – R; *P. goianensis* – Ule 52, Proc. Vargem Grande, Goiás – R; *P. klotzschianus* – A. P. Duarte 7.870 e Graziela, Proc. Diamantina, Minas Gerais – HB; E. Pereira n° 9.877, Morro do Sal, Espírito Santo – HB; *P. scoparius* – R. Mello Silva *et al.* s/n°, Proc. Lençóis Bahia – R; R.M. Harley *et al.* n° 22.699, Serra dos Lençóis, Bahia – CEPEC; *P. spartioides* – H.S. Irwin *et al.* 33.018, Proc. Chapada dos Veadeiros, Goiás – UEC; H.M. Harley 19.709, Serra das Almas, Bahia – SPF; A.M. Giulietti *et al.* s/n°, Serra do Cabral, Minas Gerais – SPF.

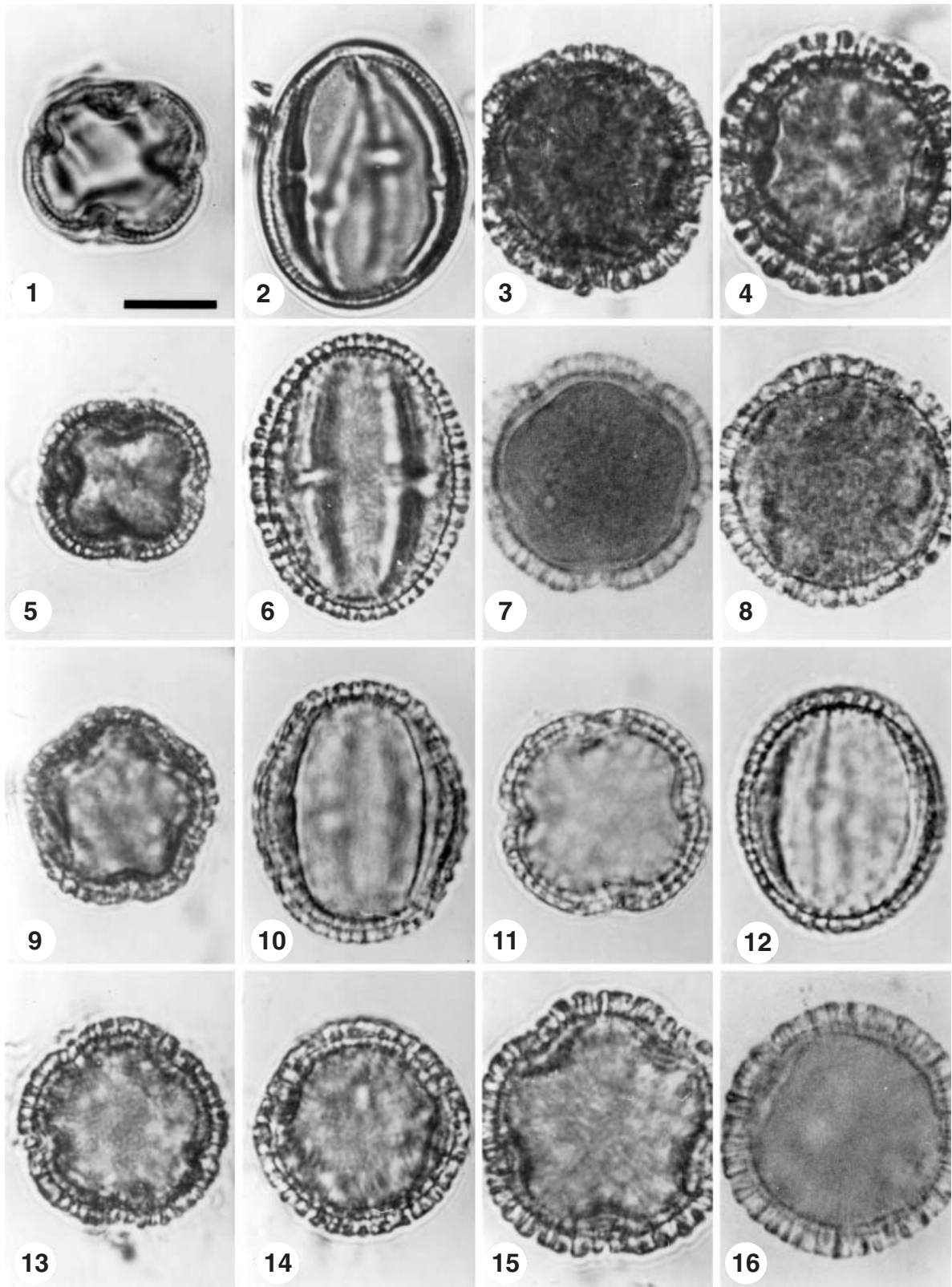
The pollen grains were obtained from anthers of herbarium specimens and acetolysed according to Erdtman (1952). Part of the acetolysed sample was mounted in glycerine jelly for light microscope analyses. The other part was dehydrated in 70% ethanol for 3 h, air-dried at room temperature, sputter-coated with gold and analysed using a Jeol 25 S-II scanning electron microscope.

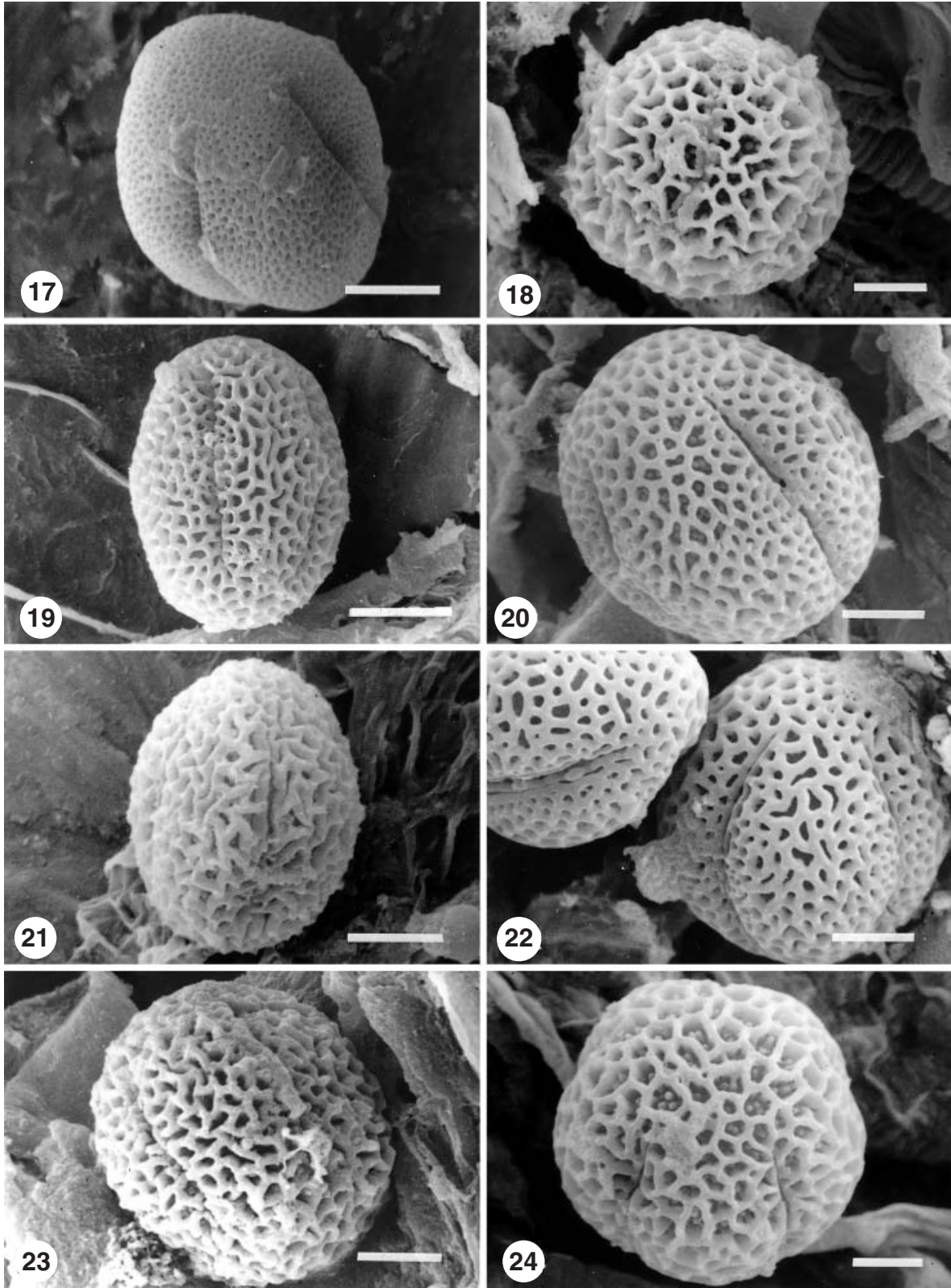
About 50 grains for each species were used for the pollen measurements. Measurements of polar length and equatorial width were taken using an eye piece micrometer adapted to a Zeiss microscope and the range, variance and standard deviation were noted. Subsequent description used the terminology of Punt *et al.* (1994).

RESULTS

The pollen grains of the eight species of *Phyllanthus* section *Choretroides* (Figs 1–24; Table 1) show a prolate sphaeroidal shape, as observed in *P. angustissimus*, *P. goianensis*, *P. klotzschianus* and *P. scoparius*, and a subprolate shape as in

Figures 1–16. Light microscope micrographs of *Phyllanthus* section *Choretropsis* pollen grains: optical sections of polar and equatorial views. Figs 1–2. *P. choretroides*. Figs 3–4. *P. goianensis*. Figs 5–6. *P. spartioides*. Figs 7–8. *P. angustissimus*. Figs 9–10. *P. flagelliformis*. Figs 11–12. *P. gladius*. Figs 13–14. *P. klotzschianus*. Figs 15–16. *P. scoparius*. Scale bars = 10 µm.





P. choretroides, *P. flagelliformis*, *P. gladius* and *P. spartioides*. The species are zonocolporate with 4–5 invaginated colpi with lalongate or circular endoapertures; however, only 5 colpi were observed in *P. angustissimus*, *P. flagelliformis* and *P. goianensis* and only 4 colpi in *P. choretroides*. The aperture configuration consists of straight and narrow colpi and strongly delimited, large, lalongate apertures in *P. choretroides* and *P. spartioides*. Wider colpi in the equatorial region of the pollen grains comprising circular endoapertures occur in all the other species examined. Costae along the colpi were observed only in *P. choretroides* and *P. spartioides* (Figs 2 and 6)

The sexine is semitectate with deep lumina in all of the species. Only in *P. choretroides* are the pollen grains microreticulate. The reticulum of the remaining species may present curvilinear muri as in *P. flagelliformis*, *P. goianensis* and *P. scoparius*, rectilinear muri as in *P. spartioides*, or simultaneously rectilinear and curvilinear muri as in *P. angustissimus*, *P. gladius* and *P. klotzschianus*. There are no margins around the colpi except in *P. gladius* (Fig. 22), which show very straight and psilate boundaries along the colpi.

In summary, the pollen type of *Phyllanthus* section *Choretropis* may be defined as prolate sphaeroidal to subprolate, zonocolporate with 4–5 colpi, sexine broadly reticulate or microreticulate. Two subtypes are established:

Subtype 1 (Figs 3–6, 17–18) showing colpi provided with costae, large lalongate endoapertures and a

microreticulate ornamentation in *P. choretroides* and a rectilinear-reticulate ornamentation in *P. spartioides*.

Subtype 2 (Figs 17, 19, 20, 22–24) showing wider colpi without costae, circular endoapertures and curvilinear or curvilinear-rectilinear reticulate ornamentation in *P. angustissimus*, *P. flagelliformis*, *P. gladius*, *P. goianensis*, *P. klotzschianus* and *P. scoparius*.

DISCUSSION

The pollen grains of the section *Choretropis*, subsections *Choretropis* and *Applanata*, showed similar characteristics in relation to pollen dimensions, number of colpi and sexine ornamentation. This suggests a basic pollen type characterized by prolate spheroidal and subprolate zonocolporate pollen grains with 4–5 invaginated colpi and a semitectate commonly broad reticulate sexine.

The number of colpi varied in *P. gladius*, *P. klotzschianus*, *P. scoparius* and *P. spartioides*. However, the range in colpi number characterized this section. It has been shown that the colpi number may vary in some *Phyllanthus* species, with unspecialized branchlets as in *P. odontadenius* and *P. urinaria* (Háïcour, 1984a,b; Rossignol, Rossignol & Háïcour, 1987; Háïcour *et al.*, 1994). The diversity in colpi number was related to the genetic variability observed among the different natural populations of these taxa, which led many authors to consider these species taxonomic

Table 1. Diameters (µm), shape, number of colpi and ornamentation patterns in pollen grains of the genus *Phyllanthus*, section *Choretropis*

Species	Polar diameter	Equatorial diameter	Shape	Number of colpi	Ornamentation
Subsection <i>Choretropis</i>					
<i>P. choretroides</i>	29.0 + 1.3 (24.0–36.0)	21.9 + 0.6 (20.0–24.0)	subprolate	4	mrr
<i>P. goianensis</i>	27.4 + 1.2 (24.0–36.0)	24.7 + 1.2 (20.0–30.0)	prolate sphaeroidal	5	rc
<i>P. spartioides</i>	23.5 + 0.9 (24.0–32.0)	22.1 + 0.6 (20.0–26.0)	subprolate	4–5	rr
Subsection <i>Applanata</i>					
<i>P. angustissimus</i>	26.8 + 0.4 (26.0–28.0)	25.8 + 1.7 (28.0–36.0)	prolate sphaeroidal	5	rc/rr
<i>P. flagelliformis</i>	25.7 + 1.2 (28.0–30.0)	21.9 + 0.9 (18.0–26.0)	subprolate	5	rc
<i>P. gladius</i>	28.0 + 0.5 (26.0–30.0)	24.3 + 0.6 (22.0–26.0)	subprolate	4–5	rc/rr
<i>P. klotzschianus</i>	28.5 + 0.6 (26.0–32.0)	26.8 + 0.8 (28.0–36.0)	prolate sphaeroidal	4–5	rc/rr
<i>P. scoparius</i>	33.0 + 0.9 (30.0–38.0)	31.4 + 0.8 (28.0–36.0)	prolate sphaeroidal	4–5	rc

mrr = microreticulate; rc = reticulate with curvilinear muri; rr = reticulate with rectilinear muri.

Figures 17–24. Scanning electron microscope micrographs of *Phyllanthus* section *Choretropis* pollen grains in equatorial views. Fig. 17. *P. choretroides*. Fig. 18. *P. goianensis*. Fig. 19. *P. spartioides*. Fig. 20. *P. angustissimus*. Fig. 21. *P. flagelliformis*. Fig. 22. *P. gladius*. Fig. 23. *P. klotzschianus*. Fig. 24. *P. scoparius*. Scale bars = 5 µm, except in Fig. 17, equals; 10 µm.

complexes as actively evolving (Háïcour, 1984a,b; Rosignol *et al.*, 1987; Háïcour *et al.*, 1994). However, vegetative and reproductive structures did not vary among different populations of *Choretropsis* species.

Although reticulate ornamentation of the sexine was constant within the section, variation in the reticulum patterns occurred, leading to two groups of species. *Phyllanthus choretroides* showed a particular pollen grain ornamentation, differing from all other species studied by its microreticulate ornamentation. The other groups were characterized by rectilinear, curvilinear or mixed configurations of muri. The presence of costae in the colpi configuration, observed only in *P. choretroides* and *P. spartioides* of subsection *Choretropsis*, may define this subsection. However, no correlation between reticulate pattern and subsection could be identified (Table 1).

The observed features suggested that the pollen type of section *Choretropsis* was closely related to the *Securinega* type proposed by Punt (1962) in respect of the subprolate spheroidal shape condition, reticulate sculpture, the 4-zonocolporate condition and the variability of endoaperture configuration. However, the studied species differed from the *Securinega* type by the prolate spheroidal shape in the 5-colporate pollen grains and the low frequency of species with costae (two of eight species). Except in *P. gladiatus*, no margins could be detected in the *Choretropsis* section.

Pollen morphology and architecture pattern of the species have been considered to be the main characteristics useful in *Phyllanthus* taxonomy (Webster, 1956). A large number of *Phyllanthus* species showed 3-colporate and reticulate pollen grains. Tricolporate pollen grains have been reported in the primitive tribes of Phyllanthoideae such as Wielandieae and Amanoeae, in the primitive petaliferous genera of Phyllanthaceae such as *Astrocasia*, *Leptopus* and *Andrachne*, in the apetalous genera related to *Phyllanthus* such as *Flueggea*, *Richeriella* and *Margaritaria*, and in some other *Phyllanthus* sections (Webster, 1956, 1994b; Levin, 1986; Simpson & Levin, 1994; Lobreau-Callen & Malécot, 2000; Lobreau-Callen, Malécot & Suarez-Cervera, 2000, 2001). The pollen grains of sections *Paraphyllanthus* and *Phyllanthus*, whose species did not develop phylloclades, are 3- or 4-colporate (Webster, 1956, 1957). However, 3-colporate pollen grains were not observed in species of section *Choretropsis*.

It has been shown that the pollen sculpture of the sections *Hemiphyllanthus* and *Phyllanthus*, which did not develop phylloclades, was divergent. Species of section *Hemiphyllanthus* developed areolated pollen and those of section *Phyllanthus*, reticulate pollen grains (Webster, 1956). The reticulate pollen grains associated with a phyllanthoid ramification with pinnatifid branchlets led Webster (1956, 1957, 1958) to

propose species of the section *Phyllanthus* as the ancestors of section *Choretropsis*.

Webster (1958) suggested parallel evolution between the section *Choretropsis*, including endemic Brazilian species characterized by the pinnatifid compound phylloclade branchlets and reticulate ornamentation of pollen grains, and the section *Xylophylla*, endemic to the West Indies, with species showing bipinnatifid compound phylloclade branchlets and areolate pollen grains.

The reticulate pattern was the predominant pollen subtype within the section *Choretropsis*, being present in all species from the subsection *Applanata*, and in *P. goianensis* and *P. spartioides* in the subsection *Choretropsis*. The difference in the pattern of pollen sculpture observed in *P. choretroides* seems to be related to the divergence between the architecture and anatomy of this species and the other species from the section *Choretropsis* (Santiago, 1988a,b). It was shown that in contrast to the last species, which are characterized by the elongation of the main axis and the development of monopodial architecture, *P. choretroides* branchlets underwent a reduction in the main axis leading to sympodial architecture. This divergence in the pattern of ramification and architecture was also observed within the species of section *Phyllanthus* with normal branchlets (Webster, 1956).

Phyllanthus gladiatus presented an uncommon architecture among *Phyllanthus* species, being characterized by increase in plant height, the elongation of the main axis and the presence of single branches, which were similar to the deciduous branchlets of the phyllanthoid branching, distributed distally (Dingler, 1885; Webster, 1956; Santiago, 1988a,b). The architecture in association with pollen morphology constitutes distinctive features for this taxon, since although its pollen grain sculpture remained similar to the other species of the section, the presence of psilate boundaries around the colpi was characteristic for this species.

The results led to the proposal of a basic pollen type in all the species of section *Choretropsis*. The pollen morphology of the eight endemic Brazilian species of the section suggested a close relationship between *P. goianensis* and *P. spartioides* in the subsection *Choretropsis*, and between this last subsection and the species of subsection *Applanata*. The divergent pattern of pollen morphology in association with the sympodial architecture and the cylindrical phylloclades of *P. choretroides* (Santiago, 1988a) are suggestive of a distinctive evolutive trend within the subsection *Choretropsis*. To further understand the relationships within the taxa of the section *Choretropsis*, and between these species and those of section *Phyllanthus*, the pollen structure of species of both sections needs to be better investigated.

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REFERENCES

- Bentham G. 1878.** Notes on Euphorbiaceae. *Botanical Journal of the Linnean Society* **14**: 185–267.
- Bentham G, Hooker JD. 1880.** *Phyllanthus*. In: *Genera plantarum* Vol. 3. London: Reeve & Co., Williams & Norgate, 272–275.
- Bor J. 1979.** Pollen morphology and the bi-reticulate exine of the *Phyllanthus* species (Euphorbiaceae) from Mauritius and Réunion. *Review of Palaeobotany and Palynology* **27**: 149–172.
- Dingler H. 1885.** *Die Flachsprosse der Phanerogamen. Vergleichende Morphologisch – Anatomische Studien*. Erstes Heft: *Phyllanthus* sect. *Xylophylla*. Muenchen: Ackermann.
- Erdtman G. 1952.** *Pollen morphology and plant taxonomy: angiosperms*. Stockholm: Alquist and Wiksell.
- Háicour R. 1984a.** Éléments d'analyse de la structure des populations et de l'évolution d'une espèce rudérale pantropicale, *Phyllanthus urinaria* L. (Euphorbiaceae).1. Étude du polymorphisme de l'entité *Purinaria* et premier essai de classification. *Bulletin du Museum National d'Histoire Naturelle, Paris*, 4^e série 6. Sect. B. *Adansonia* **1**: 63–74.
- Háicour R. 1984b.** Éléments d'analyse de la structure des populations et de l'évolution d'une espèce rudérale pantropicale, *Phyllanthus urinaria* L. (Euphorbiaceae).2. Étude de la variation génétique et de sa traduction phénotypique. *Bulletin du Museum National d'Histoire Naturelle, Paris*, 4^e série 6. Sect. B. *Adansonia* **2**: 157–191.
- Háicour R, Rossignol L, Rossignol M, Gaisne C. 1994.** Patterns of diversification and evolution in *Phyllanthus odontadenius* (Euphorbiaceae). *Annals of the Missouri Botanical Garden* **81**: 289–301.
- Levin GA. 1986.** Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic analysis. *Systematic Botany* **11**: 515–530.
- Lobreau-Callen D, Malécot V. 2000.** Le pollen des Crotonoideae apétèles (Euphorbiaceae): étude cladistique préliminaire et répartition des genres paléotropicaux. *Geo-Eco-Trop* (special no.): 177–196.
- Lobreau-Callen D, Malécot V, Suarez-Cervera M. 2000.** Comparative study of pollen from apetalous Crotonoideae and some other uniovulate Euphorbiaceae: exine ultrastructure at the aperture. In: Harley MM, Morton CM, Blackmore S, eds. *Pollen and spores: morphology and biology*. Kew, London: Royal Botanical Gardens, 301–324.
- Lobreau-Callen D, Pons D, Malécot V. 2001.** Pollen aperturé des Crotonoideae apétales actuelles et fossiles. In: Weiss R, ed. *Contributions to geology and paleontology of Gondwana in honour of Helmut Wopfner*, Cologne: Geological Institute, University of Cologne, 303–323.
- Lobreau-Callen D, Punt W, Schmid M. 1988.** Pollen morphology and taxonomy of the *Phyllanthus* species (Euphorbiaceae) native to New Caledonia. *Review of Palaeobotany and Palynology* **54**: 283–304.
- Meewis B, Punt W. 1983.** Pollen morphology and taxonomy of the subgenus *Kirganelia* (Jussieu) Webster (genus *Phyllanthus*, Euphorbiaceae) from Africa. *Review of Palaeobotany and Palynology* **39**: 131–160.
- Mueller Argoviensis JO. 1863.** *Phyllanthus*. In: de Candolle AP, ed. *Vorläufige Mitteilungen aus dem für De Candolle's Prodomus bestimmten Manuscript über diese Familie*. Linnaea, 31. Muenchen: 1–57.
- Mueller Argoviensis JO. 1866.** *Phyllanthus*. In: de Candolle AP, eds. *Prodomus systematis naturalis regni vegetabilis*. Vol. 15. Paris: 274–436.
- Mueller Argoviensis JO. 1873.** *Phyllanthus*. In: Martius KFP, ed. *Flora Brasiliensis*. Vol. 11. Muenchen: 23–76.
- Pax F. 1890.** *Phyllanthus*. In: Engler A, Prantl K, eds. *Die natürlichen Pflanzenfamilien*. Vol. 3. Leipzig: 18–23.
- Pax F, Hoffmann K. 1923.** Euphorbiaceae americanae novae. I. *Reprium Species Novarum Regni Vegetabili* **19**: 174.
- Pax F, Hoffmann K. 1931.** *Phyllanthus*. In: Engler A, Prantl K, eds. *Die Natürlichen Pflanzenfamilien* Vol. 19c. Leipzig: Engelmann, 60–66.
- Punt W. 1962.** Pollen morphology of Euphorbiaceae with special reference to taxonomy. *Wentia* **7**: 1–116.
- Punt W. 1972.** Pollen morphology and taxonomy of section *Ceramanthus* Baillon s.l. of the genus *Phyllanthus* (Euphorbiaceae). *Review of Palaeobotany and Palynology* **13**: 213–228.
- Punt W. 1980.** Pollen morphology of the *Phyllanthus* species (Euphorbiaceae) occurring in Guinea. *Review of Palaeobotany and Palynology* **31**: 155–177.
- Punt W, Blackmore S, Nilsson S, Le Thomas A. 1994.** *Glossary of pollen and spore terminology*. LPP Contributions Series no. 1. Utrecht: LPP Foundation.
- Punt W, Rentrop J. 1974.** Pollen morphology of the *Phyllanthus* species occurring in the continental United States. *Review of Palaeobotany and Palynology* **16**: 243–261.
- Rossignol L, Rossignol M, Háicour R. 1987.** A systematic revision of *Phyllanthus* subsection *Urinaria* (Euphorbiaceae). *American Journal of Botany* **74**: 1853–1862.
- Santiago. LJM. 1988a.** Estudos preliminares da seção *Choretropsis* Muell. Arg., gênero *Phyllanthus* L. (Euphorbiaceae). *Bradea* **5**: 44–49.
- Santiago. LJM. 1988b.** Contribuição ao conhecimento do gênero *Phyllanthus* L. (Euphorbiaceae) seção *Choretropsis* Muell. Arg. Unpublished Msc Thesis, Universidade Federal do Rio de Janeiro.
- Simpson MG, Levin GA. 1994.** Pollen ultrastructure of bi-ovulate Euphorbiaceae. *International Journal of Plant Science* **155**: 313–341.
- von Troll W. 1967.** *Vergleichende Morphologie der Höheren Pflanzen*. Vol. 1. Berlin: Koenigstein-Taunus Verlag Otto Koeltz.
- Webster GL. 1956.** A monographic study of West Indian species of *Phyllanthus*. *Journal of the Arnold Arboretum* **37**: 91–122, 217–268, 340–359.

- Webster GL. 1957.** A monographic study of West Indian species of *Phyllanthus*. *Journal of the Arnold Arboretum* **38**: 51–80, 170–198, 295–373.
- Webster GL. 1958.** A monographic study of West Indian species of *Phyllanthus*. *Journal of the Arnold Arboretum* **39**: 49–100, 111–212.
- Webster GL. 1967.** The genera of Euphorbiaceae in the South-eastern United States. *Journal of the Arnold Arboretum* **48**: 303–361.
- Webster GL. 1988.** A revision of *Phyllanthus* (Euphorbiaceae) in eastern Melanesia. *Pacific Science* **40**: 88–105.
- Webster GL. 1994a.** Classification of the Euphorbiaceae. *Annals of the Missouri Botanical Garden* **81**: 3–32.
- Webster GL. 1994b.** Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Annals of the Missouri Botanical Garden* **81**: 33–144.
- Webster GL. 1999.** *Phyllanthus*. In: Berry PE, Yatskievych K, Holst BK, eds. *Flora of the Venezuelan Guayana*. Vol. 5. St Louis: Missouri Botanical Garden Press, 191–205.
- Webster GL. 2002.** A synopsis of the Brazilian taxa of *Phyllanthus* section *Phyllanthus* (Euphorbiaceae). *Lundellia* **5**: 1–26.
- Webster GL, Airy Shaw HK. 1971.** A provisional synopsis of the New Guinea taxa of *Phyllanthus* (Euphorbiaceae). *Kew Bulletin* **26**: 85–105.
- Webster GL, Carpenter KJ. 2002.** Pollen morphology and phylogenetic relationships in neotropical *Phyllanthus* (Euphorbiaceae). *Botanical Journal of the Linnean Society* **138**: 325–338.
- Webster GL, Proctor GR. 1984.** A new species of *Phyllanthus* (Euphorbiaceae) from the Cayman Island. *Rhodora* **86**: 121–125.