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

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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 rectilineous muri as in *P. choretroides* and *P. spartioides*. The second subtype has wider colpi without costae, circular endoapertures and a reticulum with curvilineous muri as in *P. flagelliformis*, *P. goianensis* and *P. scoparius*, or curvilineous-rectilineous muri as in *P. angustissimus*, *P. gladiatus* 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. *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 be the most derived condition within *Phyllanthus* species architecture (Webster, 1956, 1957, 1958). It was proposed that these structures developed in xerophytic plants, with

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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 pinnatiform branchlets, and the section *Xylophylla*, whose species have areolate pollen grains and bipinnatiform branchlets (Webster, 1958). The species of the sections *Choretropsis* and *Xyllophylla* are endemic to the West Indies and South America, respectively (Mueller Argoviensis, 1863, 1866, 1873; Bentham, 1878; Bentham & 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. gladiatus*, *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. gladiatus* – 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 Lençois 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. Giullietti *et al*. s/n°, Serra do Cabral, Minas Gerais – SPF.

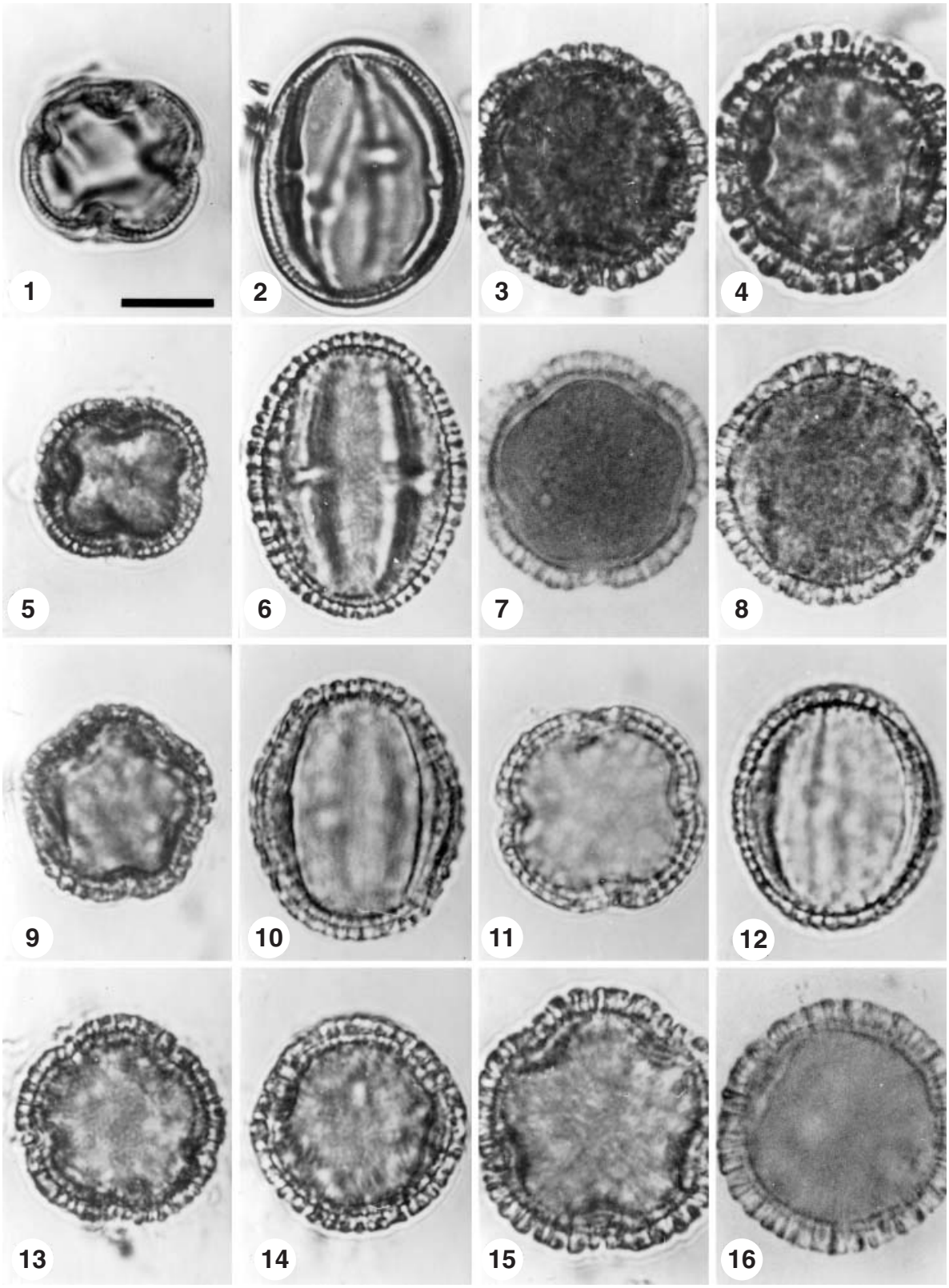
The pollen grains were obtained from anthers of herbarium specimens and acetolysed according to Erdtman (1952). Part of the acetolysed sample was mounted in glycerine jelly for light microscope analyses. The other part was dehydrated in 70% ethanol for 3 h, air-dried at room temperature, sputter-coated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

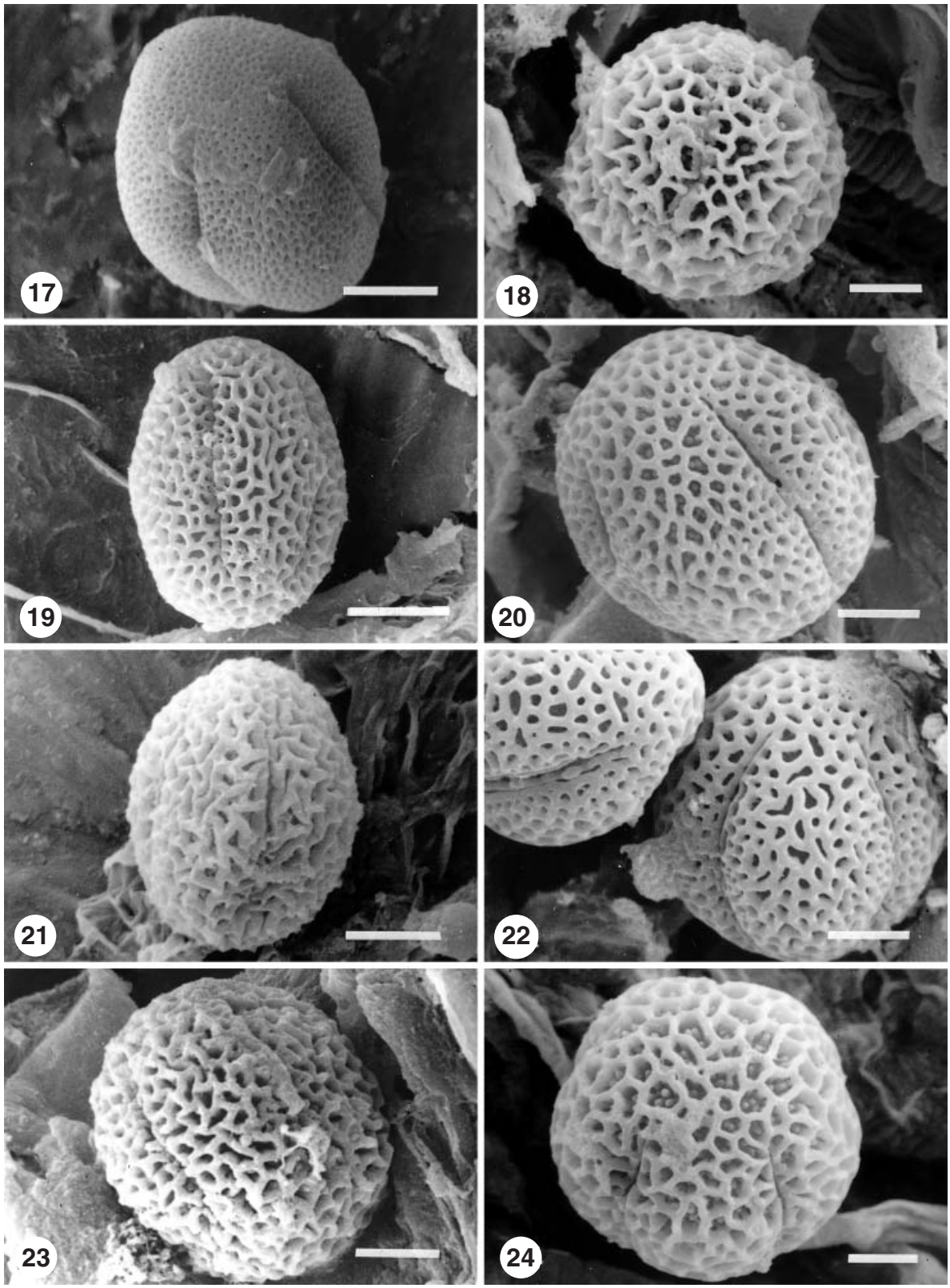
About 50 grains for each species were used for the pollen measurements. Measurements of polar length and equatorial width were taken using an eye piece micrometer adapted to a Zeiss microscope and the range, variance and standard deviation were noted. Subsequent description used the terminology of Punt *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. angustisimus*, *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. gladiatus*. Figs 13–14. *P. klotzschianus*. Figs 15–16. *P. scoparius*. Scale bars = 10 μm.





P. choretroides, *P. flagelliformis*, *P. gladiatus* 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 curvilineous muri as in *P. flagelliformis*, *P. goianensis* and *P. scoparius*, rectilineous muri as in *P. spartioides*, or simultaneously rectilineous and curvilineous muri as in *P. angustissimus*, *P. gladiatus* and *P. klotzschianus*. There are no margins around the colpi except in *P. gladiatus* (Fig. 22), which show very straight and psilate boundaries along the colpi.

In summary, the pollen type of *Phyllanthus* section *Choretroides* 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 rectilineous-reticulate ornamentation in *P. spartioides*.

Subtype 2 (Figs 17, 19, 20, 22–24) showing wider colpi without costae, circular endoaptertures and curvimurate or curvimurate-rectilineous reticulate ornamentation in *P. angustissimus*, *P. flagelliformis*, *P. gladiatus*, *P. goianensis*, *P. klotzschianius* and *P. scoparius*.

DISCUSSION

The pollen grains of the section *Choretropsis*, subsections *Choretropsis* 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. gladiatus*, *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 *Choretropsis*

Species	Polar diameter	Equatorial diameter	Shape	Number of colpi	Ornamentation
Subsection *Choretropsis*					
P. choretroides	29.0 + 1.3 (24.0–36.0)	21.9 + 0.6 (20.0–24.0)	subprolate	4	mrr
P. goianensis	27.4 + 1.2 (24.0–36.0)	24.7 + 1.2 (20.0–30.0)	prolate sphaeroidal	5	rc
P. spartioides	23.5 + 0.9 (24.0–32.0)	22.1 + 0.6 (20.0–26.0)	subprolate	4–5	rr
Subsection *Applanata*					
P. angustissimua	26.8 + 0.4 (26.0–28.0)	25.8 + 1.7 (28.0–36.0)	prolate sphaeroidal	5	rc/rr
P. flagelliformis	25.7 + 1.2 (28.0–30.0)	21.9 + 0.9 (18.0–26.0)	subprolate	5	rc
P. gladiatus	28.0 + 0.5 (26.0–30.0)	24.3 + 0.6 (22.0–26.0)	subprolate	4–5	rc/rr
P. klotzschianus	28.5 + 0.6 (26.0–32.0)	26.8 + 0.8 (28.0–36.0)	prolate sphaeroidal	4–5	rc/rr
P. scoparius	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 curvilineous muri; rr = reticulate with rectilineous muri.

Figures 17–24. Scanning electron microscope micrographs of *Phyllanthus* section *Choretropsis* 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. gladiatus*. 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; Rossignol *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 rectilineous, curvilineous 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 *Choreotropsis* 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 Phyllantheae 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 pinnatiform 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 pinnatiform compound phylloclade branchlets and reticulate ornamentation of pollen grains, and the section *Xylophylla*, endemic to the West Indies, with species showing bipinnatiform 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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