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Palynological survey of subtribe Pithecocteniinae (Bignonieae, Bignoniaceae)

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The pollen morphology of subtribe Pithecocteniinae was reviewed. Thirty species of the six genera currently recognized, namely *Amphilophium*, *Distictis*, *Distictella*, *Glaziovia*, *Haplolophium* and *Pithecoctenium*, were considered. All the species surveyed fell into one of the two pollen groups: (1) inaperturate, spheroid pollen; and (2) stephanocolpate, prolate pollen. The former group included the studied species of *Distictis*, *Distictella* and *Pithecoctenium*, the latter species of *Amphilophium*, *Glaziovia* and *Haplolophium*. The variation of exine sculpture and thickness did not show any taxonomic relationships. An argument for considering pollen features, together with other morphological characters, to elucidate monophyletic units within Pithecocteniinae is presented.

ADDITIONAL KEYWORDS: Amphilophium – Distictis – Distictella – Glaziovia – Haplolophium – palynology – Pithecoctenium – pollen morphology.

INTRODUCTION

Pollen morphology has been found to be highly conservative within the genera of Bignoniaceae and, as a result, is of high taxonomic value at the generic level in this family (Gentry & Tomb, 1979; Bove, 1993, 1994). In terms of pollen morphology, Bignonieae is the most diverse tribe in Bignoniaceae, presenting seven pollen types among its genera. Tricolpate pollen is widely represented within the genera of this tribe, being found in 22 of the 45 genera (Buurman, 1977; Gentry & Tomb, 1979).

Current knowledge of the pollen features in subtribe Pithecocteniinae Melch. comes from ten species studied in investigations of different palynological scope (Schumann, 1895; Urban, 1916; Suryakanta, 1973; Gentry & Tomb, 1979; Silvestre & Melhem, 1989; Bove, 1993, 1994): *Amphilophium paniculatum* H.B. & K., *Distictella magnoliifolia* (Kunth) Sandwith, *Distictis buccinatoria* (DC.) A.H.Gentry, *D. granulosa* Bureau & K.Schum, *Haplolophium bracteatum* Cham., *H. dusenianum* Kraenzl., *Glaziovia bauhinioides* Bureau ex Baill., *Pithecoctenium crucigerum* (L.) A.H.Gentry, *P. dolichoides* (Cham.) Bureau ex K.Schum. and *P. hatschbachii* A.H.Gentry.

In this work, we consider Pithecocteniinae to be comprised of the genera *Amphilophium*, *Distictis*, *Distictella*, *Glaziovia*, *Haplolophium* and *Pithecoctenium*, in contrast to the concept of the subtribe established by Melchior (1927). Our circumscription is based on the revision by Gentry (1973, 1974, 1976, 1993: 264–282), and the recent phylogenetic analysis of Bignoniacecae by Lohmann (2006). According to Gentry's series of floristic studies, the subtribe is composed of 43 species.

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Table 1. List of species and specimens studied

Species	Specimens
Amphilophium aschersonii Ule	Revilla 2045 (NY); Rimachi 967 (F)
A. blanchetii (DC.) Bureau & K. Schum.	Harley 21286 (SP); Harley *et al.* 18904 (NY)
A. ecuadorense A.H.Gentry	Díaz & Vázquez 2731 (NY); Boecke 2293 (NY)
A. paniculatum (L.) Kunth	García 151 (XAL); Castillo & Pedraza 2141 (XAL)
A. paniculatum var. *imatacense* A.H.Gentry	Lindeman *et al.* 11 (NY); Giulietti *et al.* 133 (HUEFS)
A. paniculatum var. *molle* (Schltdl. & Cham.) Standl.	Calzada *et al.* 6169 (XAL); Castillo & Golberg 2924 (XAL)
A. perbracteatum A.H.Gentry	Silva *et al.* 426 (HUEFS); Guedes 51578 (HUEFS)
A. sandwithii Fabris	Nee & Vargas 43424 (NY); Nee *et al.* 37394 (NY)
Distictella cuneifolia (DC.) Sandwith	Cid *et al.* 497 (NY); Amaral *et al.* 112323 (NY)
Da. dasytricha Sandwith	Maciel 4603 (NY)
Da. elongata (Vahl) Urb.	Leg 3095 (NY); Irwin *et al.* 12021 (NY)
Da. laevis (Sandwith) A.H.Gentry	Zarucchi *et al.* 2600 (NY); Anderson 10783 (NY)
Da. magnoliifolia (Kunth) Sandwith	Revilla 1790 (MEXU); Gentry 12969 (XAL)
Da. mansoana (DC.) Urb.	Montovani 1432 (XAL); Montovani 1376 (SP)
Da. monophylla Sandwith	Maguire *et al.* 41805 (NY); Hubber & Medina 5892 (NY)
Da. obovata Sandwith	Maguire *et al.* 43837 (NY); Steyermark 9380 (NY)
Da. parkeri (DC.) Sprague & Sandwith	Cowan & Sanderson 2168 (NY); Gleason 755 (NY)
Da. reticulata A.H.Gentry	Coelho & Nello 3940 (SP)
Distictis buccinatoria (DC.) A.H.Gentry	Burelo 138 (XAL); Miranda & Macias 2107 (MEXU)
D. granulosa Bureau & K.Schum.	Anderson *et al.* 35669 (RB); Lindeman 222 (NY)
D. lactiflora (Vahl) DC.	Britton & Cowell 1268 (NY); Zanoni *et al.* 34952 (NY)
D. laxiflora (DC.) Greenm.	Shilom 2140 (NY); Zolá *et al.* 355 (XAL)
D. pulverulenta (Sandwith) A.H.Gentry	Vicentini 1074 *et al.* (RB); Hopkins *et al.* 1551 (SPF)
D. staminea (Lam.) A.H.Gentry	Leonard & Leonard 12329 (NY); Alain & Liogier 22640 (NY)
Glaziovia bauhinioides Bureau ex Baill.	Herringer 2096 (SP); Kuhlmann s/n (SP)
Haplolophium bracteatum Cham.	Nadruz *et al.* 521 (NY); Brade 7045 (SP)
H. glaziovii (Bureau ex K. Schum.) A.H.Gentry	Ritz & Klein 18126 (NY); Hatschbach *et al.* 66533 (SPF).
H. rodriguesii A.H.Gentry	Sperling 5857 (NY); Sperling 5931 (NY)
Pithecoctenium crucigerum (L.) A.H.Gentry	Burelo 137 (UJAT); Luna & Zolá 304 (XAL).
P. cynanchoides DC.	Galleto 1024 (XAL); Pensiero & Morino 4288 (NY)
P. dolichoides (Cham.) Bureau ex K.Schum.	Gonçalves s/n (XAL); Silva 24 (HUEFS)
P. hatschbachii A.H.Gentry	Bernacci 25906 (UEC); Hatschbach 18505 (MBM)

We describe the pollen morphology in Pithecoctenioinae in order to provide additional information that can be used for taxonomic evaluation. Finally, we discuss the possible taxonomic implications of the morphological features found in the pollen of this group of species.

MATERIAL AND METHODS

Pollen of 30 species and three varieties of Pithecoctenioinae was studied (Table 1): six of the eight species of *Amphilophium*, ten of the 14 species of *Distictella*, six of the 12 species of *Distictis*, the only species of *Glaziovia*, three of the four species of *Haplolophium* and the four species of *Pithecoctenium*. In material borrowed from herbaria, there were no specimens with suitable flowers to obtain pollen for the remaining species.

Two samples per herbarium specimen were taken, one for light microscopy and one for observation by scanning electron microscopy (SEM). All pollen samples were subjected to standard acetolysis (Erdtman, 1952), except for the pollen of *Pithecoctenium* species, which was treated twice, as, after the first acetolysis, pollen grains were not sufficiently clear for analysis by light microscopy.

Processing for light microscopy included the immersion of acetolysed grains in a 2 : 1 glycerin and water mix, and further mounting under a glass coverslip sealed with glycerine jelly. From these samples, measurements of polar (PL) and equatorial (EL) dimensions, as well as ektexine (EK) and endexine (EN) thickness, were obtained. At least 25 pollen grains were measured for each species. A survey of the type and number of apertures, as well as exine ornamentation, was also based on these samples.

Samples of acetolysed grains for analysis by SEM were dehydrated through immersion in progressively higher concentrations of alcohol solutions.

Table 2. Pollen types in Pithecocteniinae

Inaperturate pollen, macro-reticulate	Inaperturate pollen micro-reticulate	Stephanocolpate pollen, macro-reticulate	Stephanocolpate pollen, micro-reticulate
Distictella cuneifolia	*Distictella laevis*	*Glaziovia bauhinioides*	*Amphilophium aschersonii*
Da. Dasytricha	*Da. parkeri*		*A. blanchetti*
Da. elongata			*A. ecuadorense*,
Da. magnoliifolia			*A. paniculatum*
Da. mansoana			*A. paniculatum* var. *molle*
Da. monophylla			*A. paniculatum* var. *imatacense*
Da. Obovata			*A. perbracteanum*
Da. reticulata			A. sandwithii
Distictis laxiflora	*Distictis buccinatoria*	*Haplolophium glaziovii*	*H. rodriguesii*
D. pulverulenta	*D. granulosa*		*H. bracteatum*
D. staminea	*D. lactiflora*		*H. nunezii*
Pithecoctenium crucigerum	*P. hatschbachii*		
P. cynanchoides			
P. dolichoides			

From these samples, high-resolution details of apertures and exine ornamentation were obtained.

The description of the pollen grain surface is based on the work of Bove (1994), in which the ornamentation composed of a reticulum in which the unit cells correspond to 10% or more of the longest axis is called macro-reticulate, and a surface with unit cells of the reticulum up to 2% of that axis is considered to be micro-reticulate. The rest of the terms used here for pollen descriptions were taken from Halbritter *et al.* (2005) and the studies of Bignoniaceae by Gentry & Tomb (1979) and Bove (1993, 1994).

RESULTS

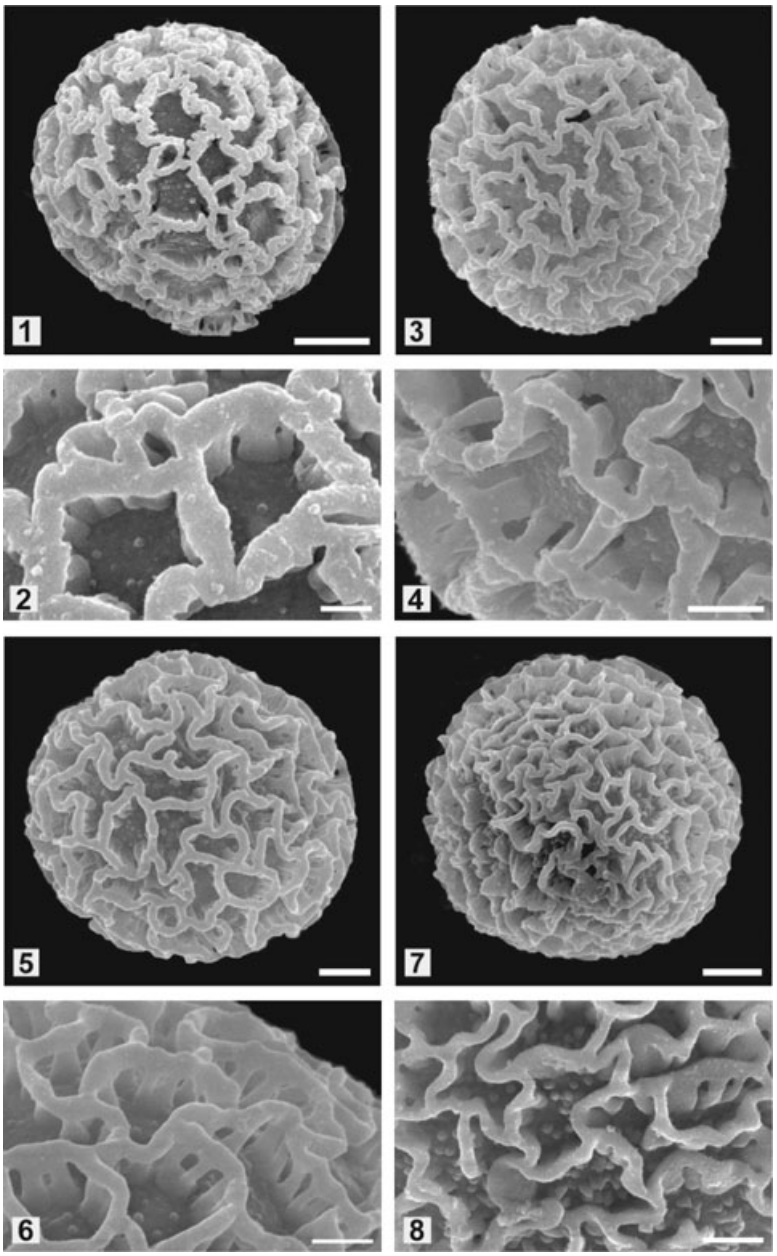
Two basic pollen types were distinguished in the studied species: (1) spheroid, inaperturate grains; and (2) prolate, 7–10-aperturate (stephanocolpate) grains. Taking into account the size of the reticulum, both types can be divided again into two groups each, namely micro-reticulate and macro-reticulate (Table 2).

Inaperturate pollen is present in all species of *Distictella*, *Distictis* and *Pithecoctenium* surveyed (Figs 1–8). A macro-reticulate pollen surface in this group is found in *Distictella cuneifolia*, *Da. dasytricha*, *Da. elongata*, *Da. magnoliifolia*, *Da. mansoana*, *Da. monophylla*, *Da. obovata*, *Da. reticulata*, *Distictis laxiflora*, *D. pulverulenta*, *D. staminea*, *Pithecoctenium crucigerum*, *P. cynanchoides* and *P. dolichoides*. A micro-reticulate surface is present in *Da. laevis*, *Da. parkeri, D. buccinatoria*, *D. granulosa*, *D. lactiflora* and *P. hatschbachii*.

Pollen grains in all the species mentioned above are radially symmetric, apolar, spheroid, with granules within the lumina of the reticulum, semitectate and with simple-baculate waved muri. Morphometric features show a wide variation among species (Table 3; Fig. 9); the smallest sized pollen grains are found in *D. staminea* (45.1 μm), with a greater diameter found in *Da. cuneifolia* and *Da. reticulata* at 71.4 μm and 70.3 μm, respectively. The thicknesses of the columns and tectum are, in most species, less than 1 μm, but, in *Da. magnoliifolia* and *Da. parkeri*, these structures can reach 2 μm, and, in *Da. cuneifolia*, they can even be 3–4 μm thick.

Stephanocolpate pollen is shown by all species of *Amphilophium* (Figs 10–18), *Glaziovia* and *Haplolophium* (Figs 19–27). A macro-reticulate pollen surface is found in *Glaziovia bauhinioides* and *Haplolophium glaziovii*. However, a micro-reticulate surface is present in *Amphilophium aschersonii*, *A. blanchetii*, *A. ecuadorense*, the three varieties of *A. paniculatum*, *A. perbracteatum*, *A. sandwithii*, *Haplolophium bracteatum* and *H. rodriguesii*.

Pollen in the group of species mentioned above is radially symmetric, prolate, seven- to ten-colpate, with granules within the lumina, and simple-baculate waved muri. Considering the average measurements of the pollen in these species (Table 4; Figs 9, 28), *H. glaziovii* had the largest pollen grains (82.4×81 μm) and *H. rodriguesii* the smallest grains (49.58×71.9 μm). Half of the studied species had columns and tectum up to 2 μm thick (*A. paniculatum*, *A. perbracteatum*, *G. bauhinioides*, *H. glaziovii* and *H. rodriguesii*), and up to 1 μm thick in the other half of the species.



Figures 1–8. Exine sculpturing of inaperturate pollen in Pithecocteniinae. Figs 1, 2. *Distictis lactiflora*. Fig. 1. ×1900; scale bar, 10 μm. Fig. 2. ×3500; scale bar, 2 μm. Figs 3, 4. *Distictella elongata*. Fig. 3. ×1300; scale bar, 10 μm. Fig. 4. ×5000; scale bar, 5 μm. Figs 5, 6. *Distictella parkerii*. Fig. 5. ×1300; scale bar, 10 μm. Fig. 6, ×4000; scale bar, 5 μm. Figs 7, 8. *Pithecoctenium hatschbachii*. Fig. 7. ×1500; scale bar, 10 μm. Fig. 8. ×4000; scale bar, 5 μm.

Pollen and systematics of the Pithecocteniinae

As stated by Gentry & Tomb (1979), pollen features can be assessed in a taxonomic context as one of several indicators of evolutionary relationships. Based on our findings, in terms of pollen morphology, we can recognize two main groups within the Pithecocteniinae: one with inaperturate, spheroid pollen, and the other with stephanocolpate, prolate pollen. As far as the sample surveyed showed, these did not interchange, i.e. all species of any genus analysed had one or other of these two pollen conditions. Using the current best phylogenetic hypothesis for Bignonieae (Lohmann, 2006) to trace pollen types, it is clear that both inaperturate and stephanocolpate types found in Pithecocteniinae have evolved independently several times within the tribe. However, only one pollen type is found in many

Table 3. Pollen measurements (μm) for species with inaperturate, spheroid pollen type (standard deviation in parentheses)

Species	Diameter	Ektexine	Endexine
Distictella cuneifolia	71.4 (3.7)	5.8 (0.5)	1 (0)
Da. dasytricha	59.6 (2.9)	5.2 (0.7)	1 (0)
Da. elongata	65.3 (4.9)	5.5 (5)	1 (0)
Da. laevis	65.2 (6.8)	4.4 (0.8)	1 (0)
Da. parkeri	68.5 (4.7)	5.1 (0.8)	1 (0)
Da. magnoliifolia	61.4 (4)	5.3 (0.7)	1 (0)
Da. mansoana	62.9 (6.9)	4.6 (0.5)	1 (0)
Da. monophylla	66.3 (9.5)	4.4 (0.5)	1 (0)
Da. obovata	64.9 (4.2)	5.6 (0.5)	1 (0)
Da. reticulata	70.3 (4.9)	5.6 (0.5)	1 (0)
Distictis buccinatoria	54.7 (3.7)	4.2 (0.6)	1 (0)
D. granulosa	66.7 (6)	5.2 (0.9)	1.7 (0.5)
D. lactiflora	56.2 (4.3)	4.4 (0.5)	1 (0)
D. laxiflora	51.9 (2.0)	3.9 (0.4)	1 (0)
D. pulverulenta	59.5 (5.3)	4.8 (0)	1.6 (0.5)
D. staminea	45.1 (5.5)	3.6 (0.5)	1 (0)
Pithecoctenium crucigerum	67.6 (5.8)	4.9 (0.5)	1 (0)
P. cynanchoides	61.1 (6)	4.7 (0.5)	1 (0)
P. dolichoides	61.4 (8.7)	4.5 (0.6)	1 (0)
P. hatschbachii	67.9 (7.8)	5.2 (0.4)	1 (0)

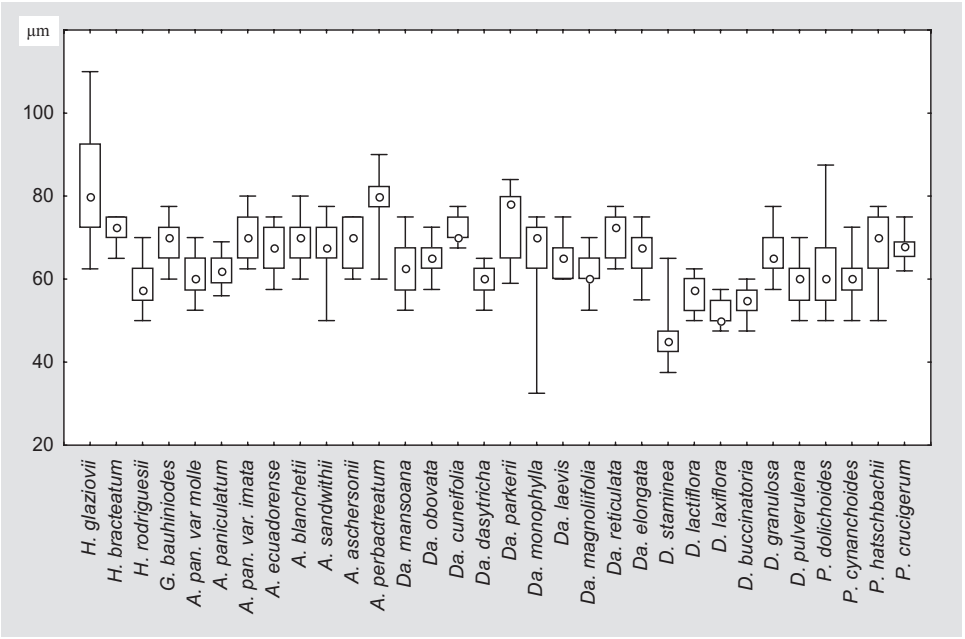
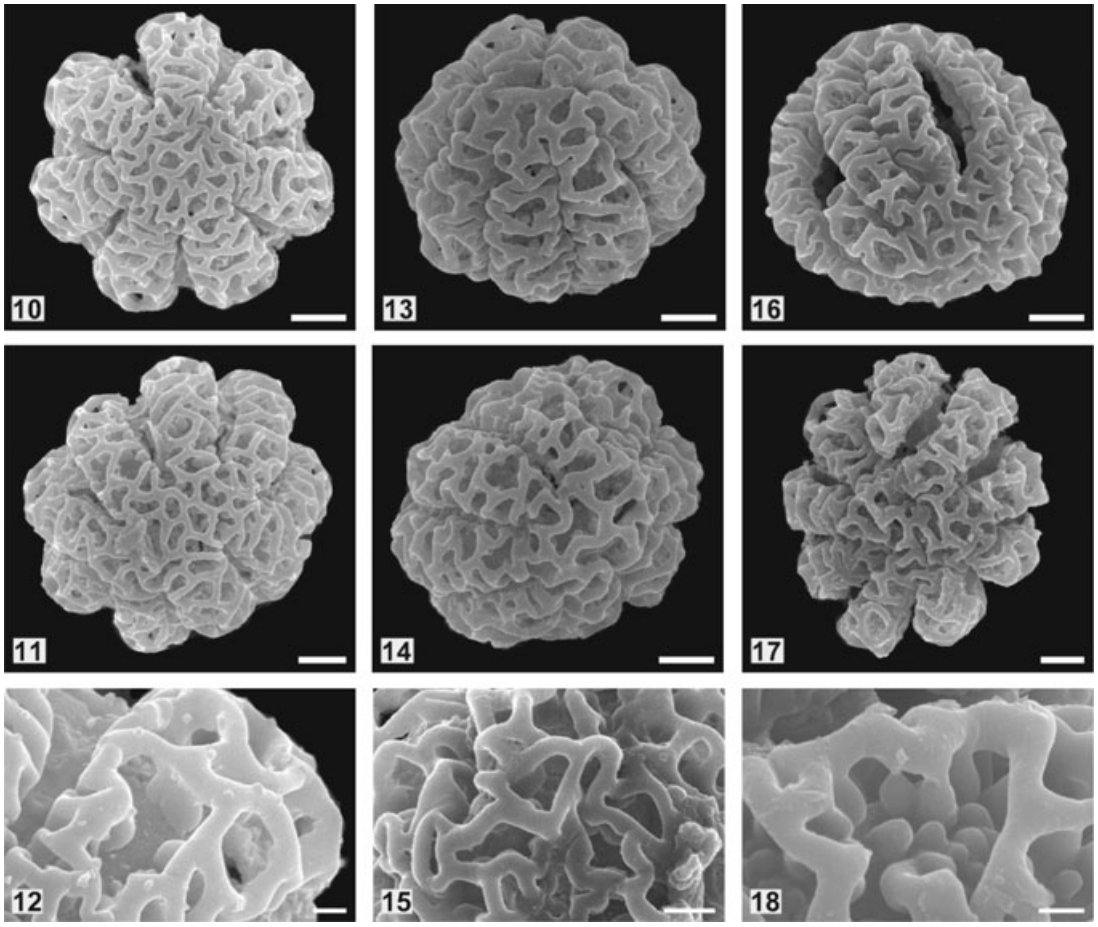


Figure 9. Equatorial diameter dimensions of pollen in Pithecocteniinae.

of the 21 species groups (genera) recognized by Lohmann (2006). Thus, in the sister clade of Pithecocteniinae, we find *Anemopegma*, *Mansoa* and *Pyrostegia* with stephanocolpate, perisyncolpate and tricolpate pollen types, respectively. Except for *Potamoganus* and *Roentgenia*, most of the so-called 'mimetic clade' in the sister group has inaperturate pollen (Lohmann, 2006). In the case of Pithecocteniinae, the clade formed by *Amphilophium*, *Glaziovia* and *Haplolophium* has stephanocolpate pollen. Genera with inaperturate pollen do not appear to constitute a monophyletic group. However, whether or not *Distictis*



Figures 10–18. Exine sculpturing of stephanocolpate pollen in Pithecocteniinae. Figs 10–12. *Amphilophium paniculatum* var. *molle*. Fig. 10. ×1500; scale bar, 10 μm. Fig. 11. ×1300; scale bar, 10 μm. Fig. 12. ×6000; scale bar, 3 μm. Figs 13–15. *A. paniculatum* var. *paniculatum*. Figs 13, 14. ×1500; scale bar, 10 μm. Fig. 15. ×3700; scale bar, 5 μm. Figs 16–18. *A. ecuadorense*. Fig. 16. ×1500; scale bar, 10 μm. Fig. 17. ×1200; scale bar, 10 μm. Fig. 18. ×8000; scale bar, 2 μm.

and *Pithecoctenium* conform to a monophyletic unit does not change the view of character evolution in this case: stephanocolpate pollen derives from the inaperturate type in Pithecocteniinae.

In addition to the pollen type, *Amphilophium*, *Glaziovia* and *Haplolophium* share other characters, such as definitely lobed calices, seed wings glabrous and tracheary elements of the wings without secondary thickenings. However, although *Distictella*, *Distictis* and *Pithecoctenium* do not form a monophyletic group, they share truncate to denticulate calices, puberulent seed wings and tracheary elements of the wings with spiral secondary thickenings. In addition, *Distictella* is distinguished by the presence of cylindrical stems, and *Pithecoctenium* by the presence of tendrils successively several times trichotomic.

In the molecular phylogenetic study of Bignonieae, Lohmann (2006) obtained a strongly supported clade equivalent to the group called, in this article, Pithecocteniinae. Beyond this point, except for the *Distictella* species, her analysis did not identify monophyletic groups corresponding to the genera currently included in the subtribe. Considering this, and putative morphological synapomorphies, she suggested to lump all the species of the subtribe into a single genus. We believe, however, that morphology, such as pollen features, can still provide additional characters to evaluate possible monophyletic groups within this aggregate of species, which might support some of the genera currently included in Pithecocteniinae.

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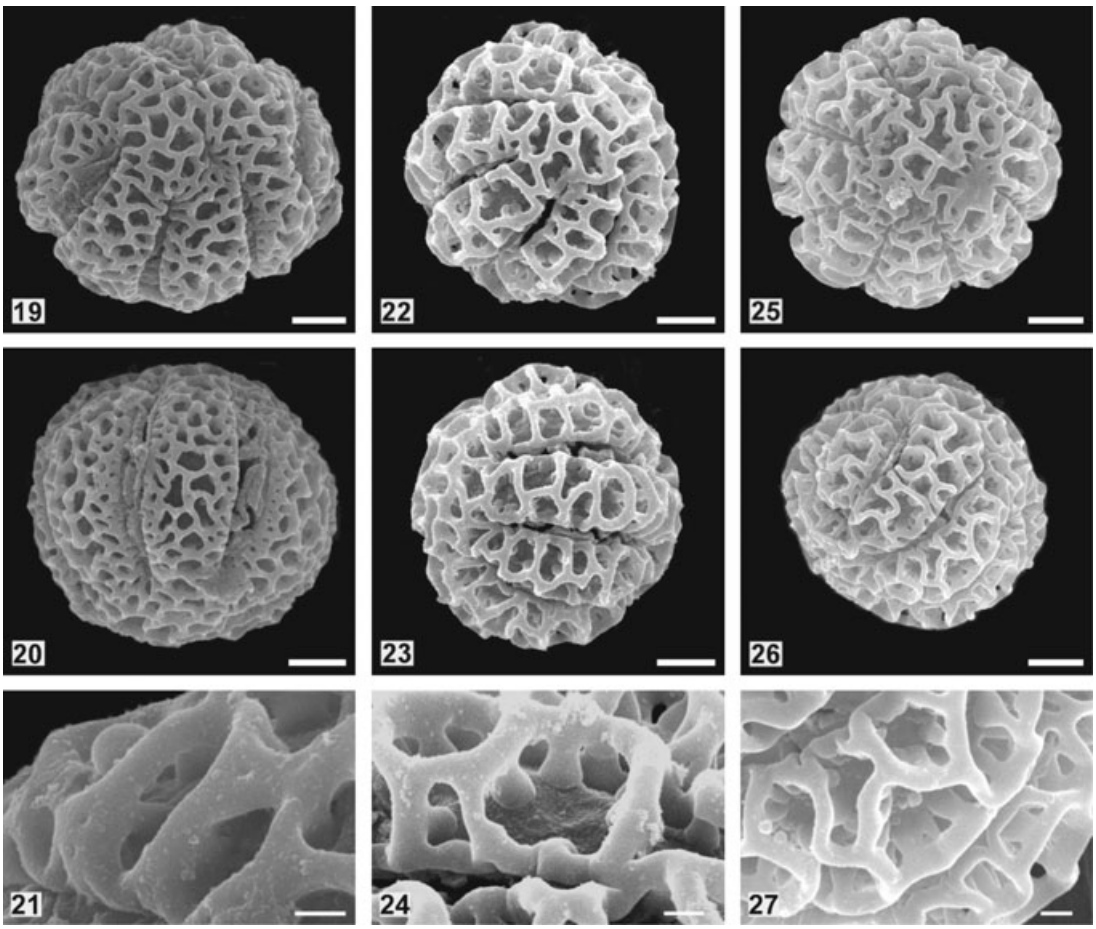

Figures 19–27. Exine sculpturing of stephanocolpate pollen in Pithecocteniinae. Figs 19–21. *Glaziovia bauhinioides*. Figs 19, 20. ×1500; scale bar, 10 μm. Fig. 21. ×9000; scale bar, 2 μm. Figs 22–24. *Haplolophium rodriguesii*. Figs 22, 23. ×1600; scale bar, 10 μm. Fig. 24. ×7000; scale bar, 2 μm. Figs 25–27. *H. glaziovii*. Figs 25, 26. ×1500; scale bar, 10 μm. Fig. 27. ×9000; scale bar, 2 μm.

Table 4. Pollen measurements (μm) for species with stephanocolpate, prolate pollen type (standard deviation in parentheses)

Species	Polar length	Equatorial length	Ektexine	Endexine
Amphilophium aschersonii	64.3 (4. 1)	68.3 (5.6)	4.9 (0.7)	1.2 (0.4)
A. blanchetii	52.8 (4.3)	68.9 (5.9)	5.6 (0.9)	1 (0)
A. ecuadorense	53.3 (4)	67.5 (5.8)	5 (0.9)	1 (0)
A. paniculatum var. paniculatum	59.5 (5.5)	60.1 (3.7)	5.1 (0.7)	1 (0)
A. paniculatum var. imatacense	54.7 (3.9)	69.8 (6.2)	4.8 (0.8)	1 (0)
A. paniculatum var. molle	53.5 (4.4)	61.4 (5.2)	5.2 (0.5)	1 (0)
A. perbracteatum	70.6 (4.5)	78.8 (7.1)	3.9 (0.7)	1 (0)
A. sandwithii	63.9 (3.9)	68.6 (6.1)	5.3 (0.2)	1.2 (0.4)
Glaziovia bauhinioides	57 (4.9)	68.9 (5.1)	5.2 (0.5)	1.3 (0.5)
Haplolophium bracteatum	59.2 (6.1)	82.6 (5.3)	7.6 (0.5)	1.12 (0.3)
H. glaziovii	81 (4.6)	82.4 (12.8)	5.3 (0.5)	1.3 (0.5)
H. rodriguesii	49.6 (3.7)	71.9 (3.5)	4.8 (0.37)	1 (0)

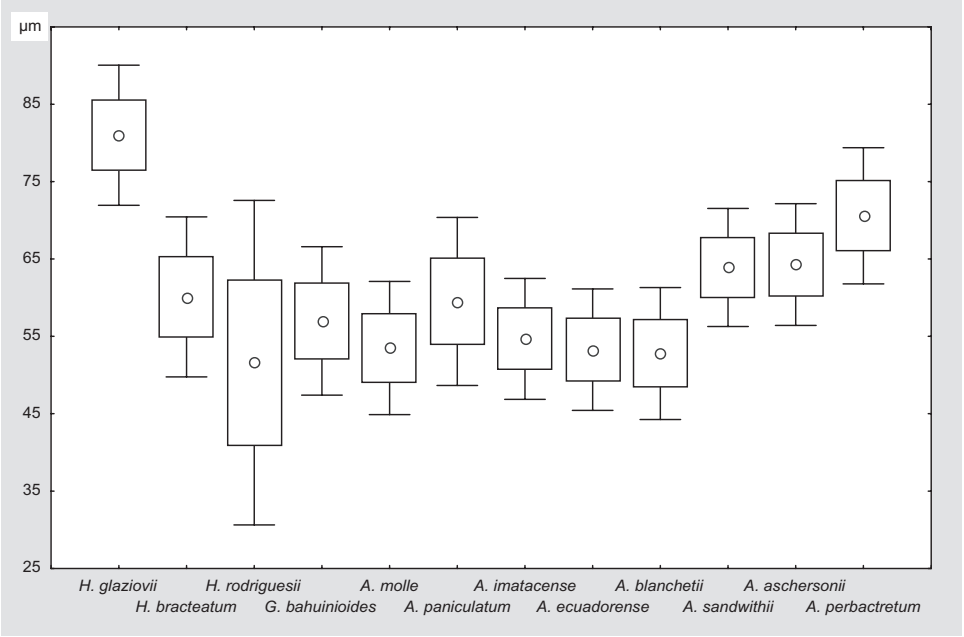

Figure 28. Polar diameter dimensions of prolate pollen in Pithecocteniinae.

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