

Morphological cladistic analysis of *Pseudobombax* Dugand (Malvaceae, Bombacoideae) and allied genera

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ABSTRACT – (Morphological cladistic analysis of *Pseudobombax* Dugand (Malvaceae, Bombacoideae) and allied genera). *Pseudobombax* Dugand belongs to the family Malvaceae subfamily Bombacoideae and aggregates 29 species restricted to the Neotropics. A morphological cladistic analysis of *Pseudobombax* and allied genera was carried out to test the monophyly of the genus and to provide hypotheses on its phylogeny. Parsimony analyses were based on 40 morphological characters and 28 species, 14 belonging to *Pseudobombax* and 14 to other species of Bombacoideae, Matisieae (Malvoideae) and Ochromeae. Nine most parsimonious trees (144 steps, ci 0.40, ri 0.67) were produced when 10 multistate characters were taken as ordered while only two most parsimonious trees (139 steps, ci 0.41, ri 0.67) were obtained when all characters were considered as unordered. *Pseudobombax* monophyly had moderate bootstrap support, appearing as sister to a clade composed of the genera *Bombacopsis* Pittier and *Pachira* Aubl., or to the genus *Bombax* L. according to the analysis. The petiole widened at the apex and the leaflets not jointed to the petiole are probably synapomorphies of *Pseudobombax*. Three main clades were found in the genus: one characterised by petiolulated leaflets and 5-angular fruits, the other by pubescent leaves and calyx, and the other by reduction of the number of leaflets. The latter includes species endemic to the Brazilian semi-arid region also characterised by the absence of phalanges in the androecium. Interspecific affinities in *Pseudobombax* as well as the morphological evolution in Bombacoideae are discussed.

Key words - biogeography, evolution, morphology, phylogeny, taxonomy

RESUMO – (Análise cladística morfológica de *Pseudobombax* Dugand (Malvaceae, Bombacoideae) e gêneros relacionados). O gênero *Pseudobombax* Dugand pertence à família Malvaceae, subfamília Bombacoideae, e compreende 29 espécies com distribuição restrita à região Neotropical. Realizou-se uma análise cladística morfológica de *Pseudobombax* e gêneros relacionados a fim de testar seu monofiletismo e elaborar hipóteses sobre sua filogenia. As análises de parcimônia foram baseadas em 40 caracteres e 28 espécies, sendo 14 de *Pseudobombax* e as demais pertencentes a Bombacoideae, Matisieae (Malvoideae) e Ochromeae. Foram obtidas nove árvores mais parcimoniosas (144 passos, ci 0,40, ri 0,67) quando 10 caracteres multiestado foram considerados como ordenados e apenas duas árvores mais parcimoniosas (139 passos, ci 0,41, ri 0,67) quando todos os caracteres foram considerados não ordenados. A monofilia de *Pseudobombax* foi moderadamente sustentada com base na análise de *bootstrap*, aparecendo como grupo-irmão de um clado formado pelos gêneros *Bombacopsis* Pittier e *Pachira* Aubl. ou do gênero *Bombax* L. de acordo com a análise. As prováveis sinapomorfias de *Pseudobombax* são o ápice do pecíolo dilatado e os folíolos não articulados com o pecíolo. Foram encontrados três cladogramas principais dentro do gênero: um caracterizado por folíolos peciolulados e frutos 5-angulares, outro caracterizado pela presença de folhas e cálice pubescentes e outro pela redução do número de folíolos. Este último inclui espécies endêmicas da região semiárida do nordeste do Brasil caracterizado também pela ausência de falanges no androceu. Apresenta-se uma discussão sobre as afinidades interespecíficas em *Pseudobombax* e sobre a evolução morfológica em Bombacoideae.

Palavras-chave - biogeografia, evolução, filogenia, morfologia, taxonomia

Introduction

Pseudobombax Dugand (Malvaceae, Bombacoideae) comprises 29 species distributed in the Neotropics (Robyns 1963, Fernández-Alonso 2001, Carvalho-Sobrinho & Queiroz 2010, IPNI 2010). It occurs in

different vegetation types, especially those associated with seasonal climate such as seasonally dry forests and Savanna. The genus is diagnosed by the combination of the trunks with vertical greenish strips, digitately compound and pulvinate leaves clustered in the apex of the branches, leaflets not jointed to the petiole, glandular receptacle, filaments joined in a tube and capsules with abundant kapok (Robyns 1963).

Pseudobombax was segregated from *Bombax* L. by Dugand (1943). He considered *Bombax* an American genus characterised by leaflets jointed to the petiole,

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flowers with filaments connate in a tube and calyx caducous in fruit that is a 5-valvate capsule with or without sparse kapok. Species with leaflets not jointed to the petiole, fruits with persistent calyx and copious kapok were thus assigned to his new genus, *Pseudobombax*. Robyns (1963) and Nicolson (1979) had a different concept of *Bombax*: they considered *Bombax* to be an Old World genus and transferred the American species to *Bombacopsis* Pittier and *Pseudobombax*. Hence, they recognised *Pseudobombax* as a New World genus distinct from *Bombacopsis*.

In traditional taxonomic systems, *Pseudobombax* was included in the family Bombacaceae (e.g. Cronquist 1981). However, phylogenetic studies based on morphological (Judd & Manchester 1997) and molecular data (Alverson *et al.* 1999, Baum *et al.* 2004) did not support the monophyly of Sterculiaceae, Tiliaceae and Bombacaceae, which are now classified into an expanded Malvaceae (Bayer *et al.* 1999, Nyffeler *et al.* 2005). Most of the traditional genera of “Bombacaceae” appears in a clade now classified as subfamily Bombacoideae, sister to subfamily Malvoideae. Together, these two subfamilies form the large Malvaceae clade defined by monotheccate anthers (Baum *et al.* 1998). Genera of tribe Durioneae (*Durio* Adans. and *Neesia* Blume) were resolved as sister to genera of the tribe Helictereeae, unrelated to Malvaceae clade (Alverson *et al.* 1999). Genera of the tribe Matisieae (*Matisia* Bonpl., *Phragmotheca* Cuatrec. and *Quararibea* Aubl.) were resolved as part of subfamily Malvoideae (Baum *et al.* 2004, Nyffeler *et al.* 2005).

Species assigned to *Pseudobombax* and allied genera have been classified in the Bombacaceae tribe Adansonieae (Benth. & Hooker 1862, Schumann 1886, 1895, van den Brink 1924, Hutchinson 1967). Van den Brink (1924) and Robyns (1963) recognised a group of closely related genera composed by *Bombax*, *Bombacopsis*, *Eriotheca* Schott. & Endl., *Pachira* Aubl., *Pseudobombax*, *Rhodognaphalon* (Ulbr.) Roberty and *Rhodognaphalopsis* A. Robyns, which they called the *Bombax*-group. These latter two genera are currently treated as synonyms of *Pachira* (Alverson 1994, Alverson & Mori 2002, Fernández-Alonso 1998, 2003, Steyermark & Stevens 1998). Moreover, the distinction between *Pachira* and *Bombacopsis* has been questioned and they were treated as congeneric by Alverson (1994), Alverson & Steyermark (1997) and Fernández-Alonso (1998).

Baum *et al.* (2004) and Nyffeler *et al.* (2005) supported the monophyly of the Adansonieae, although only four genera were sampled in each analysis: *Adansonia*

L. (two species), *Bombax* (two), *Ceiba* Mill. (two) and *Pachira* (one). In Alverson *et al.* (1999), *Eriotheca ruizii* (K. Schum.) A. Robyns and *Pseudobombax ellipticum* (H. B. K.) Dugand were included. Hence, the monophyly of *Pseudobombax* was not tested yet, its position in *Bombax*-group was not established and there is no phylogenetic hypothesis to outline the evolution and biogeography of the genus.

This work aims to investigate the phylogeny of *Pseudobombax* in order to answer the following questions: is *Pseudobombax* monophyletic? What is its putative sister group? Is the current classification supported by phylogenetic data? What are the main lines of morphological evolution in the genus? Is there correlation between diversification in the genus and occupation of different Neotropical vegetation types?

Material and methods

Taxon sampling – We included 14 species of *Pseudobombax* in the ingroup, representing the widest morphological variation and geographical range in the genus (table 1), including species from Seasonally Dry Tropical Forests (8 out of 13 species), Savanna (3/7) and Tropical Rain Forests (3/9). The morphological variation sampled included the amplitude in number of leaflets (one in *P. simplicifolium* to 10 in *P. marginatum*), indument of leaflets (glabrous in *P. campestre* to tomentose in *P. tomentosum*), length of flower (6 cm in *P. minimum* to 22 cm in *P. maximum*), organization of androecium in phalanges (absent in *P. calcicola* and present in *P. palmeri*), indument of staminal tube (glabrous in *P. grandiflorum* to pubescent in *P. millei*), number of stamens (180 in *P. campestre* to 1,200 in *P. septenatum*), ratio length/width of fruit (2.2:1 in *P. septenatum* to 8:1 in *P. calcicola*). It was avoided the inclusion of species that are diagnosed based on characters that show great phenotypic plasticity aiming to prevent noise in the analysis.

Eleven species from other genera of the *Bombax*-group and tribe Adansonieae were also taken as part of the ingroup with the aim of establishing a better supported hypothesis of sister group relationships. These included species of the genera *Adansonia* (one species), *Bombacopsis* (two), *Bombax* (one), *Cavanillesia* Ruiz & Pav. (one), *Ceiba* (two), *Eriotheca* (three) and *Pachira* (one). The placement of *Cavanillesia* is not well established, although Baum *et al.* (2004) considered that it should be included in Bombacoideae, but this assumption was not tested.

The outgroup, based on Baum *et al.* (2004), comprised (i) *Scleronema* Benth., supported as part of a sister group of the Adansonieae; (ii) *Matisia*, a representative of Matisieae formerly included in “Bombacaceae” and supported in a basal position in the Malvoideae; and (iii) *Ochroma* Sw., which is

Table 1. Taxa included in the cladistic analysis, their respective voucher and/or bibliographic source and geographical range.

Taxon	Voucher/Bibliographic source	Geographical range
<i>Adansonia digitata</i> L.	<i>Carvalho-Sobrinho 291</i>	African continent (Savanna)
<i>Bombacopsis retusa</i> (Mart. & Zucc.) A. Robyns	<i>Queiroz 4812</i>	Northeastern Brazil (Seasonally Dry Tropical Forests)
<i>Bombacopsis stenopetala</i> (Casar.) A. Robyns	<i>Carvalho-Sobrinho 251</i>	Northeastern Brazil (Seasonally Dry Tropical Forests)
<i>Bombax ceiba</i> L.	Robyns (1963)	Asian continent (Seasonally Dry and Rain Tropical Forests)
<i>Cavanillesia arborea</i> K. Schum.	<i>Carvalho-Sobrinho 475, Queiroz 1035, Leite 301</i>	Bolivia, Brazil and Peru (Seasonally Dry Tropical Forests)
<i>Ceiba glaziovii</i> (Kuntze) K. Schum.	<i>Queiroz 997, Gibbs & Semir (2003)</i>	Northeastern Brazil (Seasonally Dry Tropical Forests)
<i>Ceiba pentandra</i> (L.) Gaertn.	<i>Carvalho-Sobrinho 116, Gibbs & Semir (2003)</i>	African and American continent (Tropical Rain Forests)
<i>Eriotheca crenulicalyx</i> A. Robyns	Martins (1993)	Brazil (Atlantic Rain Forest)
<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns	<i>Carvalho 4007, Robyns (1963)</i>	Brazilian Central Plateau (Savanna)
<i>Eriotheca longipedicellata</i> (Ducke) A. Robyns	Robyns (1963)	Brazil (Amazonian Tropical Rain Forests)
<i>Matisia ochrocalyx</i> K. Schum.	Alverson & Steyermark (1997), Alverson & Mori (2002)	Costa Rica to Northern Brazil (Tropical Rain Forests)
<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urb.	Alverson & Steyermark (1997), Cascante-Marin (1997)	Mexico to Venezuela and Bolivia (Tropical Rain Forests)
<i>Pachira aquatica</i> Aubl.	<i>Mattos-Silva 3139, Robyns (1963)</i>	South Mexico to South Ecuador and Peru (Tropical Rain Forests)
<i>Pseudobombax calcicola</i> Carv.-Sobr. & L. P. Queiroz	<i>Andrade-Lima 75-8152, Carvalho- Sobrinho 485, Carvalho-Sobrinho 573</i>	Northeastern Brazil (Seasonally Dry Tropical Forests)
<i>Pseudobombax campestre</i> (Mart. & Zucc.) A. Robyns	<i>Ganev 3489, Giuliotti 1389</i>	Northeastern Brazil (Seasonally Dry Tropical Forests)
<i>Pseudobombax grandiflorum</i> (Cav.) A. Robyns	<i>Thomas 9472, Carvalho 871</i>	Southeastern and Northeastern Brazil (Atlantic Rain Forest)
<i>Pseudobombax guayasense</i> A. Robyns	<i>Asplund 17588, Robyns (1963)</i>	Ecuador (Seasonally Dry Tropical Forests)
<i>Pseudobombax longiflorum</i> (Mart. & Zucc.) A. Robyns	<i>Amorim 572, Carvalho-Sobrinho 577</i>	Bolivia, Brazil, Paraguay (Savanna)
<i>Pseudobombax marginatum</i> (A. St.- Hil., Juss. & Cambess.) A. Robyns	<i>Queiroz 3928, Carvalho-Sobrinho 580</i>	Bolivia, Brazil, Paraguay, Peru (Seasonally Dry Tropical Forests, Savanna)
<i>Pseudobombax maximum</i> A. Robyns	<i>Palmer 134, Robyns (1963)</i>	Colombia and Venezuela (Seasonally Dry Tropical Forests)
<i>Pseudobombax millei</i> (Standl.) A. Robyns	<i>Pittier 8719, Robyns (1963)</i>	Ecuador (Tropical Rain Forests)
<i>Pseudobombax minimum</i> Carv.-Sobr. & L. P. Queiroz	<i>Melo 2763, Carvalho-Sobrinho 413, Forzza 1591</i>	Brazilian Central Plateau (Savanna)
<i>Pseudobombax palmeri</i> (S. Watson) Dugand	Robyns (1963)	Mexico (Seasonally Dry Tropical Forests and Riparian Forests)
<i>Pseudobombax parvifolium</i> Carv.- Sobr. & L. P. Queiroz	<i>Queiroz 7343, Carvalho-Sobrinho 572, Carvalho-Sobrinho 751</i>	Northeastern Brazil (Seasonally Dry Tropical Forests)
<i>Pseudobombax septenatum</i> (Jacq.) Dugand	Robyns (1963)	Nicaragua to Peru and Northern Brazil (Tropical Rain Forests)
<i>Pseudobombax simplicifolium</i> A. Robyns	<i>Andrade-Lima 1210, Moss s.n. (RB 103602)</i>	Northeastern Brazil (Seasonally Dry Tropical Forests)
<i>Pseudobombax tomentosum</i> (Mart. & Zucc.) A. Robyns	<i>França 3629, Carvalho-Sobrinho 481</i>	Brazil and Paraguay (Savanna)
<i>Scleronema micranthum</i> (Ducke) Ducke	Alverson & Steyermark (1997), Esteves (2005)	Venezuela and Northern Brazil (Tropical Rain Forests)

supported as part of the Ochromeae, a small clade sister to the remaining Malvatheca (Bombacoideae + Malvoideae). Their inclusion in the analysis provided a rooting point for the trees outside the Adansonieae.

Selection and coding of characters – Morphological characters (table 2) are based on herbarium specimens and

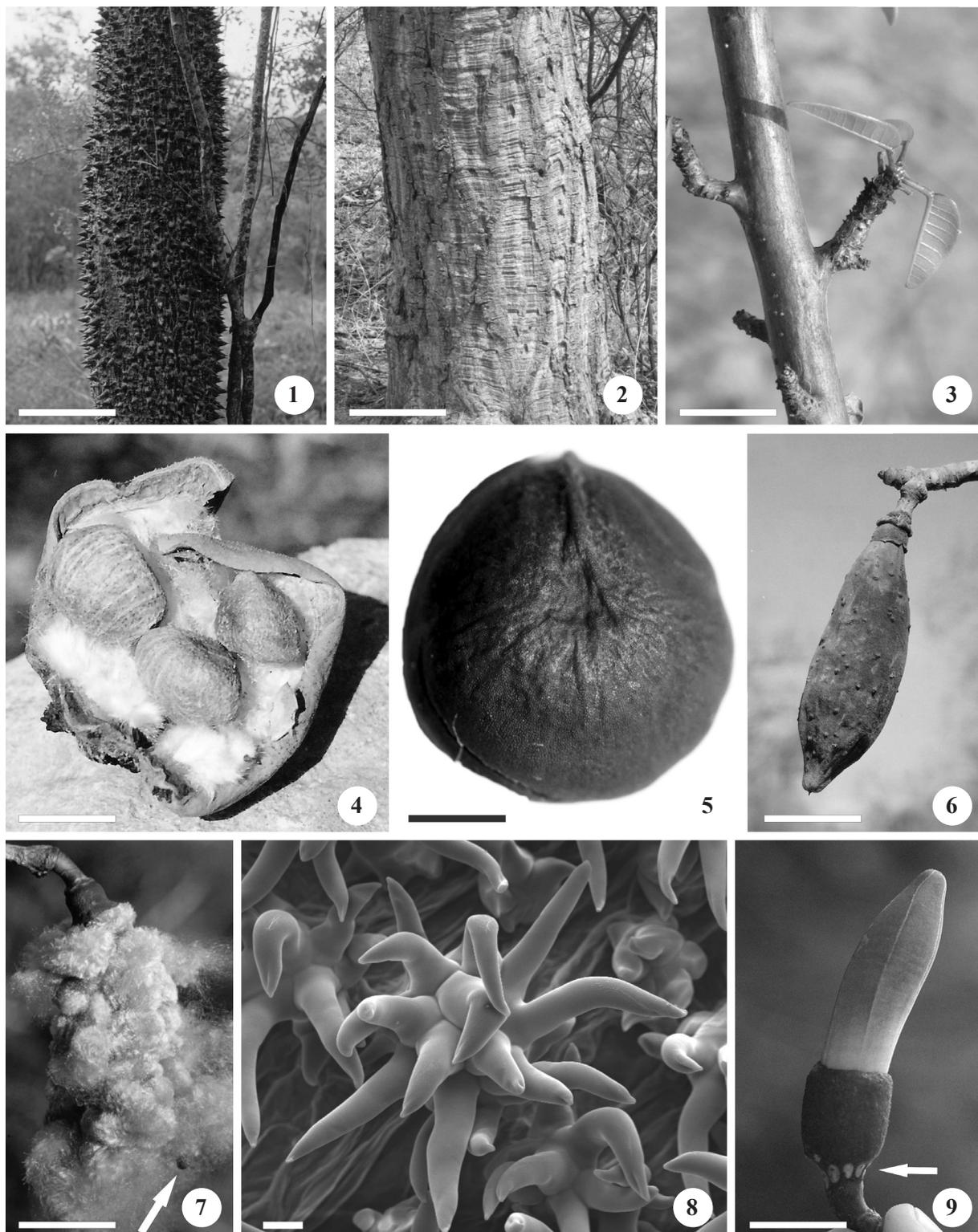
complemented by data from the following sources: Robyns (1963, 1964), Alverson & Steyermark (1997), Cascante-Marin (1997), Fernandez-Alonso (2001), Alverson & Mori (2002) and Esteves (2005). Figures 1-9 illustrate some of these characters.

Forty morphological characters were selected. Characters of plain shape (outline) were converted for

Table 2. Morphological characters utilized in the cladistic analysis of *Pseudobombax* and allied genera.

Characters	Character states
1. Habit	[0] tree; [1] shrub
2. Greenish strips on trunk (figure 2)	[0] absent; [1] present
3. Trunk (figure 4)	[0] not ventricose; [1] ventricose
4. Prickles on branches and trunk (figure 1)	[0] absent; [1] present
5. Leaves clustered in brachyblasts (figure 3)	[0] absent; [1] present
*6. Division of leaf blade	[0] simple; [1] 3 to 5 leaflets; [2] 7 to 11 leaflets; [3] one leaflet
7. Leaflets jointed to petiole	[0] absent; [1] present
8. Length of petiole (cm)	[0] 0.5-4.5; [1] 6-42
9. Apex of petiole widened	[0] absent; [1] present
10. Margin of leaf or leaflet	[0] entire; [1] lobed; [2] serrate
11. Adaxial surface of leaf/leaflet with simple hairs	[0] present; [1] absent
12. Abaxial surface of leaf/leaflet with simple hairs	[0] absent; [1] present
13. Veining pattern of leaf or leaflet	[0] pinnate; [1] palmate
*14. Petiolule	[0] absent or to 0.1 cm long; [1] 0.2 to 2 cm; [2] 2.5 to 7.5 cm
15. Inflorescence	[0] flowers isolate; [1] cymes
*16. Length of flower (cm)	[0] to 3.9; [1] 4.5-6.0; [2] 6.5-12.5; [3] 13-17; [4] 17.5-35
17. Calyx indumenta	[0] glabrous; [1] indumented
18. Glands on receptacle (figure 9)	[0] absent; [1] present
19. Margin of calyx	[0] lobed to lacinate; [1] truncate
*20. Calyx: ratio length/width	[0] to 0.6; [1] 0.8-1.5; [2] 3 or more
21. Persistence of the calyx until the fruit	[0] persistent; [1] deciduous
*22. Petal: ratio length/width	[0] to 4.5; [1] 6.0-11.5; [2] 14.0 or more
23. Tufted hairs on abaxial side of petals (figure 8)	[0] absent; [1] present
*24. Ratio length of petal/length of calyx	[0] 1.3-3.0; [1] 4.5-12.0; [2] 15.0 or more
25. Staminodes	[0] absent; [1] present
26. Indument of staminal tube	[0] glabrous; [1] pubescent
*27. Number of fertile stamens	[0] 5; [1] 20-110; [2] > 180
28. Filaments joining	[0] joined only at base; [1] joined to near apex
29. Phalanges above staminal tube	[0] absent; [1] present
30. Shape of anthers	[0] oblong, linear to reniform; [1] hipocrepiform; [2] anfractuosis
*31. Number of carpels	[0] 3; [1] 5; [2] more than 5
32. Indument of ovary	[0] glabrous; [1] indumented
*33. Locules of the ovary	[0] 3-5; [1] 5; [2] 5-15
34. Ovules per locule	[0] 2; [1] many
35. Fruit	[0] capsule; [1] samara; [2] drupe
36. Cross section of fruit	[0] circular; [1] 5-angled; [2] 5-winged
37. Fruit: ratio length/width	[0] 1.0-1.4 (figure 6); [1] 2.0-6.0; [2] more than 6.0
38. Kapok (figure 7)	[0] absent; [1] present
*39. Number of seeds per fruit	[0] up to five; [1] 15-30; [2] 50 or more
40. Shape of the seeds (figures 4-5)	[0] not angled; [1] angled

* = ordered characters.



Figures 1-9. Some morphological characters used in the cladistic analysis of *Pseudobombax*. 1. Ventricose trunk covered with woody prickles of *Ceiba glaziovii*. 2. Trunk with grayish bark and strips of exposed greenish underbark of *Pseudobombax simplicifolium*. 3. Young leaves grouped in brachyblast of *Pseudobombax simplicifolium*. 4. Overgrown seeds of *Bombacopsis retusa* showing the flat plans of contact. 5. Seed of *Pseudobombax minimum*. 6. Indehiscent capsule of *Pseudobombax marginatum*. 7. Dehiscent capsule of *Pseudobombax simplicifolium* showing abundant kapok surrounding the seeds (arrow). 8. Tufted hairs (MEV) on the outer surface of a petal of *Pseudobombax campestre*. 9. Receptacular glands (arrow) of *Pseudobombax simplicifolium*. Bar = 25 cm (1-2); 3 cm (3-4, 9); 2 mm (5); 6 cm (6, 7); 20 μ m (8).

long × width ratios in order to minimize the subjectivity present in morphological terminology. Two analyses were performed considering unordered and ordered characters (10 multistate characters that express progression series). The data matrix (table 3) was edited in the software Nexus Data Editor (Page 2001).

Phylogenetic analysis – Maximum parsimony analyses were carried out in Paup 4.0b10 for Windows (Swofford 2000) using “Branching-and-Bound” algorithm. Bootstrap support (bs) was estimated in Paup using 1,000 replicates with 10 simple addition sequences using TBR, keeping up to 15 trees per replication. The most parsimonious trees

Table 3. Data matrix for the cladistic analysis of *Pseudobombax* and allied genera. Polymorphic characters are indicated by ‘a’ (0 + 1), ‘b’ (1 + 2), ‘c’ (0 + 2), ‘d’ (2 + 3 + 4), ‘e’ (2 + 3), ‘f’ (3 + 4). (- = Inapplicable state; ? = Unknown state).

Taxon	10	20	30	40
* <i>Matisia ochrocalyx</i>	000000-000	111-001002	00000111100	1110200000
* <i>Ochroma pyramidale</i>	000000-101	111-021002	10000111102	1111012120
* <i>Scleronema micranthum</i>	000000-000	000-100001	00000011100	0000200000
<i>Adansonia digitata</i>	0010021102	0000011001	10000120?0	2121000010
<i>Bombacopsis retusa</i>	0000111000	0000020111	1111002010	1011000011
<i>Bombacopsis stenopetala</i>	0000020100	0000031011	1212011010	1111001011
<i>Bombax ceiba</i>	000102?100	1002021100	1000011011	1111001120
<i>Cavanillesia arborea</i>	001000-100	1a1-100001	1000001010	1110121000
<i>Ceiba glaziovii</i>	00110b1102	0001a20000	1000100000	1011000120
<i>Ceiba pentandra</i>	000102110c	00011a0001	10000?0a02	1?11000110
<i>Eriotheca crenulaticalyx</i>	0000011000	0000001000	1000001000	11110001?0
<i>Eriotheca gracillipes</i>	a000011100	0001a001a0	1000001000	11110011?0
<i>Eriotheca longipedicellata</i>	0000021100	0001a10002	1000001000	1?110011?0
<i>Pachira aquatica</i>	0000021100	0001a40111	1212012010	1011001011
<i>Pseudobombax calcicola</i>	0100010a10	0000021110	01110a2001	1111012120
<i>Pseudobombax campestre</i>	1100010110	00000201a0	0111002001	1111001120
<i>Pseudobombax grandiflorum</i>	0a00020110	0001ad0111	01110a2001	1111011120
<i>Pseudobombax guayasense</i>	00000?0110	000103?110	0111002011	11110??12?
<i>Pseudobombax longiflorum</i>	0000020110	0002af0111	?111002001	1a11001120
<i>Pseudobombax marginatum</i>	1100020110	0100ae1110	0111012011	1111001120
<i>Pseudobombax maximum</i>	a000020110	??010f?110	0211002011	1111011120
<i>Pseudobombax minimum</i>	0100020010	1100010111	0111002011	1111001120
<i>Pseudobombax millei</i>	0000010110	??01?31110	0111012011	11110??120
<i>Pseudobombax palmeri</i>	0000010110	1100ada110	01110a2011	1111001120
<i>Pseudobombax parvifolium</i>	0100010a10	111002111a	0111012001	1?1100?120
<i>Pseudobombax septenatum</i>	0100020110	000aa20110	0011012011	1111011120
<i>Pseudobombax simplicifolium</i>	0100130000	0000a20110	0111002001	1111001120
<i>Pseudobombax tomentosum</i>	0a00020110	110a0e1111	01?1012011	111100112?

* = Outgroups.

(MPTs) were analysed using Winclada (Nixon 2002). The characters were optimised using the “Fast optimization” (*acctrans*) option.

Results

The maximum analysis considering 10 ordered characters resulted in nine MPTs, with 144 steps, consistency index (ci) 0.40, retention index (ri) 0.67. The strict consensus tree is shown in figure 10 and one of the MPTs with optimized characters is shown in figure 11. The tribe Adansonieae appeared as monophyletic although presenting a low bootstrap support. The

Bombax-group was not supported as monophyletic due to the unresolved position of *Eriotheca crenulaticalyx* in the strict consensus tree.

At generic level, *Pseudobombax* was supported (bs 58%) as monophyletic based on the following synapomorphies: petiole with widened, disciform apex (9), leaflets not jointed to the petiole (7) and calyx persistent and enlarged in the fruit (21). *Pseudobombax* was supported as sister to the *Bombacopsis-Pachira* clade (bs 64%), based on the truncate calyx (19), narrow (tending to linear) petals (22), petals much longer than the calyx (24), presence of tufted hairs on the outer surface of the petals (23)

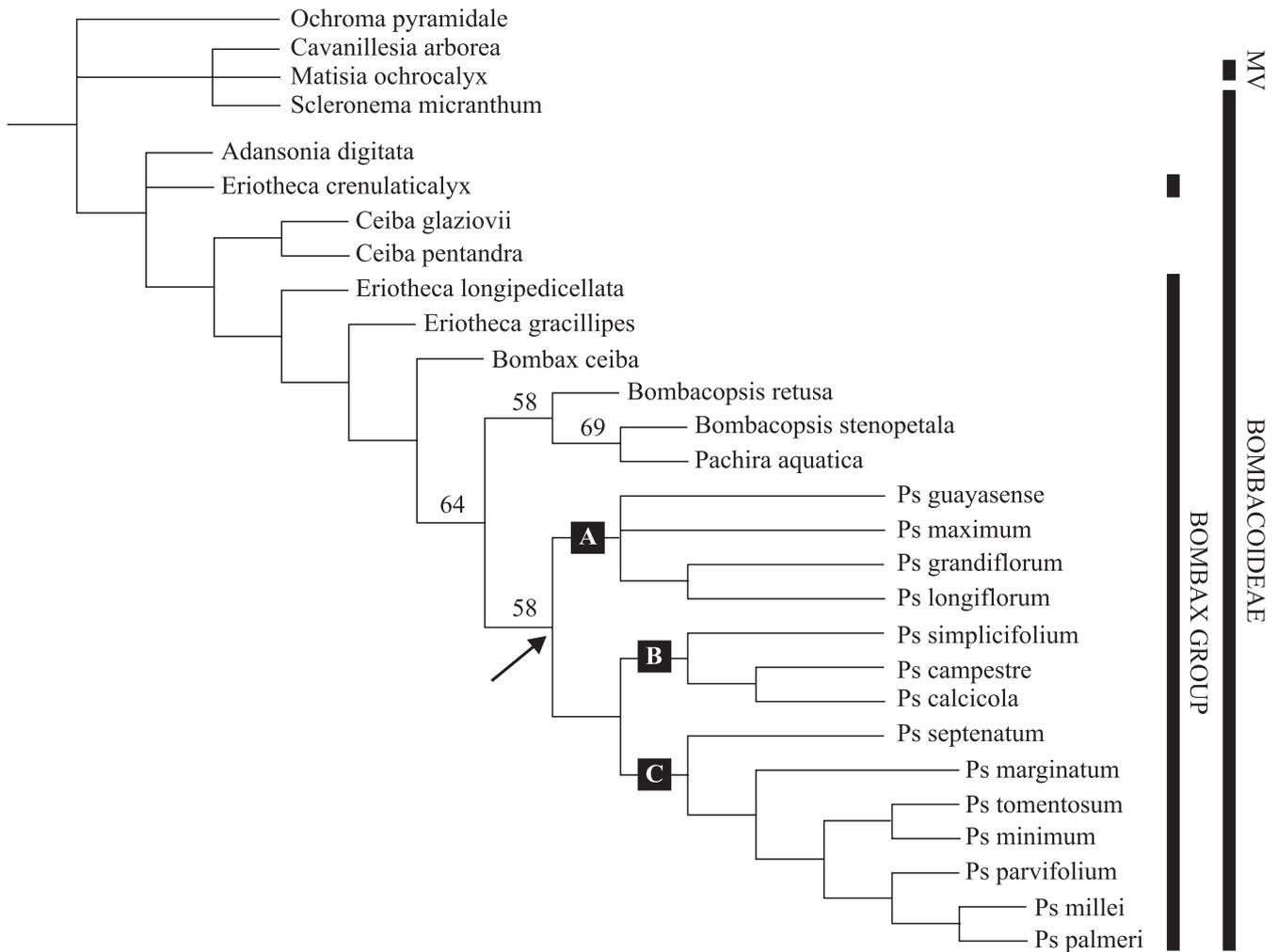


Figure 10. Strict consensus tree of the nine most parsimonious trees when considering 10 characters as ordered. Numbers above branches are bootstrap supports over 50%. The genus *Pseudobombax* is indicated by an arrow. (MV = Malvoideae; Ps = *Pseudobombax*).

and numerous stamens (27). *Pachira* appeared nested within *Bombacopsis* forming a clade with moderate support (bs 58%). The main characters that appeared as synapomorphic for this clade are the calyx almost as long as wide (20), the ovary covered by rudimentary hairs (32) and overgrown seeds (40), in addition to reversion to oblong anthers (30) and fruits without or with sparse kapok (38). The present analysis indicates the monophyly of *Ceiba* but with low support (bs < 50%). *Eriotheca* species appeared at a basal grade of the *Bombax*-group.

Within *Pseudobombax*, three main clades were recovered: clade A with four species (*P. guayasense*, *P. maximum*, *P. grandiflorum* and *P. longiflorum*, clade B including three species (*P. calcicola*, *P. campestre* and *P. simplicifolium*), and clade C including the remaining seven species (*P. marginatum*, *P. millei*, *P.*

minimum, *P. palmeri*, *P. parvifolium*, *P. septenatum* and *P. tomentosum*).

Clades B + C were defined by trunks with vertical greenish stripes (character 2). These stripes represent a chlorophyll-rich underbark which is exposed due to the opening of bands of the periderm leaving the trunk with a marbled aspect of grey and green. Clade B is characterised by reduction of leaflet number, reaching only one in *P. simplicifolium* (character 6) and androecium without phalanges (character 29). Clade C is characterised by the presence of a pubescent staminal tube (character 26). Within this clade, *P. septenatum* appears as sister of the remaining species because of the smaller ratio length/width of petals (character 22).

Cavanillesia appeared in a clade together with representatives of *Scleronema* (Bombacoideae) and *Matisia* (Malvoideae). The inclusion of *Cavanillesia* in

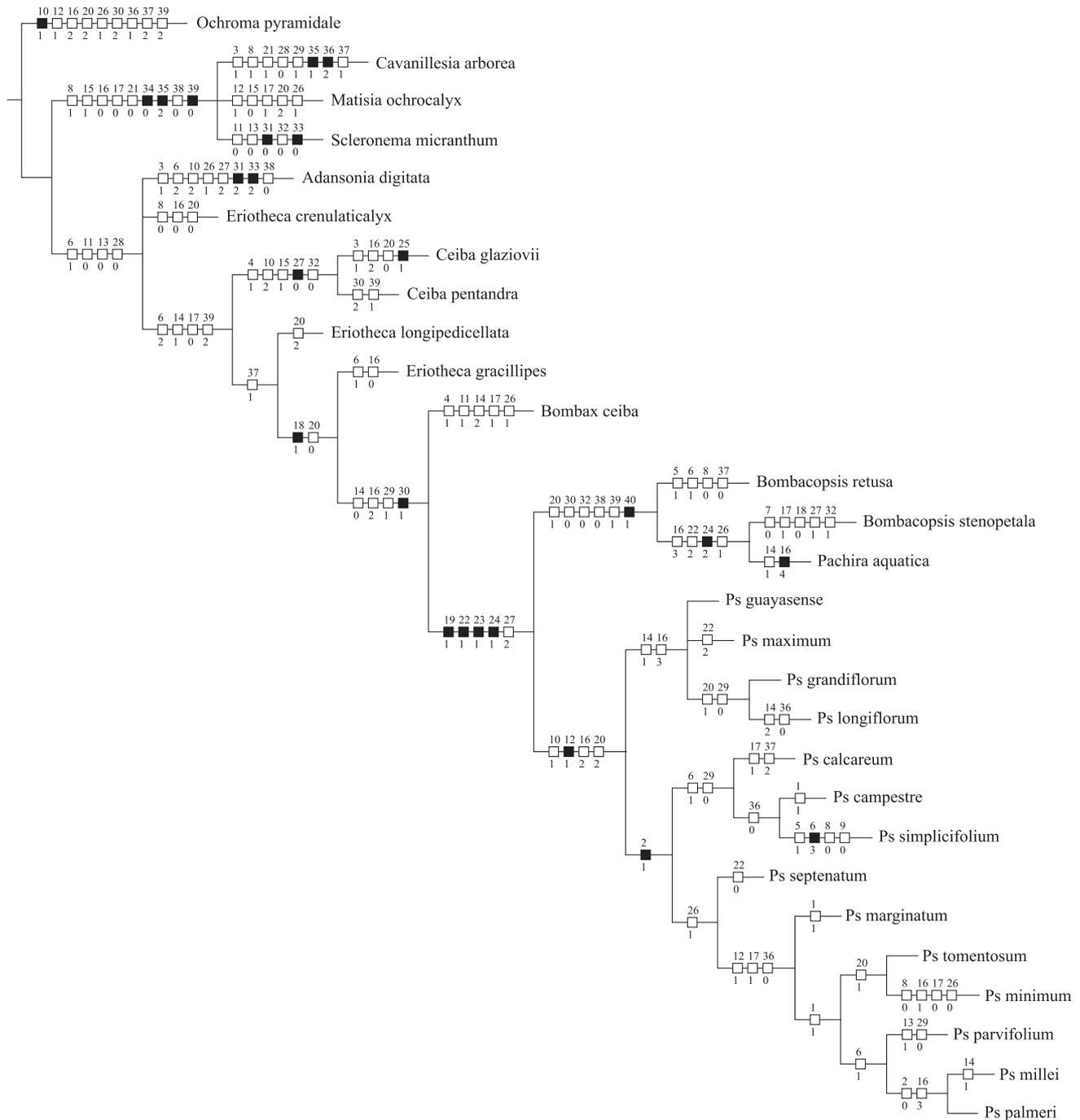


Figure 11. One of the nine most parsimonious trees, with *acctran* characters optimization. Numbers above boxes represent character and those below character state (table 2). (Ps = *Pseudobombax*).

Bombacoideae, sister to the *Eriotheca longipedicellata* – *Pseudobombax palmeri* clade, resulted in trees three steps longer.

The analysis considering unordered characters resulted in two MPTs, with 139 steps, ci 0.41, ri 0.67. The topology of strict consensus tree differed from analysis with 10 ordered characters in relation to the positioning of *Adansonia digitata*, *Bombax*

ceiba and *Pseudobombax septenatum*. *Adansonia digitata* appeared as sister to the clade *Bombacopsis-Pachira* and *Bombax ceiba* as sister of *Pseudobombax*. *Eriotheca* appeared again as a paraphyletic group together with a *Ceiba*-clade. Within *Pseudobombax*, the same clades A, B, C were recovered, but with *P. septenatum* detached of clade C and as sister to a clade A + B (figure 12).

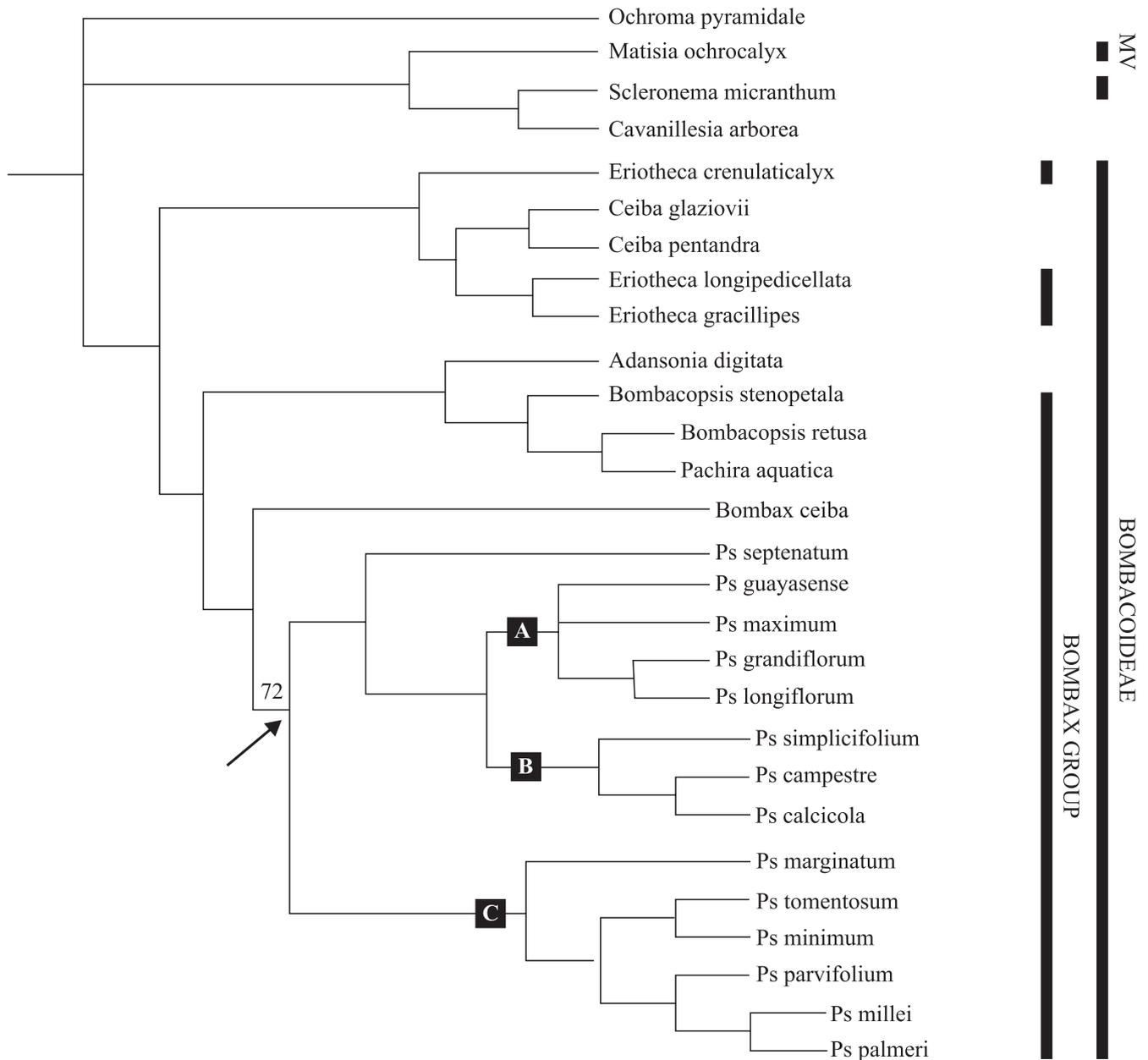


Figure 12. Strict consensus tree of the two most parsimonious trees when considering all characters unordered. Number above branch is bootstrap support over 50%. The genus *Pseudobombax* is indicated by an arrow. (MV = Malvoideae; Ps = *Pseudobombax*).

Discussion

Effect of character ordering – The topologies resulting from the ordination of 10 characters showed no influence on the interpretation of the central questions of this study. In both analyses, *Pseudobombax* and the tribe Adansoniaceae appeared as monophyletic groups while the *Bombax*-group and the infrageneric taxa of *Pseudobombax* proposed by Robyns (1963) were not supported as monophyletic in any analysis. The results

are discussed based on the analysis with 10 ordered characters because it showed greater congruence with the morphological evolution and biogeography of the group.

Phylogeny of the *Bombax*-group – The *Bombax*-group was not supported as monophyletic due the positioning of *Eriotheca crenulaticalyx*. This species appeared as sister to the remaining taxa of the *Bombax*-group in only one of the MPTs. As a consequence of the position of

E. crenulaticalyx, and also *E. longipedicellata*, the genus *Eriotheca* was likewise not supported as monophyletic. The diagnostic characters of *Eriotheca*, such as jointed leaflets, small to medium size flowers, androecium with up to 140 stamens and absence of phalanges, appeared as plesiomorphies in the present work. This genus presents complex taxonomy (Martins 1993) and was previously considered as a synonym of *Bombax* (Schumann 1886, 1895, van den Brink 1924). A larger sample than that used here seems to be necessary to advance conclusions about its monophyly and its relationship to other Bombacoideae genera.

The position of set *Bombax* apart from the American *Bombacopsis-Pachira-Pseudobombax* clade supports the separation of this Old World genus from its American allied genera (Robyns 1963, Nicolson 1979). *Pachira* appeared nested within a paraphyletic *Bombacopsis*. This result supports recent proposals for merging these genera (Alverson 1994, Alverson & Steyermark 1997, Fernández-Alonso 1998, 2003). However, because some of these characters are variable in *Bombacopsis* (Robyns 1963) a wider sampling is desirable.

Pseudobombax classification – The current classification of *Pseudobombax* was proposed by Robyns (1963) who recognised two subgenera: *Monopseudobombax* A. Robyns and *Pseudobombax*, the former characterised by simple leaves and including only one species, *P. simplicifolium*. The subgenus *Pseudobombax* was divided in two sections based on palynological characters: sect. *Pseudobombax*, including *P. septenatum* and *P. munguba* (Mart. & Zucc.) Dugand, and sect. *Heterosexinium* A. Robyns for the remaining species. The present results do not support Robyns' (1963) classification. *Pseudobombax simplicifolium* (subgen. *Monopseudobombax*) is deeply nested in the *Pseudobombax* clade, rather than sister to the remaining species of subgen. *Pseudobombax*. Likewise, at sectional level, *P. septenatum* (sect. *Pseudobombax*) is nested among the species classified by Robyns (1963) in sect. *Heterosexinium*, also refuting the monophyly of this section.

Three main clades of *Pseudobombax* were recognised in the present study. Clade A includes species that seem to be related to sandy soils in Savanna or Seasonally Dry Forests, as is the case of *P. guayasense*, *P. maximum* and *P. longiflorum*, or *restingas* and Coastal Rain Forests as *P. grandiflorum*. This clade is supported by petiolulate leaflets (character 14) and 5-angulate fruits (36) and includes species with glabrous leaflets. *Pseudobombax grandiflorum* and *P. longiflorum* form a pair of closely

related species (Robyns 1963), sharing a glabrous staminal tube without phalanges.

Clade B includes three species endemic to Seasonally Dry Tropical Forest area of north-eastern Brazil (*Caatinga*) that share triangulate bracteoles with a denticulate margin and a lower number of stamens (170 to 300), oblong, narrow fruit (1.5-2.5 cm wide) and seeds uniform, evenly coloured. *Pseudobombax simplicifolium* shares with *P. campestre* glabrous leaflets with cordate base and with only 8-13 pairs of secondary veins and 170-220 stamens. The former occurs in areas of *Caatinga* with sandy soil while *P. calcicola* is restricted to limestone outcrops in upper São Francisco River valley, in the State of Bahia. *Pseudobombax campestre* is endemic to the *Campos Rupestres* of the Espinhaço Mountain Range, in the States of Bahia and Minas Gerais, in elevations above 900 m.

The Clade C shows a trend to increase the number of stamens, usually between 400 and 1,500 per flower. However, in *P. minimum*, there is a reversion to c. 200 stamens. Most of the species included in the Clade C occurs in areas subject to seasonal climate, except for *P. septenatum* which occurs in the Amazonian Tropical Rain Forest. Within this group, *P. marginatum*, *P. tomentosum* and *P. minimum* are associated with Savanna (*Cerrado*) vegetation. *Pseudobombax minimum* is endemic to a strip of *Cerrado* in Eastern Goiás and the adjoining Western Bahia whereas *P. parvifolium* is known only from an area of *Caatinga* in Bahia and the adjoining Southern Sergipe.

Pseudobombax is more diverse in areas subject to a long dry season with xerophytic vegetation as is the case of the *Caatinga* in North-eastern Brazil and the Venezuelan Llanos (Carvalho-Sobrinho 2006) and the deciduous foliage of its species may be an adaptation to such climatic conditions. Contrary to *Pseudobombax*, the most basal taxa of the *Bombax*-group present a greater diversity in moist forests and its species are mostly evergreen as is the case with *Eriotheca* (Martins 1993), a genus with many species in the Atlantic and Amazonian forests, and with *Bombacopsis* and *Pachira*, that in sum comprise around 45 species (Alverson & Steyermark 1997, Fernández-Alonso 1998), most of which distributed in the Amazon.

Morphological evolution – A palmately compound leaf blade is a putative synapomorphy of the Bombacoideae (Baum *et al.* 2004). *Pseudobombax simplicifolium* was described by Robyns (1963) as possessing simple leaves. However, it presents leaves with a pinnately veined brochidodromous pattern which is commonly

found in leaflets of the palmately compound leaves of the Bombacoideae. We therefore interpret the leaves of *P. simplicifolium* as a reduced compound leaf with only one leaflet and thus not homologous to the simple leaf of *Cavanillesia*, *Ochroma* and the remaining Malvoideae.

The petiole widened at the apex and leaflets not jointed to the petiole were supported as derived states within the Bombacoideae and thus may be taken as synapomorphic for *Pseudobombax*. Leaflets with serrate margins seem to be plesiomorphic amongst the Bombacoideae since this condition is also found in *Ceiba* and *Adansonia*, and the entire margins may be synapomorphic for the *Bombax*-group.

It was possible to note a clear trend towards flower enlargement in the *Bombax*-group. *Eriotheca* is characterised by relatively small flowers while the species of the clade *Bombax ceiba-Pseudobombax palmeri* possess large (6.5-12 cm long) or very large (13-35 cm long) flowers. This increasing flower size seems to be associated with an increment in stamens number and their organization in phalanges. According to Rao (1952) and van Heel (1966), a primitive flower of the Malvales would have five free stamens from which three evolutionary trends have arisen: increase in stamen number; arising of monotheccate anthers from bitheccate ones; and stamen connation. Recent studies had shown that numerous and joined stamens had arisen independently in several lineages of the Malvaceae (Alverson *et al.* 1999, Baum *et al.* 2004, von Balthazar *et al.* 2006). However, monotheccate anthers seem to be an exclusive synapomorphy of the Malvateca clade ([Ochroideae [Bombacoideae, Malvoideae]]). In the *Bombax*-group, these trends seem to be linked with an increasing specialization to bat pollination. Chiropterophilous plants are often trees with 'brush' flowers that shed their leaves during flowering period and tend to flower at the apex of the branches (Faegri & van der Pijl 1971). Except for the deciduous foliage, these two traits are found in species of the *Bombax*-group, with crepuscular anthesis recorded for all studied species (Fischer *et al.* 1992). In *Pseudobombax*, the plants have also deciduous foliage during the flowering period, but it may be interpreted as a dual adaptation both to chiropterophily and to their preference for habitats subject to a long dry season since the plants flower mostly during the dry season.

Another evolutionary trend supported here is towards capsules with small and numerous seeds surrounded by abundant kapok, which is synapomorphic for the *Ceiba glaziovii-Pseudobombax palmeri* clade.

These characters may be interpreted as adaptations for wind dispersed seeds, a prevailing strategy among emergent plants (Willson 1992) as is the case of most Bombacoideae. In contrast to *Pseudobombax*, species of *Pachira* (including *Bombacopsis*) are more diverse in tropical rain forests where they form part of the canopy. This genus is supported by a reversion to fruits without or with sparse kapok and larger overgrown seeds (c. 2 cm long) which are dispersed by gravity when the fruits fall to the forest floor. Vogel (1980) found that in tropical primary forests, seeds with more massive cotyledons are common, probably because they can produce relatively robust seedlings in conditions where the sunlight may be limiting. Hence, the kapok seems to be unimportant for seed dispersal in these genera and large seeds may be a key innovation which allowed this genus to successfully colonize tropical rain forests.

Position of the genus *Cavanillesia* – Although this study focused on the phylogenetic relationships of *Pseudobombax* and allied genera, the results for *Cavanillesia* raised some interesting questions. This genus presents simple, palmately veined leaves and there is no agreement among different classification systems about its placement. Bentham & Hooker (1862) placed it in the tribe Matisieae with the genera *Durio*, *Hampea* Schldl., *Matisia*, *Ochroma*, *Quararibea* and *Scleronema*. Hutchinson (1967) removed *Cavanillesia*, *Hampea* and *Scleronema* to the tribe Hampeae. Takhtajan (1997) proposed a different arrangement with *Cavanillesia*, *Durio* and *Scleronema* (together with *Coelostegia* Bentham, *Cullenia* Wight, *Kostermansia* Soegeng and *Neesia*) in tribe Durioneae, *Matisia*, *Huberodendron* Ducke, *Ochroma* and *Quararibea* (with *Bernoullia* Oliv., *Patinoa* Cuatrec., *Phragmotheca* and *Septotheca* Ulbr.) in tribe Matisieae and *Catostemma* Benth. and *Aguaria* Ducke in tribe Catostemateae.

Molecular phylogenetic studies supported the genera *Hampea*, *Matisia* and *Quararibea* (tribe Matisieae) as more related to the Malvoideae than to the Bombacoideae (Alverson *et al.* 1999, Baum *et al.* 1998, 2004, Nyffeler *et al.* 2005). According to Alverson *et al.* (1999), *Cavanillesia* is included in the Bombacoideae but they did not present trees supporting this hypothesis since *Cavanillesia* was removed from the analysis because it produced "an excessive number of trees". Likewise, Baum *et al.* (2004) considered intuitively that *Cavanillesia* must be included in the Bombacoideae clade but this conclusion was not tested. Although not conclusive, our results do not support this view since *Cavanillesia* appeared unresolved regarding the outgroups *Matisia*

and *Scleronema*. Besides, *Cavanillesia* presents simple palmately veined leaves, traits shared with *Ochroma* and *Matisia*.

Recent molecular phylogenetic study carried out by Baum *et al.* (2004) supports *Ochroma* as part of a small clade sister to the larger Bombacoideae-Malvoideae clade. This latter study also supports the close relationship of simple leaved genera *Scleronema*, *Huberodendron* and *Catostemma*, represented here by the former, to the Bombacoideae clade. However, unlike *Ochroma*, *Matisia* and *Cavanillesia*, the leaves of these genera present a pinnate, brochidodromous pattern similar to that found in the leaflets of the palmately compound leaves of the Bombacoideae. Therefore, the simple leaves found in genera presently included in Bombacoideae (the cited *Scleronema*, *Huberodendron* and *Catostemma*) may be not homologous to the simple leaves of the remaining Malvatheca. Rather, they could be interpreted as a result of the reduction of leaflets to one and hence be taken as homologous to a leaflet. In the present work, the pinnately veined leaves of *Pseudobombax simplicifolium* was unambiguously supported as derived from palmately compound leaves. Consequently, since *Cavanillesia* presents palmately veined simple leaves, similar to those found in Matisieae (Malvoideae) and *Ochroma* (Ochomeae), the hypothesis that it belongs to the Bombacoideae needs to be better investigated.

In summary, although a better sampling and use of molecular data should improve our understanding of relationships at generic level within the *Bombax*-group, the present work is to date the most comprehensive survey that supports the monophyly of *Pseudobombax* and establishes phylogenetic hypotheses of relationships within the genus. It also raises questions to be further investigated regarding the relationship between *Pachira* and *Bombacopsis* and the possible parphyly of *Eriotheca*.

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