Taxonomy of the Babassu Complex (Orbignya spp.: Palmae)

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ABSTRACT. The taxonomic identity of the economically important group of palms known in Brazil as babassu (*Orbignya* spp.) has been a source of confusion for well over a century, largely due to a proliferation of species described from incomplete specimens obtained at a limited number of sites. To resolve this confusion, we collected complete material over a wide part of babassu's distribution in Brazil and Bolivia; additional material was obtained from Surinam. Based on the literature, biological data obtained in the field, and detailed morphological comparisons of specimens in the laboratory, we conclude that the babassu complex is comprised of two principal species, each with a pronounced tendency to hybridize. The most widely distributed species is *Orbignya phalerata* C. Martius, originally described from Bolivia, which is identical to a number of subsequently described (and consequently synonymous) species from Brazil. A second species, *O. oleifera* Burret, appears to be restricted to the São Francisco River Basin in Minas Gerais, Brazil. The wide geographic range of this complex and its propensity to hybridize have probably contributed to its high morphological variability. We suspect that this variability will prove to be a common theme in certain groups of palms currently thought to be comprised of many species.

Over widespread areas of Brazil, palms known locally as "babaçu" (spelled "babassu" in English) occur in pure stands that virtually blanket the landscape (fig. 1). Babassu stands form spontaneously on sites where the original forest cover has been cleared (Anderson and Anderson 1983). The total area of these stands in Brazil was recently estimated at 196,370 km2 (STI 1979), roughly equivalent to the U.S. state of South Dakota. Babassu palms are an important source of vegetable oil in Brazil. In 1980, 250,951 metric tons of oil-rich kernels were sold to oil pressing facilities throughout the country (IBGE 1983); the manual extraction of these kernels is a source of livelihood for hundreds of thousands of rural families (May et al. 1985). In addition to vegetable oil, babassu fruits provide a host of market and subsistence products, including flour, alcohol, charcoal, coke, tar, combustible gases, etc. (fig. 2).

Despite its ecological and economic importance, the taxonomy of babassu has been a source of confusion since it was first described well over a century ago. The confusion begins on the generic level. Although babassu is generally assigned to the Cocoeae (Attaleinae) genus *Orbignya* (currently considered to comprise ca. 18 species), the status of this and the four other

genera in the Attaleinae (sensu Dransfield and Uhl 1986) has been questioned by Wessels Boer (1965). These genera are distinguished solely on the basis of staminate flower morphology. No correlation with other characters has been observed, and staminate flower morphology spans a separation based on other characters such as endocarp pores. Lines between genera in the *Attalea* alliance are further blurred by collections of intermediate flower types, which have prompted the description of two new genera; one of these, *Markleya*, was described by Bondar (1957) as a possible intergeneric hybrid involving babassu.

A classification based solely on staminate flower morphology is of little use in the field, as most species flower for a brief period of time. Thus it is no surprise that the species of babassu are often confused with other species or even genera, notably Attalea. Oil palms commercially referred to as babassu include Orbignya agrestis (Barb. Rodr.) Burret in the Brazilian state of Pará, Attalea oleifera Barb. Rodr. in the states of Goiás and Minas Gerais, A. geraensis Barb. Rodr. in Minas Gerais, and A. pindobassu Bondar in the state of Bahia (Markley 1971). Even botanists are not immune to generic confusion when dealing with the Attalea alliance. For example,

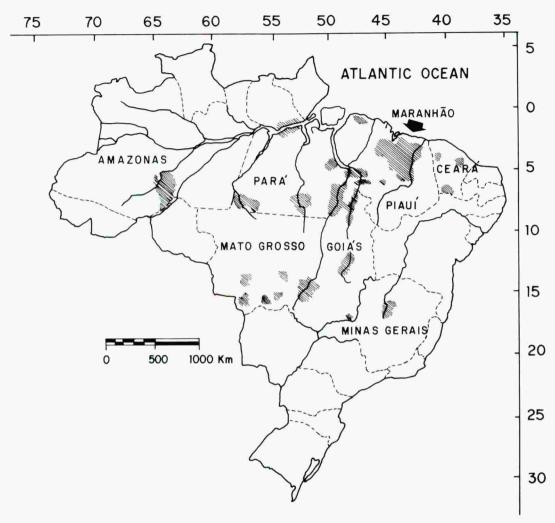


FIG. 1. Approximate distribution of high-density stands of babassu (*Orbignya* spp.) in Brazil. States containing stands are labelled. Adapted from Anonymous (1981).

the Brazilian botanist Mário Ferri (1974, 1980) evoked aboriginal dispersal to account for the apparently disjunct distribution of babassu near the town of Piraçununga in the southerly state of São Paulo; examination of male flowers collected from the local palm population has shown that it in fact pertains to the genus *Attalea* (J. T. de M. Costa, pers. comm.; A. B. Anderson, unpubl. data).

To resolve generic confusion in the Attalea alliance, Wessels Boer (1965) recommended reducing Orbignya and related genera to the single genus Attalea, but his suggestion has not been followed by other taxonomists (Dransfield and

Uhl 1986; Moore 1973; Glassman 1977a). Countervailing arguments include the weight of taxonomic tradition and the observation that Wessels Boer's scheme merely reduces the confusion to the specific level (H. E. Moore, pers. comm.). Final resolution of the confused generic limits within the *Attalea* alliance will require an exhaustive study of the entire group, which, like many large palms that occur in remote areas, is poorly represented in herbaria. In the absence of such a study, we shall consider the babassu palm to be part of the genus *Orbignya*, and thus maintain this as a distinct genus.

On the specific level, nine names associated

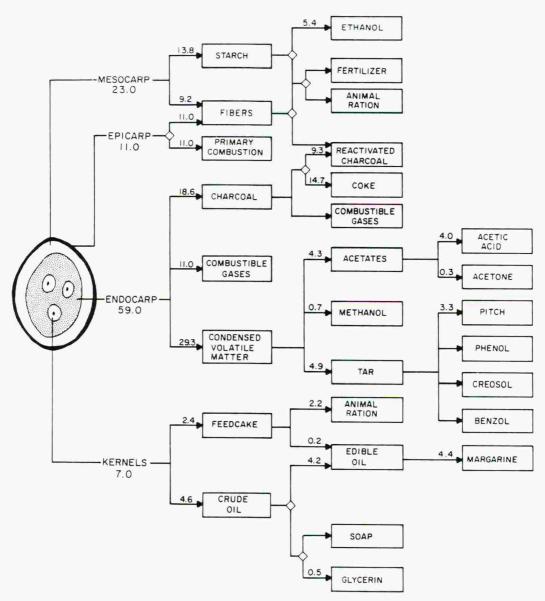


FIG. 2. Flowchart of products derivable from babassu via current technology. Diamonds represent "either/or" options. Numbers are percentages of fruit weight. Adapted from Abreu (1940), Viveiros (1943), Escola Técnica Federal do Maranhão (1976), IPT (1979), and Mendes and Carioca (1981).

with babassu have been published (table 1). Most of this proliferation has resulted from species descriptions based on inadequate botanical specimens, a problem inherent to palm taxonomy in general (Tomlinson 1979). In the more recent taxonomic literature (e.g., Bondar 1954; Glassman 1977a, 1978b; Rizzini 1963), most of the names listed in table 1 are considered syn-

onymous, and it is generally agreed that the babassu complex consists of a maximum of three species. The most commonly cited names are *Orbignya martiana* Barb. Rodr., *O. barbosiana* Burret, and *O. oleifera* Burret.

The confusion associated with the identity of the economically important babassu palm complex prompted us to undertake a long-term field study of the group's taxonomy. In conjunction with this study, we are collecting germplasm of babassu as part of a domestication effort aimed at producing more desirable strains of the palm for introduction into cultivation. The study was thus undertaken not only to resolve longstanding taxonomic confusion but to provide a basis for intensifying the utilization of babassu.

MATERIALS AND METHODS

Lack of adequate specimens has been the principal impediment to resolving the taxonomy of the babassu complex. To help remedy this situation, we collected specimens of the complex over a substantial portion of its presently known range (fig. 3). Due to the large size and bulkiness of palms in the complex, complete botanical collections required extensive field documentation; recommended procedures are described at length in Balick et al. (1982). Specimens of all collections were deposited in herbaria in the U.S., Brazil, and Bolivia (e.g., NY, CEN, MG, INPA, CPATU, LPB, and others). Detailed morphological examination and comparisons of the specimens were subsequently carried out in New York.

A first-hand familiarity with the taxa in the field provided a solid basis for reviewing the extensive and often contradictory taxonomic literature on this group. Results pertaining to the nomenclature, morphology, and distribution of taxa in the babassu complex thus represent a synthesis of literature already published, data obtained in the field, and morphological comparisons of specimens in the laboratory.

RESULTS

Examination of data on specimens obtained to-date indicates that the babassu complex is comprised of two principal species, each with a pronounced tendency to hybridize with other species. In this section, we present data on the morphology and nomenclature of the two principal species. Preliminary data on putative hybrid complexes involving these species are also provided in Appendices 1–3; final results concerning the status of these complexes and definitive nomenclature for the purported hybrids are provided in other publications (Balick et al. 1987a; Balick et al. 1987b).

OrbigNya Phalerata C. Martius, Palm. Orbig. 126, t. 13, fig. 2, t. 32A. 1844.—Type: Bolivia, Santa Cruz, Chiquitos and Moxos, n.d., d'Orbigny 20 (P).

Attalea speciosa C. Martius, Hist. Nat. Palm. 2: 138, t. 96, figs. 3-6. 1826.—Type: Brazil, Maranhão and Pará, type not designated. Orbignya speciosa (C. Martius) Barb. Rodr., Sert. Palm. Bras. 1:t. 52-53. 1903. non O. speciosa Barb. Rodr. (1891).

Orbignya martiana Barb. Rodr., Palm. Mattogross. 68, t. 22–23, figs. 1–14. 1898. Published as a new name for *O. speciosa*. t. 22–23.

Orbignya macropetala Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10:507. 1929.—TYPE: Guyana, on Rupununi River, n.d., Schomburgk s.n. (B?).

Orbignya barbosiana Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11:690. 1932. Published as a new name for O. speciosa (C. Martius) Barb. Rodr.

Stem solitary, columnar, to ca. 30 m high and 19-50 cm in diam.; leaf scars inconspicuous; leaf bases persistent just below crown. Leaves 10-25, erect-arching; sheath 40-120 cm long, usually with yellow, longitudinal striations on abaxial surface that may extend to base of rachis, abaxial surface weakly white lepidote, adaxial surface smooth; petiole 8-42 cm long, channeled adaxially, convex abaxially; rachis 560-860 cm long, base trough-shaped in cross section, middle more or less 4-sided in cross section, apex triangular in cross section, abaxial and lateral (at middle) surfaces weakly to densely orange- to brown-lepidote, adaxial surface glaucescent; pinnae 156-208 per side, 5-6 basal pinnae grouped, otherwise inserted at regular intervals and in same plane, rigid throughout when new, becoming pliant near apices with age, adaxial surface lustrous, smooth, darkgreen, abaxial surface glaucous; basal pinnae 83-185 cm long and 1.0-2.0 cm wide; middle pinnae 88-168 cm long and 2.0-6.0 cm wide; apical pinnae 22-139 cm long and 0.8-2.3 cm wide. Inflorescences androdioecious, interfoliar; prophyll 50-150 cm long; peduncular bract woody, persistent, 40-218 cm long, bearing an acumen 16-40 cm long, adaxial (interior) surface white- to yellow-lepidote at anthesis, becoming tan to rust-brown over time; all axes of inflorescences white- to yellow-lepidote at anthesis; peduncle 56-180 cm long; rachis 48-175

Table 1. Continued.

Publication				
Burret 1932	Burret 1938	W. Boer 1965	Glassman 1977a	
O. barbosiana	\$	= A. speciosa	=O. barbosiana	
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47-44-44-3 DETECTORS UPPER	=O. oleifera		=O. barbosiana	
=O. cohune			Confused name	
Part = O. barbosiana	Part =O. oleifera	=A. speciosa	=O. barbosiana	
***************		=A. speciosa	=O. barbosiana	
		- \$\dag{\psi} \cdot \cdot \dag{\psi} \dag	Uncertain species	
Proposed	9 × 4 × 4 31 22 × 5 × 5 × 5 × 5 (2) 21 × 21 × 21 × 21 × 21 × 21	=A. speciosa	=O. barbosiana	
Described		al de la fa de décidir a la rai de decidir de la rai de la rai de	=O. barbosiana	

3-6 cm long; endosperm white, oily, homogeneous; embryo cream-white.

Specimens examined. BOLIVIA. Dept. Beni: Prov. Marban, ca. 35 km S of Trinidad, 10 km S of Sachojere, Villa Alba, Jul 1982, Balick et al. 1359 (LPB, NY); 30 km S of Riberalta, island in Lake Tumi-Chucua, 2 Aug 1982, Balick et al. 1367 (LPB, NY); Prov. Mamoré, ca. 18 km S of San Joaquin, farm called "Barranquita", 18 Aug 1982, Balick et al. 1432 (LPB, NY). Dept. Santa Cruz: Prov. Velasco, ca. 105 km N of San Ignácio and 22 km S of San Simon, near Finca Bonanza, 26 Jul 1982, Hopkins et al. 158 (LPB, NY).

BRAZIL. Estado do Ceará: Mun. Ubajara, halfway between the town of Ubajara and Ubajara National Park, Dec 1981, Balick et al. 1353 (CEN, IAN, INPA, MG, NY); Mun. Ipú, on road between Ubajara (62 km) and Ipú (11 km), 12 Dec 1981, Balick et al. 1354 (CEN, IAN, INPA, MG, NY). Estado de Goiás: Mun. Tocantinópolis, 11 km from Tocantinópolis on Fazenda Mucamba, 18 Nov 1981, Balick et al. 1309 (CEN, IAN, INPA, MG, NY). Estado do Maranhão: Mun. São Félix de Balsas, community known as "Poço," 4 Dec 1982, Balick et al. 1342 (CEN, IAN, INPA, MG, NY); Mun. Bom Jardim, along Rio Pindaré at Posto Indí-

gena Carú (FUNAI Post, Guajajara Indians), 28 Aug 1983, Balick et al. 1468 (CEN, NY), 1 Sep 1983, Balick et al. 1528 (CEN, NY). Estado do Pará: Mun. Bragança, Village of Tracuateua, Nov 1981, Balick et al. 1301 (CEN, IAN, INPA, MG, NY); Mun. Itupiranga, on Rio Tocantins 20 km downstream from Itupiranga at Cajazeirinha, 23 Nov 1981, Balick et al. 1304 (CEN, IAN, INPA, MG, NY). Estado de Piauí: 32 km S of Teresina on road to Palmeiras along Parnaíba River, at locale called "Sumaré", Dec 1981, Balick et al. 1351 (CEN, IAN, INPA, MG, NY).

Nomenclature. The scientific name of this species has generated considerable confusion among taxonomists. Before initiating our fieldwork, the first taxonomic description that could definitely be attributed to babassu was that of *Orbignya martiana* Barb. Rodr., published in 1898 (table 1). A previously published name associated with babassu (*Attalea speciosa* C. Martius) was based on an incomplete collection, and its accompanying description was insufficient and could not be definitely attributed to babassu. Barbosa Rodrigues (1903) subsequently reduced



Fig. 3. Distribution of specimens of the babassu complex examined in this study.

TABLE 1. Nomenclatural history of babassu. ¹ O. speciosa (C. Martins) Barb. Rodr. is not to be confused with O. speciosa Barb. Rodr., a name currently reduced to synonymy under O. cohune (C. Martius) Dahlgren ex Standlev.

	Publication				
Scientific name	Martius 1826	Martius 1844	B. Rodrigues 1898	B. Rodrigues 1903	Burret 1929
Attalea speciosa C. Martius	Described .	(* * * * * * * * * * * * * * * * * * *	=O. martiana	=O. speciosa ¹	*************
Orbignya phalera- ta C. martius		Described .		29314723114444	************
Orbignya mar- tiana Barb. Rodr.			Described	=O. speciosa ¹	=O. martiana
Orbignya macro- stachya Drude ex Barb. Rodr.				=O. speciosa ¹	=O. dammeriana
Orbignya speciosa (C. Martius) Barb. Rodr.				Described	Part =O. martiana
Orbignya macro- petala Burret					Described
Orbignya huebneri Burret					Described
Orbignya barbo- siana Burret					
Orbignya oleifera Burret					

cm long; staminate inflorescences bearing 277-401 rachillae, the latter 10-28 cm long, erect, each rachilla subtended by a 0.5-6.0 mm long bract and bearing 17-102 staminate flowers arranged in 2(4) longitudinal rows on abaxial side only; androgynous (but functionally pistillate) inflorescences bearing 323-475 rachillae, the latter 10-24 cm long, 3-4 mm in diam., subtended by a bract 2-14 mm long, each rachilla bearing 1-2(3) pistillate flowers at base to middle and 1- several aborted staminate flowers at middle to apex, or more rarely bearing staminate flowers only. Staminate flowers yellowish, fragrant, asymmetrical, subtended by 2 bracteoles 1-4 mm long; sepals 3, lanceolate to deltate, 0.8-2.5 mm long and 0.6-2.3 mm wide, coriaceous, margins smooth; petals 2(3), incurved, coriaceous, margins smooth, 9.5-16.9 mm long, one petal 3.9-7.5 mm wide and obovate with apex dentate, the other petal(s) 2.8-5.2 mm wide and narrowly elliptic with apex acute or occasionally dentate; stamens (21)2426(30); filaments slender, 1.0-4.2 mm long; thecae united, irregularly coiled and twisted; pistillode present. Pistillate flowers yellowish, subtended by 1-2 bracteoles ca. 2 mm long; sepals 3-6, imbricate, triangular to deltate, 2.8-4.1 cm long at anthesis, coriaceous, margins smooth; petals 3(-5), imbricate, triangular to deltate, 2.3-5.0 cm long at anthesis, coriaceous, margins dentate, apex acute or dentate with 2-3 teeth; staminodial cupule leaving a ring around the pistil; stigmas (1)3-6(11), apical, erect to more or less reflexed at anthesis. Fruits broadly elliptic to oblong, 6.6-12.5 cm long, 3.7-9.9 cm wide, 40-440 g dry weight, lepidote, rust-brown at maturity, apex gray-white; stigmatic residue persistent; staminodial ring weakly to strongly defined; calyx a cupule of indurate perianth enclosing the base of the fruit, 3.8-5.8 cm long, containing a 2-4 cm long staminodial tube; epicarp fibrous, 1-4 mm thick; mesocarp mealy, dry, 2-12 mm thick; endocarp woody, 35-76 mm in diam.; seeds ovate to elliptic, (1)3-6(11), O. martiana to synonymy under the new combination, O. speciosa (C. Martius) Barb. Rodr. Although widely accepted in Brazil, the latter name is invalid because the same combination (O. speciosa Barb. Rodr.) had been previously published by Barbosa Rodrigues (1891) in reference to another species (cf. Article 64, ICBN). Before initiating our fieldwork, then, Orbignya martiana was the earliest, validly published name definitely referable to babassu.

Martius (1844) published a relatively complete description of *O. phalerata*, which he designated as the type species of the genus. The collections were obtained in northeastern Bolivia in the region around Chiquitos and Moxos from a palm known locally as "cusi." Martius' published description and illustration provides no basis for distinguishing it from *O. martiana*. However, further collections of this species had apparently not been obtained.

During two expeditions to Bolivia in 1982 and 1983, we obtained collections of the cusi palm at seven localities in northeastern Bolivia (fig. 2). Comparison of this material with collections obtained of the babassu palm in Brazil revealed no consistent differences. We thus conclude that *Orbignya phalerata* C. Martius and O. martiana Barb. Rodr. are synonymous. The former has priority and the latter name is thus reduced to synonymy.

Hybridization. Orbignya phalerata is the most widespread, morphologically variable, and economically important species in the babassu complex. It is this species that forms extensive stands in the Brazilian states of Maranhão, Piauí, Goiás, and Mato Grosso (fig. 1), with outlying populations ranging from Bolivia to Surinam (fig. 3). Contributing to its high morphological variability is its apparently pronounced tendency to hybridize. We propose that O. phalerata forms two hybrid complexes. One involves an intergeneric cross with Maximiliana maripa (Correa de Serra) Drude, producing a putative hybrid described by Bondar (1957) as Markleya dahlgreniana. We found this hybrid at two localities in the Brazilian state of Pará, and it has been reported at two other localities in Surinam (Wessels Boer 1965; see fig. 3); in all cases it occurs in association with O. phalerata and M. maripa. A morphological comparison of the three taxa (Appendix 1) reveals the intermediate nature of the purported hybrid. The second hybrid involves a cross between *O. phalerata* and *O. eichleri* Drude, producing a putative hybrid described by Bondar (1954) as *O. teixeirana*. The intermediate morphology of this taxon (Appendix 2), as well as its exclusive occurrence in association with *O. phalerata* and *O. eichleri* at four localities in the Brazilian state of Maranhão, support our contention that it represents a hybrid.

Orbignya Oleifera Burret, Notizbl. Bot. Gard. Berlin-Dahlem 14:240. 1938.—Type: Brazil, Minas Gerais, Pirapora, 18 Dec 1937, Burret & Brade 19 (RB).

Stem solitary, columnar, to ca. 20 m high and 31-53 cm in diam.; leaf scars inconspicuous; leaf bases persistent just below crown. Leaves 13-20, erect-arching; sheath 100-125 cm long, rarely with yellow, longitudinal striations on abaxial surface that may extend to base of rachis, abaxial surface densely white-lepidote, adaxial surface smooth; petiole 0-10 cm long; rachis 625-750 cm long, base trough-shaped in cross section, middle more or less 4-sided in cross section, apex triangular in cross section, abaxial and lateral (at middle) surfaces densely whitelepidote, adaxial surface smooth; pinnae 156-186 per side, 2-3 basal pinnae grouped, otherwise inserted at regular intervals and in same plane, very rigid, adaxial surface lustrous, smooth, dark-green, abaxial surface glaucous; basal pinnae 152-182 cm long and 1.5-2.5 cm wide; middle pinnae 140-168 cm long and 4.5-6.0 cm wide; apical pinnae 49-69 cm long and 0.5-1.5 cm wide. Inflorescences and rodioecious, interfoliar; prophyll ca. 75 cm long; peduncular bract woody, persistent, opening longitudinally along a more or less distinct invagination, 95-240 cm long and 28-41 cm wide, bearing an acumen 28-52 cm long, adaxial (interior) surface tan to light orange; all axes of inflorescences white- to yellow-lepidote at anthesis; peduncle 94-122 cm long; rachis 100-170 cm long; staminate inflorescences bearing up to 365 rachillae, the latter 13-32 cm long, erect, each rachilla subtended by a ca. 4 mm long bract and bearing 69-138 staminate flowers arranged in 2-3(4) longitudinal rows on abaxial side only; androgynous (but functionally pistillate?) inflorescences bearing ca. 277 rachillae, the latter reduced, 2-3 cm long, 3-4 mm in diam., sub-



FIGS. 4, 5. Orbignya. 4. O. phalerata C. Martius (M. J. Balick et al. 1392) from Ascencíon, Bolivia. 5. O. oleifera Burret (M. J. Balick et al. 1684) from Pirapora, Minas Gerais, Brazil.

tended by a contorted bract 5-6 cm long, each rachilla bearing 1-2 pistillate flowers at base to middle and 2-3 aborted staminate flowers at middle to apex, or more rarely bearing staminate flowers only. Staminate flowers yellowish, fragrant, asymmetrical, subtended by 1-2 bracteoles, the latter 1-2 mm long on staminate inflorescences, up to 1.5 cm long on androgynous inflorescences; sepals 3, deltate, ca. 1.5 mm long and ca. 1.2 mm wide, membranous to coriaceous, margins smooth; petals 2(3), incurved, coriaceous, margins smooth, 10-12 mm long, one petal 6-7 mm wide and obovate with apex dentate or lobed, the other petal(s) 4 mm wide and narrowly elliptic with apex acute; stamens 28-32(37); filaments slender, ca. 2 mm long; thecae united, irregularly coiled and twisted; pistillode present. Pistillate flowers yellowish, subtended by a straight to curved or occasionally contorted bracteole 0.8-3.0 cm long; sepals 3-6, imbricate, triangular to deltate, 1.0-3.0 cm long at anthesis, coriaceous, margins smooth;

petals 3(4-5), imbricate, triangular to deltate, ca. 2 cm long at anthesis, coriaceous, margins smooth, apex cuspidate; staminodial cupule leaving a ring around the pistil; stigmas typically 3-6, apical, erect. Fruits broadly elliptic to oblong, 13-14 cm long, 7.5-8.0 cm wide, 152-404 g dry weight, lepidote, brownish-yellow at maturity, apex brown; stigmatic residue persistent; staminodial ring strongly defined; calyx a cupule of indurate perianth enclosing the base of the fruit, 7.0-7.5 cm long, containing a ca. 1.4 cm long staminodial tube; epicarp fibrous, 1-2 mm thick; mesocarp mealy, dry, 1-2 mm thick; endocarp woody, 51-76 mm in diam.; seeds 4-6, ovate to elliptic, 4.3-6.0 cm long, endosperm white, oily, homogeneous; embryo cream-white.

Specimens examined. BRAZIL. Estado de Minas Gerais: Mun. Pirapora, ca. 10 km from town of Pirapora on N side of BR-365, adjacent to highway, 14 May 1981, A. B. Anderson 398 (MG, NY); ca. 2 km from town of Pirapora on Fazenda da Prata, 26 Nov 1984, M. J.

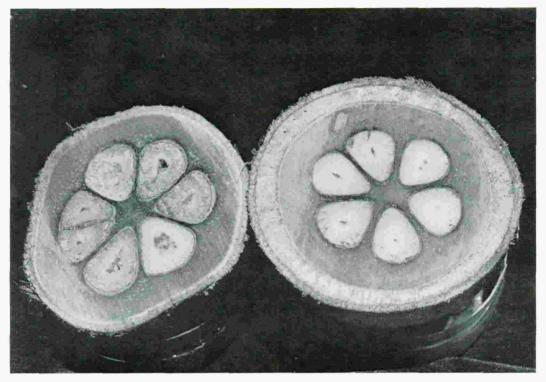


FIG. 6. A comparison of fruit cross sections in *Orbignya oleifera* (left; M. J. Balick et al. 1684) and O. phalerata (right; M. J. Balick et al. 1677). Note striking difference in thickness of mesocarp.

Balick et al. 1684 (CEN, NY), and 28 Nov 1984, M. J. Balick et al. 1686 (CEN, NY); Mun. Santa Fe, ca. 11 km from town of Santa Fe near stream called Logra do Rio, on Fazenda Santa Maria, 1 Dec 1984, M. J. Balick et al. 1696 (CEN, NY).

Nomenclature. Burret (1938) provided an incomplete description of this species based on material collected from Pirapora, Minas Gerais. Before initiating our fieldwork, the status of this species was uncertain; Glassman (1977a) reduced it to synonymy under Orbignya barbosiana Burret. In 1981 and 1984 we visited the type locality and obtained several collections. The general aspect of O. oleifera is similar to that of O. phalerata (figs. 4, 5). However, detailed morphological comparisons between these species revealed numerous differences involving both vegetative and reproductive structures (table 2; fig. 6). We feel that these differences are sufficient to consider O. oleifera as a distinct species from O. phalerata. Yet, collections of O. oleifera have only been obtained from two localities. According to local informants, the species occurs along the São Francisco River at a considerable distance from the type locality at Pirapora and may even extend into the neighboring states of Goiás and Bahia. Like *O. phalerata*, *O. oleifera* is likely to exhibit greater morphological variability than we have documented in collections from two localities, and it is possible that further collections will blur the distinctions between these two species.

Hybridization. At a single locality in the municipality of Santa Fe, Minas Gerais, we found a population of a putative hybrid resulting from an intergeneric cross between *Orbignya oleifera* and *Attalea compta* C. Martius. This was seen only in the vicinity of these two species, and a morphological comparison (Appendix 3) reveals its intermediate status.

DISCUSSION

Our results show a high degree of morphological variability in the principal species of the babassu complex, *Orbignya phalerata* (table 2). This variability encompasses characters formerly considered relatively stable and utilized to differentiate species of *Orbignya*, such as the

TABLE 2. A selective morphological comparison of Orbignya phalerata C. Martius and O. oleifera Burret.

Character	O. phalerata	O. oleifera
Leaf		
Abaxial surface of leaf		
—texture	smooth to moderately lepi- dote	densely lepidote
—yellow striations	usually present	rarely present
Petiole		
—length in adults (cm)	8-42	0-10
Pinnae		
 —angle of insertion at middle of rachis 	ca. 75-90°	ca. 45-60°
 thickness of midvein at base of middle pinnae (mm) 	ca. 1.5	ca. 2.2
—adaxial surface	lustrous	glaucescent
—firmness	rigid to slightly pliant at tips	very rigid throughout
Inflorescence		
Peduncular bract		
-longitudinal invagination	absent	present
Staminate inflorescences	present in all adults (no adults with exclusively androgynous inflores- cences)	present in most adults (some with exclusively androg- ynous inflorescences)
Androgynous inflorescence		
—length of bract subtending rachilla (mm)	2-14	50-60
—length of rachilla (cm)—bracteoles subtending pistillate flowers	10-24	2–3
number	1-3	1
length (mm)	ca. 2	8-30
Staminate flowers		
Number of stamens	(21)24-26(30)	28-32(37)
Fruit		
Color at maturity	rust-brown, apex grayish	brown-yellow, apex brown- ish
Thickness of mesocarp (mm)	2-12	1-2

number of stamens or the dimensions of leaf pinnae and fruits (Glassman 1977a). There are probably three sources of this high morphological variability: the species' wide geographic range, its apparent propensity to hybridize, and its intrinsic genetic variation. Each of these factors is discussed below.

Phytogeography. The wide distribution of Orbignya phalerata is especially noteworthy in view of the high weight of its fruits. During the course of our fieldwork, we found fruits with a fresh weight ranging from approxi-

mately 100 to 900 g. Dissemination of these massive fruits has probably been exclusively by mammals (either living or extinct) or water. Among living mammals, rodents such as pacas (Agouti paca) and agoutis (Dasyprocta punctata) are effective, short-range dispersal agents (Anderson and Anderson 1983); humans and possibly monkeys disseminate the fruits over greater distances. Coevolution between hard-fruited palms such as babassu and large Pleistocene mammals such as mastodonts and gomphotheres seems likely (Janzen and Martin 1982),

but a paucity of paleontological evidence makes it possible to assess the potential contribution of these now extinct animals to the current distribution of *Orbignya phalerata*.

Markley (1971) argued convincingly that this species [which he referred to as Orbignya speciosa (Mart.) Barb. Rodr.] originated on the Central Brazilian Shield, a major center of diversity for the entire Attalea alliance (Glassman 1977a, 1977b, 1978a, 1978b). Since its origin during the Precambrian, the Brazilian Shield has undergone considerable erosion by numerous river systems. With few exceptions (discussed below), populations of O. phalerata from eastern Bolivia to the eastern portions of the Amazon Basin are connected by watersheds to the Brazilian Shield. Throughout its range, O. phalerata is largely confined to floodplains, river valleys, and former deltas, which lends support to the idea of dissemination by rivers. Although their high specific gravity (ca. 1.4 g fresh weight/ cm3) prevents the fruits from floating, they can be carried considerable distances by runoff and rivers in flood (Anderson and Anderson 1983).

There are three important exceptions to the links between the Brazilian Shield and the present range of *Orbignya phalerata*. The first is its disjunct occurrence in Surinam (fig. 3). Until the early Pleistocene, the eastern portions of the Brazilian and Guayana Shield were connected, which probably accounts for the close floristic ties between the two regions (Maguire 1970). The Guianas represent a second center of diversity of the entire *Attalea* alliance (Wessels Boer 1965).

A second exception is the occurrence of O. phalerata in the Brazilian states of Maranhão and Piauí (figs. 1, 3). Markley (1971) suggested that the Tocantins River may have once served as a link for dissemination of the palm to these states. The Tocantins has its headwaters in the Brazilian Shield and presently drains into the Amazon River. During the Cretaceous, however, it may have flowed across the northern part of Maranhão into the Atlantic and built up the huge delta that presently covers most of the northern third of the state. It seems unlikely that this delta could have been built by the relatively insignificant rivers of Maranhão that exist today (Pindaré, Mearim, Itapecuru, and Parnaíba), most of which have their headwaters only a short distance from the delta. Uplift of

the Serra do Gurupí in western Maranhão (probably during the lower Tertiary) may have forced the Tocantins to change to its present course.

A final anomaly in the distribution of *O. phalerata* is its disjunct occurrence in the Brazilian state of Ceará (figs. 1, 3). Here the palm is confined to isolated and geologically very old uplifts, which are not connected by river systems with the Central Brazilian Shield. These uplifted areas have long served as favorable sites for human settlement and agriculture, due to their relatively cool temperatures, high rainfall, and fertile soils. Markley (1971) argued that babassu's occurrence in Ceará is due to dissemination by humans from the Parnaíba valley 200–300 km distant.

Hybridization and Intrinsic Genetic Variation. The results of our study show that both Orbignya phalerata and O. oleifera each appear to have a strong propensity to hybridize. Probably as a result, both species exhibit high morphological variability.

In at least one character, this can be attributed to intrinsic genetic factors unrelated to hybridization, as illustrated in a comparison of the distribution of androgynous (but functionally female) inflorescences per palm in six populations of babassu (fig. 7). Five of the six sites represented populations of O. phalerata; the southerly site represented a population of O. oleifera. Despite a wide range of ecological conditions, the four contiguous populations in Maranhão (forest and pasture at Lago Verde, wet site at Pindaré Mirím, and dry site at Caxias) showed no differences in the distribution of female inflorescences per palm, according to the Kolmogorov-Smirnov Test (Siegel 1956). However, distributions in the two geographically disjunct populations (northerly site in Goiás and southerly site in Minas Gerais) were significantly different from the first four populations, as well as from each other ($P \le 0.01$ in all cases). These results suggest that the distribution of female inflorescences per palm in populations of babassu is governed by genetic factors.

Characteristics unique to the population of *Orbignya oleifera* in Pirapora, Minas Gerais, could have important implications for genetic improvement of babassu. The exceptionally high percentage of female (i.e., fruit bearing) inflorescences in this population results in high fruit

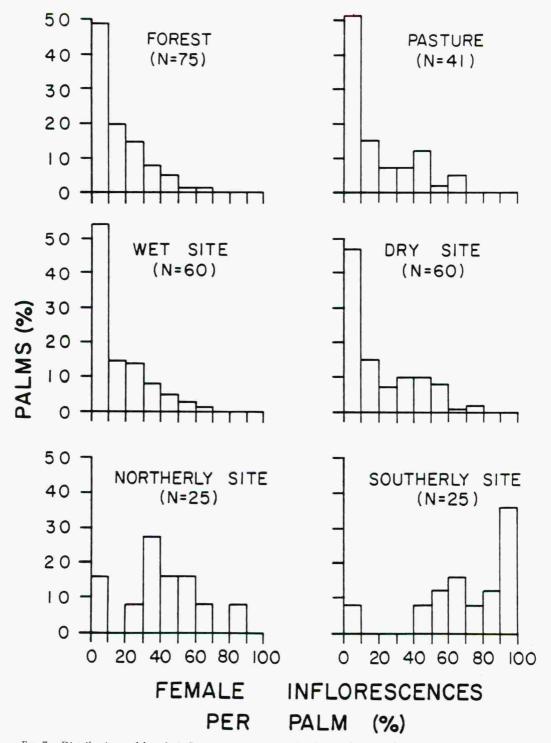


Fig. 7. Distributions of female inflorescences per palm in six populations of babassu in Brazil. Forest and pasture site = Lago Verde, Maranhão; wet site = Pindaré Mirím, Maranhão; dry site = Caxias, Maranhão; northerly site = Tocantinópolis, Goiás; and southerly site = Pirapora, Minas Gerais. N = number of palms observed per site. Source: Anderson and Anderson (1983).

production, estimated at approximately 5 or more tons per hectare (Balick, unpubl. data), compared to mean yields of ca. 1.5 tons per hectare for O. phalerata in Maranhão (STI 1979). In addition, kernels account for up to 18% of total fruit weight in the O. oleifera population (J. M. F. Frazão, pers. comm.), compared to a mean 7% in O. phalerata (see fig. 2). As a result, kernel and consequently oil yields of O. oleifera are potentially many times those of O. phalerata. Merely introducing the former into plantations could thus produce significant increases in vields, even in the absence of further selection or subsidies such as fertilizers and pesticides. In addition to higher yields, apparently precocious individuals have been observed that could attain maturity far more rapidly than the estimated minimal time span of 12 years usually required by babassu palms growing on open sites. One of the putative hybrids of babassu, the so-called Orbignya teixeirana (Appendix 2), is tolerant of soils that are infertile and relatively dry. While collecting taxonomic specimens, seeds from promising individuals and/ or from representative populations have been obtained and subsequently introduced into babassu germplasm banks administered by the Centro Nacional de Recursos Genéticos (CEN-ARGEN).

CONCLUSION

Coupling of taxonomic and agronomic research on babassu has provided a basis for genetic improvement of the complex. The direction that this improvement takes will probably be determined by babassu's unique characteristics. Because of its wide adaptability and capacity to form high density stands with little or no intentional human effort, the babassu complex appears to be especially promising for extensive land use systems rather than intensive plantations, at least within its native range.

Elucidating precise relationships on the species level is the greatest challenge facing palm taxonomists today (Tomlinson 1979). Although babassu is singular in its capacity to dominate the landscape, we suspect that its high morphological, intraspecific variability will prove to be a common theme in groups of palms currently thought to be comprised of many species. In economic palms such as babassu, this variability provides a unique opportunity for combining basic and applied research, which

can lead to deeper insight concerning the biology and utilization of these poorly known plants.

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46

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APPENDIX 1. A selective morphological comparison of *Orbignya phalerata, Maximiliana maripa*, and the putative hybrid, *Markleya dahlgreniana*.

Character	O. phalerata	Hybrid	M. maripa
Leaf			
Arrangement of leaf bases	spiralled	spiralled, in 5 ver- tical rows	spiralled in 5-7 ver- tical rows
Sheath			
—length in adults (cm) —abaxial surface	560-860 usually with pro- nounced stria- tions	603–817 usually with faint striations	420–490 without striations
Petiole			
—length in adults (cm) Pinnae	8-42	64-110	90-240
— number per side — orientation	156–208 in same plane	208–264 in same plane to moderately cris- pate	209–473 crispate
—arrangement	regular	in groups of (1)2-5	in groups of (2)3-7(14)
Staminate inflorescence			
Peduncular bract Rachilla	slightly curved	moderately curved	strongly curved
—length of subtending bract (mm)	0.5-6.0	1.5-2.5	0.5-1.0
 number of subtending bracts arrangement of staminate flowers 	in longitudinal rows on abaxial	142–190 in irregular rows on abaxial side	107-273 spiralled
	side		
Androgynous inflorescence Rachilla			
—length (cm)	10-24	10-15	10.5-14.5
 —length of subtending bract (mm) —number of pistillate flowers per rachilla 	2-14 1-2(3)	3-4 2.5	6–12 4–9
Staminate flowers			
Sepals			
—shape	lanceolate to del- tate	deltate	triangular
—length (mm)	0.8-2.5	0.6-1.2	0.4-1.5
—width (mm) Petals	0.6-2.3	0.5-0.7	0.3-1.0
—number	2(3)	3(4-7)	3
—orientation	incurved	slightly incurved	straight
—length (mm) Stamens	9.5-16.9	3.4-6.8	2.1-3.7
—number	(21)24-26(30)	6-11	6(8)
—orientation of thecae	irregularly coiled and twisted	straight to irregu- larly coiled and twisted	straight
Pistillate flowers			
Corolla			
—length of sepals (cm)	2.8-4.1	1.9-2.5	1.2-1.5
—length of petals (cm)	2.3-5.0	2.5-3.0	1.8-2.3

APPENDIX 1. Continued.

Character	O. phalerata	Hybrid	M. maripa
Fruit			
Shape	broadly elliptic to oblong	elliptic	elliptic to ovate
Length (cm)	6.6-12.5	6.5-7.0	4.0-4.5
Width (cm)	3.7-9.9	3.2-3.8	2.4-2.6
Length of calyx (cm)	3.8-5.8	3.5-4.5	ca, 2.5
Length of staminodial tube (cm)	2.0-4.0	1.2-1.5	ca. 0.5
Thickness of epicarp (mm)	1.0-4.0	1.0-1.5	0.5-0.8
Thickness of mesocarp (mm)	2.0-12.0	2.5-3.0	0.5-1.5
Consistency of mesocarp	mealy, dry	slightly oily	oily
Diameter of endocarp (mm)	35-76	21-27	18-24

APPENDIX 2. A selective morphological comparison of *Orbignya phalerata*, O. eichleri, and their hybrid, O. teixeirana.

Character	O. phalerata	Hybrid	O. eichleri
Stem			
Length in adults (cm)	500-3000	0-800	0
Diameter (cm)	19-50	19-42	0
Leaf			
Number per palm	10-25	8-13	3-8
Sheath			
—length in adults (cm)	40-120	30-100	20-33
—striations on abaxial surface	generally present	present or absent	absent
Petiole	0.40	17 00	
—length in adults (cm) Rachis	8-42	17-80	30-80
—cross section in middle	4-sided	4-sided	triangular
—abaxial surface	weakly to strongly	weakly lepidote	smooth
	lepidote	wearing represent	
Pinnae			
—number per side	156-208	96-190	63-128
—orientation	in same plane	in same plane to crispate	crispate
—disposition	regular	clustered to regu- lar	clustered
—adaxial surface	dull to lustrous	dull	dull
—abaxial surface	weakly glaucous	weakly glaucous to smooth	mostly smooth
Inflorescence			
Bracts			
-length of prophyll (cm)	50-150	30-33	20
 length of acumen of peduncular bract (cm) 	16-40	3–20	3-12
 abaxial surface of peduncular bract 	tan to rust-brown	blood red	blood red
Peduncle			
—length (cm)	56-180	37-95	5-37
—curvature	not recurved	weakly to strongly recurved	strongly recurved
Rachilla —number on staminate	277-401	41-50	15-35
inflorescence	2//-401	41-30	15-55
 number on androgynous inflorescence 	323-475	20-70	10-20
—attachment to rachis	throughout	on abaxial side only	on abaxial side only
—length of subtending bract (mm) Staminate flowers	0.5-14	0.5-30	1.0-45
—stamens per flower	(21)24-26(30)	(18)20-25(26)	14-18(20)
Pistillate flowers	V - 2 V - 2 - 2 V 2 2 V	Account markers	//
—length of sepals (mm)	2.8-4.1	2.4-3.5	1.9-3.5
—length of petals (mm)	2.3-5.0	2.2-3.4	1.3-2.8
Fruit			
Weight (g)	40-410	18-210	10-50

APPENDIX 3. A selective morphological comparison of *Orbignya oleifera* Burret, *Attalea compta* C. Martius, and their putative hybrid.

Character	O. oleifera	Hybrid	A. compta
Stem			
Diameter (cm)	31-53	35-40	20-32
Leaf			
Length of petiole (cm)	0-10	5-10	10-20
Arrangement of pinnae	regular except at extreme base of rachis	regular except at base of rachis	regular except at base meter of rachis
Length of rachis (cm)	625-750	537-550	413-657
Inflorescence			
Length of acumen on peduncular bract (cm)	28-52	17-20	13–33
Androgynous inflorescence			
Rachilla			
—length (cm)	2-3	9-12	5-15
—position of pistillate flowers	0–2 cm above in- sertion on rachis	2.5-4 cm above in- sertion on rachis	ca. 5 cm above inser- tion on rachis
Staminate flower			
Corolla			
—texture of sepals	membranous to co- riaceous	membranous to slightly coria- ceous	membranous
—number of petals	2(3)	(2)3	3
—shape of petals	narrowly elliptic to ovate	narrowly elliptic to ovate	lanceolate
Stamens			
—number	28-32(37)	11-20	11-12
-attachment of thecae to filaments	at midpoint	almost throughout length	throughout length
—orientation of thecae	irregularly twisted and coiled	more or less straight to twist- ed and coiled	straight
Fruit			
Length (cm)	13-14	9.2~10.0	7.8-9.4
Width (cm)	7.5-8.0	4.3-6.7	4.9-5.3
Shape	broadly elliptic to oblong	elliptic	obovate
Dry weight (g)	152-404	110-176	76-96
Channelling on surface	absent	moderate	pronounced
Maximum length of calyx (cm)	7.0-7.5	5.2-7.2	4.0-5.0
Color of mesocarp	white	yellow	orange
Consistency of mesocarp	dry	dry to oily	oily
Diameter of endocarp (cm)	5.1-7.6	4.0~5.2	3.7-4.1