

Systematic and Agro-ecological Studies in the Attaleinae (Palmae)

by

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Volume 1. Systematic Studies

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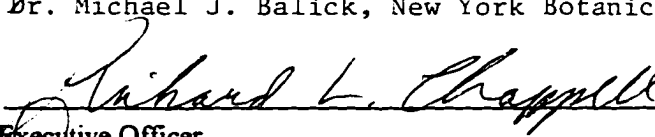
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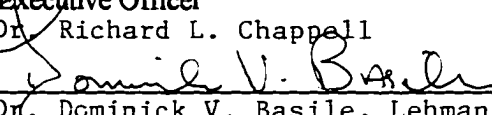
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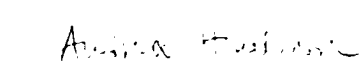
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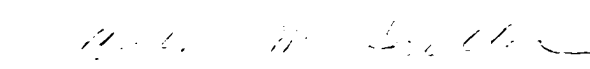

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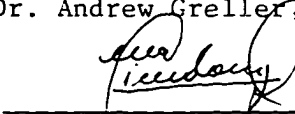
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Abstract**Systematic and Agro-ecological Studies in the Attaleinae (Palmae)****by****Claudio Urbano Bittencourt Pinheiro**

Chairman: Michael J. Balick

In Northeastern Brazil, palms play an important role in the lives of tens of thousands of people. More than a source of income for people, these plants are of great ecological importance, for their persistence as the main coverage of the soil where other less resilient species have failed. To study the palm species in the subtribe Attaleinae two lines of research were undertaken:

1. Systematic Studies. To provide new elements for the understanding of the taxonomic status of the species in the subtribe Attaleinae, a study of the leaf anatomy of representative species was carried out. The generic classification of the Attaleinae is discussed in view of the results obtained from the multivariate and cladistic approaches applied to the anatomical data collected. The results showed a significant discontinuity in the variation pattern within the subtribe Attaleinae. Groups could be separated on the basis of results from multivariate and cladistic analyses of the anatomical characters, and a high number of intermediates identified.

Multivariate analyses showed discontinuity in the patterns of variation among characters, between characters and taxa, and supported the separation of groups. The multivariate analyses showed the extreme complexity of character variation within the subtribe, particularly when a number of putative hybrids and intermediates were included. The subtribe was characterized as a monophyletic group, which diversified in three or four evolutionary directions. Overall, the results indicated that hybridization may have been a very important mechanism of speciation within the *Attaleinae*.

2. Agro-ecological Studies. This research comprised two experiments geared towards improving the management and cultivation of the babassu palm. The first experiment was set up in the *Cocaís* region of the northeastern Brazilian state of Maranhão, as a continuation of long-term studies on seed germination and nursery management. It was designed to measure the responses of babassu seedlings to different types of soil and levels of fertilization. The second experiment tested the establishment of babassu in degraded soils in the pre-Amazon region of Maranhão. It confirmed the relative ability of the babassu palm to overcome unfavorable ecological conditions such as competition, low soil fertility and degradation, and ultimately its potential use for reforestation.

DEDICATION

This dissertation is dedicated to Maria José (Zeca), my best friend, a great wife, and a devoted mother; and to my children Thales, Thalia, and Claudio Filho, the major reasons for so much effort.

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I. Systematic Studies

1. Introduction

The Subtribe *Attaleinae* - History of the Generic Delimitation

Attalea was described by Humboldt, Bonpland and Kunth (1816), with one species, *A. amygdalina*. The genus was accepted by Martius (1824, 1837) who described two closely related genera: *Maximiliana* (1826) and *Orbignya* (1837). Karsten (1857) described a new genus, *Scheelea*, which was not accepted by Drude (1881). Burret (1929) carried out the first taxonomic revision of the tribe *Attaleae*, which included the genera *Attalea* Humboldt, Bonpland et Kunth, *Maximiliana* Martius, *Orbignya* Martius ex Endlicher, and *Scheelea* Karsten. Burret (1929) treated *Attalea* and *Scheelea* as natural and distinct genera, and *Attalea* and *Orbignya* as closely related genera that could be distinguished only by the staminate flowers. He saw *Maximiliana* as closely related to *Scheelea*. Correlation between floral and fruit characters was attempted by Barbosa Rodrigues (1903) and Burret (1929). Later, two new genera were added to the tribe: *Parascheelea* Dugand (1940) and *Markleya* Bondar (1957).

Delimitation of the genera in this subtribe has always been controversial, mostly because of their remarkable overall morphological similarity and the high phenotypic plasticity of many characters, this apparently related to the edaphic and hydric conditions of their habitats (Bondar, 1942, 1964). Additionally, the high propensity for both interspecific and intergeneric hybridization in the wild makes the situation even more confusing. Tomlinson (1961) found no anatomical evidence for separating the genera; on the contrary, using anatomical characters, he could not even separate species considered as belonging to different genera. Confusion was exacerbated by the lack of complete collections of these palms, and many descriptions were based on insufficient material and their improper identification.

The intermediate types of staminate flowers described by Bondar (1957) for Markleya, made the separation even more confusing and provided additional evidence for the lumping the of the genera in the Attalea alliance into the genus Attalea: if the type of staminate flower in Markleya is the result of hybridization, the large uniform and fertile populations of this hybrid contradict the generic separation (Wessels Boer, 1965).

Wessels Boer (1965) defended the practical importance of classifying the doubtful species as a single genus; instead of 5 or 6 questionable genera. The recognition of a single one would avoid new equivocal and useless combinations. He recognized seven species of Attalea from Surinam, but within this genus he included the other

closely related genera Orbignya, Maximiliana, Scheelea, Markleya, and Parascheelea. Moore (1966) disagreed with Wessels Boer by arguing that the genera segregated from Attalea could be properly distinguished on the basis of the staminate flower morphology, and by using the morphology of the inflorescences as well. He saw no justification for adopting a single genus classification simply because staminate flowers could not be obtained according to the collector's convenience. In relation to the variation shown by the staminate flowers of Maximiliana (Wessels Boer, 1965), Moore (1966) considered this apparent variation to be the result of the use of different collections. That apparent variation would be more convincing if the flowers discussed by Wessels Boer originated from the same inflorescence, but this was not the case. The flowers were from different collections, even though each type showed uniformity within each inflorescence. Overall, Moore (1966) disagreed with the generic and specific concepts used by Wessels Boer (1965), considering them unusually broad. Later, Moore (1973) placed the genera Attalea, Scheelea, Parascheelea, Orbignya, and Maximiliana in the cocosoid group in the Cocos alliance within the Attalea unit, which corresponded to the tribe Attaleeae of the subfamily Coccoideae in the traditional scheme of Potztl (1964). He placed Bondar's genus Markleya as a putative hybrid.

In his preliminary study on the taxonomy of the genus Attalea, Glassman (1977a) considered all genera as distinct and valid, although he recognized some of Wessels Boer's arguments as valid. He urged that some other characters be found

for their proper and unquestionable differentiation. The dichotomous keys for distinguishing the genera proposed by Glassman (1977a, 1977b, 1977c, 1978) are still based on the morphology of the staminate flower. Uhl and Dransfield (1987) included the genera in the subtribe Attaleinae within the tribe Cocoeae of the subfamily Arecoideae; Parascheelea was subsumed under Orbignya. Uhl and Dransfield (1987) considered generic lumping premature because too little was known about these genera, but they conceded that the genera as traditionally delimited could be distinguished only if staminate flowers were present. Henderson and Balick (1991) resumed the discussion on the generic limits stating that many other characters, including pistillate flowers, leaves, fruits and habitat, do not correlate with staminate flower morphology. Characteristics of staminate flower were shown to be of limited value for separation of the genera, since intermediate types occur. More recently, Henderson (1995) followed Boer's morphological-geographic approach, and lumped all five genera into Attalea.

The Morphological Separation of the Genera

The subtribes in the tribe Cocoeae (Bactridinae, Butiinae, Elaeidinae, and Beccariophoenicinae) usually have only androgynous inflorescences on the same plant. The exception is the Attaleinae, which can be distinguished from the others by having staminate and androgynous inflorescences, usually on the same plant.

Glassman (1977a, 1977b, 1977c, 1978) recognized 69 species in the subtribe Attaleinae, distributed as follows: Orbignya (11 species); Attalea (25); Scheelea (31); Maximiliana (1); and Markleya (1). Uhl and Dransfield (1987) recognized 20 species of Orbignya, 22 species in Attalea, 28 species of Scheelea, and 1 in Maximiliana. These numbers are much smaller if one follows the classification by Henderson et al. (1995): only 29 species are recognized as valid in the subtribe, all in the genus Attalea.

A few principal morphological characters have been used to separate the genera in the Attaleinae (Glassman, 1977a, 1977b, 1977c, 1978; Uhl and Dransfield, 1987), including:

- . Number of stamens: 6 - 57 per flower in Orbignya, 6-75 in Attalea, and consistently 6 in Scheelea and Maximiliana.
- . Shape of anther: coiled in Orbignya and straight in the other genera.
- . Number, shape and consistency of petals: ranging from 1-8; from lanceolate to spatulate to fleshy hooked tips in Orbignya; usually 3, linear, and fleshy in Scheelea; usually 3, lanceolate, not fleshy, and usually longer than stamens in Attalea; and finally, also 3 in number, but much shorter than the stamens in Maximiliana.

The Use of Leaf Anatomy as a Taxonomic Tool in Palms

Tomlinson (1961) considered that leaf anatomical characters alone could not normally be used to distinguish palms at the specific level, but he believed they were of value, especially at the generic level when combined with other lines of evidence such as morphology. A number of workers have used leaf anatomy coupled with morphological evidence to assist in distinguishing palms at the specific level (e.g., Syagrus (Glassman, 1972); Chelyocarpus (Uhl, 1972); Thrinax (Read, 1975); Hyophorbe (Uhl, 1978); Orbignya (Balick et al., 1987); Ammandra, Palandra, and Phytelephas (Barfod, 1988); Aiphanes (Borchsenius and Bernal, 1996), and Euterpe, Prestoea, and Neonicholsonia (Henderson and Galeano, 1996).

Tomlinson (1961) was the first investigator to publish information on leaf anatomy of Orbignya, Attalea, Maximiliana, and Scheelea. He found the leaf anatomy of Attalea very similar to that of Scheelea and Maximiliana, but different from Orbignya. All anatomical evidence in this study was confined to the generic level, and a maximum of two species was used for each genus, all of them cultivated in botanical gardens.

At least four hybrids have been described within the Attaleinae, but only one has had its hybrid status confirmed (Balick et al., 1987) and that is Orbignya x teixeirana

(Bondar) Balick, Pinheiro & Anderson (Orbignya phalerata Martius x O. eichleri Drude). This was done by using both anatomical and morphological comparisons. This study showed the validity of the use of leaf anatomy as a tool for taxonomic studies, both at the generic and specific levels.

To provide new elements for the elucidation of the taxonomic status of the species in the subtribe, an anatomical study of the leaf of selected representative species in each of the five genera in the group, including the putative hybrids, was carried out. For each genus, except for the monotypic Maximiliana and Markleya, a number of species were used for anatomical studies (Table 1).

Based on previous experience, and on results reported in the few anatomical studies carried out on palm species, the hypothesis that leaf anatomy can strongly contribute to the elucidation of taxonomic problems in this group of palms, especially at the generic level, is presented and tested here. This work was undertaken to produce evidence either to support the lumping, or to show that anatomical groups can be distinguished within the subtribe, and that these groups fall or do not fall, totally or partially, into the traditional taxonomic circumscription of the former genera. Additional expected results included: 1) leaf anatomical descriptions for the taxa studied; 2) a tentative generic delimitation of the subtribe by using taximetric techniques; 3) a phylogenetic analysis of the group based on anatomical characters; and 4) confirmation of the status of the purported hybrids included in this study.

2. Material and Methods

2.1. Preparation of Leaf Material

a. Sampling

Specimens were selected primarily on the basis of their more accepted validity as species, and at the same time, adequate representativeness from the formerly recognized genera in the subtribe was sought. Availability of specimens at the herbarium of the New York Botanical Garden (NYBG) also determined the scope and size of the sample used. Three herbarium specimens collected from different locations and different habitats were used to represent each selected taxon. A total of 30 species of the subtribe Attaleinae from the palm collection of the NYBG were examined. These included 12 species of Orbignya, 10 species of Attalea, 4 species of Scheelea, Maximiliana maripa, and Markleya dahlgreniana. (Table 1). Besides M. dahlgreniana, three other putative hybrids were included to be investigated: Attalea x piassabossu (Attalea burretiana (= A. oleifera) x A. funifera); x Attabignya minarum (Orbignya oleifera x Attalea compta); and Attalea colenda (unknown species of Orbignya and Attalea; Glassman, unpublished). Three species of Syagrus (subtribe Butiinae) were also included in this study for their potential use as outgroups in a phylogenetic analysis of the Attaleinae. The identity of the specimens used was that as determined by specialists.

A total of 78 specimens were prepared and examined using three microtechniques: cross sections, epidermal peels and clearings. Information on the specimens studied is provided in Table 1. The material used in the preparation of the anatomical sections was removed from the middle portion of a pinna along the middle of the leaf. A piece, ca. 4 cm wide, including one side of the pinna plus the midrib was taken from herbarium specimens. This sample was cut into 4 smaller pieces at this point, but this can be done later on, after rehydration of the material. The four pieces cut had the following sizes and destinations: two 0.5 cm pieces for cross sections (one a spare for when the preparation was unsuccessful); one 1.0 cm piece for the epidermal peels (an extra piece may be advisable, since handling of peels during washing, staining and mounting was a difficult task, which often resulted in loss of material); and one 2.0 cm piece cleared and used in the study of venation patterns.

For the preparation of palm leaf cross sections the samples were treated according to the methodology described by Martens and Uhl (1984). Epidermal peels were made following the techniques described by O'Brien and McCully (1981). Venation patterns were analyzed in samples cleared according to the technique described by Martens and Uhl (1984). The large number and varying nature of specimens used required several modifications and adaptations to be made to the original methodology for all three techniques used. The most important steps of the modified methodology used for the three techniques are briefly described below.

Table 1. Taxa and specimens used in the study, with local of collection, collector's name and number.

Genus	species	Origin	Code#	Collector	Number
Orbignya	phalerata	Bolivia	OPH-01	Balick	1367
Orbignya	phalerata	Brazil (Pará)	OPH-02	Balick	961
Orbignya	phalerata	Brazil (M. Grosso)	OPH-03	Balick	1946
Orbignya	oleifera	Brazil (M. Gerais)	OO-04	Balick	1684
Orbignya	oleifera	Brazil (Bahia)	OO-05	Noblick	4645
Orbignya	oleifera	Brazil (Bahia)	OO-06	Noblick	4679
Orbignya	brejinhoensis	Brazil (Bahia)	OB-07	Noblick	4515
Orbignya	brejinhoensis	Brazil (Bahia)	OB-08	Noblick	4385
Orbignya	brejinhoensis	Brazil (Bahia)	OB-09	Noblick	4614
Orbignya	eichleri	Brazil (Maranhao)	OE-10	Balick	1319
Orbignya	eichleri	Brazil (Tocantins)	OE-11	Balick	1597
Orbignya	eichleri	Brazil (M. Grosso)	OE-12	Henderson	811
Orbignya	luetzelburgii	Venezuela	OL-13	W. Boer	2374
Orbignya	luetzelburgii	Venezuela	OL-14	W. Boer	2357
Orbignya	polysticha	Peru	OPO-15	F. Kahn	1724
Orbignya	polysticha	Brazil (Amazonas)	OPO-16	Henderson	833
Orbignya	polysticha	Venezuela	OPO-17	W. Boer	2273
Orbignya	sagotii	French Gyiana	OSA-18	S. Mori	14954
Orbignya	sagotii	Brazil (Pará)	OSA-19	Lobo	109
Orbignya	sagotii	Suriname	OSA-20	W. Boer	165
Orbignya	cohune	Honduras	OCO-21	Balick	1720
Orbignya	crassipatha	Haiti	OCR-22	Henderson	805
Orbignya	crassipatha	Haiti	OCR-23	Zanoni	26102
Orbignya	cuatrecasana	Colombia	OCU-24	Balick	1637
Orbignya	cuatrecasana	Colombia	OCU-25	Gentry	47842
Orbignya	cuatrecasana	Colombia	OCU-26	Balick	1630
Orbignya	guacuyule	Mexico	OG-27	Pennington	9488
Orbignya	spectabilis	Brazil (Pará)	OSP-28	Pardini	70
Orbignya	spectabilis	Suriname	OSP-29	W. Boer	1503
Orbignya	spectabilis	Brazil (Amapá)	OSP-30	S. Mori	17421
Scheelea	phalerata	Peru	SP-31	F. Khan	2148
Scheelea	phalerata	Brazil (Goiás)	SP-32	Noblick	4864
Scheelea	phalerata	Brazil (Pará)	SP-33	Noblick	5018
Scheelea	insignis	Brazil (Amazonas)	SI-34	Henderson	856
Scheelea	insignis	Brazil (Amazonas)	SI-35	Pardini	20
Scheelea	insignis	Brazil (Amazonas)	SI-36	Henderson	821
Scheelea	butyracea	Venezuela	SB-37	W. Boer	1990
Scheelea	butyracea	Brazil (Acre)	SB-38	Henderson	1648
Scheelea	butyracea	Ecuador	SB-39	H. Balslev	4339
Scheelea	attaleoides	Brazil (Amazonas)	SA-40	Prance	17572
Scheelea	attaleoides	Suriname	SA-41	W. Boer	1431
Scheelea	attaleoides	Brazil (Amazonas)	SA-42	Henderson	1170

Table 1. (Cont'd)

Genus	species	Origin	Code#	Collector	Number
Attalea	oleifera	Brazil (Bahia)	AO-43	Noblick	4595
Attalea	oleifera	Brazil (Bahia)	AO-44	Noblick	4855
Attalea	oleifera	Brazil (Bahia)	AO-45	Noblick	3733
Attalea	dubia	Brazil (Sao Paulo)	AD-46	Krapovickas	23154
Attalea	dubia	Brazil (Sao Paulo)	AD-47	Pardini	83
Attalea	funifera	Brazil (Bahia)	AF-48	A. Amorim	1160
Attalea	funifera	Brazil (Bahia)	AF-49	Noblick	4245
Attalea	funifera	Brazil (Bahia)	AF-50	A. Amorim	1531
Attalea	geraensis	Brazil (M. Gerais)	AG-51	J.G. Vieira	421
Attalea	geraensis	Brazil (M. Gerais)	AG-52	Noblick	4851
Attalea	geraensis	Brazil (Bahia)	AG-53	Noblick	4524
Attalea	humilis	Brazil (Bahia)	AH-54	S. Mori	9611
Attalea	humilis	Brazil (Bahia)	AH-55	Noblick	3732
Attalea	pindobassu	Brazil (Bahia)	AP-56	Noblick	4604
Attalea	pindobassu	Brazil (Bahia)	AP-57	Noblick	3828
Attalea	nucifera	Colombia	AN-58	Galeano	1276
Attalea	nucifera	Colombia	AN-59	Renteria	1499
Attalea	tessmannii	Brazil (Acre)	AT-60	J. Jangoux	85027
Attalea	tessmannii	Peru	AT-61	P. Nuñez	14976
Attalea	tessmannii	Brazil (Acre)	AT-62	Henderson	1656
Attalea	racemosa	Peru	AR-63	R. Vásquez	14323
Attalea	racemosa	Venezuela	AR-64	W. Boer	1894
Attalea	racemosa	Colombia	AR-65	Torres	3206
Maximiliana	maripa	Peru	MM-66	Gentry	52306
Maximiliana	maripa	Suriname	MM-67	W. Boer	1329
Maximiliana	maripa	Brazil (Pará)	MM-68	Balick	960
Markleya	dahlgreniana	Suriname	MD-69	W. Boer	805
Markleya	dahlgreniana	Brazil (Pará)	MD-70	Balick	1305
Markleya	dahlgreniana	Brazil (Maranhao)	MD-71	Pinheiro	899
Attalea	colenda	Ecuador	YC-72	Balslev	62027
Attalea	colenda	Ecuador	YC-73	Blicher-Mathiesen	62617
Attalea	piassabossu	Brazil (Bahia)	AXP-74	Noblick	4508
Attabignya	minarum	Brazil (M. Gerais)	AXM-75	Balick	1694
Syagrus	amara	Dominica	SYA-76	S. Hill	24818
Syagrus	comosa	Brazil (M. Grosso)	SYC-77	H.S. Irwin	6525
Syagrus	cocoides	Brazil (Tocantins)	SC-78	Balick	1616

b. Rehydration and Fixing

The herbarium material used was rehydrated in a solution of glycerin alcohol , 10% aerosol OT, and distilled/deionized water (10:3:87) and kept overnight in a vacuum chamber at -20 psi, to aid penetration of the solution. Samples were then washed in 3 changes of deionized water and then treated according to the procedures for the different techniques as follows: samples for cross sections were fixed in FAP (formalin, propionic acid, 50% ETOH; 5:5:90) for 48 hours and then stored in a glycerin alcohol solution (1 part glycerin, 6 parts 70% ETOH) for at least one week for initial softening; samples for epidermal peels and clearings were stored in glycerin alcohol immediately after rehydration until use.

c. Cross Sections

Preparation of the material for the study of cross sections included rehydration, fixing, desilification, softening, embedding in Paraplast Plus, and sectioning. Desilification is crucial for successful sectioning of the material. This was achieved by treating the samples with a solution of glycerin alcohol and hydrofluoric acid (2:1) for a period of 6 days which worked well for all specimens. However, due to the large sample size and the differences in the hardness of the material used, some samples could possibly stay longer in the acid treatment, for better results. From my

observations though, this treatment should not be longer than ten days, since cells walls may collapse, ruining the preparation. After the acid treatment, samples were washed in running water for 24 hours, before embedding and sectioning. Before sectioning, additional softening in glycerin alcohol for at least 2 weeks is strongly recommended. This can be done right after the acid treatment, or later, after embedding the material in Paraplast and cutting of the blocks. These can be stored directly in glycerin alcohol for extra softening. If time is not a problem, additional softening after the acid treatment, and after embedding as well, is recommended.

Embedding of the samples in Paraplast Plus followed a protocol using a Toluene series, although a standard series of tertiary butyl alcohol (TBA) was recommended by Martens & Uhl (1980). Changes of solution in the Toluene series (Appendix I) were made at 1-hour intervals, accompanied by vacuum aspiration up to 100% Toluene; from this point, samples were left in the solution for at least 12 hours, in each remaining step of the series. At this point, the blocks were stored in glycerin alcohol for additional softening, for at least two weeks. As mentioned, softening of the material after the HF acid treatment is very important for its successful sectioning. The embedded material was sectioned with an A. O. Spencer 820 Rotary Microtome in 15 μ sections. Sections from palm leaves are known to have difficulty in affixing firmly to slides, and often fall off during staining. To solve this problem, the modification of the Sass' adhesive recommended by Martens and Uhl (1980) was tried. The results were not totally satisfactory as some sections continued to fall off.

A combination of two adhesives solved the problem completely. Sections were allowed to float in Sass' adhesive in a petri dish, while a thin layer of Haupt's adhesive was put on the slide and spread out with a finger. This was followed by the placement of a layer of 4% formalin on the slide with the adhesive. Sections were transferred from the petri dish to the slide (with the use of a paintbrush), and then allowed to dry overnight. A modified standard dehydration-staining series for 0.5% aqueous Safranin and Fast Green was used (Appendix II). A minimum of three hours in Safranin and not longer than 20 seconds in Fast Green, produced the best stainings. The only problem found by using the two-adhesive method was that the Haupt's adhesive gets stained by Fast Green, and cleaning the slide becomes necessary before it can finally be mounted. Scraping the slide with a razor blade around the sections and rinsing with Hemo-De removes the undesirable green staining on the slide. Kleermount was used as the mounting medium.

d. Epidermal Peels

Samples for epidermal macerations (1.0 cm wide, including leaf margin) were taken out of the glycerin alcohol solution (where they were stored after the rehydration procedure), and washed three times for 15 minutes each in deionized water. The bleach procedure for macerations recommended by Martens and Uhl (1980) did not produce good results with my samples: 1) peels did not separate well; 2) when separated, the peels were very fragile and easily damaged during handling;

3) distortions to cells (especially guard-cells) occurred making them dark, and giving them a “burned” look. Because of the overall unsatisfactory results of this method, Jeffrey’s Solution was used instead of bleach. Samples were left in Jeffrey’s solution for a period of 4-5 days, at which point the epidermis were almost entirely separated. Final separation was achieved during washing (three times, 15 minutes each). Only one change of solution was made (after 48 hours); this accelerated the separation and allowed better handling of the peels during washing, since the first solution becomes very dark, and peels cannot be seen well, thus increasing the risk of their loss during washing. The washed samples were covered in the vials with 0.5% aqueous Safranin and left to stain overnight. For mounting, samples were moved to a petri dish with water (to wash out the excess Safranin), and then put through a modified dehydration series (Appendix III). The use of a paintbrush for handling the samples during the entire procedure is recommended. Samples were mounted with Kleermount.

e. Clearings

Samples 2.0 cm wide were placed in 10% NaOH in an oven at 58°C overnight or longer until they were completely clear. For some, the overnight exposure was enough; for others, up to three days were necessary, and for a few, 8 days were required with a change of solution made after the third day. Samples were moved to 5% NaOH for further clearing. Samples should not be left in 10% NaOH for a long

time, because this made them brittle. They should be moved to a 5% solution if they are difficult to clear, and should stay longer in the clearing solution. When cleared, samples were washed in three changes of deionized water for 15 minutes each. Then they were placed in one-third strength commercial bleach until completely clear (usually 30-60 minutes, depending on the sample). Samples were washed again in three changes of deionized water (15 minutes each), placed in small petri dishes, covered with 0.5% aqueous Safranin, and left to stain for at least 30 minutes. Afterwards, the stained samples were moved to a petri dish with water (to wash out the excess Safranin), and dehydrated through the same modified series used for the epidermal peels (Appendix III). Samples were finally mounted with Kleermount.

2.2. Data Collection

“Those who look for differences between ‘species’ will surely find them” (Henderson et al., 1995). To avoid either subjective extreme or my own opinion on the generic controversy to interfere with my viewing of the data during its collection, the samples were treated on the same lowest level: as a large sample of specific entities united only by the same treatment given to their leaf material. No groups were formed “*a priori*”, and no names were assigned to the samples; only numbers to identify the specimens. This proved to be a useful strategy, since no differences (or similarities) were defined beforehand, unless they existed and were detected

during the examination of the specimens, which also did not follow a pre-determined order. Only after all specimens were examined and the data had been collected, a more nominal approach was applied to the sample. To understand the information obtained, the “ups and downs” within the range of the same specific entity (which consisted of three specimens), names had to be defined. The data was then sorted out still at the very lowest level, and descriptions were made for each taxon. Based on examination of the specimens, 87 anatomical characters (both quantitative and qualitative) were identified. A preliminary grouping based on a number of characters was attempted; however, no names were assigned for the preliminary groups formed, until they were submitted to the multivariate and cladistic analyses. Finally, the names of former genera were then applied to the anatomical groups. The exceptions to the anatomical groups ended up being even more interesting than those that fell into the generic/anatomical groups. These exceptions, discussed later, supported the hypothesis of the high propensity of these palms to hybridize in the wild, and showed the usefulness of leaf anatomy in the identification of such cases.

In order to be able to compare the Attaleinae specimens to other groups, three species of Syagrus were included in this study. The inclusion of this genus is also based on the fact that it belongs to a subtribe that is thought to be the closest to the Attaleinae (Uhl and Dransfield, 1987). Syagrus was then, a natural choice for an outgroup, in the study of the phylogeny of the Attaleinae. Another reason for

choosing was to investigate whether the morphological resemblance of Maximiliana maripa and Syagrus would correlate with their leaf anatomical structures.

Optimal methods and procedures for treating biological data have always been the goal of taxonomists, attempting to make their classificatory work more objective; some of these methods have always been available, but difficult due to the large amount of time and labor required. After computers and computer programs became more widespread, many of these methods are now used by biological researchers. Considering the availability of these electronic tools, I decided to use three different treatments for the data collected:

- 1) Descriptive Analysis - anatomical descriptions of taxa based on qualitative and quantitative characters, overall resemblance and differences within the sample.
- 2) Multivariate Analysis - a taximetric treatment of the data, for a more "objective" approach of the information collected. The data were subject to two multivariate analyses, principal components analysis and cluster analysis.
- 3) Cladistic analysis - study of the phylogeny of the subtribe using anatomical data.

2.3. Multivariate Analyses

Consistent evidence has been produced and reported in many papers that numerical methods can be extremely helpful in taxonomic work, in many different plant groups (Davis and Heywood, 1963; Clifford and Goodal, 1967; Gilmartin, 1967; Sneath, 1969; Prance et al., 1969; Clifford and Stephenson, 1975; Hassal, 1976). The development of the phenetic approach to classification has been for many considered greatly stimulating to taxonomy (Stuessy, 1990). One of its major contributions has been a better understanding of the characters used and their correlation in taxonomic work. Several statistical techniques have been designed or modified to search for taxonomic patterns in complex data sets. Duncan and Baum (1981) reviewed the use of these techniques and indicated that cluster analysis has been the most utilized by plant taxonomists.

This is probably the first account of a study in which taximetric techniques are used in the palm family. It is based on the anatomical data collected from 75 specimens of 30 species of the subtribe Attaleinae (plus three species of Syagrus). The data were analyzed by two methods utilizing JMP version 3.1.6.2 (SAS Institute, Inc., Cary, North Carolina) statistical package. Two main classes of analytical techniques were used in this study: ordination (principal component) and cluster analysis. In the principal components analysis (PCA), quantitative (continuous and meristic) and qualitative characters were analyzed separately and combined to

derive correlation matrices from which the components were extracted. In the cluster analysis, only the combination of quantitative and qualitative (double-state and multi-state) characters was used.

The purpose of these analyses were to test the existing classification of the species in the Attaleinae, produced by traditional taxonomic methods, to confirm the existence and the membership of the groups, and compare them, statistically, on the basis of the correlation of their characters and similarities among them. The complexity in the variation of patterns among characters could be first observed during collection and description of the data. To understand the patterns of character variation within the anatomical data set, the principal components method was used. Cluster analysis was used after PCA to study the grouping patterns of the groups of taxa. Details on advantages and constraints of the two methods (PCA and Cluster) are provided by Sokal and Sneath (1963), Prance et al. (1969), Pimentel (1979), and Grisp and Weston (1993).

A number of putative hybrids were included in the study, and the possibilities of new cases were examined. These possibilities were suggested by a number of “mixed” and/or conflicting patterns seen during collection and sorting of data, and confirmed after the first analysis with all taxa was performed. The specimens which fell into this category were termed “intermediates”, just as a way of distinguishing them from the others, for the purpose of analytical comparison only. Numerical

approaches have been used in the study of hybrids, and the two oldest and most widely used methods of studying introgression are the hybrid index (Anderson, 1949) and the pictorialized scatter diagram (Anderson and Gage, 1952). Both methods are based on the partial and interlocking linkage (multifactorial linkage) between quantitative characters. Multifactorial linkage and character coherence provide a basis for detecting and quantifying the effects of introgression (Grant, 1981). Refinements in the hybrid index method were made by several workers using several multivariate methods of analysis including: principal components (Namkoong, 1966; Olivieri and Jain, 1977); cluster analysis (Flake, Urbatsch, and Turner, 1978); and discriminant functions (Namkoong, 1966). Principal components and cluster analyses are both utilized to study character correlation, similarities, and dissimilarities between "good" species, putative hybrids, and those specimens which showed conflicting patterns in character variation (the "intermediates").

Principal Components Analysis

This multivariate method is based on the principle that specimens more similar to one another in the ways their characters covary can be placed closer to each other along the principal axes (components) extracted. Linear combinations of the original variables are taken such that the first principal component has maximum variation, the second principal component has the next most variation, subject to being orthogonal to the first, and so on (JMP, 1995). The percentage of the total variance

explained by each extracted component and the loadings (eigenvectors) for each character are calculated. These are very helpful in the visualization of the characters that are most important in relation to the variance explained by each component.

The methodology used by Rogstad (1993) for PCA analysis was partially adopted in this study. The principal components analysis included 47 quantitative characters (28 measurements, 19 counts), and 40 qualitative characters coded as double-state (13) and multi-state (27). The characters used in the analyses are shown in Table 2. A total of 74 specimens (one specimen, AT-61 shown in Table 1, had to be eliminated because it was misidentified) representing 30 different taxa in the subtribe Attaleinae were analyzed.

Table 2. List of quantitative and qualitative anatomical characters used in the multivariate analyses.

Adaxial Cuticle -Thickness (μ)
Adaxial Trichome - Length (μ)
Adaxial Epidermis -Thickness: Thin; Thick.
Adaxial Epidermis - Cell Extension: Longitudinal; Oblique; Mixed.
Adaxial Epidermis - Cell Shape: Rectangular; Rhombohedral; Spindle-shaped; Oblique; Mixed.
Adaxial Epidermis - Cell Walls: Linear; Undulate; Slightly undulate.
Over Fiber Cells - Length (μ)
Over Fiber Cells - Width (μ)
Inter Fiber Cells - Length(μ)
Inter Fiber Cells - Width (μ)
Adaxial Silica Bodies - Size (mm)
Abaxial Cuticle - Thickness (μ)
Abaxial Trichome - Size (μ)
Abaxial Epidermis - Thickness: Thin; Thick.
Costal Bands (# cells)
Costal Bands - Width(freq.)
Costal Bands - Width (μ)
Costal Cells - Length (μ)
Costal Cells - Width (μ)
Costal Cells - Shape: Rectangular; Spindle-shaped; Mixed.
Costal Cells - Walls: Linear; Undulate; Slightly undulate.
Intercostal Bands (# cells)
Intercostal Bands - Width (μ)
Intercostal Cells - Length (μ)
Intercostal Cells - Width (μ)
Intercostal Cells - Walls: Linear; Undulate; Slightly undulate.
Stomates - Arrangement: In files; Not in files.
Stomates - # rows
Guard cells - position: Superficial; Sunken; Slightly sunken.
Subs. Lateral - position: Above normal epidermal cells; Below normal epidermal cells; At the same level.
Abaxial Silica Bodies -Size (mm)
Adaxial Hypodermis - # Layers
Adaxial Hypodermal Cells - Shape: Round; Rectangular; Mixed.
Adaxial Hypodermal cells - Size(μ)
Adaxial Hypodermis -Tannins: absent; present.
Abaxial Hypodermis - # Layers
Abaxial Hypodermal Cells - Shape: Absent; Square; Round; Mixed.
Abaxial Hypodermal Cells-Size(μ)
Adaxial Fibers - Type: Non-lignified; Lignified; Slightly lignified.
Adaxial Fibers - # Groups
Adaxial Fibers - # Fibers/group
Adaxial Fibers-Shape/Groups: Groups&Rows; Rows; Bunches; Groups&Bunches.
Adaxial Fibers - Location: Between, Above & Below Hypodermal cells; Above hypodermis; Below hypodermis.

Table 2. (cont'd.)

Abaxial Fibers - # Groups
Abaxial Fibers- # Fibers/group
Abaxial Fibers - Arrangement: Absent; Present-regular; Present-irregular.
Abaxial Fibers - Shape of Groups: Absent; Roundish; Square.
Abaxial Fibers - Location: Absent; Above hypodermis; Between Hypodermis&Epidermis; On hypodermis.
Palisade mesophyll - # Layers
Palisade mesophyll - Differentiation: Absent; Well differentiated; Poorly differentiated.
Palisade mesophyll - Thickness (μ)
Palisade mesophyll - Cell Walls: No palisade; Thick; Thin.
Palisade mesophyll - Tannins: Absent; Infrequent; Frequent.
Spongy mesophyll - # Layers
Spongy mesophyll - Differentiation: Well differentiated; Poorly differentiated.
Spongy mesophyll - Thickness (μ)
Spongy mesophyll - Cell Walls: Thick; Thin.
Spongy mesophyll - Tannins: frequent; Infrequent.
Chlorenchyma - Total Thickness(μ)
Primary Veins - Shape: Pear-shaped; Round; Ovate; Mixed.
Primary Veins - Number
Primary Veins - Height(μ)
Primary Veins - Width (μ)
Primary Veins - Position: Centered; Closer-abaxial-surface; Mixed.
Primary Veins - Type/fiber: Large-thick walls; Large-thin walls; Small-thick walls; Mixed.
Primary Veins - # Layers
Secondary & Tertiary Veins - Number
Secondary & Tertiary Veins - Number in Between Large Veins
Mid-secondary Veins: Absent; Present.
Sec. Veins - Height (μ)
Tert. Veins - Height (μ)
Secondary & Tertiary Veins- Inner sheath: Complete; Incomplete; Mixed.
Secondary & Tertiary Veins - Buttresses: Absent; Present.
Secondary & Tertiary Veins - # Layers
Secondary & Tertiary Veins - Type/fiber: Large-thick walls; Large-thin walls; Mixed.
Expansion cells - Location: Only on midrib; Midrib&Leaf margin.
Midrib - Shape: Rectangular; Round; Square; Irregular.
Midrib - Size (mm)
Midrib - # Vasc.bundles
Sclerotic sheath - shape: Pointed; Very Pointed.
Midrib - Cuticle (μ)
Midrib Hypodermis - # Layers
Midrib Spongy mesophyll - # Layers
Midrib Fibers - location: Around midrib; Upper portion.
Midrib Exp.cells - #layers
Mid Exp. Cells - Confluence: Confluent; Not confluent.
Transverse Veins: Short; Long; Mixed.

Although some workers have successfully used both quantitative and qualitative characters combined (Prance et al. 1969; Crisp and Weston, 1993), principal component analysis has been mostly recommended with exclusively or predominantly quantitative data, when it supposedly produces components which account for a greater fraction of the variation (Prance et al., 1969). The data used in this analysis consisted of 47 quantitative and 40 qualitative characters, as shown above. To test whether purely morphometric and coded qualitative characters used separately in the PCA could still distinguish the groups, and produce components with a higher percentage of the variation, two other analyses were separately rerun. To test whether the groups could be distinguished on the basis of separate sets of anatomical characters, six PCAs were rerun (without the putative hybrids and intermediates), each including only characters from: 1) epidermis; 2) hypodermis; 3) fibers; 4) chlorenchyma; 5) veins; and 6) midrib. Finally, to examine how characters would vary within the entire group of hybrids/intermediates, a new PCA was run including only those specimens with observed mixed patterns as well as the reported hybrids as well.

In principal components analysis a method called rotation can be used to better align the directions of the factors with the original variable so that the factors may be more interpretable. The rotation method is called varimax, and tries to make elements of the matrix go toward 1 or 0 to show the clustering of variables (JMP,

1995). Although rotation may improve the interpretability of components, it did not help much in this study; therefore, only unrotated components are reported.

Cluster Analysis

Clustering is the technique of grouping rows (in this case taxa) together that share similar values across a number of variables. The principle behind the method is the idea that data are not scattered evenly through n-dimensional space, but rather form clumps, locally dense areas, modes, clusters. The identification of these clumps goes a long way towards characterizing the distribution of values (JMP, 1995). Instead of a correlation matrix as for the PCA, the first step in this method involves the computation of a similarity matrix in which all the objects are compared with each other (Prance et al., 1969). As pointed out before, cluster analysis has been the most widely used multivariate method among plant taxonomists (Duncan and Baum, 1981). Criticism on the method includes the view of it as a technique that always gives clusters even if a random data set is utilized (Rogstad, 1989). In this study, principal components analysis was used to demonstrate that groups can be distinguished based upon character variation. Cluster analysis was used to test the existence of groups on the basis of a taxa-character relationship. It also allowed the study of the clustering pattern within the sample as a whole, and within and among

separate groups of “good” species, putative hybrids and their parents, and intermediates.

The analyses were performed with the same number of specimens (74) and characters (87), shown respectively in Tables 1 and 2, with the exclusion of the three species of Syagrus. The hierarchical clustering method was used; it is also called agglomerative clustering because it a combining process. The method starts with each row as it own cluster. At each step the distance between each cluster is calculated, and the two clusters that are closest together are combined. This combining continues until all the points are in one final cluster (JMP, 1995). The clustering distances were calculated by using two methods: Ward's minimum variance and single linkage.

2.4. Cladistic Analysis

The evolutionary relationships of the members of this subtribe are studied and their characterization as a monophyletic group is attempted. Taxa within the subtribe are tested in relation to their monophyly and their relationship to each other is analyzed. Additionally, the effects of the putative hybrids on the analysis are examined and compared to the effects reported in the literature for other groups of plants. These subjects are approached by the cladistic analyses of anatomical characters.

a. Taxa Analyzed

Thirty taxa of the subtribe Attaleinae were included (Table 3). Syagrus amara, S. comosa, and S. cocooides, species of a genus grouped in the subtribe Butiinae (one of the five subtribes in the tribe Cocoeae), were taken as the outgroups.

b. Methods

Only qualitative characters (binary and multi-state) were used in the cladistic analyses (Table 4). Different analyses were performed to investigate different situations:

1. Analysis including all taxa - one outgroup. A data matrix of thirty-one taxa including the hybrids and intermediates and 47 characters (Table 3) was first set up to observe the complex character-taxa variation within the subtribe, and the effect of the presence of hybrids/intermediates in the analysis and in the overall topology of the cladogram. Syagrus amara was used as the outgroup (S. comosa and S. cocooides were excluded).

2. Analysis without intermediates - one outgroup. The matrix shown in Table 3 was reduced to analyze the relationships within the group without the putative hybrids

and intermediates. The hypothesis tested was that without the presence of those putative hybrids and the conflicting intermediates in the analysis, a more resolved cladogram would be obtained. This analysis involved 15 taxa and the same 47 anatomical characters. S. amara was used as the outgroup. The taxa excluded from the matrix shown in Table 3 were: O. luetzelburgii, O. polysticha, O. sagotii, O. crassispata, O. spectabilis, S. phalerata, S. butyracea, A. dubia, A. nucifera, A. tessmannii, A. racemosa, M. dahlgreniana, A. colenda, A. x piassabossu, x A. minarum, S. comosa, and S. cocoides.

3. Analyses with and without putative hybrids and intermediates- three outgroups. The two other species of Syagrus were included as outgroups. Analyses with and without the putative hybrids and intermediates were rerun, and data matrices were constructed, respectively, with 33 and 15 taxa; 47 characters were used in the two matrices. Syagrus amara, S. comosa and S. cocoides were taken as outgroups.

4. Analyses with the inclusion of one or more putative hybrids and intermediates at a time. Putative hybrids and intermediates were individually included in the analysis to observe the position of these taxa in the cladogram, and the overall effect on the topology. The taxa individually re-included in the analysis were those listed above.

After the results from the analysis with selected inclusion and exclusion of putative hybrids and intermediates were obtained, and the effects on the cladogram

observed, the taxa which did produce significant changes in the topology were re-included in the original matrix and the analysis rerun. This final analysis was performed with three outgroups.

Characters were analyzed using the Wagner parsimony method. *Nona* version 0.97 (Goloboff, 1993), and Hennig86 (Farris, 1988) were used to generate the trees. The commands, hold/20 and mult*1000, were used to search for trees in *Nona*. Swapping of the 20 most parsimonious trees (using the command max*) was used when recommended by the program (which was necessary only in the all-taxa analyses, with all putative hybrids and intermediates included). The trees were saved in *Nona*, and retrieved in Hennig86, where the strict consensus tree was generated. The polarity of characters was determined by outgroup comparison (Stevens, 1980; Watrous and Wheeler, 1981). Dada version 0.88 (Nixon, 1993) and Clados version 0.88 (Nixon, 1992) were used to examine and manipulate the data matrix and the trees. Syagrus amara was used alone in two one-outgroup analyses (with and without putative hybrids and intermediates), and combined with S. comosa and S. cocoides in two three-outgroup analyses. The cladistic analyses were performed on a IBM compatible computer.

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Table 4. Character states used in the cladistic analysis.

-
0. Adaxial Epidermis: thick (0); thin (1). Polymorphisms: *O. polysticha* (0,1), *O. spectabilis* (0,1), *S. phalerata* (0,1), *S. butyracea* (0,1), *A. tessmannii* (0,1).
 1. Adaxial Epidermis - Cell Extension: longitudinal (0); oblique (1); mixed (2).
Polymorphisms: *S. butyracea* (0,1), *M. dahlgreniana* (0,1).
 2. Adaxial Epidermal Cells - Shape: rectangular (0); rhombohedral (1); spindle-shaped (2); mixed (3). Polymorphisms: *S. butyracea* (0,1), *M. dahlgreniana* (2,3).
 3. Adaxial Epidermal Cells - Walls: linear (0); undulate (1); slightly-undulate (2).
Polymorphisms: *O. polysticha* (0,2), *O. spectabilis* (0,2), *S. butyracea* (1,2), *A. tessmannii* (0,2), *A. racemosa* (1,2).
 4. Abaxial Epidermis - Thickness: thick (0); thin (1). *O. polysticha* (0,1), *O. spectabilis* (0,1), *S. phalerata* (0,1), *S. butyracea* (0,1).
 5. Costal Cells - Shape: rectangular (0); spindle-shaped (1); mixed (2). Polymorphisms: *S. butyracea* (0,1), *A. geraensis* (1,2), *M. maripa* (0,2), *M. dahlgreniana* (1,2).
 6. Costal Cells - Walls: linear (0); undulate (1); slightly-undulate (2). Polymorphisms: *O. polysticha* (0,2), *S. butyracea* (0,1), *A. tessmannii* (0,2), *A. racemosa* (1,2).
 7. Intercostal Cells - Walls: linear (0); undulate (1); slightly-undulate (2). Polymorphisms: *O. polysticha* (0,2), *S. butyracea* (0,1), *A. tessmannii* (0,2), *A. racemosa* (0,2).
 8. Stomates - Arrangement: in files (0); not in files (1). Polymorphisms: *O. sagotii* (0,1), *S. butyracea* (0,1), *A. dubia* (0,1), *A. nucifera* (0,1), *M. maripa* (0,1).
 9. Guard-cells: superficial (0); sunken (1); slightly sunken (2). Polymorphisms: *O. polysticha* (1,2), *S. butyracea* (0,1), *A. dubia* (1,2), *A. racemosa* (0,2), *M. dahlgreniana* (0,1).
 10. Adaxial Hypodermis - Layers: single (0); double (1).
 11. Adaxial Hypodermal Cells - Shape: octagonal (0); round (1); rectangular (2); mixed-one layer (3); both-two layers (4). Polymorphisms: *O. polysticha* (1,3), *O. spectabilis* (1,3), *A. dubia* (2,3), *A. tessmannii* (2,3), *M. dahlgreniana* (1,4).
 12. Adaxial Hypodermis - Tannins: absent (0); Moderately present (1); Strongly present (2).
Polymorphisms: *O. eichleri* (0,1), *S. butyracea* (0,1), *A. geraensis* (0,1), *A. tessmannii* (0,1), *A. racemosa* (0,1).
 13. Abaxial Hypodermis: absent (0); present (1).
 14. Abaxial Hypodermal Cells - Shape: absent (0); square (1); round (2); mixed (3).
Polymorphisms: *O. cuatrecasana* (1,3), *O. spectabilis* (1,3), *S. phalerata* (2,3), *S. butyracea* (1,2), *A. dubia* (1,3), *A. racemosa* (1,2), *M. maripa* (1,2,3), *M. dahlgreniana* (1,3).
 15. Adaxial Fibers -Type: non-lignified (0); lignified (1); slightly lignified (2). Polymorphisms: *O. eichleri* (1,2), *O. sagotii* (0,1), *O. spectabilis* (0,1), *S. attaleoides* (0,2), *A. oleifera* (1,2), *A. pindobassu* (0,2).
 16. Adaxial Fibers - Arrangement of Bundles: Groups&Rows (0); Rows (1); Bunches (2); Groups&Bunches (3). Polymorphisms: *O. polysticha* (1,2), *O. spectabilis* (1,2), *S. phalerata* (0,1), *A. oleifera* (0,2), *A. dubia* (0,1), *A. geraensis* (0,2), *A. pindobassu* (0,2), *A. tessmannii* (0,2), *M. maripa* (0,1).

Table 4 (cont'd.)

17. Adaxial Fibers - Location: between-above-below hypodermis (0); above hypodermis only (1); below hypodermis only (2); in between layers (3); between hypodermal cells (4). Polymorphisms: *O. polysticha* (0,2), *O. sagotii* (0,4), *O. spectabilis* (0,2), *S. phalerata* (0,1), *S. attaleoides* (0,4), *A. oleifera* (0,2), *A. dubia* (0,2), *A. geraensis* (0,2), *A. tessmannii* (0,2), *A. racemosa* (0,1), *M. maripa* (0,4), *M. dahlgreniana* (0,1).
18. Abaxial Fibers - Arrangement: absent (0); present-regular (1); present-irregular (2). Polymorphisms: *O. eichleri* (0,2), *O. polysticha* (1,2), *S. phalerata* (1,2), *A. oleifera* (1,2), *A. dubia* (0,2), *A. funifera* (1,2), *A. nucifera* (1,2), *M. dahlgreniana* (1,2), *A. colenda* (0,1).
19. Abaxial Fibers - Shape of Bundles: absent (0); roundish (1); square (2). Polymorphisms: *O. eichleri* (0,1), *O. spectabilis* (1,2), *S. butyracea* (1,2), *A. dubia* (0,1), *A. colenda* (0,1).
20. Abaxial Fibers Bundles - Location: absent (0); above hypodermis (1); between hypodermis & epidermis (2); in between hypodermal cells (3). Polymorphisms: *O. eichleri* (0,2), *O. sagotii* (1,3), *O. spectabilis* (1,3), *S. butyracea* (1,2), *A. dubia* (0,1).
21. Palisade Mesophyll - Layers: absent (0); single (1); multiple (2).
22. Palisade Mesophyll-Differentiation: absent (0); well differentiated (1); poorly differentiated (2). Polymorphisms: *O. polysticha* (1,2), *O. spectabilis* (1,2), *A. tessmannii* (1,2).
23. Palisade Mesophyll - Cell Walls: no palisade (0); thick (1); thin (2). Polymorphisms: *O. polysticha* (1,2), *O. spectabilis* (1,2).
24. Palisade Mesophyll - Tannins: absent (0); infrequent (1); frequent (2). Polymorphisms: *O. phalerata* (1,2), *O. oleifera* (1,2), *O. breijinhoensis* (1,2), *O. polysticha* (1,2), *O. spectabilis* (0,1), *S. phalerata* (1,2), *S. butyracea* (0,1,2), *A. oleifera* (1,2), *A. humilis* (0,2), *A. pindobassu* (0,1), *A. racemosa* (0,2).
25. Spongy Mesophyll - Layers: up-to-5 (0); more-than-5 (1).
26. Spongy Mesophyll - Differentiation: well differentiated (0); poorly differentiated (1). Polymorphisms: *O. cuatrecasana* (0,1), *A. tessmannii* (0,1).
27. Spongy Cells - Walls: thick (0); thin (1). Polymorphisms: *O. cuatrecasana* (0,1), *A. tessmannii* (0,1).
28. Spongy Mesophyll - Tannins: absent (0); infrequent (1); frequent (2). Polymorphisms: *O. polysticha* (1,2), *S. butyracea* (1,2), *A. humilis* (1,2), *A. racemosa* (1,2), *M. maripa* (1,2).
29. Primary Veins - Shape: pear-shaped (0); round (1); ovate (2); mixed:pear-round (3). Polymorphisms: *O. polysticha* (1,3), *O. spectabilis* (1,3), *S. phalerata* (0,3), *A. nucifera* (1,3), *M. dahlgreniana* (0,1,2).
30. Primary Veins - Position: centered (0); closer-abaxial surface (1); mixed-both types (2). Polymorphisms: *O. polysticha* (1,2), *S. phalerata* (0,2), *A. racemosa* (0,1).
31. Primary Veins - Fibers: large-thick walls (0); large-thin walls (1); small-thick walls (2); mixed (3). Polymorphisms: *O. spectabilis* (1,3), *S. butyracea* (0,1), *A. tessmannii* (0,3), *A. racemosa* (0,1), *M. dahlgreniana* (2,3).
32. Mid-secondary Vein: absent (0); present (1). Polymorphisms: *O. eichleri* (0,1), *O. polysticha* (0,1), *O. sagotii* (0,1), *S. butyracea* (0,1), *A. oleifera* (0,1), *A. dubia* (0,1), *M. dahlgreniana* (0,1).

Table 4 (Cont'd.)

33. Inner Sheath - Secondary & Tertiary Veins: complete (0); incomplete (1). Polymorphisms: O. sagotii (0,1), O. spectabilis (0,1), S. butyracea (0,1), M. dahlgreniana (0,1).
 34. Buttresses: absent (0); present-pointed (1); present-flat (2). Polymorphisms: S. butyracea (0,1), A. dubia (0,1), A. pindobassu (0,1), M. dahlgreniana (0,1).
 35. Secondary & Tertiary Veins - Fibers: large-thick walls (0); large-thin walls (1); mixed (2). Polymorphisms: O. sagotii (1,2), A. racemosa (0,1), M. dahlgreniana (0,1).
 36. Expansion Cells - Location only on midrib (0); midrib & leaf margin (1). Polymorphisms: O. phalerata (0,1), O. sagotii (0,1), S. phalerata (0,1), S. butyracea (0,1), S. attaleoides (0,1), A. dubia (0,1), A. geraensis (0,1), A. humilis (0,1), A. nucifera (0,1), A. racemosa (0,1), M. maripa (0,1), A. colenda (0,1).
 37. Midrib - Shape: rectangular (0); round (1); square (2); irregular (3). Polymorphisms: O. oleifera (0,1).
 38. Midrib - Sclerotic Sheath: pointed (0); very pointed (1). Polymorphisms: O. sagotii (0,1), S. phalerata (0,1), S. butyracea (0,1), A. racemosa (0,1).
 39. Midrib Fibers - Location: around midrib (0); upper portion (1). Polymorphisms: A. tessmannii (0,1), M. dahlgreniana (0,1).
 40. Midrib Expansion Cell Bands - Confluence: confluent (0); not confluent (1). Polymorphisms: O. sagotii (0,1), A. geraensis (0,1).
 41. Transverse Veins: short (0) long (1); mixed (2). Polymorphisms: O. polysticha (1,2), O. spectabilis (1,2), S. phalerata (0,2).
 42. Primary Veins - Bumps: absent (0); both surfaces (1); abaxial only (2).
 43. Hypodermal Fibers: absent (0); present-adaxial (1); present-abaxial (2).
 44. Hypodermal Fibers - Midrib: absent (0); present (1).
 45. Trichomes: flush (0); sunken (1).
 46. Trichomes - Shape: flask (0); clavate (1).
-

3. Results

3.1. Anatomical Descriptions

For the most part, the descriptions contain mostly qualitative characters; additional quantitative data for characters are shown in Tables 5 - 11.

1. Orbignya phalerata Martius. *Adaxial epidermal cells* smaller and of different shape and orientation compared to the abaxial epidermal cells, in cross section; *adaxial hypodermis* with two layers of cells, the upper layer with cells more rectangularly shaped and smaller than those in lower layer, with cells of more variable shape and size; *abaxial hypodermis* a single layer of somewhat regularly shaped (square) and sized cells, not interrupted by fiber bundles; *adaxial fibers* usually slightly lignified, 260-375 in number (mean=317), regularly distributed, and occurring mostly in between the two layers of hypodermal cells, as groups or rows of 4-9 fibers (mean=7 fibers/group); *abaxial fibers* also regularly distributed, in small roundish groups of 3 fibers, usually located in between hypodermis and epidermis; *palisade mesophyll* poorly differentiated, ca. 50 μ thick, usually formed by two layers of elongate thin-walled palisade cells; *spongy mesophyll* also poorly differentiated, with 6-7 layers (80-100 μ thick; mean=90 μ) of compact, roundish, thin walled-cells; *primary veins* round, ranging from 10 to 13 in number (mean= 11), centered (located

in the middle of the mesophyll), fibrous inner sheath complete, 0.128 mm tall x 0.122 mm wide on average, always formed by small fibers of thick walls; a distinctive *mid-secondary vein*, usually bigger and located slightly higher than the others, positioned mid way between two large veins; *secondary and tertiary veins* 115-123 in number, secondary (mean=0.071 mm) slightly bigger than tertiary vein (mean=0.050 mm) but both on the same plane on mesophyll, with their lower fibrous portions always located above the hypodermal layer; no buttresses are formed; *stomates with sunken guard-cells*, not arranged in definite files, usually in rows of 2-3 on intercostal bands; *adaxial epidermal cells* longitudinally or obliquely extended of either rectangular or rhombohedral shape, undulate or linear walls; *abaxial epidermis* consisting of one layer of longitudinally extended, spindle-shaped *costal cells* of linear walls; *intercostal cells* of variable shape and linear walls; *midrib* 2.2-2.7 mm in length (mean=2.4 mm), rectangular, with 3-6 layers of *expansion cells* on each side of the midrib, not confluent below the sclerotic sheath; ca. 20 *vascular bundles* enclosed in the sclerotic sheath; *small fiber groups* located on upper portion of the midrib only; *transverse veins* short, connecting up to 3 large veins (most frequently 2). Specimens examined: OPH-02, OPH-03.

2. Orbignya oleifera Burret. *Adaxial epidermal cells* smaller and of different shape and orientation compared to the abaxial epidermal cells, in cross section; *adaxial hypodermis* with two layers of cells, the upper layer with cells more rectangularly shaped and smaller than those in lower layer, with cells of more variable shape and

size; *abaxial hypodermis* a single layer of somewhat regularly shaped (square) and sized cells, not interrupted by fiber bundles; *adaxial fibers* usually slightly lignified, 345-390 in number (mean=365), regularly distributed, and occurring mostly in between the two layers of hypodermal cells, as groups or rows of 7-9 fibers (mean=8 fibers/group); *abaxial fibers* also regularly distributed, in small roundish groups of 3-4 fibers, usually located in between hypodermis and epidermis; *palisade mesophyll* poorly differentiated, 92-120 μ thick (mean=104 μ), usually formed by two layers of elongate thin-walled palisade cells; *spongy mesophyll* also poorly differentiated, with 6-8 layers (150-190 μ thick; mean=165 μ) of compact, roundish, thin walled-cells; *primary veins* round, ranging 8-13 in number (mean=11), centered (located in the middle of the mesophyll), fibrous inner sheath complete, 0.199 mm tall x 0.171 mm wide on average, always formed by small fibers of thick walls; a distinctive *mid-secondary vein*, usually bigger and located slightly higher than the others, positioned mid way between two large veins; *secondary and tertiary veins* 116-138 in number (mean=127), secondary (mean=0.091 mm) slightly bigger than tertiary vein (mean=0.054 mm), on the same plane on mesophyll, with their lower fibrous portions always located above the hypodermal layer; no buttresses are formed; *stomates with sunken guard-cells*, arranged not in definite files, usually in rows of 2-3 on intercostal bands; *adaxial epidermal cells* obliquely extended, of usually rhombohedral shape, linear walls; *abaxial epidermis* consisting of one layer of longitudinally extended, spindle-shaped *costal cells* of linear walls; *intercostal cells* of variable shape and linear walls; *midrib* 2.7-3.1 mm in length (mean=2.9 mm),

rectangular, with 3-6 layers of *expansion cells* on each side of the midrib, not confluent below the sclerotic sheath; ca. 20 *vascular bundles* enclosed in the sclerotic sheath; *small fiber groups* located on upper portion of the midrib only; *transverse veins* short, connecting up to 3 large veins (most frequently 2).

Specimens examined: OO-04, OO-05, OO-06.

3. Orbignya brejinhoensis Glassman sp. nv. (unpublished). *Adaxial epidermal cells* smaller and of different shape and orientation compared to the abaxial epidermal cells, in cross section; *adaxial hypodermis* with two layers of cells, the upper layer with cells more rectangularly shaped and smaller than those in lower layer, with cells of more variable shape and size; *abaxial hypodermis* a single layer of regularly shaped (square) and sized cells, not interrupted by fiber bundles; *adaxial fibers* usually slightly lignified, 215-390 in number (mean=301), regularly distributed, and occurring usually in between the two layers of hypodermal cells, as groups or rows of 4-9 fibers (mean=6 fibers/group); *abaxial fibers* also regularly distributed, in small roundish groups of 3-4 fibers, often located in between hypodermis and epidermis; *palisade mesophyll* poorly differentiated, 60-80 μ thick (mean=73 μ), usually formed by two layers of elongate thin-walled palisade cells; *spongy mesophyll* also poorly differentiated, with 7-8 layers (130-160 μ thick; mean=143 μ) of compact, roundish, thin walled-cells; *primary veins* round, 8-12 in number (mean=9), centered (located in the middle of the mesophyll), fibrous inner sheath complete, 0.176 mm tall x 0.161 mm wide on average, always formed by small fibers of thick walls; a distinctive *mid-*

secondary vein, usually bigger and located slightly higher than the others, positioned mid way between two large veins; *secondary and tertiary veins* 92-114 in number (mean=101), *secondary* (mean=0.080 mm) slightly bigger than *tertiary vein* (mean=0.048 mm), on the same plane on mesophyll, with their lower fibrous portions always located above the hypodermal layer; no buttresses are formed; *stomates with sunken guard-cells*, arranged not in definite files, usually in rows of 2-3 on intercostal bands; *adaxial epidermal cells* obliquely extended, of mostly rhombohedral shape, linear walls; *abaxial epidermis* one layer of longitudinally extended, spindle-shaped *costal cells* of linear walls; *intercostal cells* of variable shape and linear walls; *midrib* 1.7-2.6 mm in length (mean=2.0 mm), rectangular, with 3-6 layers of *expansion cells* on each side of the midrib, not confluent below the sclerotic sheath; ca. 20 *vascular bundles* enclosed in the sclerotic sheath; *small fiber groups* located on upper portion of the midrib only; *transverse veins* short, connecting up to 3 large veins (most frequently 2). Specimens examined: OB-07, OB-08, OB-09.

4. Orbignya eichleri Drude. *Adaxial epidermal cells* are smaller and of different shape and orientation compared to the *abaxial epidermal cells* (bigger and square); *adaxial hypodermis* with one single layer of large, rectangular to square large cells, frequently interrupted by fiber groups; one-layered *abaxial hypodermis* of square cells, frequently interrupted by fibrous lower portions of secondary and tertiary veins (buttresses); *adaxial fibers* lignified or not, 110-170 in number (mean=145), small-

medium size (6-7 fibers/group), always in between hypodermal and epidermal layers; *abaxial fibers* lacking, or very small in number (5), of very small groups (2-3 fibers/group), irregularly distributed, located in between hypodermis and epidermis; *palisade mesophyll* poorly differentiated, ca. 60-70 μ thick (mean=64.6 μ), in 2 layers of elongate thin-walled cells, with strong occurrence of tannins; *spongy mesophyll* poorly differentiated, with 6 layers (ca. 90-100 μ thick; mean=93.3 μ) of roundish, compact, thin-walled cells, also with strong presence of tanniniferous cells among normal spongy cells; *primary veins* large, taking up most of the mesophyll, centered, mostly ovate, 6-8 in number, 0.171 mm tall x 0.124 mm wide on average, inner sheath complete, formed by one layer of large fibers of thick walls; *mid-secondary vein* not discernible; *secondary and tertiary veins* 57-69 in number, nearly on same plane, secondary (mean=0.067 mm) slightly bigger than tertiary veins (mean=.046 mm), inner sheath of large fibers of thick walls, incomplete on upper portion, with lower portions going through hypodermis, touching epidermis and forming large buttresses; *stomates with sunken guard-cells*, not arranged in definite files, mostly in rows of 2-4 on intercostal bands; *adaxial epidermis* of mostly obliquely extended rhombohedral cells, with some mixture of longitudinally oriented cells (rectangular), of slightly undulate walls; *abaxial epidermis* with longitudinally oriented, spindle-shaped *costal cells*, of linear walls; *intercostal cells* of variable shape and size, and linear walls; *midrib* mostly square-shaped, 0.64-0.84 mm long (mean=0.74mm), with 3 layers of confluent expansion cells on each side of the midrib; *transverse veins*

short, connecting up to 2 large veins. Specimens examined: OE-10, OE-11, OE-12, MB -1313, MB-131, and MB-1317.

5. Orbignya luetzelburgii (Burret) Wess. Boer. *Epidermal cells* of different size, shape and orientation on adaxial and abaxial surfaces; one layer of roundish large *adaxial hypodermal cells*; *abaxial hypodermis* completely replaced by an entire layer of large, thin-walled fibers (*hypodermal fibers*); lignified *adaxial fibers* which occur in large groups, 190-285 in number, above hypodermis, or in bunches below it; individual fibers are large, 7 fibers/group; *abaxial fibers* lacking (hypodermal fibers are dominant); *palisade mesophyll* poorly differentiated (ca. 50 μ thick), formed by very thin-walled and elongate, but somewhat short palisade cells in one layer; *spongy mesophyll* also poorly differentiated (ca. 90-100 μ thick), of thin-walled cells; mesophyll with several *cells inclusions* (oil globules, mucilage, sclereids); *primary veins* 5-8 in number, centered, pear-shaped of small, thick-walled fibers (although with some mixture of large thick-walled fibers), 0.148 mm long x 0.142 mm wide on average; no *mid-secondary vein*; *secondary and tertiary veins* of 118-122 in number (secondary=0.057mm; tertiary= 0.041 mm), with elongate lower portions sitting right on layer of *hypodermal fibers*, which replaces abaxial hypodermal layer; veins are surrounded by a complete inner sheath of large, thick-walled fibers; no buttresses are formed; *stomates with guard-cells* slightly sunken, not in definite files, arranged in rows of 2-3 on intercostal bands; a thick *adaxial epidermal layer* with obliquely extended rhombohedral cells of undulate walls; a thick *abaxial epidermis* of

longitudinally extended spindle-shaped *costal cells* of undulate walls; *intercostal cells* variously shaped and sized of undulate walls; *midrib* irregularly shaped, 0.6 mm long on average, with very pointed sclerotic sheath enclosing 8-10 vascular bundles; 3 layers of confluent *expansion cells* on each side of midrib; *transverse veins* long. Specimens examined: OL-13 and OL-14.

6. Orbignya polysticha Burret. Adaxial *epidermal cells* with approximately the same size, shape and orientation on both surfaces (except OPO-17); a single layer of roundish large *adaxial hypodermal cells* (mixed rectangular and roundish cells in OPO-17); usually non-lignified *adaxial fibers* 365-395 in number, mostly in small groups (vertical rows more frequent) of 6-7 fibers/group, above, in between, and below hypodermal cells; OPO-17 with *adaxial fiber bundles* in the bunches pattern, below hypodermis; *abaxial fiber groups* ranging from 80-145 per lamina, in groups of 7, somewhat square, regularly distributed, and usually located in between hypodermal cells or directly on it, irregularly distributed, above hypodermal layer); *palisade mesophyll* well differentiated with one layer of elongate thick-walled palisade cells (ca. 30-70 μ thick) (poorly differentiated, thin-walled cells in OPO-17); *spongy mesophyll* also well differentiated, formed by cells of thick walls, with 5-8 layers (ca. 60-90 μ thick); *primary veins* 9-13, formed mostly by large fibers of thin or thick walls, either closer to the abaxial surface (more frequent), or centered, 0.117 mm long x 0.114 mm wide on average; *mid-secondary* vein not easily distinguishable; *secondary and tertiary veins* 65-98 in number, small (secondary=

0.063; tertiary= 0.042 mm), formed by large fibers of thin walls (less frequently thick walls) with fibrous lower portion located on hypodermis or going through it, forming small buttresses; *stomates* with sunken or slightly sunken guard-cells, in files (OPO-15) or not with rows of 2-3 stomates on intercostal bands; *adaxial epidermis* a thin layer of longitudinally extended cells of rectangular and rhombohedral shape, slightly undulate to undulate wall (except OPO-17, with linear walls); *abaxial epidermis* of thin-walled cells; *costal cells* always longitudinally extended, spindle-shaped or rectangular, of slightly undulate to undulate walls (linear in OPO-17); *intercostal cells* of variable shape and size, slightly undulate to undulate walls (linear in OPO-17); *midrib* irregularly shaped, but mostly rectangular, 0.6-2.3 m long (mean=1.4 mm), with 8-18 small vascular bundles in sclerotic sheath; 3-4 layers of confluent *expansion cells* on each side of midrib; *small fiber groups* all way around midrib; *transverse veins* long (mixed short and long transverse veins in OPO-17).
Specimens examined: OPO-15, OPO-16 & OPO-17.

7. Orbignya sagotii Trail ex Thurn. *Adaxial epidermal cells* with approximately the same shape, size and orientation compared to the abaxial surface; a single layer of roundish large *adaxial hypodermal cells*; non-lignified *adaxial fibers* (except in OSA-19) occurring mostly in small groups, 350-480 in number (mean=413), mostly vertical rows, 3-5 fibers/group, located above, in between, and below hypodermal cells; *abaxial fiber groups* 50-80 in number, in groups of 6-7 (mean=6), somewhat square, located above or in between hypodermal cells; *palisade mesophyll* well

differentiated, with one layer of elongate thick-walled palisade cells (ca. 40-70 μ thick); *spongy mesophyll* also well differentiated, formed 6-7 layers (100-180 μ thick; mean=125.5 μ) of thick-walled cells; *primary veins* 10-14 in number (mean=12), 0.119 mm long x 0.121 mm wide on average, formed mostly by large fibers of thin walls, closer to the abaxial surface; *mid-secondary veins* not distinguishable (except in OSA-18); secondary and tertiary veins 48-104 in number, small (secondary=0.067; tertiary=0.046 mm), roundish or of slightly elongate lower end, usually formed by large fibers of thin walls (less frequently thick walls), inner sheath complete or incomplete (OSA-20), with fibrous lower portions going through hypodermis, forming small buttresses; *stomates with superficial guard-cells*, in files of 1-2, or not in definite files (OSA-18) with rows of 2-3 stomates on intercostal bands; *adaxial epidermis* a thin layer of longitudinally extended cells of rectangular and rhombohedral shape, of undulate walls; *abaxial epidermis* thin, longitudinally extended costal cells, spindle-shaped or rectangular, of undulate walls; *intercostal cells* of variable shape and size, and undulate walls; *midrib* somewhat irregular, but mostly rectangular, 1.1-1.2 mm long; usually 3 layers of *expansion cells* (5-6 in OSA-18), confluent or not (OSA-19) below the sclerotic sheath; *transverse veins* long. Specimens examined: OSA-18, OSA-19 & OSA-20.

8. Orbignya cohune (Mart.) Dahlgren ex Standl. *Adaxial epidermal cells* smaller and of different shape (more rectangular on upper surface, more square on lower) and orientation (more obliquely oriented on upper, more longitudinally extended on

lower) compared to *abaxial epidermal cells* in cross section view; *adaxial hypodermis* with one layer of large roundish cells, frequently interrupted by usually small fiber groups; *abaxial hypodermis* also one-layered, with mostly square cells; *adaxial fibers* in ca. 400 small groups of 3–4 fibers/groups (lignified or non-lignified), located above, in between or below hypodermal cells; *abaxial fibers* approximately 80 groups in number, regularly arranged in small, roundish groups (3 fibers/group), located in between hypodermis and epidermis; *palisade mesophyll* poorly differentiated, ca. 40 μ thick, with 1-2 layers of elongate thin-walled palisade cells, tanniniferous cells weakly present; *spongy mesophyll* poorly differentiated, composed of approximately 8 layers (ca. 100 μ thick) of compact spongy cells of thin walls; tanniniferous cells also weakly present in this mesophyll; *primary veins* round, formed mostly by up to 4 layers of small fibers of thick walls, centered, ca. 12 in number, 0.110 m tall x 0.100 mm wide; *mid-secondary* vein distinguishable, located approximately mid way in between two primary veins; *secondary and tertiary veins* ca. 90 in number, secondary (mean=0.055 mm) slightly bigger than tertiary veins (mean=0.042 mm), inner sheath incomplete, of elongate fibrous lower portions; most of the secondary veins located directly above or on the hypodermis (touching it or not), and tertiary veins usually going through hypodermis, forming small buttresses; *stomates with sunken guard-cells*, arranged not in definite files, in rows of 2-3 on intercostal bands; *adaxial epidermis* thick, with a mixture of obliquely and longitudinally extended cells (rhombohedral and rectangular) of slightly undulate to undulate walls; *abaxial epidermis* with longitudinally extended, spindle-shaped or

rectangular *costal cells*, of slightly undulate to undulate walls; *intercostal cells* variously shaped and sized, and cell walls also varying from slightly undulate to linear; *midrib* roundish, ca. 1.28 mm long on average, 18 vascular bundles enclosed in the sclerotic sheath; 3-5 layers of expansion cells not confluent below the sclerotic sheath; *transverse veins* short. Specimens examined: 1466, 1467, OCO-21.

9. Orbignya crassispatha (Mart.) Glassman. *Adaxial epidermal cells* smaller and of different shape and orientation compared to the abaxial epidermal cells; *adaxial hypodermis* single layered, of rectangular hypodermal cells; this layer is usually continuous, not interrupted by fibers; *abaxial hypodermis* formed by one layer of mostly square cells of regular size; *adaxial fiber groups* lignified, in number of 300-360 (mean=330), in large *bunches*, ranging from 9-11 fibers/group (mean=10), below the hypodermal layer; *abaxial fibers* 95-100, of large groups (3-9 fibers/group; mean=6), located in between hypodermis and epidermis, or above hypodermis, in spongy mesophyll; *palisade mesophyll* poorly differentiated, 50-60 μ thick (mean= 55 μ), of 2 layers of elongate thin-walled cells; spongy mesophyll also poorly differentiated, approximately 90 μ thick, formed by 7 layers of roundish, compact, thin-walled spongy cells; *primary veins* in number 12, large, 0.168 mm long x 0.113 mm wide, pear-shaped, and usually of fibrous upper portions (top buttresses); primary veins centered, but closer and sometimes connected to the adaxial surface, because of the top buttresses; inner sheath complete, formed by large fibers of thick walls; *secondary and tertiary veins* 96-127 in number

(mean=111), usually elongate; secondary (mean=0.062 mm) bigger than tertiary veins (mean=0.056 mm), inner sheath incomplete, of fibrous lower portions (large fibers of thick walls), which go through hypodermis, forming buttresses; *stomates of sunken guard-cells*, not arranged in definite files, usually in rows of 3-4 (most frequently 1-2) on intercostal bands; *adaxial epidermis* thick, of obliquely extended, rhombohedral cells, of linear walls; *abaxial epidermis* thick, of longitudinally extended, spindle-shaped *costal cells*, of linear walls; *intercostal cells* of variable shape and size, and linear walls; *midrib* ca. 1.2 mm long, somewhat square; *vascular bundles* 20-22, enclosed in sclerotic sheath; *small fiber bundles* mostly located at the upper portion of the midrib; *transverse veins* short, connecting up to 3 large veins (most frequently 2). Specimens examined: OCR-22, OCR-23.

10. Orbignya cuatrecasana Dugand. *Epidermal cells* of approximately same size, shape and orientation on both upper and lower surfaces; *adaxial hypodermis* with one layer of large, roundish cells; *abaxial hypodermis* single-layered, of mostly roundish cells; lignified *adaxial fibers* 300-320 (mean=311) small groups and horizontal rows (4-6 fibers/group), always located above the hypodermal layer; *abaxial fibers* 60-75 in number (mean=68), regularly distributed and arranged in somewhat roundish groups of 6-9 fibers/group, located in between hypodermis and epidermis; *palisade mesophyll* poorly differentiated (60-70 μ thick; mean=63.3 μ), of thin-walled cells mostly taken by tannins; *spongy mesophyll* also poorly differentiated, with 5-6 layers (80-100 μ thick; mean=90 μ), of roundish, compact,

tannin-filled spongy cells of thin walls; *primary veins* 11-16 (mean=13) in number, 0.125 mm tall x 0.139 mm wide on average, round, located closer to the abaxial surface, inner sheath complete, formed by a mixture of large fibers of thick and thin walls; *mid-secondary* not distinguishable from the others; *secondary and tertiary veins* 91-138 in number (mean=108), small; secondary (mean=0.071 mm long) slightly bigger than tertiary mean=0.053 mm long), mostly elongate, inner sheath incomplete, formed by large fibers of thick walls, with fibrous lower portions always through hypodermis, forming buttresses; *stomates with superficial guard-cells*, mostly arranged in definite files of 1-2 stomates on intercostal bands; *adaxial epidermis* a thin layer of longitudinally extended (cells mostly rectangularly shaped, but of oblique ends) cells, of linear walls; *abaxial epidermis* also thin, with longitudinally extended rectangularly shaped *costal cells*, of linear walls; *intercostal cells* variable, of linear walls; *midrib* 1.68-2.20 mm long (mean=2.0 mm) rectangular, or square; 18-20 *vascular bundles* enclosed in the sclerotic sheath; 5-6 layers of confluent *expansion cells* on each side of midrib; *transverse veins* long. Specimens examined: OCU-24, OCU-25, and OCU-26.

11. Orbignya guacuyule (Liebm. ex Mart.) E. Hern. *Adaxial epidermal cells* smaller and of different shape (more rectangular on upper surface, more square on lower) and orientation (more obliquely oriented on upper, more longitudinally extended on lower) compared to *abaxial epidermal cells* in cross section view; *adaxial hypodermis* with basically one layer of large roundish cells, frequently interrupted by usually

small fiber groups; *abaxial hypodermis* also one-layered, with mostly square cells; *adaxial fibers* in ca. 490 small groups of usually 4 fibers/groups (lignified or non-lignified), located above, in between or below hypodermal cells; *abaxial fibers* usually 80 in number, regularly arranged in small, roundish groups (3 fibers/group), located in between hypodermis and epidermis; *palisade mesophyll* poorly differentiated, ca. 50 μ thick, with 1-2 layers of elongate thin-walled palisade cells, tanniniferous cells weakly present; *spongy mesophyll* poorly differentiated, composed of 8 layers (ca. 100 μ thick) of compact spongy cells of thin walls; tanniniferous cells also very weak in this mesophyll; *primary veins* round, formed mostly by up to 4 layers of small fibers of thick walls, centered, 13 in number, 0.115 m tall x 0.125 mm wide; *mid-secondary vein* distinguishable, located approximately mid way in between two primary veins; *secondary and tertiary veins* ca. 130 in number, secondary (mean=0.069 mm) slightly bigger than tertiary veins (mean=0.051 mm), inner sheath incomplete, of elongate fibrous lower portions; most of the secondary veins located right above or on the hypodermis (touching it or not), and tertiary veins usually going through hypodermis, forming small buttresses; *stomates with sunken guard-cells*, arranged not in definite files, in rows of 2-3 on intercostal bands; *adaxial epidermis* thick, with a mixture of longitudinally extended, spindle-shaped cells of linear walls; *abaxial epidermis* with longitudinally extended, spindle-shaped or rectangular *costal cells*, of linear walls); *intercostal cells* variously shaped and sized, and cell walls also varying from slightly undulate to linear; *midrib* roundish, ca. 1.9 mm long on average, 18 vascular bundles enclosed in the sclerotic

sheath; 3-5 layers of expansion cells not confluent below the sclerotic sheath;
transverse veins short. Specimens examined: OG-27).

12. Orbignya spectabilis Mart. *Epidermal cells* equally shaped, sized and oriented on both surfaces; one single layer of roundish large adaxial *hypodermal cells*, but mixed rectangular and roundish in OSP-30); *abaxial hypodermis* also single layered, but cells are somewhat more regularly shaped (square); *adaxial fibers* lignified (OSP-28) or not, 300-502 groups, 3-7 fibers/group (mean=4-5), mostly in vertical rows located above, in between and below hypodermal cells, or in bunches (6-8 fibers/group) below the hypodermis (OSP-30); *abaxial fibers* 82-98 groups, in square arrangement in between hypodermal cells (OSP-28 & OSP-29, and more roundish, located above hypodermis in OSP-30; *palisade mesophyll* well differentiated (ca. 50-100 μ thick), with one layer of thick-walled cells (OSP-28 & OSP-29, or poorly differentiated, with two layers (ca. 100 μ thick) of thin-walled cells (OSP-30); all three specimens have a well differentiated spongy mesophyll, although the number of layers ranged from 5, ca. 80 μ thick (OSP-28) to 6-8, 100-140 μ thick (OSP-29 & OSP-30; all three specimens have *primary veins* formed by large fibers of thin or thick walls, 9-13 in number, 0.133 mm long x 0.131 mm wide on average, located closer to abaxial surface; shape of primary veins is mostly round, but some slight pear-shaping can be noticed in (OSP-29); *mid-secondary* vein not distinguishable; *secondary and tertiary veins* 67-82 in number, small (secondary=0.068 mm; tertiary=0.059 mm), mostly of elongate fibrous lower ends, which go through

hypodermis, forming very small to medium buttresses; secondary and tertiary veins are mostly formed by mixture of large fibers of thick or thin walls, inner sheath complete (except in OSP-30), *stomates with superficial guard-cells*; mostly arranged in definite files of 1-2 (except OSP-30) on the intercostal bands; *adaxial epidermis* thin (except in OSP-30)), in a mixed pattern of obliquely and longitudinally extended cells (rhombohedral and rectangular), of slightly undulate walls (except in OSP-28, which is linear); *abaxial epidermis* thin, with longitudinally extended costal cells (rectangular), of slightly undulate to undulate walls; intercostal cells of variable shape and size, and slightly undulate walls; *midrib* somewhat irregular, but mostly rectangular, 1.6-2.3 mm long (mean=1.9 mm), 16-18 vascular bundles inside sclerotic sheath; 3-4 layers of confluent *expansion cells* on each side of midrib; *small fiber bundles* all way around midrib; hypodermis with 2 layers in OSP-29 & OSP-30; *transverse veins* long (mixed in OSP-29), connecting up to 6 large veins. Specimens examined: OSP-28, OSP-29 & OSP-30.

13. Scheelea phalerata (Mart. ex Spreng.) Burret. *Adaxial and abaxial epidermal cells* of different shape, size and orientation; *adaxial epidermal cells* are smaller and more regularly shaped than the abaxial cells; *adaxial hypodermis* is a mixture of rectangular and roundish large cells in SP-31; only roundish cells in SP-32; rectangular cells in SP-33; *abaxial hypodermis* a single layer varying from roundish to regularly shaped cells (square); *adaxial fibers* lignified (SP-31 & SP-33) or non-lignified (SP-32), arranged in small groups and rows (350-401 in number), of mostly

3 fibers per group, located above, in between and below hypodermal cells; *abaxial fibers* 70-90 in number (SP-31 & SP-32), regularly distributed, arranged in small roundish groups of 2-3 fibers/group, above hypodermis in the spongy mesophyll (SP-31 & SP-33); abaxial fibers missing in SP-32; palisade mesophyll well differentiated ca. 40-60 μ thick), with one layer of thick-walled elongate palisade cells (all three specimens); spongy mesophyll also very well differentiated (ca. 80-90 μ thick), 5-8 layers of roundish, compact spongy cells; tanniniferous cells frequent on both mesophylls; primary veins 7-13, 0.160 mm long x 0.126 mm wide on average, mostly pear-shaped with top buttresses (SP-31 & SP-32) or not (SP-33), centered, and formed by large fibers of thick walls (common in mixed patterns); *secondary and tertiary veins* large (secondary=0.067 mm; tertiary=0.050 mm), nearly on same plane, elongate, with upper inner sheath incomplete, and fibrous lower portions which go through hypodermis, forming large buttresses; *stomates with superficial guard-cells*, and mostly in files of 1-3 stomates on intercostal bands; *adaxial epidermis* a thick layer of mostly obliquely extended cells, of rhombohedral shape and linear walls, although some longitudinally extended cells (rectangular) can be observed; *abaxial epidermis* thick, of mostly longitudinally extended costal cells, of rectangular shape, and linear walls; *intercostal cells* variable, of linear walls; midrib 1.2-2.3 mm long (mean=1.7 mm), irregularly shaped, of very pointed sclerotic sheath; 3-4 layers of *expansion cells* not confluent below sclerotic sheath; *transverse veins* short (SP-32), or mixed (basically short, but with some long ones).
Specimens examined: SP-31, SP-32 & SP-33.

14. Scheelea insignis (Mart.) H. Karst. *Adaxial and abaxial epidermal cells* very similar in shape (rectangular), size (small) and orientation (longitudinal) when compared in cross section; *adaxial hypodermis* single-layered, formed by roundish, large, hypodermal cells; *abaxial hypodermis* also of roundish large cells, similar to those on adaxial hypodermis, usually interrupted by fiber bundles; *adaxial fibers* usually non-lignified, 260-303 in number (mean=288), occurring in very small groups (frequently 2-3 fibers/group) below or in between hypodermal cells; *abaxial fibers* 70-92 in number (mean=84), in groups larger than those in adaxial surface occurring in a somewhat square arrangement and frequently located on the hypodermal layer or in between hypodermal cells, interrupting the layer; *palisade mesophyll* very well differentiated, 40 μ thick, formed by one layer of elongate thick-walled cells; *spongy mesophyll* also very well differentiated, 50-60 μ thick (mean 56.6 μ), formed by 4-5 (usually 4) layers of thick-walled cells; *primary veins* 9-12 in number (mean=10.6), usually round, smaller than in the other groups (0.095 mm long x 0.112 mm wide), inner sheath complete, formed by large fibers of thin walls, which gives it a "chain" look, especially on the upper portion; primary veins not centered in the mesophyll - they are located closer to the abaxial surface; *secondary and tertiary veins* 75-119 in number (mean=99.6), usually small and roundish, secondary veins (mean=0.046 mm long) slightly bigger than tertiary veins (mean=0.034 mm long), inner sheath complete, with fibrous lower portions located on hypodermis, or going through it forming small buttresses; secondary and tertiary veins are also formed by large

fibers of thin walls; *stomates with superficial guard-cells*, arranged in definite files of 1-2 on intercostal bands; *adaxial epidermis* thin composed of longitudinally extended cells rectangular cells with undulate or slightly undulate walls; *abaxial epidermis* also a thin layer, formed by longitudinally extended rectangular *costal cells*, of usually undulate walls; *intercostal cells* variously shaped and sized, of undulate or slightly undulate walls; *midrib* 1.2-1.6 mm long (mean=1.4 mm), usually irregularly shaped (mostly pentagonal), with a very pointed sclerotic sheath; 12-20 vascular bundles (mean=15) enclosed in the sclerotic sheath; *small fiber bundles* all way the midrib; *transverse veins* long, connecting 4 to all large veins (most frequently 4-6).

Specimens examined: SI-34, SI-35, SI-36.

15. Scheelea butyracea (Mutis ex L.f.) H. Karst. ex H. Wendl. *Adaxial epidermal cells* of different shape, size (smaller) and orientation in comparison with abaxial epidermis; *adaxial hypodermis* one layer of roundish cells, (large in SB-38, smaller in SB-37 & SB-39); *abaxial hypodermis* one layer of regularly shaped (square) and sized (SB-37 & SB-39), or mostly roundish (SB-38); *adaxial fibers* slightly lignified (SB-37 & SB-39), or non-lignified (SB-38), regularly arranged in small groups of 2-3 fibers, groups (330-550 in number; mean=410)) located above, in between, and below hypodermal cells; *abaxial fibers* groups 62-75 in number (mean=69), small size (3 fibers/group), roundish, and located above hypodermis in spongy mesophyll (SB-37 & SB-39), or in between hypodermis and epidermis (SB-38); *palisade mesophyll* well differentiated (ca. 30-40 μ in SB-37 & SB-38; 60-65 μ in SB-39), with

one (SB-37 & SB-38) or two layers (SB-39) of elongate thick-walled cells; *spongy mesophyll* 5-6 (SB-37 & SB-38), or 7-8 layers (SB-39) of roundish, compact thick-walled cells, 80-135 μ (mean=101.6 μ); *primary veins* 9-13 in number (0.111 mm long x 0.112 mm wide on average), centered (SB-37 & SB-39), or closer to abaxial surface (SB-38), formed by large fibers of thin walls mostly; mid-secondary vein distinguishable (SB-37 & SB-39), or not (SB-38); *secondary and tertiary veins* small, elongate, with lower portions always above hypodermis, not forming buttresses (SB-37 & SB-39), or going through hypodermis, forming small buttresses (SB-38); secondary and tertiary veins about the same size in SB-38; secondary bigger than tertiary veins in SB-37 & SB-39 (secondary= 0.059 mm; tertiary=0.044 mm); veins are formed by large fibers of thick walls in SB-37, and thin walls in SB-38 & SB-39; veins with incomplete upper inner sheath in SB-37 & SB-39; complete in SB-38; *stomates* with sunken (SB-37 & SB-39) or superficial (SB-38) *guard-cells*, arranged in definite files of 1-2 (SB-38), or not in definite files with rows of 2-4 on intercostal bands (SB-37 & SB-39); *adaxial epidermis* thick in SB-37 and SB-39, and thin in SB-38; cells obliquely extended and mostly rhombohedral in SB-37 & SB-39, longitudinally extended and mostly rectangular in SB-38; all three specimens of undulate walls; *abaxial epidermis* thick (SB-37- & SB-39), or thin (SB-38), with longitudinally extended, spindle-shaped *costal cells* of linear walls (SB-37 & SB-39), or rectangular of undulate walls (SB-38); *intercostal cells* variable in shape and size, of linear (SB-37 & SB-39), or undulate walls (SB-38); *midrib* irregularly shaped (1.1-2.4 mm long; mean=1.6 mm), with 3-5 layers of confluent expansion cells below the

sclerotic sheath; *small fiber bundles* all way around midrib; *transverse veins* long, connecting 2-7 large veins. Specimens examined: SB-37, SB-38 & SB-39.

16. Scheelea attaleoides (Barb. Rodr.) Wess. Boer. *Adaxial and abaxial epidermal cells* very similar in shape (rectangular), size (small) and orientation (longitudinal) compared in cross section view; *adaxial hypodermis* single-layered, formed by roundish, large, hypodermal cells; *abaxial hypodermis* also of roundish large cells, similar to those on adaxial hypodermis, usually interrupted by fiber bundles; *adaxial fibers* usually non-lignified, 282-545 in number (mean=401), occurring in very small groups (usually 3 fibers/group), below or in between hypodermal cells; *abaxial fibers* 103-230 in number (mean=155.3), in groups larger than those in adaxial surface (3-6 fibers/group), in a somewhat square arrangement, and frequently located on the hypodermal layer or in between hypodermal cells, interrupting the layer; *palisade mesophyll* very well differentiated, 30-50 μ thick (mean=40 μ), formed by one layer of elongate thick-walled cells; *spongy mesophyll* also very well differentiated, 60-70 μ thick (mean=66.5 μ), formed by 4 layers of thick-walled cells; *primary veins* 6-7 in number (mean=6.6), usually round, small (0.110 mm long x 0.113 mm wide), inner sheath complete, formed by large fibers of thin walls, which gives the a "chain" look, especially on the upper portion; *primary veins* not centered in the mesophyll - they are located closer to the abaxial surface; *secondary and tertiary veins* 38-82 in number (mean=63), usually small and roundish, *secondary veins* (mean=0.046 mm long) slightly bigger than *tertiary veins* (mean=0.034 mm long), inner sheath

complete, with fibrous lower portions located on hypodermis, or going through it forming small buttresses; secondary and tertiary veins are also formed by large fibers of thin walls; *stomates with superficial guard-cells*, arranged in definite files of 1-2 on intercostal bands; a thin *adaxial epidermis* of longitudinally extended cells rectangular cells of undulate or slightly undulate walls; *abaxial epidermis* also a thin layer, formed by longitudinally extended rectangular *costal cells*, of usually undulate walls; *intercostal cells* variously shaped and sized, of undulate or slightly undulate walls; *midrib* 0.8-1.2 mm long (mean=1.3 mm), usually irregularly shaped (mostly pentagonal), with a very pointed sclerotic sheath; 8-12 vascular bundles (mean=10) enclosed in the sclerotic sheath; *small fiber bundles* all way the midrib; *transverse veins* long, connecting 4 to all large veins (most frequently 4-6). Specimens examined: SI-34, SI-35, SI-36.

17. Attalea oleifera Barb. Rodr. *Adaxial epidermal cells* smaller and of different shape and orientation compared with the abaxial epidermal cells; *adaxial hypodermis* single layered, formed by regularly rectangular hypodermal cells; *abaxial hypodermis* formed by one layer of mostly square cells; *adaxial fiber groups* lignified, 184-262 in number, in large *bunches*, ranging from 9-12 fibers/group, below the hypodermal layer; 21-68 groups of *abaxial fibers*, (3-4 fibers/group), located above hypodermis, in spongy mesophyll; *palisade mesophyll* poorly differentiated, 60-80 μ thick (mean=73.4 μ), of usually 2 layers of elongate thin-walled cells; *spongy mesophyll* also poorly differentiated, 120-140 μ thick

(mean=130 μ), formed by 7-10 layers of roundish, compact, thin-walled spongy cells; *primary veins* 10-12 in number, large, 0.197 mm long x 0.169 mm wide, pear-shaped, and usually of fibrous upper portions (top buttresses); primary veins are centered; inner sheath complete, formed by small or large fibers of thick walls; *secondary and tertiary veins* 83-126 in number (mean=102), usually elongate; secondary (mean= 0.083mm) bigger than tertiary veins (mean= 0.064 mm), inner sheath incomplete, of fibrous lower portions (large fibers of thick walls), forming buttresses; *stomates of slightly sunken guard-cells*, not arranged in definite files, usually in rows of 1-4 (most frequently 2-3) on intercostal bands; *adaxial epidermis* thick, of obliquely extended, rhombohedral cells, of linear walls; *abaxial epidermis* thick, of longitudinally extended, spindle-shaped *costal cells*, of linear walls; *intercostal cells* of variable shape and size, and linear walls; *midrib* 1.5-2.0 mm long (mean=1.8 mm), rectangular, 10-16 *vascular bundles* enclosed in sclerotic sheath; *small fiber bundles* mostly located at the upper portion of the midrib; *transverse veins* short, connecting up to 3 large veins (most frequently 2). Specimens examined: AO-43, AO-44, AO-45.

18. Attalea dubia (Mart.) Burret. *Epidermal cells* about the same size in both surfaces, but shaped and oriented differently; *adaxial hypodermis* one-layered, with regularly shaped (rectangular) and sized cells (a mixed layer of round and rectangular cells in AD-47); single *abaxial hypodermal layer* with cells of mostly regular shape (square & rectangular) and size; *adaxial fiber bundles* in number of

160-180 (mean=170), non-lignified, regularly arranged in small bunches (3-6 fibers per group) below hypodermis (AD-46), or medium groups and horizontal rows (2-5 fibers per group) in between and above hypodermal cells (AD-47); *abaxial fibers* lacking or very small in number (30 in AD-46), irregularly distributed, in small roundish groups of 1-2 fibers, located above hypodermis in the spongy mesophyll; *palisade mesophyll* poorly differentiated (60-80 μ thick; mean=70 μ), in two layers of elongate thin-walled palisade cells; *spongy mesophyll* poorly differentiated (80-120 μ ; mean= 100 μ), in 6-7 layers of roundish, compact, thin-walled spongy cells; *primary veins* 8-12 in number (mean=12), pear-shaped, 0.182 mm long x 0.163 mm wide on average, some with the top buttresses, centered, formed by small fibers of thick walls; *mid-secondary vein* discernible in AD-46, located slightly higher than the others, mid way in between large veins; secondary slightly bigger than tertiary veins in AD-46, inner sheath incomplete on upper portion, with lower fibrous portion always located above hypodermis, not forming buttresses; *secondary and tertiary veins* 53-90 in number (mean=71), of approximately same size in AD-47, inner sheath also incomplete on upper portion, with fibrous lower portions going through hypodermis, and forming medium buttresses; secondary= 0.067 mm; tertiary=0.045 mm, formed of large fibers of thick walls in both specimens examined; *stomates with sunken* (AD-46) or *slightly sunken* (AD-47) *guard-cells*, not in definite files (AD-46), or files of 1 (AD-47) on intercostal bands; *adaxial epidermis* thick, of obliquely extended, spindle-shaped cells, of linear walls; *abaxial epidermis* also a thick layer, with longitudinally extended, spindle-shaped *costal cells*, of linear walls; *intercostal*

cells variable in shape and size, of linear walls; *midrib* 1.2-1.6 mm long (mean=1.4 mm), irregularly shaped, but somewhat ovate (AD-46), or triangular (AD-47); 4 layers of confluent *expansion cells* on each side of the midrib; *small fiber bundles* (when present), on upper portion of the midrib; *transverse veins* short. Specimens examined: AD-46 & AD-47.

19. Attalea funifera Mart. ex Spreng. *Adaxial epidermal cells* bigger and of different shape and orientation compared with the abaxial epidermal cells; *adaxial hypodermis* single layered, formed by very regularly shaped (rectangular) and sized hypodermal cells; all adaxial hypodermal cells filled with tannins; some hypodermal cells replaced by large fibers (*hypodermal fibers*); *abaxial hypodermis* formed by one layer of mostly square and also tannin-filled cells of somewhat regular size; *adaxial fiber groups* lignified, 254-265 in number (mean=260), in large *bunches*, ranging 4-8 fibers/group (mean=6), below the hypodermal layer; *abaxial fibers* in small number (31-53), of medium groups (4-5 fibers/group), located above hypodermis, in spongy mesophyll; *palisade mesophyll* poorly differentiated, 80-120 μ thick (mean=100 μ), of 1-2 layers of elongate thin-walled cells; *spongy mesophyll* also poorly differentiated, 100-120 μ thick (mean=106.6 μ), formed by 6-7 layers of roundish, compact, thin-walled spongy cells; *primary veins* 10-13 in number (mean=11.6), large, 0.212 mm long x 0.156 mm wide, pear-shaped with fibrous upper portions (top buttresses); primary veins are centered, but closer and sometimes connected to the adaxial surface, because of the top buttresses; inner sheath complete, formed by small and

large fibers of thick walls; *secondary and tertiary veins* 77-108 in number (mean=89), elongate; secondary (mean=0.097 mm) bigger than tertiary veins (mean=0.074 mm) inner sheath incomplete, of fibrous lower portions (large fibers of thick walls), forming large buttresses; *stomates of superficial guard-cells*, not arranged in definite files, usually in rows of 2-7 (most frequently 3-4) on intercostal bands; *adaxial epidermis* thick, of obliquely extended, rhombohedral cells, of linear walls; *abaxial epidermis* thick, of longitudinally extended, spindle-shaped *costal cells*, of linear walls; *intercostal cells* of variable shape and size, and linear walls; *midrib* 1.1-1.2 mm long, round; *vascular bundles* enclosed in sclerotic sheath; *small fiber bundles* lacking on midrib; instead, a layer of hypodermal fibers around the sclerotic sheath; *transverse veins* short, connecting up to 3 large veins (most frequently 2).
Specimens examined: AF-48, AF-49, AF-50.

20. Attalea geraensis Barb. Rodr. *Adaxial epidermal cells* smaller and of different shape and orientation compared to the abaxial epidermal cells; *adaxial hypodermis* single layered, formed by regularly shaped (rectangular) hypodermal cells; *abaxial hypodermis* formed by one layer of mostly square cells regularly sized; *adaxial fiber groups* non-lignified, 152-160 in number (mean=156), in large groups or *bunches*, ranging 7-8 fibers/group (mean=7), below (most frequently), above and in between hypodermal cells; *abaxial fibers* lacking, or very small in number (up to 10; 2-3 fibers/group), located above hypodermis, in spongy mesophyll; *palisade mesophyll* poorly differentiated, 60-90 μ thick (mean=80 μ), of usually 2 layers of elongate thin-

walled cells; *spongy mesophyll* also poorly differentiated, 90-100 μ thick (mean=93.3 μ), formed by 6-7 layers (mean=6) of roundish, compact, thin-walled spongy cells; *primary veins* 8-11 in number (mean=9), large, 0.165 mm long x 0.130 mm wide, pear-shaped, and usually of fibrous upper portions (top buttresses); primary veins are centered; inner sheath complete, formed by small or large fibers of thick walls; *secondary and tertiary veins* 70-89 in number (mean=78), usually elongate; secondary (mean= 0.087 mm) bigger than tertiary veins (mean= 0.067 mm), inner sheath incomplete, of fibrous lower portions (large fibers of thick walls), which go through hypodermis, forming buttresses; *stomates of slightly sunken guard-cells*, not arranged in definite files, usually in rows of 1-5 (most frequently 2-3) on intercostal bands; *adaxial epidermis* thick, of obliquely extended, rhombohedral cells, of linear walls; *abaxial epidermis* thick, of longitudinally extended, spindle-shaped *costal cells*, of linear walls; *intercostal cells* of variable shape and size, and linear walls; *midrib* 1.1-1.2 mm long, usually rectangular; 8-10 *vascular bundles* enclosed in sclerotic sheath; *small fiber bundles* mostly located at the upper portion of the midrib; *transverse veins* short, connecting up to 3 large veins (most frequently 2).

Specimens examined: AG-51, AG-52, and AG-53.

21. Attalea humilis Mart. ex Spreng. *Epidermal cells* of different shape, size and orientation on each surface; *adaxial hypodermis* one layer of mostly rectangular cells of approximately same size, but mixed with some roundish cells; *abaxial hypodermal cells* square or rectangular, and mostly of regular size; *adaxial fiber*

bundles in number of 320-358 (mean=339), non-lignified, regularly arranged in small-medium bunches (5 fibers/group), below hypodermal layer; *abaxial fibers* in number of 110-129 (mean=119), regularly arranged in small roundish groups (4-6 fibers/groups), mostly located right on hypodermis, or less frequently above it, in spongy mesophyll; *palisade mesophyll* poorly differentiated, 1-2 layers (70-80 μ ; mean= 75 μ) of thin-walled elongate palisade cells; *spongy mesophyll* poorly differentiated, but with 4-6 layers (ca. 100 μ) of roundish, compact cells; *primary veins* 10-12, 0.160 mm long x 0.131 mm wide on average, pear-shaped (some with top buttresses), centered, formed by small fibers of thick walls; in AH-54, however, there is both, pear-shaped (centered) and round (closer to abaxial surface) veins, formed by large fibers of thick (bigger, pear-shaped veins) and thin (smaller, round veins) walls; *secondary and tertiary veins* 91-127 in number (secondary=0.063 mm; tertiary=0.048mm), mostly elongate, formed by large fibers of thick walls, with incomplete upper inner sheath, located mostly right on the hypodermal layer, with fibrous lower portion going through hypodermis, forming buttresses; *stomates with superficial guard-cells*, in files 1-2 (AH-54), or not in definite files (AH-55), but still 1-2 on intercostal bands; *adaxial epidermis* thick, of mostly obliquely extended (but mixed with some rectangular cells) of linear walls; a thick *abaxial epidermis* with longitudinally extended costal cells, spindle-shaped (mixed with rectangular in AH-54), or mostly rectangular (mixed with spindle-shaped cells in AH-55), of linear walls; intercostal cells variously shaped and sized, of linear walls; *midrib* rather irregular, but mostly rectangular, 1.2-1.7 mm long (mean=1.5 mm); 3 layers of not *confluent*

expansion cells on each side of the midrib; *small fiber bundles* all way around midrib; *transverse veins* short (AH-54), or mixed (short transverse veins mostly with some long ones - AH-55). Specimens examined: AH-54 & AH-55.

22. Attalea pindobassu Bondar. *Adaxial epidermal cells* smaller and of different shape and orientation compared to the abaxial epidermal cells; *adaxial hypodermis* single layered, formed by very regularly rectangular hypodermal cells; *abaxial hypodermis* formed by one layer of mostly square cells of somewhat regular size; *adaxial fiber groups* slightly lignified or lignified, 164-202 in number (mean=183), arranged in *bunches* or groups with 6 fibers/group on average, below or above the hypodermal layer; *abaxial fibers* in small number (up to 20), of small groups (2-3 fibers/group), located above hypodermis, in spongy mesophyll; *palisade mesophyll* poorly differentiated, 80-90 μ thick (mean=85 μ), of 2 layers of elongate thin-walled cells; *spongy mesophyll* also poorly differentiated, ca. 120 μ thick, formed by 6-7 layers (mean=6) of roundish, compact, thin-walled spongy cells; *primary veins* 9-12 in number (mean=10), large, 0.186 mm long x 0.154 mm wide on average, pear-shaped, and usually of fibrous upper portions (forming top buttresses); primary veins are centered, but closer and sometimes connected to the adaxial surface, because of the top buttresses; inner sheath complete, formed by small or large fibers of thick walls; *secondary and tertiary veins* 66-74 in number (mean=70), usually elongate; secondary (mean= 0.091mm) bigger than tertiary veins (mean= 0.075 mm), inner sheath incomplete, of fibrous lower portions (small fibers of thick walls), which go

through hypodermis, forming buttresses; *stomates of slightly sunken guard-cells*, not arranged in definite files, usually in rows of 2-6 (most frequently 2-4) on intercostal bands; *adaxial epidermis* thick, of obliquely extended, rhombohedral cells, of linear walls; *abaxial epidermis* thick, of longitudinally extended, spindle-shaped *costal cells*, of linear walls; *intercostal cells* of variable shape and size, and linear walls; *midrib* ca. 1.0 mm long, usually rectangular; *vascular bundles* enclosed in sclerotic sheath; *small fiber bundles* mostly located at the upper portion of the midrib; *transverse veins* short, usually connecting up to 2 large veins. Specimens examined: AP-56, and AP-57.

23. Attalea nucifera H. Karsten. *Epidermal cells* of approximately same size, shape, and orientation on both surfaces; *adaxial hypodermis* with one layer of large, roundish cells; *abaxial hypodermis* also one layered of variously shaped (but mostly roundish) cells; non-lignified *adaxial fiber bundles* (366-378 in number), arranged mostly in small groups (3-4 fibers/group) and/or horizontal and vertical rows, in between and/or above hypodermal cells; *abaxial fibers* (27 -78) , irregularly (AN-58) or regularly (AN-59) distributed in a somewhat square arrangement of mostly 6 fibers, in between hypodermal cells, frequently interrupting the layer; *palisade mesophyll*, one well differentiated layer (40-50 μ thick; mean=45 μ) of thick-walled elongate palisade cells; a well differentiated *spongy mesophyll* with 5 layers (50-90 μ thick; mean=70 μ) of thick-walled, compact spongy cells; *primary veins* 9-13 in number (mean=11), 0.102 mm long x 0.108 mm wide, round, closer to the abaxial

surface, formed by large fibers of thin walls (the “chain” pattern); *secondary and tertiary veins* 69-83 in number, small (secondary=0.059 mm; tertiary=0.045 mm), roundish, inner sheath complete, formed by large fibers of thin walls; with fibrous lower portions going through hypodermis, forming small buttresses; *stomates with superficial guard-cells*, not in definite files, but in rows of 1-2 on intercostal bands; *adaxial epidermis* thin, of longitudinally extended, rectangular cells (with some mixture of rhombohedral cells?), of undulate walls; *abaxial epidermis* thin, with longitudinally extended, rectangular costal cells, of undulate walls; intercostal cells variable, of undulate walls; *midrib* ca. 1.2 mm long, irregularly shaped, with a very pointed sclerotic sheath; *small fiber bundles* all way around midrib; 2-3 layers of not confluent *expansion cells* on each side of the midrib; *transverse veins* long.

Specimens examined: AN-58 & AN-59.

24. Attalea tessmannii Burret. *Epidermal cells* of different size, shape and orientation on both surfaces: smaller and obliquely extended on adaxial surface, bigger and longitudinally extended on abaxial; *adaxial hypodermis* a continuous layer of regularly shaped (rectangular) and sized cells in AT-60, and more roundish and of variable size in AT-62; *abaxial hypodermis* one layer of mostly square/rectangular, regularly sized cells in AT-60, and less regularly shaped (although still mostly square) and sized in At-62; lignified *adaxial fibers*, 402-406 groups, regularly arranged in bunches (4-6 fibers/group), mostly below hypodermal layer, or small-medium groups (2-4 fibers/group) above or in between hypodermal

cells; *abaxial fibers* lacking in the two specimens; *palisade mesophyll* poorly differentiated in AT-60 (50-60 μ), well differentiated in AT-62 (60-70 μ), both with one layer of elongate palisade cells (thin-walled in AT-60, thick-walled in AT-62) with frequent presence of tannins; *spongy mesophyll* poorly differentiated, with 7 layers (80-100 μ) of thin-walled cells in AT-60, and well differentiated 6 layers (?) of thick-walled spongy cells in AT-62; *primary veins* 12-13 in number, 0.136 mm long x 0.138 mm wide on average, round, closer to the abaxial surface, forming bumps on lamina below them, with a inner sheath formed mostly by large and small fibers of thick walls; big *secondary and tertiary veins* (92-114 in number; secondary=0.100 mm; tertiary=0.078 mm), with lower portions going through hypodermis, forming large buttresses and bumps on lamina below them; veins are formed by large fibers of thin walls, with complete fibrous inner sheaths; *stomates with slightly sunken guard-cells*, located in the grooves formed in between the bumps of two secondary or tertiary veins; stomates not in definite files, occurring in rows of 3-6 on intercostal bands; *adaxial epidermis* (thin in AT-60) with obliquely extended, rhombohedral cells of slightly undulate to linear walls (AT-62); *abaxial epidermis* (thin in AT-60) with longitudinally extended, spindle-shaped costal cells, of slightly undulate to linear walls (AT-62); *intercostal cells* variable, of slightly undulate to linear walls; midrib 1.5-2.0 mm long, irregularly shaped, mostly roundish and pointed on upper portion; *small fiber bundles* only on upper portion (AT-60), or all way around midrib (AT-62); 3-4 layers of confluent *expansion cells* on each side of the midrib; *transverse veins*

long, connecting 3-8 large veins. Specimens examined: AT-60 & AT-62. Specimen AT-61 was mistakenly identified, and turned out to be a specimen of Syagrus.

25. Attalea racemosa Spruce. *Epidermal cells* of different size, shape and orientation in AR-63 & AR-64; same shape, size and orientation in AR-65; *adaxial hypodermis* with one layer of large roundish hypodermal cells; *abaxial hypodermis* one layer of roundish large cells (AR-63 & AR-65), or of more regular shape (square) and size (AR-64); lignified *adaxial fiber bundles* (253-484 in number, mean=396), occurring in small groups and rows (mostly 3 fibers/group), above, in between or below hypodermal cells; *abaxial fiber bundles* in number of 84-148 (mean=118) in AR-63 & AR-64, in a regular somewhat square arrangement (4-8 fibers/group), in between hypodermal cells; bundles in number of 80, more roundish, with 5-8 fibers/group, located in between hypodermis and epidermis in AR-64; *palisade mesophyll* well differentiated (40 μ thick), with 1 layer of elongate (but rather "fat") thick-walled palisade cells; *spongy mesophyll* well differentiated (ca. 60 μ thick) with 4-5 layers of roundish thick-walled spongy cells; *primary veins* in number of 7-10, 0.096 mm long x 0.105 mm wide, round, closer to abaxial surface in AR-63 & AR-65, centered in AR-64, formed mostly by large fibers of thin walls in AR-63, and large fibers of thick walls in AR-64 and AR-65; *secondary and tertiary veins* 57-115 in number, small (secondary=0.055 mm; tertiary=0.042 mm); , roundish, inner sheath complete, formed by large fibers of thin walls, with lower portions forming small buttresses in AR-63 & AR-65; bigger, more elongate, inner

sheath complete, formed by large fibers of thick walls, with lower portions forming large buttresses in AR-64; stomates with superficial guard-cells in AR-63 and AR-65, mostly in arranged in files of 1-2 on intercostal bands; *stomates* with slightly sunken *guard-cells* in AR-64, also occurring in files of 1-2; *adaxial epidermis* thin, cells longitudinally extended, rectangular, of slightly undulate to undulate walls (or linear in AR-64); *abaxial epidermis* thin, of longitudinally extended, rectangular *costal cells*, of slightly undulate to undulate walls; or mixed spindle-shaped-rectangular of linear walls in AR-64; *intercostal cells* of variable shape and size, slightly undulate walls (linear in AR-64); *midrib* 0.8-2.0 mm long (mean=1.5 mm), irregularly shaped; *small fiber bundles* all way around midrib; 3 layers of confluent *expansion cells* on each side of midrib; *transverse veins* long, connecting up to 7 large veins in AR-63 and AR-65; *transverse veins* short or mixed short-long in AR-64 (connecting up to 3 large veins). Specimens examined: AR-63, AR-64, and AR-65.

26. Maximiliana maripa (Corr. Serra) Drude. *Adaxial epidermal cells* bigger of approximately same shape and orientation compared to the abaxial epidermal cells; *adaxial hypodermis* of one layer of roundish cells; *abaxial hypodermis* also one-layered, with cells smaller than on adaxial hypodermis, variously shaped and sized; *adaxial fibers* in 289-352 groups (mean=324), usually non-lignified, small (2-3 fibers per group), mostly in vertical rows, located usually in between hypodermal cells (or less frequently, above and/or below hypodermis); *abaxial fibers* 94-104 (mean=98) groups, usually 4-6 per group, located right on the hypodermal layer or in between

the hypodermis and epidermis; *palisade mesophyll* 50-60 μ thick (mean=56.6), with one well differentiated layer of elongate palisade cells of thick walls; *spongy mesophyll* usually 6-layered, 90-120 μ thick (mean=100 μ), of roundish, compact, thick-walled spongy cells; *primary veins* 5-7 in number (mean=6), constitute the most distinctive character in this species; these are the big: 0.293 mm long x 0.228 mm wide on average, pear-shaped, centered, inner sheath complete, formed by up to 9 layers of small fibers of thick walls, forming conspicuous bumps on both upper and lower surfaces of lamina, right above and below each primary vein; *secondary and tertiary veins* 98-145 in number (mean=119); secondary (0.065 mm long) bigger than tertiary veins (0.042 mm long), inner sheath complete, of large, thin-walled fibers, with elongate fibrous lower portions going through hypodermis or not, technically forming buttresses, although not much pressure is put on the epidermis, since the lower pointed tip of the veins only touches it; *stomates with superficial guard-cells*, arranged not in definite files, in rows of usually 2-3 on intercostal bands; *adaxial epidermis* thick, of longitudinally extended, spindle-shaped cells, of linear walls; *abaxial epidermis* also thick, of longitudinally extended, mostly rectangular *costal cells*, of linear walls; *intercostal cells* variously shaped and sized, of linear walls; *midrib* 2.1-2.8 mm long (mean=2.4 mm), irregularly shaped, but somewhat triangular; 18-20 vascular bundles (mean=18), enclosed in sclerotic sheath; 4 layers of *expansion cells* not confluent below sclerotic sheath; *transverse veins* short, connecting up to 3 large veins (most frequently 2). Specimens examined: MM-66, MM-67, and MM-68.

27. Markleya dahlgreniana Bondar. *Epidermal cells* in cross section are smaller on the adaxial surface and of different shape and orientation when compared to the abaxial epidermal cells; *adaxial hypodermis* show some variation: it is one-layered in one specimen examined (MD-69, from Suriname), and two-layered in the other two specimens (MD-70 and MD-71, from Brazil); in the two-layered specimens, hypodermal cells in the upper layer are more regularly shaped (square/rectangular) and sized, and more roundish in the lower layer; in the one-layered specimen hypodermal cells are roundish; *abaxial hypodermis* one-layered, of regularly shaped (square) cells; slightly lignified *adaxial fibers*, 190-526 groups (mean=390), mostly small to medium size (groups or rows with 3-6 fibers/group), usually above, in between and less frequently below the two hypodermal layers (when 2-layered), or mostly above hypodermis when 1-layered; *abaxial fiber bundles* quite variable in number (range=25-273; mean=147), but mostly regularly distributed and arranged in roundish groups of 2-5 fibers per group, and usually located in between hypodermis and hypodermis, or less frequently, right on the hypodermal layer; *palisade mesophyll* poorly differentiated, 40-60 μ thick (mean=53.4 μ), formed usually by one layer of elongate thin-walled palisade cells of thin walls; *spongy mesophyll* well differentiated, 90-120 μ thick (mean=110 μ), with 6 layers of compact thick-walled spongy cells; *primary veins* 8-14 in number (mean=10), pear-shaped or round, 0.173 mm long x 0.156 mm wide on average, centered, inner sheath complete, formed by small fibers of thick walls, frequently forming slight bumps on lamina,

above and below veins; *mid-secondary* only discernible in MD-70; *secondary and tertiary veins* 77-162 in number (mean=120), secondary (mean=0.075 mm long) slightly bigger than tertiary veins (0.060 mm long), usually of elongate fibrous lower portions, inner sheath incomplete, formed by large fibers of thick walls in MD-70 & MD-71, and complete, of thinner walls in MD-69; location of secondary and tertiary veins varying from one specimen to another: with lower portions going through hypodermis and slightly touching epidermis in MD-69; above hypodermis, with no buttresses formed in MD-70; and, in a mixed pattern, with most of the veins above, but close to the hypodermis, with some going through hypodermis, touching the epidermis, in MD-71; *stomates with superficial guard-cells* in MD-69, and sunken in MD-70 and MD-71, not in definite files, with 2-4 rows on intercostal bands; *adaxial epidermis* thick, longitudinally extended, spindle-shaped in MD-69, and obliquely extended, rhombohedral, with some mixture of longitudinally extended, rectangular cells, in MD-70 and MD-71, always of linear walls; *abaxial epidermis* thick, of longitudinally extended, usually spindle-shaped *costal cells* (a mixture of rectangular and spindle-shaped cells in MD-69), of linear walls; *intercostal cells* variously shaped, of linear walls; *midrib* 1.4-2.5 mm long (mean=2.0 mm), rectangular, with 3-5 layers of expansion cells (confluent in MD-69 & MD-70, not confluent in MD-71) on each side of midrib; *small fiber bundles* all way around midrib in MD-69 and MD-70, and only on upper portion in MD-71; *transverse veins* short, connecting up to 2 large veins. Specimens examined (MD-69, MD-70 & MD-71).

28. Attalea colenda (O. F. Cook) Balslev & Henderson. *Adaxial epidermal cells* are smaller and of different shape and orientation compared to the abaxial cells; *adaxial hypodermis* with one layer of very regularly shaped (rectangular) and sized cells; *abaxial hypodermis* also one layer of regular rectangular/square cells; *adaxial fibers* non-lignified, 245-283 groups (mean=264), in large bunches (18-20 fibers per group; mean=19) below hypodermis; *abaxial fiber groups* up to 15, or lacking completely; when present, arranged in small groups of 1-2 fibers, irregularly distributed, located in between hypodermis and epidermis; *palisade mesophyll* ca. 100-110 μ thick (mean=105 μ), poorly differentiated, with 2-3 layers of elongate thin-walled cells; *spongy mesophyll* poorly differentiated, 140-150 μ thick (mean=145 μ), with 9-10 layers of compact, thin-walled spongy cells; *primary veins* 14 in number, 0.194 mm long x 0.165 mm wide on average, mostly pear-shaped, although some smaller, roundish ones can be found; pear-shaped veins in number of 6-8, sometimes with upper portions more fibrous (top buttresses), centered, inner sheath complete, formed by small fibers of thick walls; roundish veins, centered or closer to abaxial surface, inner sheath complete, formed by large (on upper portion) and small (on lower portion) fibers of thick walls; *mid-secondary* vein distinguishable; *secondary and tertiary veins* 143-158 in number (mean=150), secondary (0.101 mm long) bigger than tertiary veins (0.074 mm long), both elongate, located nearly on same plane, with lower fibrous portions always above hypodermis, with no buttresses formed; inner sheath of both secondary and tertiary veins incomplete, formed by 1-3 layers of large fibers of thick walls; *stomates with sunken guard-cells*,

not arranged in definite files, usually in rows of 3-6 on intercostal bands; *adaxial epidermis* thick, of obliquely extended, rhombohedral cells, of linear walls; *abaxial epidermis* thick, of longitudinally extended, spindle-shaped cells, of linear walls; *intercostal cells* variable, of linear walls; *midrib* 2.3-2.4 long (mean=2.4 mm), mostly rectangular, with 4 layers of not confluent expansion cells on each side of midrib, below sclerotic sheath; *small fiber bundles* on upper portion of midrib; *transverse veins* short. Specimens examined: YC-72 & YC-73.

29. Attalea x piassabossu Bondar. *Adaxial cuticle* very thick (0.020 mm); *abaxial cuticle* 0.010 mm thick; *epidermal cells* slightly bigger and of different shape and orientation compared to the abaxial cells; *adaxial hypodermis* one layer of regularly rectangular very-thick walled cells; large hypodermal fibers eventually replacing a few of the hypodermal cells (taking the exact shape and size of the replaced cell); *abaxial hypodermis* also one layer of regularly shaped (square) and sized cells; *adaxial fibers* lignified, ca. 153 groups arranged in bunches of ca. 16 fibers/group, below the hypodermal layer; *abaxial fibers* very small in number of groups (21), with ca. 3 fibers per group on average; *palisade mesophyll* poorly differentiated, ca. 120 μ thick, with 2-3 layers of elongate thin-walled palisade cells, with strong presence of tannins; *spongy mesophyll* also poorly differentiated, 160 μ thick, with 8 layers of compact, thin-walled spongy cells; both palisade and spongy mesophylls with strong presence of tannins (from A. funifera, whose hypodermis and mesophyll are completely darkened by the strong occurrence of tannins); *primary veins* in number

of 7, 0.242 mm long x 0.150 mm wide, pear-shaped with large top-buttresses and 1-2 layers of big hypodermal fibers on the upper and lower portions of the veins; primary veins centered, inner sheath complete, formed by small and large thick-walled fibers; *secondary and tertiary veins* 94 in number, secondary veins bigger (0.110 mm long; tertiary veins 0.079 mm long), elongate, positioned nearly on same plane, with lower fibrous portions (1-5 layers) of secondary veins frequently going through hypodermis, forming buttresses (tertiary above hypodermis); *stomates with unusually superficial guard-cells* (from *A. funifera*), not in definite files, occurring in rows of 2-3 on intercostal bands; *adaxial epidermis* a thick layer of obliquely extended, rhombohedral cells, of linear walls; *abaxial epidermis* thick, of longitudinally extended, spindle-shaped cells, of linear walls; *intercostal cells* variable in shape and size, of linear walls; *midrib* 1.1 mm long, round, with a layer of hypodermal big fibers replacing the hypodermis all way around it; *midrib cuticle* very thick (0.024 mm); *expansion cells* in 3 layers on each side of midrib, not confluent below the sclerotic sheath; *transverse veins* short. Specimen examined: AXP-74.

30. x *Attabignya minarum* Balick, Anderson & Medeiros-Costa. *Adaxial epidermal* cells smaller and of different size and shape, compared to the abaxial cells; *adaxial hypodermis* with two layers: upper layer with regularly rectangular cells, and lower layer of roundish cells; *abaxial hypodermis* one single layer of regularly shaped (square) and sized cells; *adaxial fibers* in number of 255 groups, slightly lignified, regularly distributed in a mixed arrangement of medium-size groups and bunches,

more frequently with 8 fibers per group on average, usually below the upper hypodermal layer, and in between the hypodermal cells of the lower layer; *abaxial fiber groups* in small number (42), of small size (3 fibers/group), irregularly distributed, and usually located above hypodermis in the spongy mesophyll; *palisade mesophyll* poorly differentiated, with 2 layers (ca. 100 μ thick) of elongate narrow thin-walled palisade cells; *spongy mesophyll* poorly differentiated, ca. 180 μ thick, with 9 layers of compact, thin-walled spongy cells; *tannins* present in both mesophylls; *primary veins* 12, ca. 0.188 mm long x 0.152 mm wide, a mixture of pear-shaped veins with upper buttresses, and some round ones; in any case, centered, inner sheath complete, formed by small fibers of thick walls; mid-secondary present; *secondary an tertiary veins* 145 in number, secondary (0.088 mm long) bigger than tertiary veins (0.071 mm long), positioned nearly on same plane, with fibrous lower portions of veins always located above hypodermal layer, inner sheath of secondary and tertiary veins 1/2 incomplete, formed by small fibers of thick walls; *stomates with sunken guard-cells*, not in definite files, usually in rows of 2-5 on the intercostal bands; *adaxial epidermis* thick, with obliquely extended rhombohedral cells, of linear walls; *abaxial epidermis* thick, with longitudinally extended, spindle-shaped *costal cells*, of linear walls; *intercostal cells* variously shaped and sized, of linear walls; *midrib* 1.9 mm long, rectangular, with 3-4 layers of expansion cells on each side of the midrib, confluent below the sclerotic sheath; *midrib cuticle* thick (0.014 mm), *hypodermis* 2-layered; *transverse veins* short.

Specimen examined: AXM-75.

31. Syagrus amara (Jacq.) Mart. *Trichomes* present, but very infrequent on both surfaces, flask-shaped (club-shaped basal cell expanded distally in a wide filament of thin-walled cells), irregularly distributed, partially sunken, 0.030-0.040 mm long. *Adaxial cuticle* ca. 0.006 mm thick; *abaxial cuticle* 0.003-0.004 mm thick. *Adaxial epidermal cells* more regularly shaped, sized and oriented than *abaxial cells*; *adaxial hypodermis* one layer (regularly interrupted by fiber groups) of large thin-walled cells, octagonally shaped; *abaxial hypodermis* also one layer of cells slightly smaller than the *adaxial cells*, frequently interrupted by fiber bundles; *adaxial fiber groups* in number of 125, small (5 fibers/group), non-lignified, located in between or below *hypodermal cells*; *abaxial fiber groups* in number of 55, regularly distributed and somewhat in a square arrangement of ca. 8 fibers per group, in between lower *hypodermal cells*; *palisade mesophyll* lacking; *mesophyll* is entirely filled with large, mostly rectangular *spongy cells*, transversely oriented, and arranged in 4 layers (60 μ thick); *primary veins* in number of 6, 0.106 m long x 0.085 mm wide, somewhat pear-shaped, centered, but forming bumps on both sides of the lamina, inner sheath complete, formed by large fibers of thick (on lower portion) and thin (upper portion) walls; *secondary* (0.068 mm) slightly bigger than *tertiary veins* (0.044 mm), but in smaller number (37 in number, both *secondary* and *tertiary veins*), both with most of the inner sheath formed by large fibers of thin walls, with large, flat buttresses on lower portions (formed by non-lignified smaller fibers of thicker walls); *stomates* with *superficial guard-cells*, mostly arranged in regularly spaced files of 1-2 on intercostal

bands; *adaxial epidermal cells* a very uniform layer of mostly longitudinally extended cells, of rectangular shape (although frequently with oblique ends), and linear walls; *abaxial epidermal cells* of longitudinally extended elongate rectangular costal cells, of linear walls; *intercostal cells* variable in shape and size, of linear walls; *midrib* ca. 1.0 mm long, mostly rectangular, with *expansion cells* in 3-4 layers on each side of the midrib, confluent below the sclerotic sheath; *small fiber bundles* very regularly spaced all way around the midrib; *transverse veins* short, few, and connecting not only two large veins, but secondary and tertiary veins between them. Specimen examined: SYA-76.

32. Syagrus comosa (Mart.) Mart. *Trichomes* present on both surfaces, flask-shaped, irregularly distributed, slightly sunken, ca. 0.015-0.020 mm long, more frequent on adaxial surface. *Adaxial cuticle* ca. 0.008 mm thick; *abaxial cuticle* ca. 0.010 mm thick. *Adaxial epidermal cells* more regularly shaped, sized and oriented than abaxial cells; adaxial hypodermis with one mostly continuous layer of regularly shaped (rectangular to square) and sized cells; *abaxial hypodermis* also single-layered, of more variable shape and size, often interrupted by lower portions of secondary and tertiary veins; *adaxial fibers* in ca. 96 groups, regularly arranged in massive (up to 50 fibers/group, but most frequently 18-22; mean=20) non-lignified bunches below the hypodermal layer; *abaxial fibers* practically lacking (just a few); *palisade mesophyll* poorly differentiated, with apparently 2 or more layers of elongate (ca. 100 μ thick), very thin-walled palisade cells; *spongy mesophyll* poorly

differentiated (ca. 120 μ thick), with 6-7 layers of also very thin-walled compact spongy cells; no tannins on both mesophylls; *primary veins* 5, 0.230 mm long x 0.118 mm wide, pear-shaped with upper portion buttresses, inner sheath complete, formed by small fibers of thick walls; *secondary and tertiary veins* 60 in number, very distinctive by having inner sheath divided by fibers into two sections of phloem elements; *secondary* (0.097 mm) bigger than *tertiary veins* 0.067 mm), both mostly with inner sheath incomplete on upper portions, formed by large fibers of thin walls; *stomates with superficial guard-cells*, in files of 1-2, on intercostal bands; *adaxial epidermal cells* obliquely extended, mostly rhombohedral or cubical, but also rectangular (on over-fiber bands), of undulate walls; *abaxial epidermal cells* longitudinally extended, rectangular (but with oblique ends), of undulate walls; *intercostal cells* mostly rectangular, of undulate walls; *midrib* small (0.5 mm long) round, with 4-5 layers of *expansion cells* on each side, confluent below the sclerotic sheath; *transverse veins* short and thick. Specimen examined: SYC-77.

33. Syagrus cocooides Mart. *Trichomes* present on both surfaces, very infrequent, however, especially on abaxial surface, flask-shaped, irregularly distributed, slightly sunken, 0.030-0.040 mm long. *Adaxial cuticle* ca. 0.006 mm thick; *abaxial cuticle* very thin, ca. 0.002-0.003 mm thick. *Adaxial epidermal cells* more regularly shaped, sized and oriented than abaxial cells; *adaxial hypodermis* one layer of regularly shaped (mostly roundish or octagonal) cells, often interrupted by small groups of fibers, some tannin-filled; *abaxial hypodermis* one layer, frequently interrupted by

the lower portions of secondary and tertiary veins, with mostly square cells; *adaxial fibers* lignified, in very small groups (152 in number, 1-2 fibers per group), mostly horizontal rows, located in between hypodermal cells; *abaxial fibers* lacking; *palisade mesophyll* well differentiated (ca. 40 μ thick), with 2 layers of short palisade cells, darkened by tannins; *spongy mesophyll* ca. 30 μ thick, poorly differentiated, with 3 layers of compact, mostly tannin-filled cells; *primary veins* 8, 0.127 mm long x 0.075 mm wide, pear-shaped with upper buttresses, forming bumps on both sides of lamina; inner sheath of primary veins complete, formed by large fibers of thick walls; *secondary and tertiary veins* ca. 50 in number, of slight different size (secondary=0.059 mm; tertiary=0.044 mm), elongate (deltoid shape - more *Attaleinae* type), inner sheath shortly incomplete on upper portion, formed by large fibers of thick walls; lower fibrous portions with buttresses; *stomates with superficial guard-cells*, not in definite files in rows of 2-6 (most frequently 3) on intercostal bands; *adaxial epidermal cells* mostly obliquely extended, rhombohedral or cubical, of undulate walls; *abaxial epidermis* of longitudinally extended mostly rectangular (of oblique ends) *costal cells*, and undulate walls; *intercostal cells* variously shaped and sized, of linear to slightly undulate walls; *midrib* small (0.5 mm long), irregularly shaped, but somewhat rectangular, with 3 layers of confluent *expansion cells* on each side; *transverse veins* short, but in a very unusual pattern: very few transverse veins connect two large veins; they are mostly connecting the large veins to secondary and tertiary veins. Specimen examined: SC-78.

Table 5. Quantitative data for leaf anatomical characters of taxa from the Attaleinae - Cuticle and trichomes.

Taxa	Adaxial Cuticle (μ)			Abaxial Cuticle (μ)			Adaxial Trichomes(μ)			Abaxial Trichomes (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	8	8	-	8	8	-	50-60	55	7.07	50	50	-
<i>O. oleifera</i>	8	8	-	4	6	2	40-60	46.6	11.54	40-44	41.3	2.30
<i>O. brejinhoensis</i>	7-10	8	1	8-10	9	1	40-50	46.5	5.77	40-50	46.6	5.77
<i>O. eichleri</i>	4-6	4	1	4-7	5	1	30-40	34.6	5.03	34-50	38	3.46
<i>O. luetzelburgii</i>	10-12	11	1	14-15	14	7	50-70	60	14.14	40-60	50	14.1
<i>O. polysticha</i>	4-10	6	3	4-8	5	2	50-60	53.3	10.60	30-50	40	10.0
<i>O. sagotii</i>	6-7	6	5	3-5	4	1	40-80	60	20.0	40-60	50	10.0
<i>O. cohune</i>	6	6	-	6	6	-	50	50	-	40	40	-
<i>O. crassipatha</i>	4	4	-	1	1	-	50-60	55	7.07	40-45	42.5	-
<i>O. cuatrecasana</i>	4-8	6	2	3-6	4	-	40-60	53.3	11.54	50-60	55	5.0
<i>O. guacuyule</i>	10	10	-	9	9	-	40	40	-	40	40	-
<i>O. spectabilis</i>	8-10	8	1	3-9	5	3	60	60	-	40-60	50	10.0
<i>S. phalerata</i>	4-6	5	1	1	1	-	60	60	-	35-45	40	5.00
<i>S. insignis</i>	2-3	2	5	1-3	2	1	40-60	50	10.00	30-40	36.6	5.77
<i>S. butyracea</i>	7	7	-	3-10	6	3	40-50	43.3	5.77	30-60	43.3	15.2
<i>S. attaleoides</i>	3	3	-	2-3	2	0.6	50-60	53.3	5.77	40	40	-
<i>A. oleifera</i>	8-10	9	1	8-12	10	2	50	50	-	50-60	56.6	5.77
<i>A. dubia</i>	4-8	6	2	1	1	-	50-60	55	7.07	50-60	55	7.07
<i>A. funifera</i>	14-22	19	4	4-8	5	2	60-70	63.3	5.77	40-50	56.6	5.77
<i>A. geraensis</i>	3-4	3	0.5	2-4	3	1	40-50	43.2	5.77	40-50	46.5	5.77
<i>A. humilis</i>	6-8	7	1	2-3	2	7	60	60	-	40-50	45	7.07
<i>A. pindobassu</i>	10	10	-	10	10	-	50-60	55	7.07	60	60	-
<i>A. nucifera</i>	3	3	-	2-3	2	0.7	50	50	-	40	40	-
<i>A. tessmannii</i>	6	6	-	8-9	8	0.7	50	50	-	40	40	-
<i>A. racemosa</i>	3-6	4	1	2-7	4	2	40-60	50	10.0	50	50	-
<i>M. maripa</i>	7-8	7	0.5	3-4	3	0.5	40-50	46.7	5.77	40-50	46.6	5.77
<i>M. dahlgreniana</i>	10	10	-	9-10	9	0.5	50	50	-	40-50	43.3	5.77
<i>A. colenda</i>	9-10	9	0.7	10	10	-	50	50	-	50	50	-
<i>A. x piassabossu</i>	20	20	-	10	10	-	80	80	-	60	60	-
<i>x A. minarum</i>	10	10	-	10	10	-	60	60	-	50	50	-
<i>S. amara</i>	6	6	-	3	3	-	40	40	-	30	30	-
<i>S. comosa</i>	8	8	-	10	10	-	20	20	-	30	30	-
<i>S. cocoides</i>	6	6	-	3	3	-	40	40	-	30	30	-

Table 6. Quantitative data for leaf anatomical characters of taxa from the Attaleinae - Silica bodies.

Taxa	Adaxial Silica Bodies (mm)			Abaxial Silica Bodies (mm)		
	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	0.006	0.006	-	0.006	0.006	-
<i>O. oleifera</i>	0.006-0.008	0.007	0.001	0.006	0.006	-
<i>O. brejinhoensis</i>	0.006-0.007	0.006	0.0005	0.006	0.006	-
<i>O. eichleri</i>	0.006-0.007	0.006	0.0005	0.006-0.007	0.006	0.0005
<i>O. luetzelburgii</i>	0.006-0.009	0.007	0.001	0.004-0.006	0.005	0.001
<i>O. polysticha</i>	0.006-0.007	0.006	0.005	0.006	0.006	-
<i>O. sagotii</i>	0.005-0.008	0.006	0.001	0.006-0.007	0.006	0.0005
<i>O. cohune</i>	0.006	0.006	-	0.006	0.006	-
<i>O. crassipatha</i>	0.004-0.005	0.004	0.0007	0.005	0.005	-
<i>O. cuatrecasana</i>	0.003-0.007	0.005	0.002	0.006	0.006	-
<i>O. guacuyule</i>	0.007	0.007	-	0.008	0.008	-
<i>O. spectabilis</i>	0.006-0.008	0.006	0.001	0.006-0.009	0.007	0.001
<i>S. phalerata</i>	0.005-0.007	0.006	0.001	0.006	0.006	-
<i>S. insignis</i>	0.004-0.008	0.006	0.002	0.006-0.009	0.007	0.001
<i>S. butyracea</i>	0.005-0.006	0.005	0.0005	0.004-0.006	0.005	0.001
<i>S. attaleoides</i>	0.006-0.008	0.007	0.001	0.006-0.008	0.007	0.001
<i>A. oleifera</i>	0.007	0.007	-	0.005-0.007	0.006	0.001
<i>A. dubia</i>	0.006-0.007	0.006	0.0007	0.007	0.007	-
<i>A. funifera</i>	0.007-0.008	0.007	0.0005	0.007	0.007	-
<i>A. geraensis</i>	0.006-0.008	0.007	0.001	0.006-0.007	0.006	0.0005
<i>A. humilis</i>	0.005	0.005	-	0.004-0.006	0.005	0.001
<i>A. pindobassu</i>	0.007-0.008	0.007	0.0007	0.007	0.007	-
<i>A. nucifera</i>	0.007	0.007	-	0.007	0.007	-
<i>A. tessmannii</i>	0.007	0.007	-	0.007-0.008	0.007	0.0007
<i>A. racemosa</i>	0.006-0.007	0.006	0.0005	0.005-0.007	0.006	0.001
<i>M. maripa</i>	0.009-0.012	0.010	0.001	0.008-0.010	0.009	0.001
<i>M. dahlgreniana</i>	0.007	0.007	-	0.007-0.008	0.007	0.0005
<i>A. colenda</i>	0.007-0.008	0.007	0.0007	0.007-0.008	0.007	0.0007
<i>A. X piassabossu</i>	0.008	0.008	-	0.008	0.008	-
<i>x A. minarum</i>	0.007	0.007	-	0.007	0.007	-
<i>S. amara</i>	0.004	0.004	-	0.009	0.009	-
<i>S. comosa</i>	0.008	0.008	-	0.005	0.005	-
<i>S. cocoides</i>	0.006	0.006	-	0.006	0.006	-

Table 7. Quantitative data for leaf anatomical characters of taxa from the
Attaleinae - Non-vascular fibers.

Taxa	Adaxial Fibers - Number of Groups			Adaxial Fibers - Number- Fibers/Group			Abaxial Fibers - Number of Groups			Abaxial Fibers - Number of Fibers/Group		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	260-375	317.5	81.31	4-9	6.5	3.53	75-80	77.5	3.53	3	3	-
<i>O. oleifera</i>	345-390	365.0	22.91	7-9	8.3	1.15	110-187	137.3	43.08	3-4	3.6	0.57
<i>O. brejinhoensis</i>	215-390	301.6	87.51	4-9	6.0	2.64	65-95	83.3	16.07	3-4	3.3	0.57
<i>O. eichleri</i>	110-170	145.0	31.22	6-7	6.3	0.57	0-5	3.3	2.88	0-4	2.0	2.00
<i>O. luetzelburgii</i>	190-285	237.5	67.17	7	7	-	-	-	-	-	-	-
<i>O. polysticha</i>	365-395	383.3	16.07	6-7	6.2	0.57	80-145	116.6	33.29	7	7	-
<i>O. sagotii</i>	350-480	413.3	65.06	3-5	4.2	1.15	50-82	69.0	16.82	6-7	6.6	0.57
<i>O. cohune</i>	400	400	-	3	3	-	85	85	-	3	3	-
<i>O. crassipatha</i>	300-360	330.0	42.42	9-11	10.0	1.41	95-100	97.5	3.53	3-9	6.0	4.24
<i>O. cuatrecasana</i>	300-320	311.6	10.41	4-6	4.6	1.15	60-75	68.3	7.6	6-9	7	1.73
<i>O. guacuyule</i>	490	490	-	4	4	-	80	80	-	3	3	-
<i>O. spectabilis</i>	300-502	369.3	114.9	3-7	4.5	2.08	82-98	87.6	8.96	5-9	7.0	2.00
<i>S. phalerata</i>	350-401	367.6	28.88	3	3	-	10-90	58.2	42.52	2-3	2.6	0.57
<i>S. insignis</i>	260-303	288.0	24.26	2-3	2.5	0.57	70-92	84.2	12.42	3-4	3.3	0.57
<i>S. butyracea</i>	330-550	410.0	121.6	3	3	-	62-75	69.3	6.65	3	3	-
<i>S. attaleoides</i>	282-545	401.0	133.2	3	3	-	103-230	155.3	66.38	3-6	4.3	1.52
<i>A. oleifera</i>	184-262	226.6	39.51	9-12	10.3	1.52	21-68	39.0	25.35	3-4	3.2	0.57
<i>A. dubia</i>	160-180	170.0	14.14	4-5	4.5	0.70	0-30	15.2	21.21	0-3	1.7	2.12
<i>A. funifera</i>	254-265	260.0	5.56	4-8	6.3	2.08	31-53	40.6	11.23	4-5	4.3	0.57
<i>A. geraensis</i>	152-160	156.5	4.16	7-8	7.6	0.57	-	-	-	-	-	-
<i>A. humilis</i>	320-358	339.0	26.87	5	5	-	110-129	119.5	13.43	4-6	5.0	1.41
<i>A. pindobassu</i>	164-202	183.0	26.87	6	6	-	18-20	19.0	1.41	2-3	2.5	0.70
<i>A. nucifera</i>	366-378	372.0	8.48	3-4	3.5	0.70	27-78	52.5	36.06	6	6	-
<i>A. tessmannii</i>	402-406	404.0	2.82	4-6	5	1.41	-	-	-	-	-	-
<i>A. racemosa</i>	253-484	396.0	124.9	3	3	-	84-148	118.0	32.18	6-8	6.6	1.15
<i>M. maripa</i>	289-352	324.0	32.07	2-3	2.3	0.57	94-104	98.2	5.13	4-6	4.5	1.15
<i>M. dahlgreniana</i>	190-526	390.0	176.9	3-6	4.3	1.52	25-273	147.0	124.0	2-5	3.2	1.52
<i>A. colenda</i>	245-283	264.0	26.87	18-20	19	1.41	0-15	7.5	10.60	0-2	1.0	1.41
<i>A. x piassabossu</i>	153	153	-	16	16	-	21	21	-	3	3	-
<i>x A. minarum</i>	255	255	-	8	8	-	42	42	-	3	3	-
<i>S. amara</i>	125	125	-	5	5	-	55	55	-	8	8	-
<i>S. comosa</i>	96	96	-	20	20	-	7	7	-	5	5	-
<i>S. cocoides</i>	152	152	-	2	2	-	-	-	-	-	-	-

Table 8. Quantitative data for leaf anatomical characters of taxa from the Attaleinae - Chlorenchyma.

Taxa	Palisade - Thickness (μ)			Spongy Mesophyll - #layers			Spongy Mesophyll - Thickness (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	50	50.0	-	6-7	6.5	0.70	80-100	90.0	14.14
<i>O. oleifera</i>	92-120	104.0	14.42	6-8	7.0	1.00	150-190	165.3	21.57
<i>O. brejinhoensis</i>	60-80	73.3	11.54	7-8	7.2	0.57	130-160	143.2	15.27
<i>O. eichleri</i>	60-70	64.6	5.03	6	6	-	90-100	93.3	5.77
<i>O. luetzelburgii</i>	50.0	50.0	-	6-8	7.0	1.41	90-100	95.0	7.07
<i>O. polysticha</i>	30-70	46.6	20.81	5-8	6.3	1.52	60-90	80.0	17.32
<i>O. sagotii</i>	40-70	53.2	15.27	6-7	6.5	0.57	100-180	126.5	46.18
<i>O. cohune</i>	40	40.0	-	8	8	-	100	100.0	-
<i>O. crassispatha</i>	50-60	55.0	7.07	7	7	-	90.0	90.0	-
<i>O. cuatrecasana</i>	60-70	63.3	5.77	5-6	5.6	0.57	80-100	90.0	10.00
<i>O. guacuyule</i>	50	50.0	-	8	8	-	100	100	-
<i>O. spectabilis</i>	50-100	76.6	25.16	5-8	6.6	1.52	80-140	106.6	30.55
<i>S. phalerata</i>	40-60	46.7	11.54	5-8	6.3	1.52	80-90	83.3	5.77
<i>S. insignis</i>	40	40.0	-	4-5	4.2	0.57	50-60	56.6	5.77
<i>S. butyracea</i>	30-65	45.0	18.02	5-8	6.3	1.52	80-135	101.6	29.29
<i>S. attaleoides</i>	30-50	40.0	10.00	4	4	-	60-70	66.5	5.77
<i>A. oleifera</i>	60-80	73.4	11.54	7-10	8.2	1.52	120-140	130.0	10.00
<i>A. dubia</i>	60-80	70.0	14.14	6-7	6.5	0.70	80-120	100.0	28.28
<i>A. funifera</i>	80-120	100.0	20.00	6-7	6.3	0.57	100-120	106.6	11.54
<i>A. geraensis</i>	70-90	80.0	10.00	6-7	6.3	0.57	90-100	93.3	5.77
<i>A. humilis</i>	70-80	75.0	7.07	4-6	5.0	1.41	100	100.0	-
<i>A. pindobassu</i>	80-90	85.0	7.07	6-7	6.5	0.70	120	120.0	-
<i>A. nucifera</i>	40-50	45.0	7.07	5	5.0	-	50-90	70.0	28.28
<i>A. tessmannii</i>	60-70	65.0	7.07	6-7	6.5	0.70	90-100	95.0	7.07
<i>A. racemosa</i>	40	40	-	4-5	4.3	0.57	60	60.0	-
<i>M. maripa</i>	50-60	56.6	5.77	6	6.0	-	90-120	100.0	17.32
<i>M. dahlgreniana</i>	40-60	53.4	11.54	5-7	6.0	1.0	90-120	110.0	17.32
<i>A. colenda</i>	100-110	105.0	7.07	9-10	9.5	0.70	140-150	145.0	7.07
<i>A. x piassabossu</i>	120	120.0	-	8	8.0	-	160	160.0	-
<i>x A. minarum</i>	100	100.0	-	9	9.0	-	180	180.0	-
<i>S. amara</i>	0	0.0	-	4	4.0	-	60	60.0	-
<i>S. comosa</i>	100	100.0	-	7	7.0	-	120	120.0	-
<i>S. cocoides</i>	40.0	40.0	-	3	3.0	-	30	30.0	-

Table 9. Quantitative data for leaf anatomical characters of taxa from the
Attaleinae - Primary veins.

Taxa	Primary Veins - Number			Primary Veins - Height (μ)			Primary Veins - Width (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	10-13	11.5	2.12	120.7-136.6	128.6	11.24	112.8-131.5	122.1	13.22
<i>O. oleifera</i>	8-13	11.0	2.64	184.4-211.7	199.8	13.98	152.8-182.8	171.4	16.24
<i>O. brejinhoensis</i>	8-12	9.3	2.30	159.3-203.0	176.7	23.13	144.0-190.2	161.0	25.35
<i>O. eichleri</i>	6-8	6.6	1.15	161.3-178.8	171.6	9.24	114.6-136	124.6	10.76
<i>O. luetzelburgii</i>	5-8	6.5	2.12	136.2-160.0	148.1	16.82	127.2-157.0	142.1	21.07
<i>O. polysticha</i>	9-13	10.6	2.08	87.6-136.8	117.7	26.38	90.5-134.8	114.6	22.41
<i>O. sagotii</i>	10-14	12.3	2.08	98.7-158.0	119.3	33.48	98.6-155.0	121.5	29.63
<i>O. cohune</i>	12	12.0	-	105.9	105.9	-	100.0	100.0	-
<i>O. crassispatha</i>	12	12.0	-	161.6-175.0	168.3	9.47	110.0-116.2	113.1	4.38
<i>O. cuatrecasana</i>	11-16	13.3	2.51	122-132.5	125.7	5.87	133.1-144	139.4	5.66
<i>O. guacuyule</i>	13	13.0	-	115.8	115.8	-	125.0	125.0	-
<i>O. spectabilis</i>	9-13	10.3	2.30	105.0-152.8	133.6	25.24	105.0-148.0	131.9	23.49
<i>S. phalerata</i>	7-13	9.4	3.21	137.3-200.0	160.7	34.19	108.4-146.7	126.1	19.30
<i>S. insignis</i>	9-12	10.6	1.52	82.8-111.6	95.9	14.56	102.8-126.7	112.6	12.51
<i>S. butyracea</i>	9-13	11.0	2.00	101.0-128.0	111.1	14.70	101.0-132.0	112.0	17.29
<i>S. attaleoides</i>	6-7	6.6	0.57	103.0-115.7	110.0	6.47	110.0-118.3	113.2	4.44
<i>A. oleifera</i>	10-12	11.0	1.00	171.0-215.3	197.2	23.26	161.0-178.5	169.4	8.76
<i>A. dubia</i>	8-12	10.0	2.82	173.0-912.5	182.7	13.78	153.7-173.0	163.3	13.64
<i>A. funifera</i>	10-13	11.6	1.52	188.0-240.0	212.6	26.10	141.5-166.2	156.2	13.04
<i>A. geraensis</i>	8-11	9.00	1.73	154.4-185.4	165.6	17.14	124.3-142.7	130.6	10.42
<i>A. humilis</i>	10-12	11.0	1.41	152.0-168.2	160.1	11.45	114.0-149.1	131.5	24.81
<i>A. pindobassu</i>	9-12	10.5	2.12	166.7-206.6	186.6	28.21	142.2-166.7	154.4	17.32
<i>A. nucifera</i>	9-13	11.0	2.82	84.5-121.1	102.8	25.88	91.8-124.4	108.1	23.05
<i>A. tessmannii</i>	12-13	12.5	0.70	130.8-141.2	136.0	7.35	129.2-147.5	138.3	12.94
<i>A. racemosa</i>	7-10	8.6	1.52	90.0-107.1	96.1	9.54	100.0-112.8	105.5	6.58
<i>M. maripa</i>	5-7	6.0	1.00	263.0-316.0	293.9	27.37	211.6-242.5	228.7	15.71
<i>M. dahlgreniana</i>	8-14	10.6	3.05	165.7-186.2	173.4	11.16	150.0-161.4	156.3	5.80
<i>A. colenda</i>	14	14.0	-	175.4-214.3	194.8	27.50	158.4-172.1	165.2	9.68
<i>A. x piassabossu</i>	7	7.0	-	242.8	242.8	-	150.0	150.0	-
<i>x A. minarum</i>	12	12.0	-	188.8	188.8	-	152.7	152.7	-
<i>S. amara</i>	6.0	6.0	-	106.6	106.6	-	85.0	85.0	-
<i>S. comosa</i>	5	5.0	-	230.0	230.0	-	118.0	118.0	-
<i>S. cocoides</i>	8	8.0	-	127.5	127.5	-	75.0	75.0	-

Table 10. Quantitative data for leaf anatomical characters of taxa from the
Attaleinae - Secondary and tertiary veins.

Taxa	Sec./Tert. Veins Number			Sec./Tert. Veins - Number/Between L. V.			Secondary Veins Height (μ)			Tertiary Veins Height (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	115-132	123.5	12.02	14	14.0	-	62.8-80.0	71.4	12.16	45.0-55.0	51.5	-
<i>O. oleifera</i>	116-138	127.3	11.01	13-16	14.6	1.52	80.7-112.0	91.9	17.44	48.2-63.1	54.0	7.94
<i>O. brejinhensis</i>	92-114	101.0	11.53	15-16	15.6	0.57	72.0-94.3	80.6	11.95	41.6-55.5	48.1	6.99
<i>O. eichleri</i>	57-69	64.6	6.65	9-16	12.3	3.51	61.6-74.5	67.5	6.50	45.7-49.3	46.9	2.07
<i>O. luetzelburgii</i>	118-122	120.0	2.82	16-18	17.0	1.41	56.2-59.0	57.6	1.97	39.1-44.5	41.8	3.81
<i>O. polysticha</i>	65-98	85.0	17.57	9-14	11.3	2.51	45-79.3	63.3	17.27	32.0-48.0	42.1	8.83
<i>O. sagotii</i>	48-104	78.0	28.21	9-14	12.4	2.88	56.3-89.6	67.6	19.02	40.0-60.3	46.7	11.7
<i>O. cohune</i>	88	88.0	-	8	8.0	-	55.0	55.0	-	42.0	42.0	-
<i>O. crassispatha</i>	96-127	111.5	21.92	14	14.0	-	62.5-62.8	62.6	0.21	55.3-58.0	56.6	1.90
<i>O. cuatrecasana</i>	91-138	108.3	25.81	14	14.0	-	70-73.2	71.1	1.79	51.2-58	53.7	3.71
<i>O. guacuyule</i>	132	132.0	-	14	14.0	-	69.8	69.8	-	50.8	50.8	-
<i>O. spectabilis</i>	67-82	73.0	7.93	7-14	10.3	3.51	58.7-81.6	68.4	11.82	50.0-77.6	59.8	15.3
<i>S. phalerata</i>	82-138	117.6	30.98	9-25	17.3	8.02	61.8-71.0	67.6	5.04	48.2-52.7	50.8	2.33
<i>S. insignis</i>	75-119	99.6	22.47	9-14	10.6	2.88	41.2-50.8	46.5	4.87	31.4-37.6	34.2	3.13
<i>S. butyracea</i>	64-142	111.6	41.78	8-15	10.6	3.78	57.6-62.8	59.5	2.86	38.3-49.8	44.0	5.75
<i>S. attaleoides</i>	38-82	63.0	22.60	7-15	12.0	4.35	42.8-50.0	46.5	3.60	32.2-38.7	34.8	3.43
<i>A. oleifera</i>	83-126	102.6	21.73	10-14	12.3	2.08	69.6-90.8	83.1	11.77	51.7-72.0	64.2	10.9
<i>A. dubia</i>	53-90	71.5	26.16	8-9	8.5	0.70	47.8-87.6	67.7	28.14	36.8-53.2	45.0	11.5
<i>A. funifera</i>	77-108	89.0	16.64	8	8.0	-	92.8-106.1	97.7	7.26	73.3-77.0	74.8	1.92
<i>A. geraensis</i>	70-89	78.0	9.84	7-10	8.0	1.73	85.4-90.0	87.6	2.30	64.8-72.8	67.5	4.56
<i>A. humilis</i>	91-127	109.0	25.48	8-11	9.5	2.12	60.4-65.7	63.0	3.74	45.0-52.1	48.5	5.02
<i>A. pindobassu</i>	66-74	70.0	5.65	7-9	8.0	1.41	83.7-98.5	91.1	10.46	66.6-85.2	75.9	13.1
<i>A. nucifera</i>	69-83	76.0	9.89	8	8.0	-	52.2-67.6	59.9	10.88	39-52	45.5	9.19
<i>A. tessmannii</i>	92-114	103.0	15.55	7-10	8.5	2.12	98.7-102.2	100.4	2.47	74.6-81.4	78.0	4.80
<i>A. racemosa</i>	57-115	80.6	30.43	7-10	8.6	1.52	49.2-67.8	55.6	10.51	37.3-51.1	42.6	7.39
<i>M. maripa</i>	98-145	119.6	23.71	24-32	27.6	4.04	63.0-67.7	65.2	2.36	41.1-43.2	42.3	1.09
<i>M. dahlgreniana</i>	77-162	120.3	42.52	7-12	10.0	2.64	65.6-82.2	75.7	8.90	48.7-67.0	60.4	10.1
<i>A. colenda</i>	143-158	150.5	10.60	9-15	12.0	4.24	96.2-107.7	101.9	8-13	74.7-75.1	74.9	0.28
<i>A. x piassabossu</i>	94	94.0	-	14	14.0	-	110.8	110.8	-	79.0	79.0	-
<i>x A. minarum</i>	145	145.0	-	11	11.0	-	88.0	88.0	-	71.5	71.5	-
<i>S. amara</i>	37	37.0	-	9	9.0	-	68.6	68.6	-	44.8	44.8	-
<i>S. comosa</i>	60	60.0	-	14	14.0	-	97.0	97.0	-	67.7	67.7	-
<i>S. cocoides</i>	50	50.0	-	7	7.0	-	59.1	59.1	-	44.5	44.5	-

Table 11. Quantitative data for leaf anatomical characters of taxa from the Attaleinae - Midrib.

Taxa	Midrib - Size			Midrib - Number of VBs		
	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	2.2-2.7	2.4	0.36	20	20.0	-
<i>O. oleifera</i>	2.7-3.1	2.9	0.20	20	20.0	-
<i>O. brejinhoensis</i>	1.7-2.6	2.0	0.50	18-22	20.0	2.00
<i>O. eichleri</i>	0.64-0.84	0.7	0.10	5-12	7.6	3.78
<i>O. luetzelburgii</i>	0.6-0.7	0.6	0.08	8-10	9.0	1.41
<i>O. polysticha</i>	0.6-2.3	1.4	0.84	8-18	14.6	5.77
<i>O. sagotii</i>	1.1-4.1	2.2	1.69	10-26	16.0	8.71
<i>O. cohune</i>	1.3	1.3	-	18	18.0	-
<i>O. crassipatha</i>	1.2	1.2	-	20-22	21.0	1.41
<i>O. cuatrecasana</i>	1.68-2.20	2	0.28	18-20	19.3	1.15
<i>O. guacuyule</i>	1.8	1.8	-	18	18.0	-
<i>O. spectabilis</i>	1.6-2.3	1.9	0.36	16-18	16.6	1.15
<i>S. phalerata</i>	1.2-2.3	1.7	0.57	12-28	20.0	8.00
<i>S. insignis</i>	1.2-1.6	1.4	0.21	12-20	15.0	4.35
<i>S. butyracea</i>	1.1-2.4	1.6	0.68	12-16	14.6	2.30
<i>S. attaleoides</i>	0.8-1.8	1.3	0.53	8-12	10.0	2.00
<i>A. oleifera</i>	1.5-2.0	1.8	0.24	10-16	12.6	3.05
<i>A. dubia</i>	1.2-1.6	1.4	0.26	12	12.0	-
<i>A. funifera</i>	1.1-1.2	1.1	0.03	8-10	9.3	1.15
<i>A. geraensis</i>	1.1-1.2	1.2	0.02	8-10	8.6	1.15
<i>A. humilis</i>	1.2-1.7	1.5	0.38	9-13	11.0	2.82
<i>A. pindobassu</i>	0.9-1.0	0.9	0.04	6-7	6.5	0.70
<i>A. nucifera</i>	1.1-1.2	1.2	0.04	10	10	-
<i>A. tessmannii</i>	1.5-2.0	1.8	0.33	22-25	23.5	2.12
<i>A. racemosa</i>	0.8-2.0	1.5	0.60	6-16	11.3	5.03
<i>M. maripa</i>	2.1-2.8	2.4	0.37	18-20	18.6	1.15
<i>M. dahlgreniana</i>	1.4-2.5	2.0	0.52	8-24	18.0	8.71
<i>A. colenda</i>	2.3-2.4	2.4	0.04	20	20.0	-
<i>A. x piassabossu</i>	1.1	1.1	-	9	9.0	-
<i>x A. minarum</i>	1.9	1.9	-	14	14.0	-
<i>S. amara</i>	1.0	1.0	-	6	6.0	-
<i>S. comosa</i>	0.5	0.5	-	6	6	-
<i>S. cocoides</i>	0.5	0.5	-	5	5.0	-

3.2. Multivariate Analyses

a. Principal Components

All-taxa PCA

The first PCA was performed including all specimens and taxa in the sample (except *Syagrus*), and all quantitative and qualitative characters were used. The first step was to run the analysis with all characters included, and the loadings for each character were examined. Characters with low loadings on any component could be removed from the data matrix and the analysis re-calculated. This may be a useful strategy for the removal of characters that vary randomly in comparison with strongly covarying characters, since these low-weighted characters do not contribute much to the analysis and can be safely eliminated (Rogstad, 1993). Table 12 shows the loadings for the first five components derived from the PCA. Removal of few low-weighted characters was tried, but it did not improve the results of the analyses. Therefore, only results including all characters are reported.

The results showed that the first five components are necessary to represent a large portion of the variation within the sample. The first two components accounted for only 34.4% of the total variation. The loadings for each character are shown in

Table 12, with the higher loadings in bold. The fact that the total variation in five components was only 52.5%, and that the first and the second components accounted for only 26.7% and 7.73%, respectively, indicated the complexity of anatomical character variation within the subtribe Attaleinae. The components beyond the fifth accounted for less than 5% each and are not worth considering in the analysis of the results.

Examination of the pattern of grouping based on character correlation shown in Figures 1 and 2, indicated in some cases a conflicting distribution of a number of specimens supposedly of the same species. These species had their specimens distributed over different portions of the scatterplot (e.g., *O. polysticha*, *O. sagotii*, *O. spectabilis*, *S. butyracea*, *S. phalerata*), a pattern that was also observed in putative hybrids included in the study (e.g. *M. dahlgreniana*). In a PCA, the dispersion of the points in the space represents patterns of similarities between the specimens; the distance between these points is actually a measure of their dissimilarity. Such a large distance between specimens supposedly of the same species attracted attention for those particular specimens. This fact, plus the observation of crossed or “mixed” patterns during the phase of collection of data and anatomical descriptions of the taxa studied, and the very low percentage of variation explained by the first two components, led to the suggestion that a number of intermediates or specimens with conflicting patterns existed within the sample. These intermediates were then hypothesized as a possible cause for the spreading of variation over a greater

number of components. Because this group of specimens showed characteristics similar to the putative hybrids in terms of crossed, conflicting or unusual characters (in comparison with other specimens), this group of specimens (therein called intermediates) were then more carefully observed and tested as new possibilities of hybridization in the subtribe.

The scatterplot for the first and second components (Figure 1 and 2) shows that no groups can be clearly demarcated, except the Brazilian Orbignya group, which also includes two specimens of the putative hybrid Markleya dahlgreniana (MD-70 and MD-71). The location of the third specimen of M. dahlgreniana (MD-69, located closer to M. maripa, shown in Figure 1) correlates with the observations during collection of data. That particular specimen (collected in Surinam) showed a number of characters closer to M. maripa, as opposed to the other two specimens (collected in Brazil), closer to Orbignya.

Attalea and their closer intermediates formed a large cluster on the right upper portion of the scatterplot, including Orbignya luetzelburgii, O. crassispata, Attalea colenda, A. tessmannii, A. dubia, and with O. eichleri close to A. geraensis. Maximiliana can still be distinguished in the middle lower portion of the scatterplot (Figures 1 and 2). The other groups are more complex: O. cohune and O. cuatrecasana, placed in the same group of non-Brazilian Orbignya, are located in the middle portion of the diagram, along with a number of specimens whose

character variation lies half way between Scheelea and the other groups. Scheelea specimens clusters with a variety of other specimens: all identified as part of those conflicting intermediates. (Figures 1 and 2). All specimens of S. phalerata are located exactly in between Scheelea and Attalea specimens, but not close to each other. It is also interesting to observe the position of S. butyracea specimens in the diagram: one specimen is closer to Orbignya, one is closer to Scheelea, and the third one is in between the two groups (Figure 2). All specimens of A. nucifera and A. racemosa grouped with Scheelea specimens and their related intermediates (Figures 1 and 2).

Table 12. Loadings for the first five components derived from the Principal Components Analysis of anatomical characters from 74 specimens of species in the Attaleinae - PCA with all taxa included.

EigenValue:	22.9921	6.6535	5.9361	5.3395	4.2543
Percent:	26.7350	7.7367	6.9024	6.2088	4.9468
Cum. Percent:	26.7350	34.4716	41.3741	47.5828	52.5297
Eigenvectors:					
Adaxial Cuticle -Thickness (μ)	0.11923	0.10598	0.14204	0.12986	0.12771
Adaxial Trichome-Length (μ)	0.01530	0.10392	0.13589	0.15830	0.07611
Adaxial Epidermis-Thickness	0.16131	-0.03667	0.03509	-0.12057	0.04800
Adaxial Epidermis- Cell Extension	0.06016	-0.04231	-0.10984	0.06930	0.12903
Adaxial Epidermis- Cell Shape	0.06493	-0.05604	-0.16985	0.07620	0.11738
Adaxial Epidermis- Cell Walls	-0.11939	0.04672	-0.15784	0.04995	0.14984
Over Fiber Cells - Length (μ)	-0.13044	-0.03247	0.10232	-0.01545	0.13117
Over Fiber Cells - Width (μ)	0.06181	0.07782	0.13156	0.05524	0.14871
Inter Fiber Cells - Length(μ)	-0.11542	0.01664	0.04882	0.05209	0.20671
Inter Fiber Cells - Width (μ)	0.09942	0.19545	0.09020	0.04433	0.07936
Adaxial Silica Body - Size (mm)	0.01755	0.01350	0.21361	-0.06381	0.12165
Abaxial Cuticle - Thickness (μ)	0.11483	-0.01859	-0.04936	0.12705	0.15609
Abaxial Trichome Size (μ)	0.07819	0.00594	0.11211	0.13054	0.04763
Abaxial Epidermis-Thickness (μ)	0.16828	-0.02687	-0.11011	-0.03806	0.03976
Costal Bands (#cells)	0.01301	0.20515	-0.08482	0.10737	-0.20891
Costal Bands - Width(f)	0.06835	0.18915	-0.10622	0.14034	-0.06557
Costal Bands - Width (μ)	0.04874	0.19191	-0.09645	0.18490	-0.07670
Costal Cell - Length (μ)	-0.03916	0.14528	0.20088	0.08413	0.10100
Costal Cell - Width (μ)	0.09682	-0.01812	-0.11754	0.17320	0.16123
Costal Cell - Shape	-0.11693	0.01856	0.14971	-0.04733	-0.07687
Costal Cells - Walls	-0.14623	0.04232	-0.08296	0.13475	0.13844
Intercostal Bands (#cells)	0.11359	0.10487	0.04152	0.07023	0.00070
Intercostal Bands - Width (μ)	0.10085	0.09762	0.04396	0.07852	0.01518
Intercostal Cell - Length (μ)	-0.02267	0.10127	0.06269	0.10847	0.25591
Intercostal Cell - Width (μ)	0.07150	0.03791	-0.06399	0.02873	0.17274
Intercostal Cells - Walls	-0.14592	0.05003	-0.07547	0.13886	0.14065
Stomates - Arrangement	0.14118	-0.01188	-0.09847	-0.03196	0.00670
Stomates - # rows	0.15025	0.05669	-0.00875	0.00473	-0.04172
Guard cells - position	-0.04605	0.18327	-0.00238	-0.02775	-0.14092
Subs. Lateral - position	0.09254	-0.02121	-0.20943	-0.02599	-0.07214
Abax Silica Bodies -Size (mm)	-0.00559	0.05626	0.19395	-0.00809	0.02235
Adaxial Hypodermis - #Layers	0.08958	-0.25733	-0.03241	0.04758	0.05420
Adax Hypodermal Cells - Shape	0.14168	-0.15731	-0.04562	0.00717	-0.01658
Adax Hypodermal cells - Size(μ)	-0.07897	0.04076	0.09962	0.09882	0.03244
Adax Hypodermis -Tannins	0.02709	0.20164	0.02362	0.04223	-0.09511
Abax Hypodermis - Shape	0.10698	-0.05225	0.09178	-0.02896	-0.21817
Abax Hypodermal Cells-Size(μ)	0.06098	0.02320	0.06421	0.16856	-0.14125
Adaxial Fibers - Type	0.03032	0.13080	0.04486	0.06991	-0.01902
Adaxial Fibers - #Groups	-0.09453	-0.13244	0.03207	0.20177	-0.12560
Adax Fibers - #Fibers/group	0.13961	0.04113	0.00408	0.03009	0.05380
Adaxial Fibers-Shape/Groups	0.14968	0.12211	0.02778	-0.03553	-0.01837
Adaxial Fibers - Location	0.05958	-0.08858	0.13225	-0.02919	0.06935

Table 12. (cont'd.)

Abaxial Fibers - #Groups	-0.08198	-0.21865	0.09563	0.07823	-0.00855
Abax Fibers-#Fibers/group	-0.09939	-0.05964	0.10842	0.16799	0.04331
Abax Fibers - Arrangement	0.01318	-0.01855	0.03569	-0.00765	0.19483
Abaxial Fibers - Shape	-0.14604	-0.07233	0.06005	0.14287	0.07624
Abaxial Fibers - Location	-0.13316	-0.15386	0.03897	0.08500	0.10072
Palisade - #Layers	0.16074	-0.00871	-0.04183	-0.07416	0.05358
Palisade Differentiation	0.17032	0.00894	-0.04192	-0.00689	0.02691
Palisade - Thickness	0.15815	0.04783	0.11555	0.10107	0.05349
Palisade - Cell Walls	-0.16614	-0.00299	0.03074	0.01831	-0.01969
Palisade - Tannins	0.08153	0.11664	-0.09355	-0.01766	-0.09287
Spongy - #Layers	0.14233	-0.03714	0.00507	0.11602	0.02586
Spongy - Differentiation	0.17113	0.00630	-0.08365	-0.04097	0.05753
Spongy - Thickness	0.15264	-0.10490	0.08608	0.15792	0.08273
Spongy - Cell Walls	-0.17346	-0.00393	0.06328	0.04907	-0.05508
Spongy - Tannins	0.06958	0.09716	0.00324	-0.10413	-0.09913
Chlorenchyma	0.16594	-0.04246	0.10502	0.14206	0.07595
Primary Veins - Shape	0.05083	0.10952	-0.03364	-0.22044	0.15267
Primary Veins - Number	0.04411	-0.01254	-0.06067	0.23258	-0.21524
Primary Veins - Height(μ)	0.12879	-0.00189	0.26016	-0.09813	0.03179
Primary Veins - Width (μ)	0.10576	-0.06444	0.26269	-0.01733	0.00989
Primary Veins - Position	-0.12099	0.07468	-0.10798	0.14010	0.07670
Primary Veins - Type/fiber	-0.07969	0.13233	-0.08342	0.16665	-0.01679
Primary Veins - #Layers	0.07878	0.01991	0.25460	-0.10050	0.02754
Sec & Tertiary Veins - Number	0.06361	-0.13406	0.09121	0.02010	-0.16441
Sec&TertVeins-Betw Large Veins	-0.00312	-0.12969	0.21924	-0.11493	0.00162
Mid-secondary Vein	0.10684	-0.15874	-0.14011	0.03869	0.12080
Sec. Veins - Height (μ)	0.15851	0.07160	0.07412	0.11949	-0.04517
Tert. Veins - Height (μ)	0.14213	0.14474	0.04941	0.12644	-0.08336
Sec&Tert Veins- Inn. sheath	0.13345	-0.04949	-0.05714	-0.11711	-0.04443
Sec&Tert veins - Buttresses	-0.09765	0.20497	0.08656	-0.02138	-0.10269
Sec&Tert Veins - #Layers	0.10312	0.17495	0.09810	-0.06450	-0.16960
Sec&Tert Veins - Type/fiber	0.12700	0.04215	-0.10073	-0.08627	0.03261
Expansion cells - Location	-0.05330	-0.00157	0.02374	-0.13573	0.01658
Midrib - Shape	-0.13409	0.08034	0.00229	-0.01257	-0.09619
Midrib - Size (mm)	0.03156	-0.21905	0.14744	0.19838	-0.13468
Midrib - # Vasc.bundles	0.01168	-0.17254	0.08112	0.16367	-0.25111
Sclerotic sheath - shape	-0.12386	0.03756	0.10244	-0.15122	0.07160
Midrib - Cuticle (μ)	0.12835	0.06302	0.08200	0.12763	0.15202
Midrib - Hypodermis	0.07475	-0.25871	-0.05536	0.01419	0.00192
Midrib - Spongy mesophyll	0.00123	-0.08190	0.03341	-0.03695	-0.12653
Midrib Fibers - location	-0.14461	0.08242	0.12048	0.08822	-0.01339
Midrib Exp.cells - #layers	0.06321	-0.12310	0.07243	0.19863	-0.14493
Mid Exp. Cells - Confluence	0.02995	-0.06588	-0.14652	0.19313	-0.02602
Transverse Veins	-0.13690	0.02957	-0.04037	0.14288	-0.01653

Fig 1. Projection of the first two components using 87 leaf anatomical characters from specimens of the Attaleinae - Distribution of specimens - PCA with all taxa included.

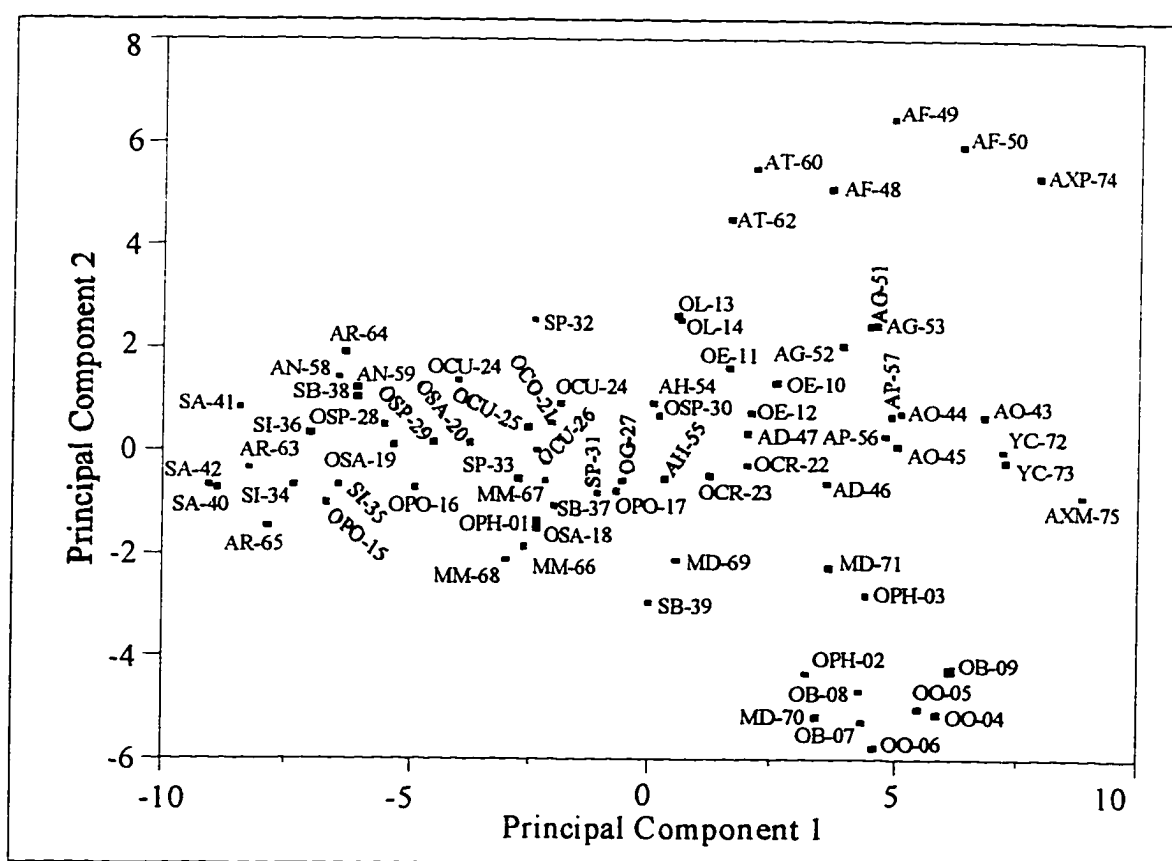
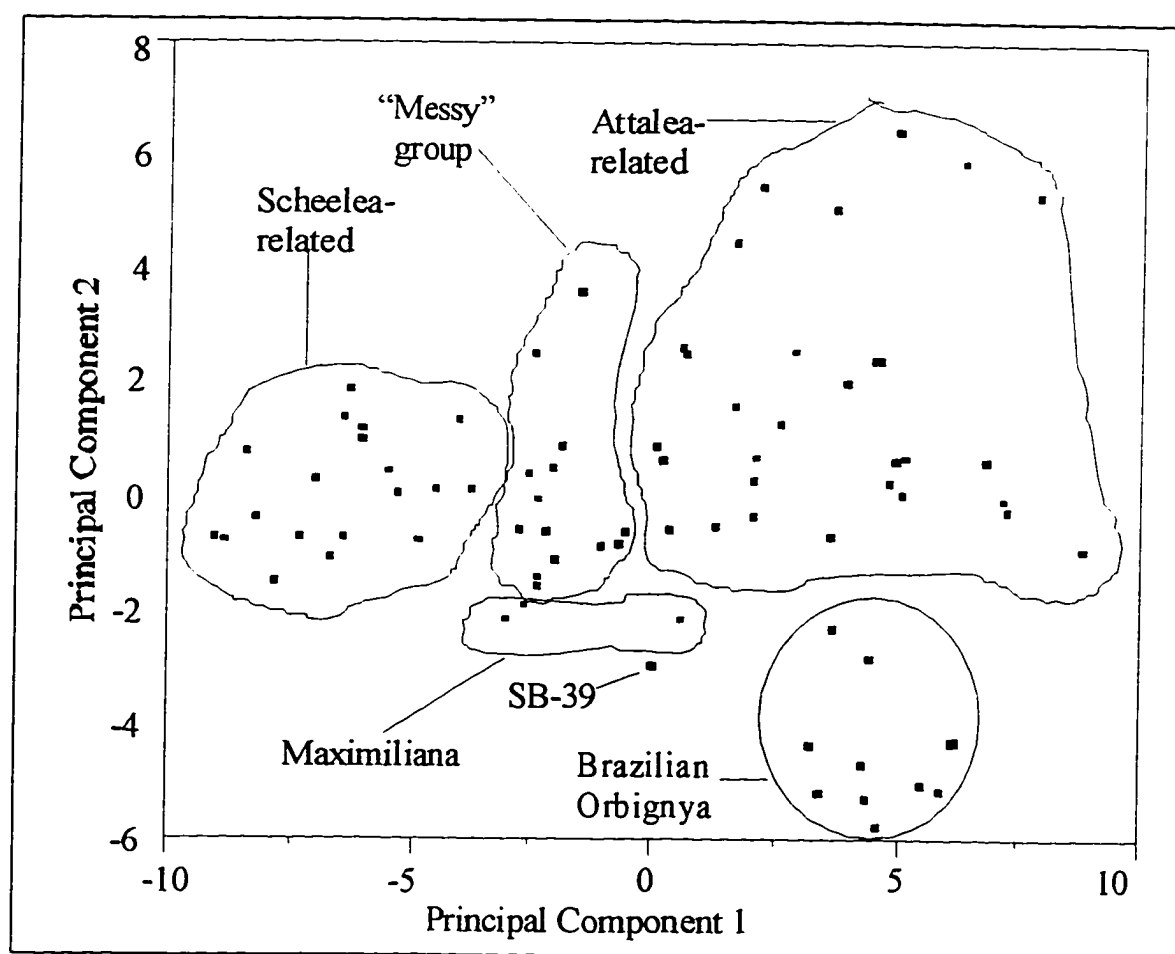


Fig 2. Projection of the first two components using 87 leaf anatomical characters from specimens of the Attaleinae - Grouping of specimens - PCA with all taxa included.



Plotting of the first three components (41% of the total variation in the five components) showed basically the same picture shown by the first two components. That is because the variation explained by the third component is nearly the same as the second component. The same situation applies to the fourth and fifth components. The same analysis was performed including the three specimens of Syagrus, just to observe what possible effects in the analysis would result from the addition of characters from species of genera in another subtribe, and to see how these species would correlate with the groups in the Attaleinae on the basis of their character variation. Their inclusion in the PCA only contributed to a slight decrease in the total variation of the five components by ca. 1.5%, especially in the first component. The Syagrus specimens appeared clearly isolated from the other taxa in the scatterplot; only S. cocooides tended to be closer to the Attalea group, probably because of a few features similar to the latter, as it can be observed from the description of the species.

PCA Without Putative Hybrids and Intermediates

It was then hypothesized that the presence of the putative hybrids and intermediates in this first PCA significantly contributed to the weak resolution of in terms of grouping patterns, by contributing to spread the character variation within a greater number of components. To test the hypothesis of the “messy” effect of the putative hybrids and intermediates in the analysis, a new PCA was performed

without those specimens. The results showed that the first five components were still necessary to explain a large amount of the variation (Table 13). However, the total percentage of the five components increased by ca. 14% in this analysis without those specimens, compared to that including them. More importantly, the variation explained by the first two components increased by 10%, which made the plotting of the first and second components very informative in terms of the delimitation of the taxa involved on the basis of the character correlation. The amount of variation explained by the components beyond the fifth was again less than 5% for each one, and they were still not considered.

The exclusion of the purported hybrids and intermediates from the PCA provided more structure to the data, so that the first and second components (especially the first) retained a disproportional portion of the variation in relation to the other components (43.7% of the total). This can be observed by analyzing the characters in each component (Table 13). Approximately the same number of characters (and basically the same characters) with the higher loadings was maintained when compared to the loadings of the components derived from the analysis with the putative hybrids and intermediates. This suggests that the putative hybrids and the intermediates with either their intermediacy in many characters, or the proximity to one of the parents, and character conflict caused many of them not covary uniformly, and significantly contributed to splitting the variation into a greater number of components. Still, the total percentage of the variation explained by the first five

components (66.5%) was not very high, and here are some possible reasons for this: 1) the complexity of anatomical character variation within the Attaleinae; 2) the type of data used in the analysis, combining both quantitative and coded qualitative data (this possibility was tested and is discussed later); 3) different parts sets of anatomical characters may be uncorrelated, just like characters from different plant parts (this possibility was also tested and discussed later).

Table 13. Loadings for the first five components derived from the Principal Components Analysis of anatomical characters from 74 specimens of species in the Attaleinae. PCA without putative hybrids and intermediates.

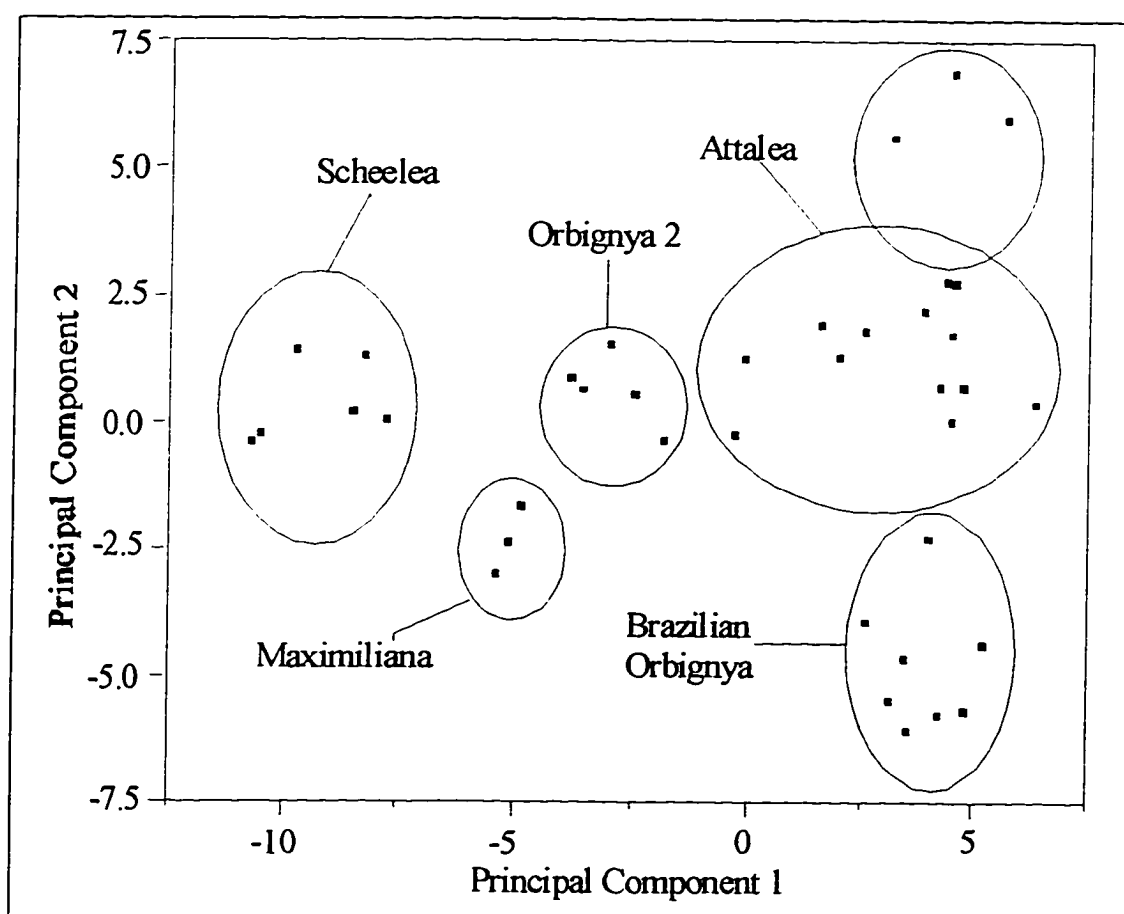
EigenValue:	27.6372	9.9732	7.8975	7.1562	4.5475
Percent:	32.1363	11.5967	9.1831	8.3212	5.2877
CumPercent:	32.1363	43.7330	52.9161	61.2373	66.5250
Eigenvectors:					
Adaxial Cuticle -Thickness (μ)	0.09795	0.08656	0.18020	0.08055	0.21708
Adaxial Trichome-Length (μ)	-0.00691	0.08656	0.10790	0.08846	0.24468
Adaxial Epidermis-Thickness	0.14922	-0.03674	0.03250	-0.17208	0.05537
Adaxial Epidermis- Cell Extension	0.14113	-0.08051	-0.11618	-0.03731	0.09143
Adaxial Epidermis- Cell Shape	0.13830	-0.06804	-0.17131	0.01622	0.11819
Adaxial Epidermis- Cell Walls	-0.08930	0.05808	-0.22246	-0.05334	0.03860
Over Fiber Cells - Length (μ)	-0.11736	-0.03152	0.02012	-0.10646	0.05623
Over Fiber Cells - Width (μ)	0.04846	-0.04163	0.09825	-0.00116	-0.16492
Inter Fiber Cells - Length(μ)	-0.11376	0.01127	-0.06571	-0.03397	0.18390
Inter Fiber Cells - Width(μ)	0.08926	0.18500	0.11743	0.03040	-0.01446
Adax Silica Bodies - Size(mm)	-0.01765	-0.02778	0.17104	-0.18054	0.01998
Abaxial Cuticle - Thickness(μ)	0.12503	-0.07680	0.00336	0.09466	0.02189
Abaxial Trichome - Size(μ)	0.07100	0.01906	0.14551	0.05679	-0.11976
Abaxial Epidermis -Thickness	0.16985	0.00255	-0.10070	-0.00755	0.06412
Costal Bands - Width(#cls)	0.04462	0.14968	-0.01671	0.07306	0.05091
Costal Bands - Width(f)	0.11191	0.11716	-0.08164	0.00390	0.14400
Costal Bands - Width(μ)	0.06704	0.17603	-0.09665	0.03685	0.03408
Costal Cells - Length(μ)	-0.06534	0.12390	0.13254	0.03434	0.26233
Costal Cells - Width(μ)	0.11014	-0.01618	-0.04764	0.13541	-0.06325
Costal Cells - Shape	-0.10686	0.03513	0.07195	-0.10139	-0.18002
Costal Cells - Walls	-0.13742	0.02216	-0.14405	0.00248	0.11760
Intercostal Bands-Width(#cells)	0.09576	0.17080	0.05259	-0.02538	0.04558
Intercostal Bands - Width(μ)	0.09677	0.21329	0.05374	-0.02672	0.06154
Intercostal Cells - Length(μ)	-0.02851	0.14281	0.02891	-0.04229	0.17574
Intercostal Cells - Width(μ)	0.08975	0.02681	-0.03517	0.00689	-0.11861
Intercostal Cells - walls	-0.13742	0.02216	-0.14405	0.00248	0.11760
Stomates - Arrangement	0.16298	-0.01077	-0.05843	-0.05360	0.06953
Stomates - #rows	0.15427	0.03278	0.01341	-0.07498	0.05259
Guard cells - Position	-0.02403	0.14775	0.04555	-0.06014	-0.16712
Subs. Lateral - Position	0.12184	-0.03364	-0.14311	-0.04987	-0.18713
Abax Silica Bodies - Size(mm)	-0.06534	0.03470	0.13230	-0.14351	-0.00064
Adaxial Hypodermis -#Layers	0.07243	-0.24590	-0.04030	0.06830	0.13677
Adax Hypodermal Cells-Shape	0.13195	-0.17364	-0.06273	0.01040	0.12344
Adax Hypodermal Cells-Size(μ)	-0.09034	0.05552	0.10420	0.13549	-0.19763
Adaxial Hypodermis -Tannins	0.03509	0.20302	0.13048	0.12415	0.10396
Abax Hypodermal Cells-Shape	0.10734	-0.01944	0.14075	0.02550	-0.10650
Abax Hypodermal Cells-Size(μ)	0.11147	0.08747	0.06963	0.11709	-0.02587
Adaxial Fibers -Type	0.02597	0.08084	0.13036	0.18385	-0.00538
Adaxial Fibers - #Groups	-0.09034	-0.13637	0.06087	0.13310	0.13428
Adax Fibers-#Fibers/group	0.15017	-0.00656	-0.02131	0.01178	-0.03597
Adaxial Fibers - Shape	0.13288	0.11161	0.08439	-0.00637	0.00548
Adaxial Fibers -Location	0.01135	-0.13475	0.08759	-0.07050	0.21903
Abaxial Fibers -#Groups	-0.09801	-0.16673	0.05012	0.04924	0.19954

Table 13. (cont'd.)

Abax Fibers- #Fibers/group	-0.07362	-0.02813	0.18274	0.17619	0.08212
Abax Fibers - Arrangement	0.02027	0.01583	0.03452	0.05883	0.12798
Abaxial Fibers - Shape	-0.13784	-0.01727	0.02781	0.18247	0.09714
Abaxial Fibers - Location	-0.13760	-0.12755	-0.02796	0.10318	0.13315
Palisade - #Layers	0.17235	0.00018	-0.06538	-0.06621	0.09593
Palisade - Differentiation	0.16172	0.01900	-0.00690	0.11237	-0.04501
Palisade -Thickness(μ)	0.14061	0.01308	0.11125	-0.00108	0.09484
Palisade Cells -Walls	-0.15587	-0.00593	-0.00242	-0.10622	0.09246
Palisade - Tannins	0.09581	0.08791	-0.06895	0.14202	-0.10522
Spongy - #Layers	0.13083	-0.07389	0.04742	0.04275	-0.09956
Spongy - Differentiation	0.16116	0.00480	-0.08740	0.05501	-0.00483
Spongy -Thickness(μ)	0.13418	-0.14949	0.08123	0.02285	0.04446
Spongy Cells - Walls	-0.16354	-0.00108	0.05401	-0.03502	-0.00388
Spongy - Tannins	0.06868	0.06227	0.04383	0.03347	-0.15916
Chlorenchyma	0.14745	-0.08593	0.10105	0.01307	0.06546
Primary Veins - Shape	0.06017	0.13288	-0.03990	-0.19081	-0.06699
Primary Veins - Number	0.04563	0.02309	0.03027	0.27076	-0.04269
Primary Veins - Height(μ)	0.07141	-0.03492	0.24254	-0.19265	0.02242
Primary Veins - Width(μ)	0.04373	-0.09520	0.27714	-0.12767	-0.01086
Primary Veins - Position	-0.12585	0.03312	-0.07829	0.19732	-0.07832
Primary Veins -Type/fiber	-0.06588	0.13926	0.03974	0.25067	0.02183
Primary Veins - #Layers	0.05955	-0.01799	0.20436	-0.15988	0.00442
Sec&Tert Veins - Number	0.01018	-0.16426	0.14705	0.09658	-0.02826
Sec&Tert Veins-Betw Large Veins	-0.04896	-0.17529	0.18810	-0.10084	-0.05721
Mid-secondary Vein	0.10837	-0.13158	-0.12153	0.00663	-0.05035
Sec Veins - Height (μ)	0.15534	0.02062	0.09914	0.01654	0.02304
Tert Veins (μ) - Height	0.13853	0.12701	0.08821	0.02363	-0.01525
Sec&Tert Veins-Inn. sheath	0.13090	0.01125	-0.12139	-0.05826	0.10034
Sec&Tert Veins - Buttresses	-0.07964	0.22401	0.04487	-0.05926	-0.14578
Sec&Tert Veins -#Layers	0.10427	0.14938	0.11394	-0.11324	0.03056
Sec&Tert Veins-Type/fiber	0.15100	0.00695	-0.12031	-0.02610	0.07321
Exp. Cells - Location	-0.05079	-0.02907	0.03778	-0.16803	0.00017
Midrib - Shape	-0.16269	0.04606	0.05165	0.04483	-0.06447
Midrib - Size(mm)	0.01003	-0.24204	0.14885	0.07833	-0.01309
Midrib - #Vasc.bundles	-0.02061	-0.22144	0.10664	0.14252	-0.05527
Sclerotic sheath - Shape	-0.16178	-0.02381	0.04340	-0.13804	0.05641
Midrib -Cuticle (μ)	0.12394	-0.00802	0.15957	0.07511	0.16068
Midrib - Hypodermis	0.05574	-0.25762	-0.07561	0.02461	-0.06639
Midrib - Spongy	0.01594	-0.12204	0.06411	-0.16218	-0.16452
Midrib Fibers - Location	-0.13410	0.10516	0.16587	0.02110	0.10745
Midrib Exp.Cells - #layers	0.04108	-0.09707	0.15598	0.21877	-0.16074
Midrib Exp. Cells-Confluence	0.08545	-0.00462	-0.07253	0.22099	-0.00157
Transverse Veins	-0.13274	0.03054	-0.02788	0.18692	-0.07218

The effect of the exclusion of the purported hybrids and intermediates from the analysis can be observed graphically in Figure 3. The scatterplot of the first and second components clearly reproduce the groups differentiated in the descriptive analysis of the data, and five groups are obtained on the basis of the correlation among anatomical characters. On the lower right portion of the scatterplot, all eight specimens of the Brazilian Orbignya cluster together, re-confirming their anatomical homogeneity as a group. The Attalea group include most of the specimens traditionally differentiated as belonging to that group; only A. funifera, which was shown to be distinctive on the basis of several characters, appears separated from the group, on the right upper portion the diagram. Again, O. eichleri clusters in the Attalea group. The non-Brazilian Orbignya occupy a central position in the scatterplot. Maximiliana and Scheelea are closer to each other than they are to any other group. Due to the fact that many components were derived from the PCA, no single pair of components will be 100% informative. However, the plotting of the first and second components (which detained a larger percentage of the variation) can be the most informative of all.

Fig. 3. Projection of the first two components using 87 leaf anatomical characters from specimens of the Attaleinae - PCA without hybrids and intermediates.



Separate PCAs of Quantitative and Qualitative Data

In the PCA with only quantitative data the first five components accounted for 67.3% of the total variation (Table 14), which is about the same as in the PCA of the two types of data combined (66.5%). The analysis of only coded qualitative data produced a slightly higher percentage for the total variation in the first five components (76.6%) (Table 15), which is not significantly different from the other results. What seems to be the major difference between the results of the two analyses is the distribution of the variation among the five components: the use of qualitative data produced a first component with a higher percentage of the variation (42.3%), compared to that of the quantitative data (26.5%), and to the combination qualitative-quantitative data (32.1%). The number of characters in each component with high loadings was approximately the same in the two separate PCAs (ranging 19-30 per component). Tables 14 and 15 show the loadings derived from the two separate analyses.

Table 14. Loadings for the first five components derived from the Principal Components Analysis of anatomical characters from specimens of the Attaleinae - PCA without putative hybrids and intermediates using only quantitative data.

EigenValue:	12.2355	7.5672	4.7534	3.7647	2.6387
Percent:	26.5990	16.4504	10.3335	8.1841	5.7362
CumPercent:	26.5990	43.0494	53.3829	61.5670	67.3032
Eigenvectors:					
Adaxial Cuticle - Thickness(μ)	0.19256	-0.01455	0.17998	0.22885	0.15228
Adaxial Trichome - Size(μ)	0.03604	-0.07409	0.10271	0.32581	0.14399
Over Fiber Cells -Length(μ)	-0.17665	0.01531	0.17090	-0.05760	0.01293
Over Fiber Cells - Width(μ)	0.08894	0.12256	0.05126	-0.07082	-0.19815
Inter Fiber Cells - Length(μ)	-0.17636	-0.07029	0.07891	0.02253	0.22067
Inter Fiber Cells - Width(μ)	0.18316	-0.12254	0.11974	0.10351	-0.13173
Adaxial Silica Bodies-Size(mm)	-0.00303	0.06691	0.32453	-0.15478	0.05111
Abaxial Cuticle-Thickness (μ)	0.18324	0.10969	-0.09695	-0.00853	0.05046
Abaxial Trichome - Size(μ)	0.13639	0.04987	0.03413	0.08360	-0.31176
Costal Bands - Width(#cells)	0.09247	-0.15302	-0.03834	0.15567	0.12173
Costal Bands Width(f)	0.16650	-0.15487	-0.07306	0.00291	0.25361
Costal Bands - Width(μ)	0.11488	-0.22058	-0.06763	-0.00400	0.07868
Costal Cells - Length(μ)	-0.05183	-0.10987	0.23959	0.28514	0.10715
Costal Cells - Width(μ)	0.16030	0.02985	-0.15383	-0.01308	-0.05679
Intercostal Bands-Width(#cells)	0.18533	-0.16347	0.08843	0.00656	-0.04451
Intercostal Bands - Width(μ)	0.18900	-0.20239	0.11939	0.03351	-0.02017
Intercostal Cells - Length(μ)	-0.02409	-0.15667	0.19592	0.03640	0.13088
Intercostal Cells - Width(μ)	0.12731	-0.03393	-0.07693	-0.12834	-0.19188
Abaxial Silica Bodies-Size(mm)	-0.05804	-0.01786	0.30107	-0.12953	-0.03159
Adaxial Hypodermis-#Layers	0.06101	0.23342	-0.16962	0.00149	0.24965
Adax Hypodermal Cells-Size(μ)	-0.10816	-0.00389	0.05858	0.17123	-0.43837
Abax Hypodermal Cells-Size(μ)	0.18404	-0.03950	-0.05754	0.17415	-0.11505
Adaxial Fibers - #Groups	-0.13495	0.15752	0.01337	0.26671	0.16221
Adaxial Fibers - #Fib/group	0.22201	0.03408	-0.12917	-0.06911	0.05724
Abaxial Fibers - #Groups	-0.15067	0.16766	0.04071	0.18904	0.25411
Abaxial Fibers-Fibers/group	-0.07843	0.10374	0.10712	0.33922	-0.08390
Palisade - #Layers	0.22402	-0.01992	-0.11110	-0.11609	0.18984
Palisade - Thickness(μ)	0.22597	0.04209	0.06679	0.04213	0.08041
Spongy - #Layers	0.19376	0.14419	-0.05222	-0.06924	-0.03036
Spongy - Thickness (μ)	0.19355	0.21356	-0.01753	-0.03634	0.09636
Chlorenchyma	0.22431	0.15201	0.01894	-0.00725	0.09213
Primary Veins - Number	0.08682	0.02671	-0.16503	0.33724	-0.14059
Primary Veins - Height(μ)	0.13034	0.12358	0.33271	-0.14154	0.02961
Primary Veins - Width(μ)	0.09844	0.20170	0.31290	-0.07998	-0.02956
Primary Veins - #Layers	0.12455	0.08807	0.25245	-0.08440	-0.00818
SecTert Veins - Number	0.00652	0.24219	0.00533	0.16010	0.04366
SecTert Veins - #Layers	0.19002	-0.11331	0.15283	-0.01704	-0.03384
Sec&Tert Veins-Betw Large Veins	-0.08173	0.24131	0.21637	-0.09335	-0.01777
Sec Veins - Height (μ)	0.24775	0.03395	0.03468	0.00285	0.00144
Tert Veins - Height (μ)	0.24016	-0.07993	0.04482	0.05593	-0.09901
Midrib - Size(mm)	0.00543	0.31853	0.00570	0.09755	0.02449
Midrib - #Vasc.bundles	-0.03893	0.28757	-0.04526	0.13638	-0.05712
Midrib - Cuticle (μ)	0.21030	0.09139	0.11880	0.16146	0.16705
Midrib - Hypodermis	0.03605	0.25648	-0.23250	-0.13079	0.09898
Midrib - Spongy	0.00178	0.15196	0.09781	-0.22815	-0.04381
Mid Exp. Cells - #layers	0.08176	0.20428	-0.02828	0.18233	-0.28723

Table 15. Loadings for the first five components derived from the Principal Components Analysis of anatomical characters from specimens of the Attaleinae - PCA without putative hybrids and intermediates using only qualitative data.

EigenValue:	16.5299	4.4453	3.8208	2.9210	2.1625
Percent:	42.3843	11.3981	9.7968	7.4897	5.5447
CumPercent:	42.3843	53.7824	63.5792	71.0690	76.6137
Eigenvectors:					
Adax Epidermis-Thickness	0.20013	-0.08225	-0.17754	0.02772	0.14530
Adax Epid-Cell Extension	0.19668	-0.12842	0.06956	0.00387	0.18310
Adax Epidermis-Cell Shape	0.19872	-0.12641	0.14837	0.03187	0.13344
Adax Epidermis-Cell Walls	-0.09435	-0.07641	0.14920	0.32644	0.34223
Abax Epidermis-Thickness	0.22732	-0.02249	0.05346	0.11347	0.01836
Costal Cells - Shape	-0.14826	-0.00838	-0.23046	0.05066	-0.21220
Costal Cells - Walls	-0.17299	-0.14965	0.14179	0.25901	0.04258
Intercostal Cells - Walls	-0.17299	-0.14965	0.14179	0.25901	0.04258
Stomates - Arrangement	0.21874	-0.03928	-0.00651	0.07024	0.02871
Guard cells	-0.05252	0.14200	-0.23614	0.32321	-0.17174
Subs. Lateral - Position	0.16058	-0.06911	0.02116	0.32474	-0.20501
Adax Hypod Cells - Shape	0.18509	-0.20771	0.09870	-0.16838	-0.08216
Adax Hypodermis-Tannins	0.02182	0.35362	0.00242	-0.09817	0.10743
Abax Hypod Cells - Shape	0.13670	0.15907	-0.11693	-0.24412	-0.08924
Adaxial Fibers -Type	0.01780	0.33919	0.13031	-0.10231	0.08947
Adaxial Fibers - Shape	0.15951	0.18599	-0.16959	-0.06136	-0.00775
Adaxial Fibers -Location	0.02300	-0.19321	-0.09536	-0.27099	-0.02296
Abax Fibers - Arrangement	0.01942	0.06043	0.17364	-0.11627	0.37496
Abax Fibers - Shape	-0.18573	0.03789	0.22086	-0.17329	0.07375
Abaxial Fibers - Location	-0.16988	-0.14049	0.25452	-0.15801	0.08126
Palisade - Differentiation	0.20793	0.14816	0.04760	-0.11126	-0.08497
Palisade Cells - Walls	-0.20369	-0.16034	-0.04302	0.00639	0.10408
Palisade -Tannins	0.12533	0.24408	0.08931	0.14548	-0.08130
Spongy - Differentiation	0.20629	0.04265	0.15407	0.11019	-0.07159
Spongy Cells - Walls	-0.20747	-0.04453	-0.10373	0.00731	0.05287
Spongy - Tannins	0.08746	0.22927	-0.08861	0.12026	-0.00236
Primary Veins - Shape	0.08826	0.10706	-0.18833	0.16908	0.42775
Primary Veins - Position	-0.16598	0.08563	0.25734	0.17155	-0.21014
Primary Veins-Type/fiber	-0.10485	0.28600	0.22219	0.07284	-0.13974
Mid-secondary Vein	0.14950	-0.19583	0.14355	0.06275	-0.28991
Sec&Tert - Inn. sheath	0.17636	-0.08403	0.00796	0.02498	0.16116
Sec&Tert Veins-Buttresses	-0.11767	0.24863	-0.19324	0.26372	0.12221
Sec&Tert veins-Type/fiber	0.20508	-0.05248	0.04686	0.21096	0.07707
Exp Cells - Location	-0.05234	-0.13674	-0.28456	-0.00273	-0.12491
Midrib - Shape	-0.21306	0.11372	0.05141	-0.00051	0.07877
Sclerotic sheath	-0.21017	-0.15052	-0.10353	-0.01602	0.10791
Midrib Fibers - Location	-0.18681	0.13805	-0.13529	-0.17045	0.12320
Midrib Exp Cells-Confluence	0.10451	0.14111	0.35567	-0.03540	0.03280
Transverse Veins	-0.17900	0.10176	0.20029	-0.02560	-0.20435

The groups of taxa previously observed could still be separated using the results from both analyses, although the visualization of the groups was slightly better in those plottings of components from the qualitative data (Figures 4 and 5). However, they were both inferior in terms of group delimitation compared to that produced by the components derived from the PCA of quantitative-qualitative data combined. Therefore, the results used in this study are those derived from the combination of data.

Fig. 4. Scatterplot of the first two components derived from PCA with exclusively qualitative data.

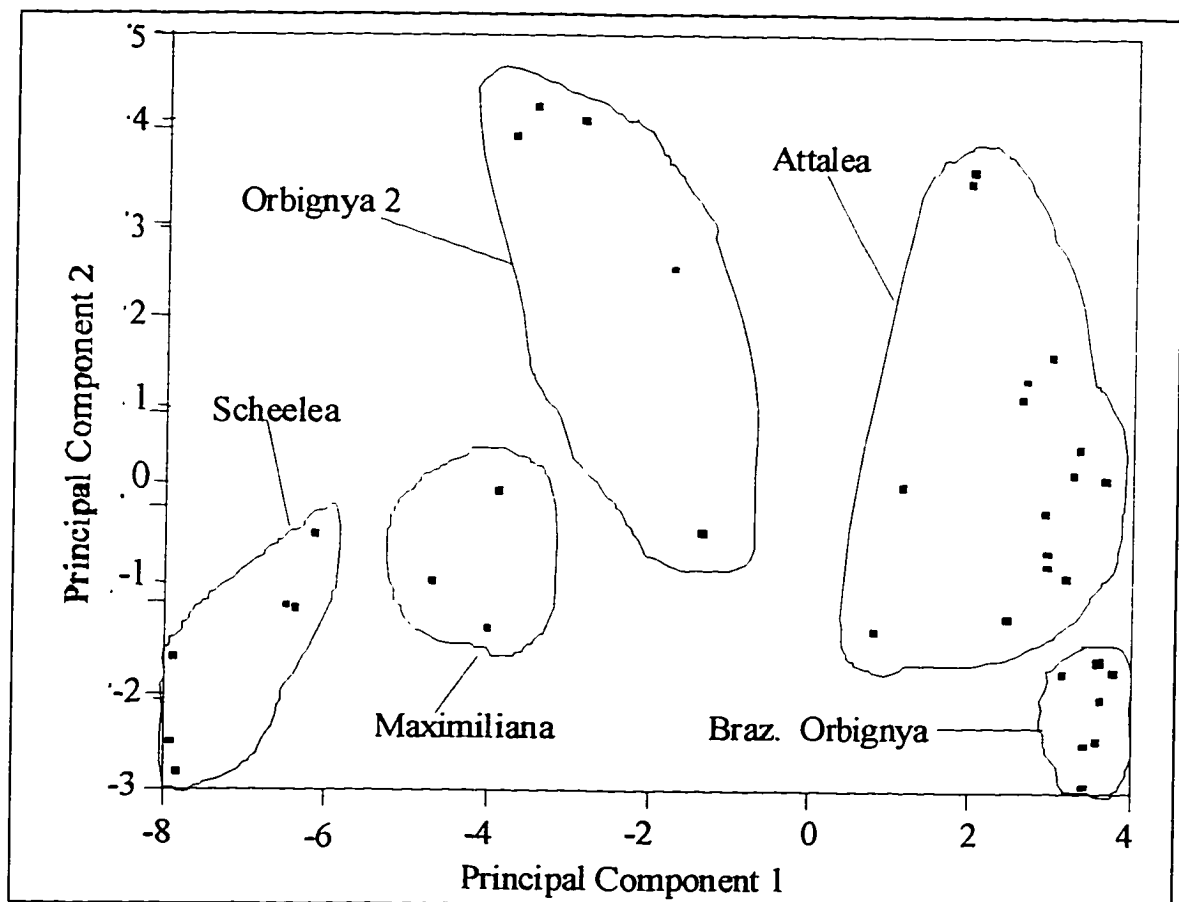
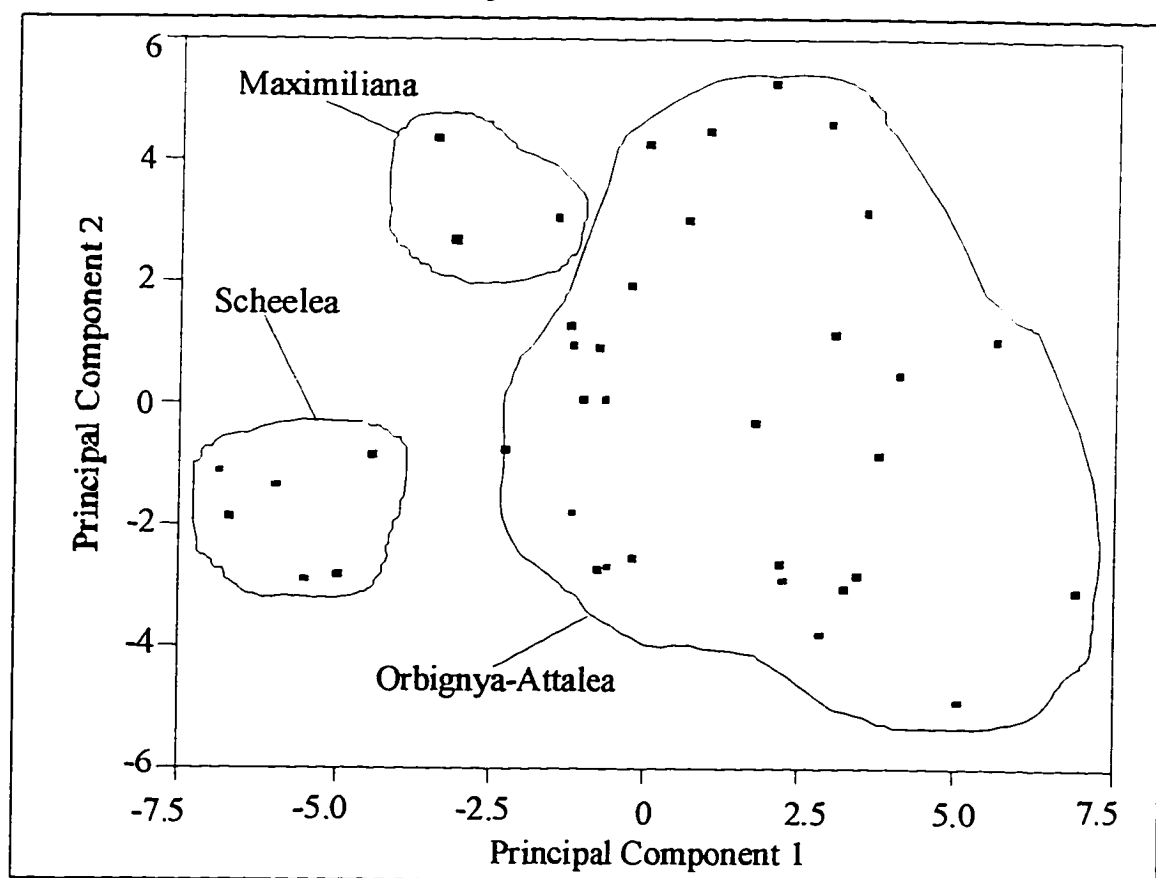


Fig.5. Scatterplot of the first two components derived from PCA with exclusively quantitative data.



PCAs with Separate Sets of Characters

Epidermal characters alone showed the lowest total percentage of variation explained by five components (69.7%); Scheelea and Maximiliana were distinctively separated from the others; Attalea and Orbignya could not be easily separated. The highest loadings in the first component (32% of variation) were found in epidermal characters such as orientation, size, and walls of adaxial cells, width of costal and intercostal bands, stomatal arrangement, and position of guard-cells. In the other extreme, variation of six components could be 100% explained in six components derived from the PCA of hypodermal characters, but in this case, only the Brazilian Orbignya could be easily separated as a group; the highest loadings in the first component (40.4% of the variation) were recorded in the number of layers and shape of hypodermal cells; in the other direction, the shape of cells in the abaxial hypodermis. Non-vascular fibers (87.4% of variation in five components) could separate Attalea and Orbignya from each other and from other groups, but clustered Maximiliana and Scheelea together. Location, and shape of abaxial groups, and number of adaxial and abaxial groups of fibers received the highest loadings in the first component derived. Characters from the palisade and spongy mesophylls (93.3% in five components) separated Scheelea and Maximiliana from the other groups and from each other (although close to each other), but failed to separate Attalea from Orbignya. The highest loadings for chlorenchyma characters appeared

for the thickness and differentiation of both palisade and spongy mesophylls, in one direction; in the opposite direction, tannins in palisade and spongy cells. Five of the many components (especially the first and second) derived from the analysis of venation characters (84.6% of total variation), produced a clear separation of three groups: Scheelea, Maximiliana, and Attalea mixed with Orbignya. This correlates with the observations made during data collection, which revealed distinct patterns of venation in Scheelea, Maximiliana and Attalea-Orbignya. In this regard, Attalea and Orbignya differ in just a few characters such as shape of primary veins, and location of secondary and tertiary veins, which obviously were not enough to split them apart in this case. The highest loadings of venation characters were recorded as follows: as grouping characters, the width and position of primary veins, height, type of fibers, and buttresses of secondary and tertiary veins; as separating characters, the type of fibers and the number of fibrous layers of primary veins. A similar situation was found in the results of the analysis of midrib characters, with clear distinction between Scheelea and Maximiliana from themselves and from the others, and a more close grouping of Orbignya and Attalea specimens. In this case, particular characters such as size, number of vascular bundles, and number of expansion cell layers received the highest loadings. These results show that no single set of anatomical characters is good enough for a clear and easy separation of the groups; as shown before, one or two groups can be distinguished this way, but for separation of all groups previously observed, the combination of anatomical characters from the epidermis, mesophyll and midrib is necessary.

PCA With Putative Hybrids and Intermediates Only

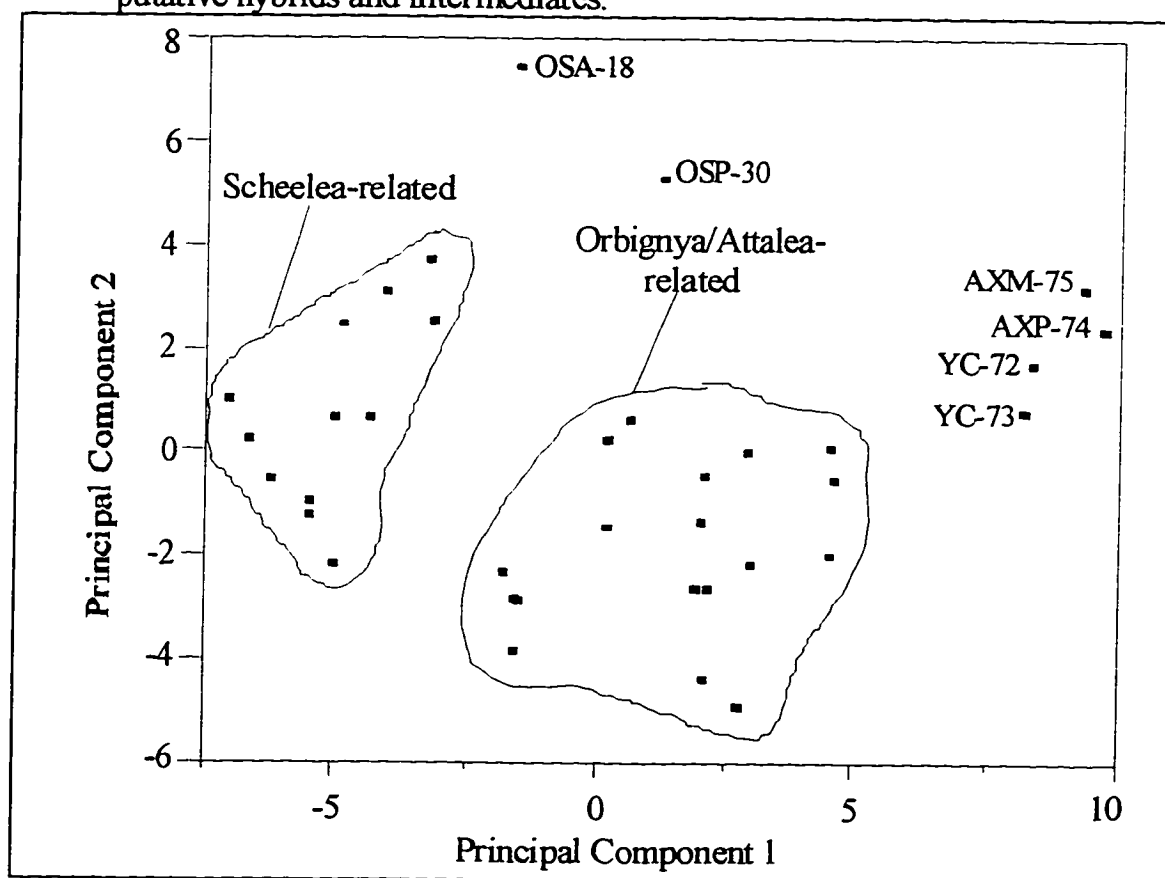
The data lose a great amount of structure and the variation becomes more complex when putative hybrids and intermediates are analyzed as a group. The results from this PCA were very similar to those obtained from the analysis which included all taxa. The total amount of variation explained by the first five components was only 54.9%, approximately the same obtained from the all-taxa included PCA. The first two components accounted only for 33.7% of the total variation (in the all-taxa PCA=34.4%). These results show that this group of specimens carry a great amount of uncorrelated (or less correlated) characters varying in a more complex pattern. The number of characters with the highest loadings was approximately the same as that from the all-taxa analysis; however, the variation was spread over a higher number of components.

Plotting the first two components (Figure 6) basically shows two large groups of taxa and two or three small satellite clusters of 1-2 taxa. In confirming the high levels of variation in the *O. polysticha-sagotii-spectabilis* complex, six specimens of these species clustered in the more *Scheelea*-related group. One specimen fell into the mostly-*Orbignya-Attalea* group, and two other specimens appeared as satellite taxa, away from each other and from the others (Figure 5). Almost all specimens of *S. butyracea* (except SB-38) and *S. phalerata* clustered in the *Orbignya-Attalea*-related

group. Since the distance between points in the space represents a measure of similarity or dissimilarity, it is understandable the location of M. dahlgreniana, A. dubia, A. tessmannii, O. luetzelburgii, O. crassispata, S. butyracea, and S. phalerata in the scatterplot: all these species carry characters related to Orbignya and Attalea. The clustering of A. racemosa and A. nucifera in the mostly Scheelea-related group is not surprising; the descriptive analysis revealed many features of that group. A. nucifera strengthens the doubt about its proper identity, and raises the possibility of a mistake.

Among the satellite taxa were A. colenda, A. x piassabossu, and x A. minarum. The size of its non-vascular fiber bundles is probably one of the major features separating A. colenda from the others; A. x piassabossu possesses two character states shared only with its putative parent, A. funifera: hypodermal fibers around midrib, and completely tannin-filled hypodermal cells; and x A. minarum had the double-layered hypodermis as one of its strongest separating characters, since this feature is only present in the Brazilian-Orbignya group, from which no specimens were included in this analysis.

Fig. 6. Scatterplot of the first two components derived from PCA with only putative hybrids and intermediates.



A final PCA was performed with the re-inclusion of a number of intermediates. These were specimens that were recorded as possessing conflicting patterns and/or “mixed” features during the collection and description of the data. These conflicts, however, were not detected statistically in the PCAs previously performed, and the specimens were re-included in the data set. The specimens were: A. colenda, A. dubia, O. crassispata, O. luetzelburgii, and A. nucifera. Indeed, the presence of these specimens did not change much the situation recorded without them. The first five components accounted for 61.1% of the (as opposed to 66.5% without these specimens). The variation explained by the first and second components was 29.9% and 10.6%, respectively (as opposed to 32.1% and 11.5% with those specimens excluded).

The scatterplot derived from the first two components (Figure 7) shows the same pattern of grouping observed before, and the specimens included grouped as follows: 1) A. nucifera joined the Scheelea group, strengthening the suggestion that this species has been placed in the wrong group; 2) O. luetzelburgii grouped with non-Brazilian species of Orbignya; 3) A. dubia, O. crassispata, and A. colenda grouped with Attalea.

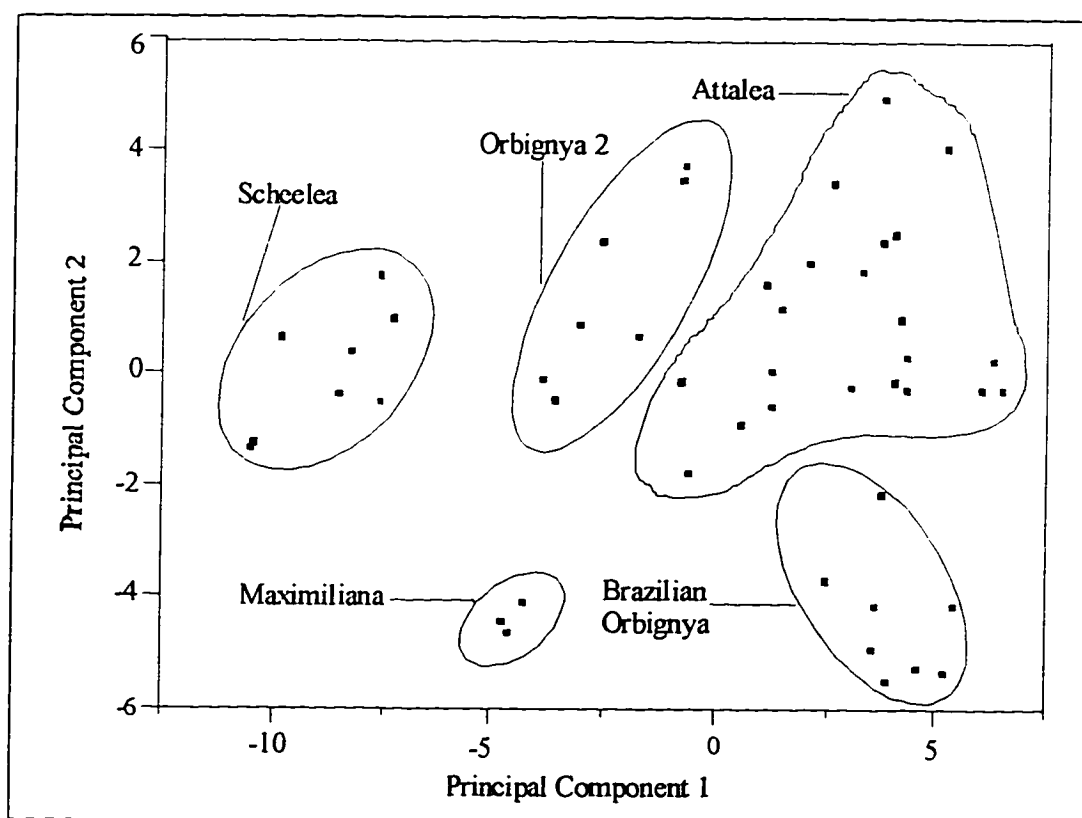
Table 16. Loadings for the first five components derived from the Principal Components Analysis of anatomical characters from specimens of the Attaleinae - PCA with intermediates re-included.

EigenValue:	25.3614	8.3881	6.9144	5.6746	5.4588
Percent:	29.4901	9.7536	8.0399	6.5984	6.3474
CumPercent:	29.4901	39.2437	47.2836	53.8821	60.2295
Eigenvectors:					
Adaxial Cuticle-Thickness	0.10260	-0.07095	0.17652	0.04525	0.18958
Adaxial Trichome-Size	-0.00508	-0.07266	0.10241	0.08361	0.07627
Adax Epidermis-Thickness	0.15927	0.01726	0.01546	-0.15902	-0.04457
Adax Epid Cell Extension	0.11161	0.00512	-0.16948	-0.03857	-0.01862
Adax Epidermis-Cell Shape	0.11187	-0.00970	-0.21773	0.02999	-0.04411
Adax Epidermis-Cell Wall	-0.10400	-0.12448	-0.18651	-0.09036	0.01281
Over Fiber Cells-Length(μ)	-0.12476	0.02666	0.02177	-0.12649	0.05274
Over Fiber Cells-Width(μ)	0.05155	0.02705	0.06098	-0.07602	0.14069
Inter Fiber Cells-Length(μ)	-0.12441	-0.03440	-0.05673	-0.07061	0.07105
Inter Fiber Cells-Width(μ)	0.06639	-0.16281	0.16337	0.03534	0.06558
Adax Silica Bodies-Size(mm)	-0.01121	0.03928	0.15976	-0.24851	0.10491
Abaxia Cuticle-Thickness	0.10119	-0.01696	-0.05172	-0.05524	0.27970
Abaxial Trichome-Size	0.07970	-0.00307	0.11653	0.03071	0.05886
Abaxial Epidermis-Thickness	0.17000	-0.05270	-0.11377	-0.02649	0.04797
Costal Bands-Width(#cls)	0.02400	-0.14600	0.01975	0.10666	-0.04635
Costal Bands-Width(f)	0.10622	-0.15884	-0.04457	-0.02115	0.04015
Costal Bands-Width(μ)	0.07295	-0.19071	-0.02151	-0.02380	0.06849
Costal Cells-Length(μ)	-0.08483	-0.07405	0.16136	0.06580	0.02195
Costal Cells-Width(μ)	0.11207	-0.03611	-0.07928	0.04019	0.22262
Costal Cells-Shape	-0.11664	0.00969	0.10771	-0.07648	-0.06934
Costal Cells-Walls	-0.14562	-0.07009	-0.12695	-0.05146	0.07338
Intercostal Bands-Width(f)	0.10061	-0.11586	0.11291	-0.02779	-0.00236
Intercostal Bands-Width(μ)	0.10366	-0.16732	0.12220	-0.03038	0.01069
Intercost Cells-Length(μ)	-0.00342	-0.11707	0.09770	-0.08326	0.11307
Intercostal Cells-Width(μ)	0.05518	-0.10750	-0.07226	-0.07288	0.14238
Intercostal Cells-Walls	-0.14562	-0.07009	-0.12695	-0.05146	0.07338
Stomates-Arrangement	0.15247	-0.04026	-0.07925	-0.04666	0.01612
Stomates-#rows	0.15769	-0.04925	0.02903	-0.09382	0.04966
Guard-cells	-0.03695	-0.10845	0.08078	0.01610	-0.14010
Subs. Lateral-Position	0.12633	0.00875	-0.12776	-0.03999	-0.11375
Abax Silica Bodies-Size(mm)	-0.04637	0.02190	0.17371	-0.15802	-0.00571
Adaxial Hypodermis-#Layers	0.07054	0.23272	-0.13632	0.04410	0.08047
Adaxial Hypod Cells-Shape	0.13528	0.16352	-0.11548	0.02681	-0.04156
Adaxial Hypod Cells-Size(μ)	-0.09649	-0.07208	0.05851	0.03539	0.18881
Adaxial Hypodermis-Tannins	0.02969	-0.13942	0.17800	0.20817	-0.00318
Abaxial Hypod Cells-Shape	0.09813	0.10451	0.12533	0.09998	-0.15519
Abaxial Hypod Cells-Size(μ)	0.07542	0.03599	0.11530	0.20390	-0.17307
Adaxial Fibers-Type	0.02246	-0.05338	0.08415	0.13324	0.23382
Adaxial Fibers-#Groups	-0.09375	0.15720	0.00128	0.12440	0.10959
Adaxial Fibers-#fib/group	0.13410	-0.01037	-0.00303	-0.00604	0.01572
Adaxial Fibers-Shape/Groups	0.12866	-0.09208	0.09253	0.02781	0.00178
Adaxial Fibers-Location	0.03289	0.17974	0.05956	-0.04342	-0.00258
Abaxial Fibers-#Groups	-0.08928	0.21276	0.00854	0.08294	0.00592

Table 16. (Cont'd.)

Abaxial Fibers-Fibers/group	-0.07831	0.09667	0.11700	0.22233	-0.01618
Abaxial Fibers-Arrangement	-0.00219	-0.02221	0.00729	0.05989	0.04782
Abaxial Fibers-Shape/groups	-0.13421	0.06993	0.02847	0.20151	-0.00253
Abaxial Fibers-Location	-0.12845	0.14336	-0.04477	0.11560	-0.00141
Palisade-#Layers	0.17329	0.00924	-0.03766	0.01377	-0.16660
Palisade-Differentiation	0.16684	-0.03636	-0.02712	0.11243	0.03446
Palisade-Thickness	0.15033	0.01851	0.12134	0.01756	0.01117
Palisade Cells-Walls	-0.16250	0.02389	0.02368	-0.09294	-0.05583
Palisade-Tannins	0.06363	-0.12360	-0.07304	0.16288	0.04446
Spongy-#Layers	0.14295	0.03961	0.00255	-0.03070	0.12396
Spongy-Differentiation	0.16727	-0.05644	-0.10369	0.01726	0.06833
Spongy-Thickness(μ)	0.14779	0.13996	0.02450	-0.02050	0.11141
Spongy Cells-Walls	-0.16916	0.04469	0.07368	-0.00776	-0.05156
Spongy-Tannins	0.05089	-0.07647	0.03012	0.05305	0.03264
Chlorenchyma	0.15845	0.09266	0.07048	-0.00561	0.07336
Primary Veins-Shape	0.04764	-0.18443	-0.01340	-0.18260	-0.05518
Primary Veins-Number	0.04875	0.01479	0.02994	0.29405	-0.01590
Primary Veins-Height(μ)	0.09201	0.08881	0.23390	-0.19064	-0.00087
Primary Veins-Width(μ)	0.06518	0.14242	0.23613	-0.17446	0.08388
Primary Veins-Position	-0.12131	-0.09920	-0.10108	0.05494	0.24615
Primary Veins-Type/fiber	-0.06684	-0.15208	0.03159	0.15559	0.20970
Primary Veins-#Layers	0.06763	0.07501	0.20629	-0.13052	-0.06166
Sec&Tert Veins-Number	0.03828	0.15731	0.06208	0.04079	0.13307
Sec&Terc-Betw Large Veins	-0.03105	0.19569	0.10627	-0.16220	0.13248
Mid-secondary Veins	0.11576	0.04437	-0.16276	-0.09665	0.14652
Sec. Veins-Height(μ)	0.15254	0.00927	0.11152	0.02784	0.00671
Tert Veins-Height(μ)	0.13890	-0.08277	0.13845	0.07090	-0.04341
Sec&Tert Veins-Inner sheath	0.13696	0.00877	-0.06260	0.03971	-0.21794
Sec&Tert Veins-Buttresses	-0.09237	-0.12432	0.13424	0.06025	-0.19427
Sec&Tert Veins-#Layers	0.09948	-0.08451	0.18677	-0.00538	-0.18961
SecTert Veins-Type/fiber	0.15705	-0.05738	-0.11979	-0.02327	-0.02706
Expansion Cells-Location	-0.04119	-0.00514	0.02205	-0.19289	0.01195
Midrib-Shape	-0.15578	-0.03428	0.03240	0.02082	0.03110
Midrib-Size(mm)	0.03454	0.28120	0.07341	0.04949	0.07619
Midrib-#Vasc. bundles	0.01143	0.25327	0.02051	0.11770	0.08411
Sclerotic sheath	-0.16033	-0.00459	0.02312	-0.17997	0.06785
Midrib-Cuticle(μ)	0.11475	-0.02510	0.08763	-0.01208	0.24849
Midrib-Hypodermis	0.05996	0.21969	-0.17245	-0.02322	0.00513
Midrib-Spongy	0.00788	0.09900	0.01743	-0.17155	-0.03716
Midrib Fibers-Location	-0.14387	-0.06750	0.17249	0.02247	0.07718
Midrib Exp. Cells-#Layers	0.05977	0.14732	0.09527	0.18252	0.14791
Midrib Exp. Cells-Confluence	0.06962	0.01986	-0.05731	0.19201	0.03127
Transverse Veins	-0.14144	-0.05950	-0.04528	0.10517	0.17698

Fig. 7. Scatterplot of the first two components derived from the final PCA with intermediates re-included.



b. Cluster Analysis

All-taxa Analysis

The first analysis was performed by including all taxa (except Syagrus). Both Ward's minimum variance and single linkage methods were tried for calculation of the clustering distances. However, only the results from the single linkage method are reported in this first analysis, since the definition of the clusters produced was superior compared to Ward's method. That is probably because the taxa including putative hybrids and intermediates do not form compact clusters (for which Ward's method is better); instead, irregular clusters are produced (as it can be seen from the PCA results) for which the single linkage method is more sensitive (Sneath and Sokal, 1973). In single linkage, also called the nearest neighbor technique (Lance and Williams, 1967), the distance between two clusters is the minimum distance between an observation in one cluster and an observation in the other cluster. A taxon that is a candidate for an extant cluster has similarity to that cluster equal to its similarity to the closest member within the cluster. Connections between clusters and taxa and between two clusters are established by single links between pairs of taxa. Single linkage usually leads to long straggly clusters (Sneath and Sokal, 1973). By imposing no constraints on the shape of clusters, this method sacrifices

performance in the recovery of compact clusters in return for the ability to detect elongated and irregular clusters (JMP, 1995).

Figure 8 shows the clustering patterns for all taxa. It is approximately a repeat of the PCA results. There is not much taxa clustering resolution, even though the arrangement of specimens with “mixed” patterns (the putative hybrids and intermediates) follow a certain pattern regarding the position of these specimens in relation to the groups to which they are related. The following situations can be discerned:

1) In the upper portion of the dendrogram, the first cluster (from OPH-01 down to OSA-19) join all “good” Scheelea, which are surrounded by their closest intermediates.

2) In the next group S. phalerata (SP) and S. butyracea (SB) are bordered by the non-Brazilian Orbignya: on one side, O. cohune (OCO) and O. cuatrecasana (OCU), and on the other side, O. guacuyule.

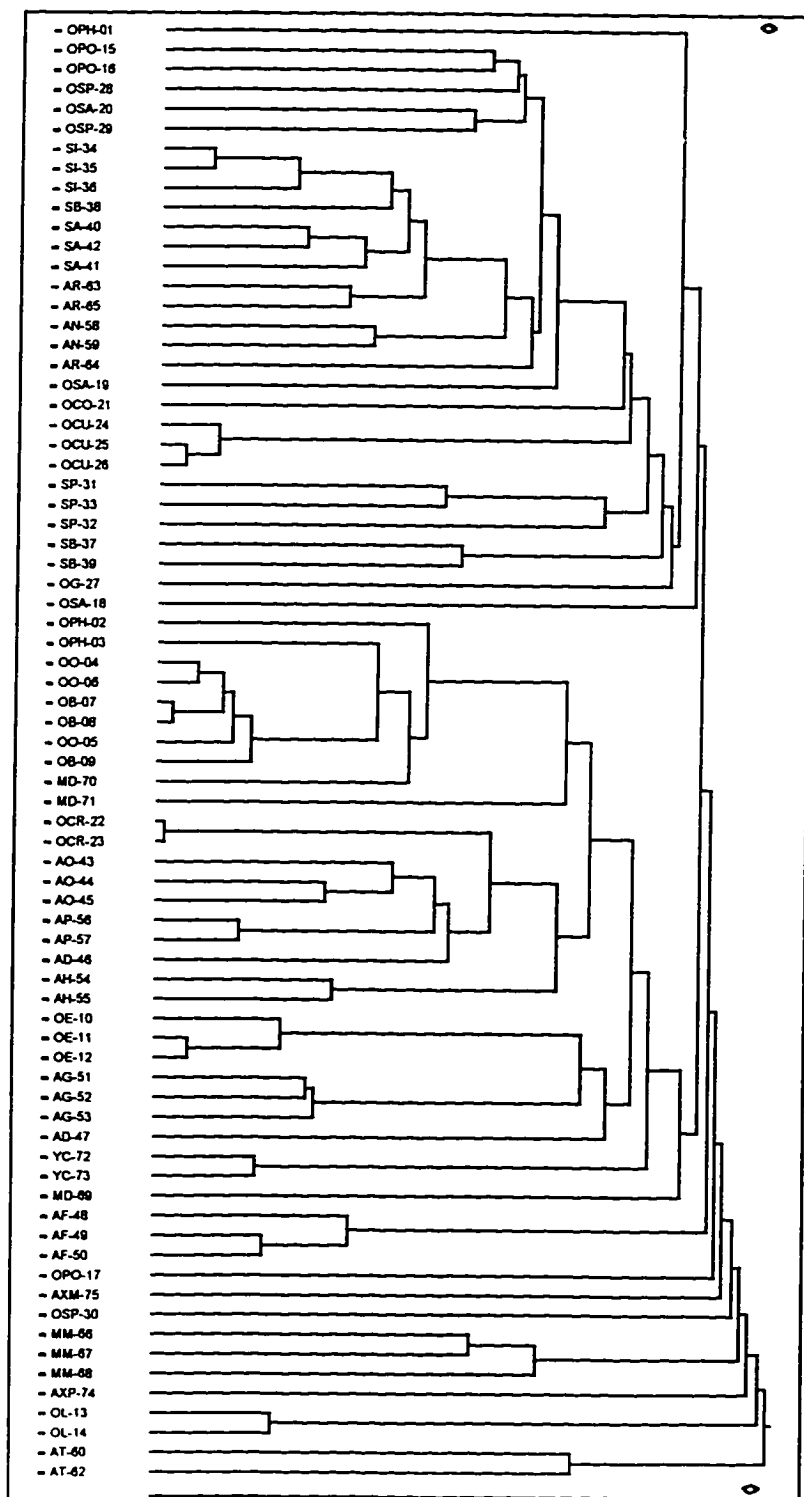
3) One of the specimens of O. sagotii (OSA-18) does not join any cluster; this is the same specimen that appeared as a satellite taxon in the PCA analysis, along with OSP-30, which is also isolated further down in the dendrogram.

4) The next cluster comprises all Brazilian Orbignya (OPH-02 to OB-09) and Markleya hybrids (MD-70 and MD-71), showing again the homogeneity of this group.

5) The “good” Attalea and their related intermediates appear in the following 5 clusters, up to A. colenda (YC-72 and YC-73); O. eichleri clusters in this group, close to the Brazilian Orbignya; A. funifera again forms a small cluster on its own.

6) All Maximiliana specimens are joined in the same group, followed by those intermediates with the most distinctive (some unique) features, which have certainly driven them to those isolated positions in the dendrogram: A. x piassabossu, O. luetzelburgii, and A. tessmannii.

Fig. 8. Hierarchical clustering using the single linkage method.
Dendrogram with all taxa included



Analysis Without Putative Hybrids and Intermediates

The Ward's minimum variance method was used for the cluster analysis without the putative hybrids and intermediates, because without the "messy" presence of those with conflicting patterns, better delineated, compact clusters of taxa would be expected. In this method, the distance between two clusters is the ANOVA sum of squares between the two clusters added up over all variables. At each generation, the within-cluster sum of squares is minimized over all partitions obtainable by merging two clusters from the previous generation (JMP, 1995). The results produced by using this method are summarized below.

1) At the lowest level, five major clusters were distinguished in the dendrogram (Figure 9), from top to bottom: a) Brazilian Orbignya; b) Attalea; c) non-Brazilian Orbignya; d) Scheelea; e) Maximiliana.

2) The Brazilian Orbignya formed a single cluster. The specimens of O. phalerata were separated from the other two species, O. oleifera and O. brejinhoensis, which in turn clustered together.

3) Orbignya eichleri appeared in the Attalea cluster, and once again, A. funifera was isolated within the Attalea group.

4) The non-Brazilian Orbignya (O. cohune, O. guacuyule, and O. cuatrecasana) comprised the next cluster; at a higher level they are included with Scheelea and Maximiliana.

5) All specimens of Scheelea clustered together, close to Maximiliana.

6) Maximiliana formed the last cluster, on the bottom portion of the dendrogram.

In the two analyses performed (with and without putative hybrids and intermediates), O. phalerata specimens always ended up separated from O. oleifera and O. breijinhoensis. In the descriptive phase of this study, distinction among these species was possible only by using a few quantitative characters (e.g., size of primary veins), as qualitative characters did not do so due to the great anatomical proximity between them. This was confirmed by the numerical analyses (both PCA and cluster): O. phalerata was consistently separated from the other two species, while, on the other hand, O. oleifera could not be distinguished from O. breijinhoensis on the basis of anatomy.

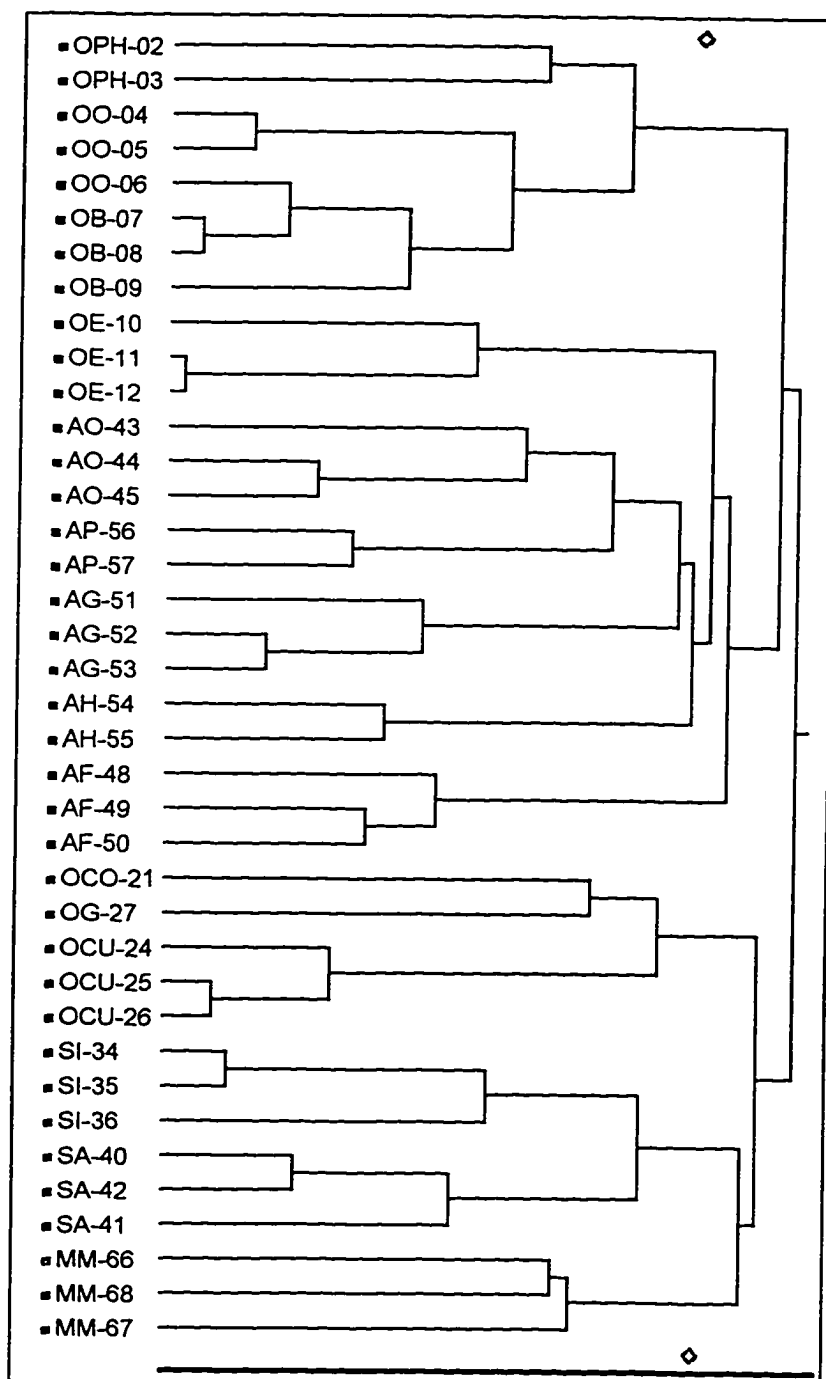
The repeated clustering of O. eichleri in the Attalea group is due to a combination of reasons. It differs from the other Brazilian Orbignya species by having a single-

layered hypodermis, and by forming buttresses in secondary and tertiary veins. The presence of buttresses also separates O. eichleri from the non-Brazilian Orbignya species. Although O. eichleri still shares many other features with O. phalerata, O. oleifera, and O. breijinhoensis, these two characters have been decisive in separating them, as can be concluded from the loadings for these features in the PCA analyses.

At the higher levels, the Brazilian Orbignya and Attalea formed a major single cluster, and Maximiliana joins Scheelea. The surprise was that the non-Brazilian Orbignya ended up in the same group with Scheelea and Maximiliana.

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Fig. 9. Hierarchical Clustering using Ward's Method.
Dendrogram without putative hybrids and intermediates

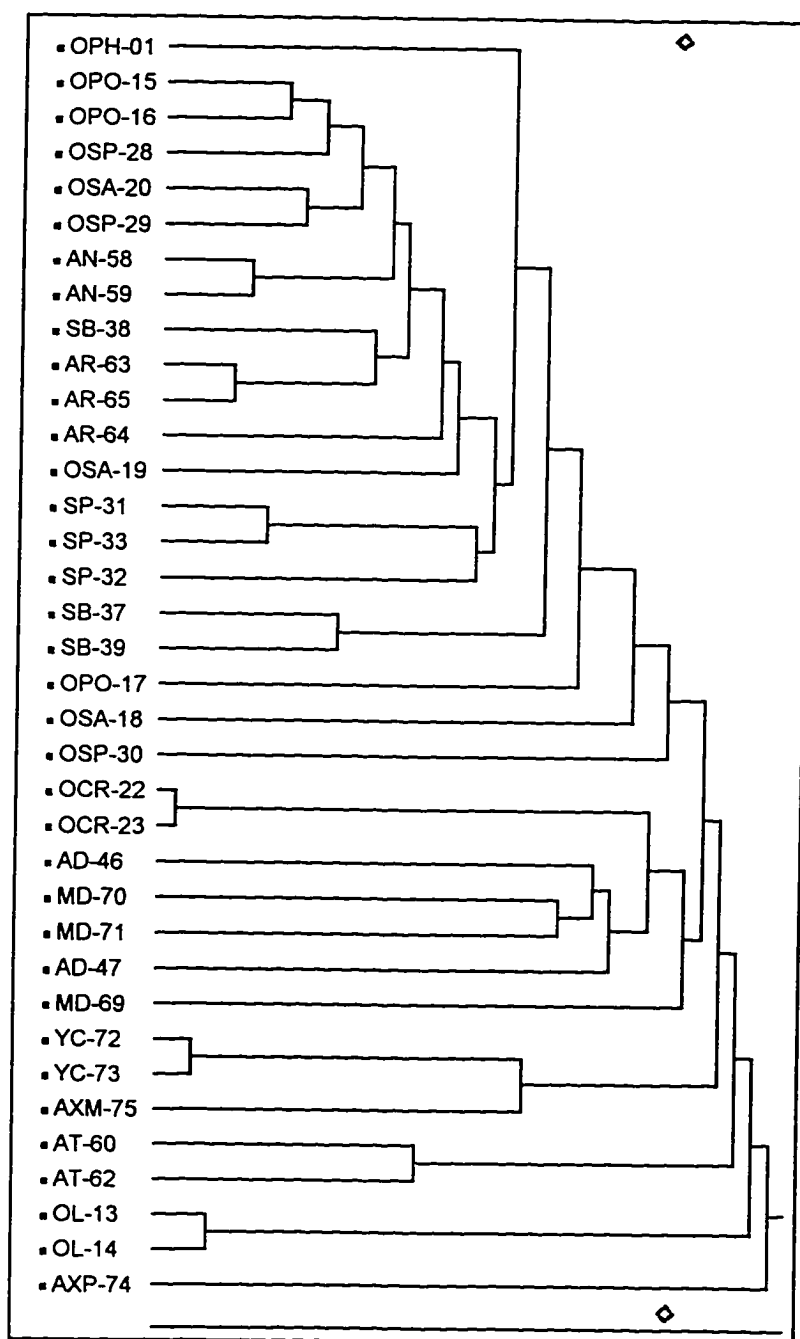


Analysis With Putative Hybrids and Intermediates Only

The cluster analysis including only the putative hybrids and intermediates virtually repeated the patterns resulting from the analysis of all taxa together. Again, using the single linkage method, all Scheelea-related intermediates clustered together (from the top down to OSA-19 in the dendrogram shown in Figure 10). This clustering pattern was expected: these specimens, although “mixed” with patterns from other groups, had a strong overall resemblance to Scheelea. This group is followed by S. butyracea and S. phalerata in the middle of the dendrogram (Figure 10), half way between the Scheelea-related group and the Orbignya-Attalea-related group (down to MD-69). The lower portion of the dendrogram is like previously observed in the all-taxa analysis, only the order of the clusters changed: A. colenda joins x A. minarum; and A. tessmannii, O. luetzelburgii, and A. x piassabossu appear isolated. This isolation is probably related to the absence of any other specimen with some of the unique characters in these taxa (e.g., bumps on lower portion of lamina in A. tessmannii; an entire abaxial layer of hypodermal fibers in O. luetzelburgii; and tannin-filled hypodermal cells and hypodermal fibers on the upper portion of primary veins and around midrib in A. x piassabossu). The repetition of the same clustering patterns resulting from the two different analyses (with all taxa, and with the conflicting specimens alone) indicate that these specimens (of putative hybrids and/or intermediates) produce a strong effect on the patterns observed. This

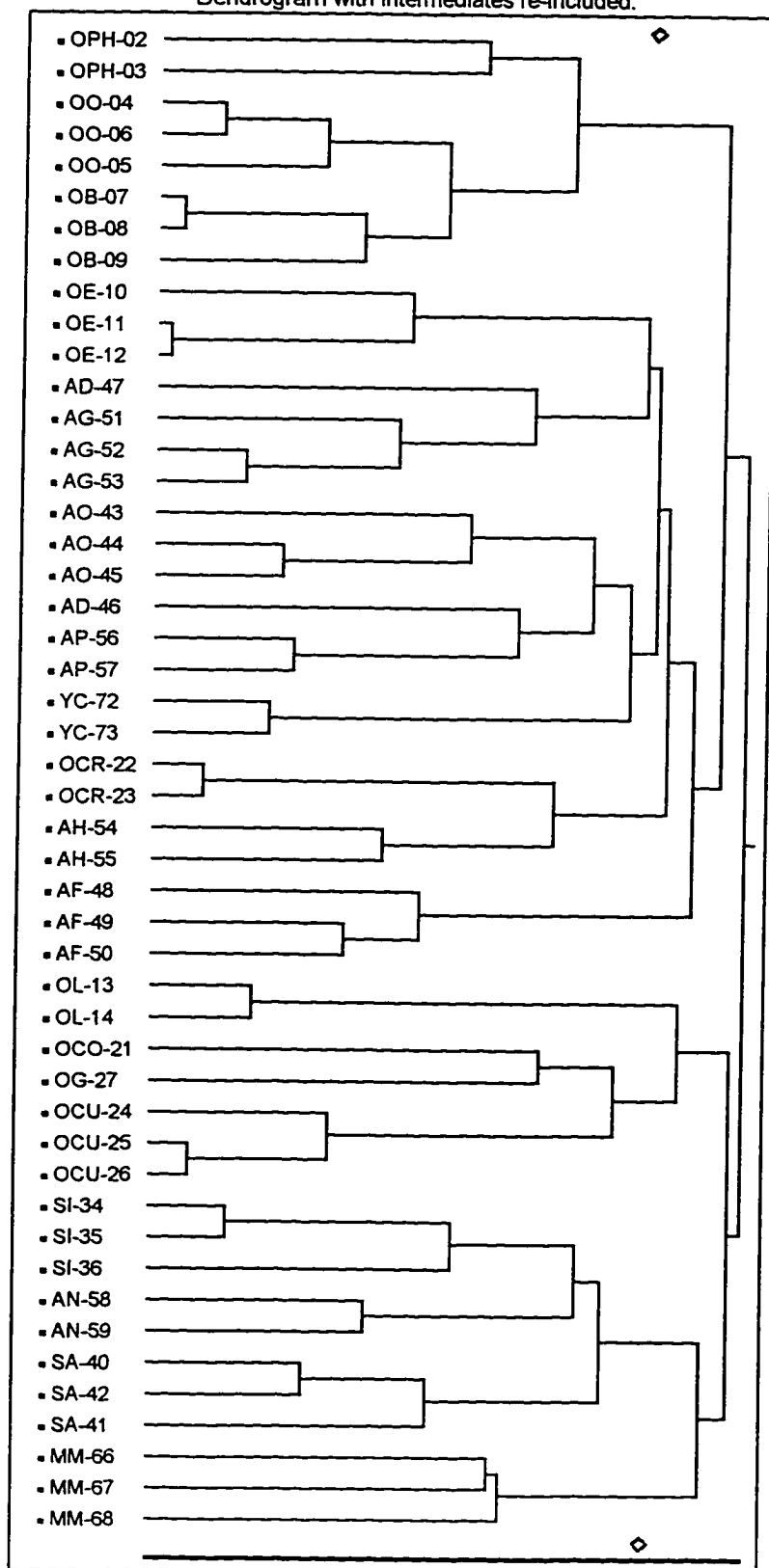
probably is the result of the more complex variation present in their characters, which ultimately results in conflicting relationships among them (within the groups to which they are most closely related), and among the groups as well. A similar situation resulted from the PCA analyses performed with and without these specimens.

Fig. 10. Hierarchical clustering using the single linkage method.
Dendrogram with only putative hybrids and intermediates



As for the PCA, those specimens labeled as intermediates but which showed no conflicting pattern of clustering in the previous analyses were returned to the data matrix, and a new cluster analysis rerun. The results, depicted in Figure 11, show exactly the same clustering pattern obtained from the PCA without these specimens (shown in Figure 7). At the high level, two major clusters were formed: one includes all Brazilian Orbignya and Attalea specimens; the other grouped the non-Brazilian Orbignya, Scheelea, and Maximiliana. At the lower level, all specimens of Brazilian Orbignya formed a separate cluster. Within this major cluster, all specimens of O. eichleri clustered with A. geraensis, and one specimen of A. dubia. Attalea oleifera, one specimen of A. dubia, A. pindobassu, and A. colenda formed a large cluster. A smaller cluster was formed by O. crassispatha and A. humilis; and repeating a pattern many times observed, A. funifera was isolated in its own cluster inside the Attalea group. In the other major cluster, the non-Brazilian Orbignya were joined by O. luetzelburgii; A. nucifera, not surprisingly, clustered in the Scheelea group, closer to S. insignis; and Maximiliana maripa formed a cluster on its own. From the specimens re-introduced in the analysis, only those of A. dubia showed erratic clustering. One of the specimens clustered in between O. eichleri and A. geraensis, and the other ended in another cluster in between specimens of A. oleifera and A. pindobassu. Attalea nucifera confirmed its great similarity to Scheelea, putting more weight on the doubt about the proper identity of this species.

Fig. 11. Hierarchical clustering using Ward's method.
Dendrogram with intermediates re-included.



3.3. Cladistic Analysis

All-taxa Analysis - One Outgroup

The analysis with all taxa resulted in 60 trees of 209 steps each, generated and retained by *Nona*. Swapping of these trees resulted in 109 trees of 209 steps. The strict consensus tree was 239 steps long, with a CI= 0.35, and a RI= 0.60 (Figure 12). The hypothesis of monophyly of the subtribe is supported by 8 synapomorphies as follows: 1) a thin abaxial epidermis; 2) round adaxial hypodermal cells; 3) a poorly differentiated palisade mesophyll; 4) frequent presence of tannins in palisade cells; 5) more than five layers of spongy cells; 6) long transverse veins; 7) sunken trichomes; 8) clavate trichomes. The cladogram, however, is mostly unresolved. The upper portion of a large clade is a polytomy that includes those mostly Scheelea-related species and intermediates; M. maripa is part of this polytomy. The lower portion is formed by Attalea-Orbignya-related species and their hybrids/intermediates; there is no resolution in this portion of the cladogram either.

The cladogram is mostly polytomic, as expected from the presence of the putative hybrids and intermediates in the analysis. In the Scheelea-related group, the synapomorphy observed in S. phalerata consists of a mixture of round and rectangular cells in a single hypodermal layer, a character state that is intermediate

in this putative hybrid; this “mixed” character is derived from the parent-groups Scheelea and Attalea, respectively, for the two different shapes of hypodermal cells (round and rectangular cells, respectively).

Three synapomorphies supported the Orbignya-Attalea-related clades, both of which are polytomic: 1) the oblique arrangement of adaxial epidermal cells; 2) a poorly differentiated spongy mesophyll; 3) mixed types of fibers (large and small fibers of thin and thick walls). Of these, only one is also present in the putative hybrids and intermediates. The clade, therefore, could probably still be supported if they were excluded. The upper unresolved group of Orbignya-Attalea species includes O. cohune, O. guacuyule, O. luetzelburgii, and A. tessmannii, each of them separated by one synapomorphy, except for O. luetzelburgii, which is separated by: 1) absence of an abaxial hypodermis; 2) the presence of two shapes of primary veins; 3) and hypodermal fibers replacing the entire abaxial hypodermis. O. cohune is distinguished by having two types of fibers forming the secondary and tertiary veins; O. guacuyule by its mixed pattern of long and short transverse veins; and A. tessmannii by its unique pattern of venation with the formation of bumps on the lower surface of the lamina.

The other clade is supported by homoplasies only, except for the synapomorphy shown by O. eichleri (its ovate primary veins). Attalea funifera and its putative hybrid, A. x piassabossu appear as sister to each other. This is supported by unique

character states, e.g. the presence of hypodermal fibers around the midrib, which also replace cells in the upper hypodermis, and a rounded midrib as well. The descriptive analysis of the data showed great anatomical proximity between these two taxa, and as a consequence of that, the hybrid status of *A. x piassabossu* could not be confirmed, since it closely resembles one of the putative parents (*A. funifera*). The placement of these two species in the cladogram as sister taxa supports the previous findings.

The Brazilian *Orbignya* group is not resolved in this cladogram; they are part of a polytomic clade with their hybrids and *Attalea* species. The synapomorphic character states of the group collapse because of the presence of hybrids and their polymorphisms for many characters. This hybrid-provoked collapse is tested and discussed later, with the individual re-inclusion of these putative hybrids in the analysis.

Analysis Without Putative Hybrids and Intermediates - One Outgroup

The analysis without the putative hybrids and intermediates produced markedly different results. Only 2 trees of 120 steps were retained after 1000 replications by *Nona*. Swapping of trees was not necessary. The strict consensus tree had 121 steps, CI= 0.64, and RI= 0.70, and it was mostly resolved (Figure 13). The

monophyly of the group was well supported again by a high number of synapomorphies (12), which are basically the same recorded from the all-taxa-one-outgroup analysis, added by:

- 1) presence of a single layer of palisade cells.
- 2) thin-walled palisade cells occurring in the entire Orbignya-Attalea group and in M. maripa.
- 3) frequent occurrence of tannins in spongy cells.
- 4) large fibers of thin walls forming the secondary and tertiary veins.
- 5) irregular shape of the midrib.
- 6) an acute sclerotic sheath.

O. cuatrecasana is placed in the Orbignya-Attalea group, and along with O. guacuyule and O. cohune they constitute sister species to two inner clades of Orbignya and Attalea species. All four character states that separate M. maripa from the rest of the subtribe are synapomorphies. The separation of Scheelea species from the Orbignya-Attalea species is differentiated by one synapomorphy (a poorly differentiated palisade mesophyll). The clade, on the other hand, is well supported by 3 synapomorphies: adaxial epidermal cells of undulate walls, thick-walled palisade cells, and large fibers with thin walls forming primary veins. These synapomorphies differentiated the clade formed by S. insignis and S. attaleoides. Attalea funifera and A. humilis are joined as sister taxa on the basis of two character

states. Excluding the putative hybrids and intermediates, they are the only two species that have adaxial non-vascular fibers arranged in bunches and to occur exclusively below the hypodermal layer. The other Attalea species ended up polymorphic for these characters.

The Orbignya-Attalea clade, with O. cuatrecasana included, is supported by only one synapomorphic character state (a poorly differentiated palisade mesophyll); without O. cuatrecasana the clade is better supported by seven synapomorphies: spindle-shaped costal cells; stomates not arranged in files; a poorly differentiated spongy mesophyll; primary veins that may occur both centered in the mesophyll or closer to the abaxial surface; two types of fibers forming primary veins (from O. guacuyule); a presence of a mid-secondary vein (mostly in the Orbignya group); and fibers in the midrib located only on its upper portion.

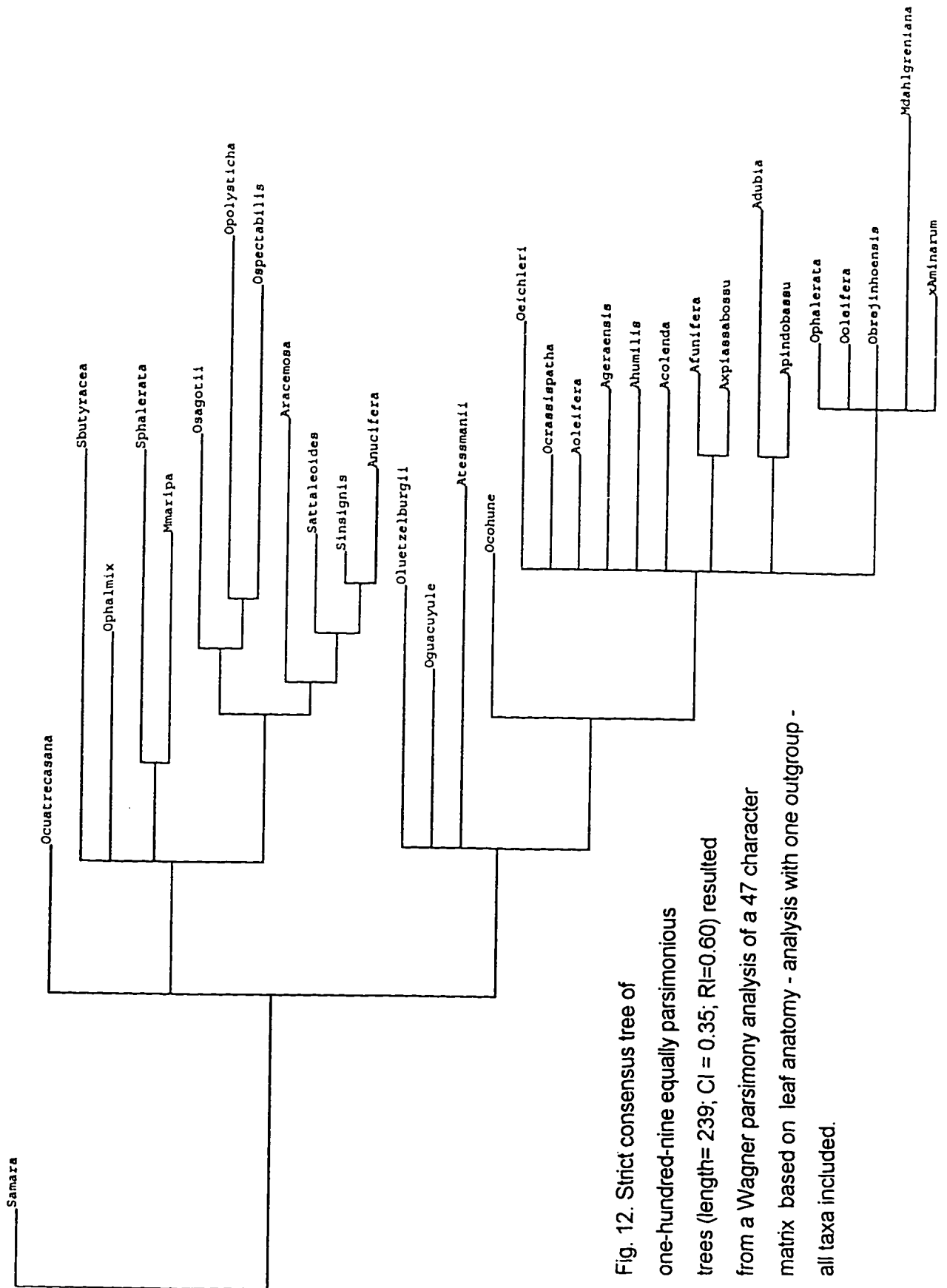


Fig. 12. Strict consensus tree of one-hundred-nine equally parsimonious trees (length= 239; CI = 0.35; RI=0.60) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with one outgroup - all taxa included.

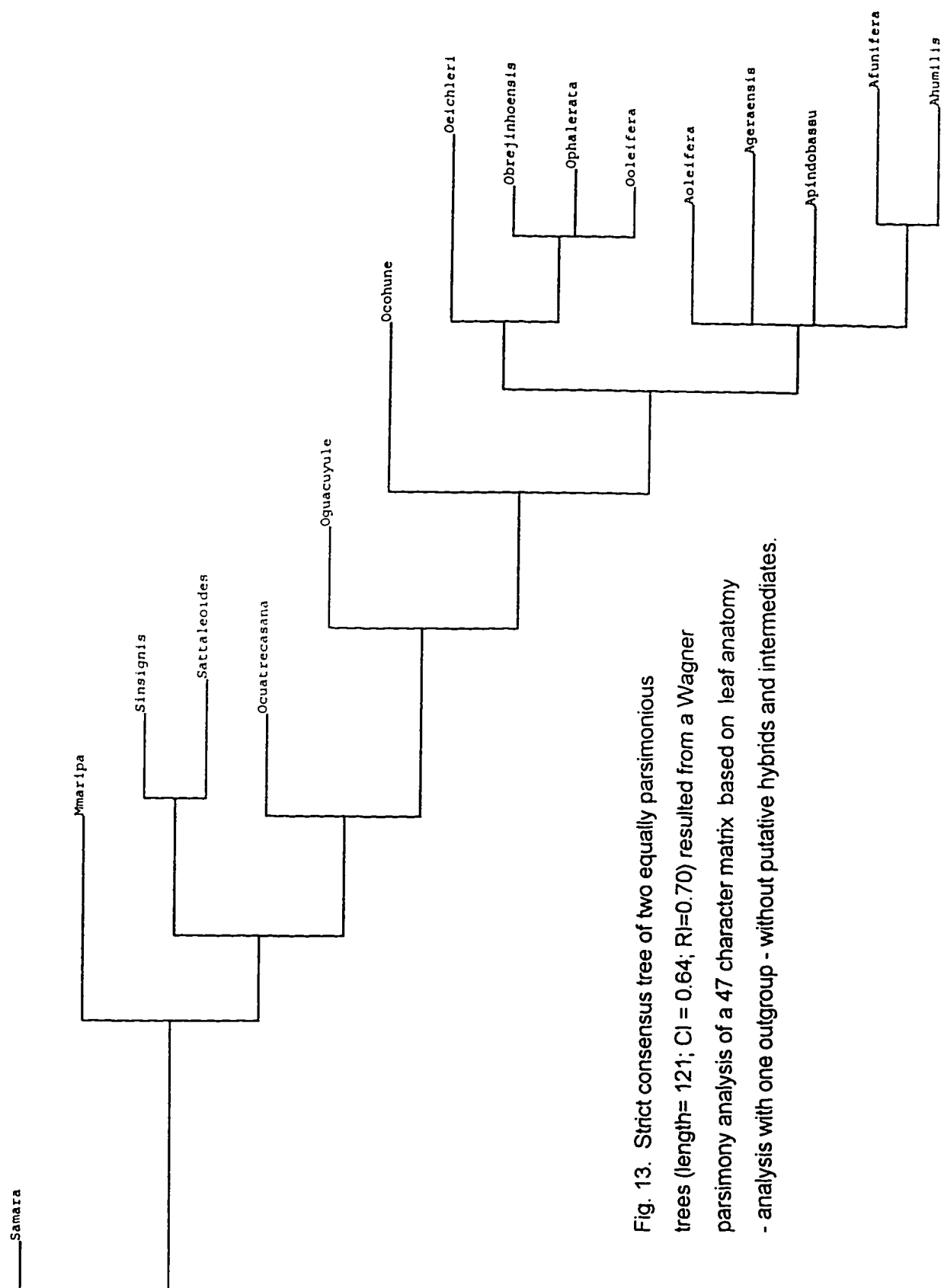


Fig. 13. Strict consensus tree of two equally parsimonious trees (length= 121; CI = 0.64; RI=0.70) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with one outgroup - without putative hybrids and intermediates.

Analysis With Three Outgroups

Syagrus amara (Jacq.) Mart. is one of the largest species of Syagrus, and until recently it was treated as a monotypic genus, Rhyticocos; Uhl and Dransfield (1987) included Rhyticocos under Syagrus. It is the only species in the genus that ranges beyond South America into the Lesser Antilles. Glassman (1987) considered this species to be a distinct taxon without close living relatives and supposedly more closely related to Chrysallidosperma (included under Syagrus by Uhl and Dransfield, 1987). Because of these peculiar characteristics, S. amara was selected as one of the outgroups. Syagrus comosa (Mart.) Mart. is a Brazilian species that apparently has no close relatives in the genus Syagrus (Glassman, 1987). Syagrus cocooides Mart. is the type species of the genus, which grows only in Brazil and Guyana (Henderson et al. 1995). To select these species as the outgroups for this study, it was taken into consideration that they are not closely related, they have no close relatives in the genus (except for maybe S. cocooides), one of them is the type species for the genus, and that S. amara is geographically and possibly evolutionarily disjunct from the others. Indeed, these three species resulted very heterogeneous anatomically, although united by a set of characters that separate them from the Attaleinae, as shown later.

Anatomical differences among S. amara, S. comosa, and S. cocoides, on the other hand, are very conspicuous, and characterize well the great distance that exists between them (see descriptions of species). Syagrus amara alone worked well as an outgroup in the single-outgroup analysis and not much resolution was added to the results by the inclusion of the two other species as outgroups. It was helpful, however, to test the strength of the characters used in the analysis and their validity as indicators of the evolutionary relationships within the Attaleinae.

All-taxa Analysis - Three Outgroups

After 1000 replications by *Nona*, 876 trees of 232 steps were found, and 98 of those were retained (CI=0.36; RI=0.66). Swapping of these trees found 108 trees of 232 steps; the strict consensus had 308 steps (CI=0.27; RI=0.49), and it resulted in being completely unresolved (Figure 14). Topologically this tree was very similar to the strict consensus obtained from the analysis performed with only one outgroup. In this case, the addition of outgroups did not contribute to any significant change in the topology. The two polytomic clades formed by Orbignya-Attalea species and their related intermediates (upper clade) contrasted with that formed by a mostly Scheelea-related group.

Analysis Without Putative Hybrids and Intermediates - Three Outgroups

Wagner parsimony analysis resulted in three equally parsimonious trees of 145 steps retained after 1000 replications performed by *Nona* (876 trees had 145 steps); the strict consensus tree (Figure 15) was 146 steps long, with a consistency index of 0.54, and 36% homoplasy. The cladogram derived from the analysis is fully resolved and it is very similar topologically to the tree obtained and previously discussed in the without-hybrids/intermediates-one-outgroup analysis. Three major clades are clearly distinguished within the Attaleinae: an Orbignya-Attalea group, formed by O. cuatrecasana, O. guacuyule, and O. cohune, each separately a sister species to the rest of the group, and further inside, a larger clade with the Brazilian Orbignya and the Attalea species; the Scheelea species group formed their own clade; and M. maripa appeared as the outermost sister taxon to the others.

The first dichotomy separates S. amara from the other two species of Syagrus (S. comosa and S. cocoides) and from the Attaleinae species. The two Syagrus form a clade of their own, and are sister species to each other; this clade is separated from the Attaleinae in the second dichotomy. The third dichotomy separates M. maripa from the rest of the subtribe; M. maripa is then the sister species to Scheelea and Orbignya-Attalea species. The fourth dichotomy separates the Scheelea clade from the other members of the Attaleinae; S. insignis is the sister species to S.

attaleoides. Orbignya cuatrecasana is the sister species to O. guacuyule, O. cohune and to the species of the Orbignya and Attalea in two inner clades. These two clades (with O. cohune as the sister species), are composed as follows: 1) the Orbignya clade is a trichotomy formed by O. phalerata, O. oleifera, and O. breijinhoensis, with O. eichleri as the sister species; 2) in the Attalea clade A. oleifera resolved with A. pindobassu; and A. geraensis ended up unresolved, as sister species to a crown clade formed by A. funifera and A. humilis (sister species to each other).

There were 36 anatomical synapomorphies for the subtribe Attaleinae (Figure 15). The monophyly of the group is well supported by seven synapomorphies as it dichotomizes from the outgroup species. Maximiliana maripa's separation from the rest of the subtribe is differentiated by four synapomorphies. The node where the Scheelea group dichotomizes is entirely homoplastic; however, the sister group formed by S. insignis and S. attaleoides is supported by at least by one synapomorphy and by a high number of other character states that occur independently in other groups. The dichotomy that makes O. cuatrecasana a sister species to the rest of the subtribe is supported by five synapomorphies; the separation of O. guacuyule is supported by one synapomorphy; O. cohune separated as a sister species is supported only by homoplasies; the dichotomy in the Orbignya clade is supported by two synapomorphies; and that in the Attalea clade is supported by only one. O. eichleri, (supported by one synapomorphy)

constitutes a sister species to the unresolved clade formed by the other Brazilian Orbignya, which is well supported by four synapomorphies. The clade formed by A. oleifera and A. pindobassu is supported by one homoplasy; the separation of A. geraensis and the the crown clade formed by A. funifera and A. humilis is supported by one synapomorphy. The crown clade is supported by one synapomorphy.

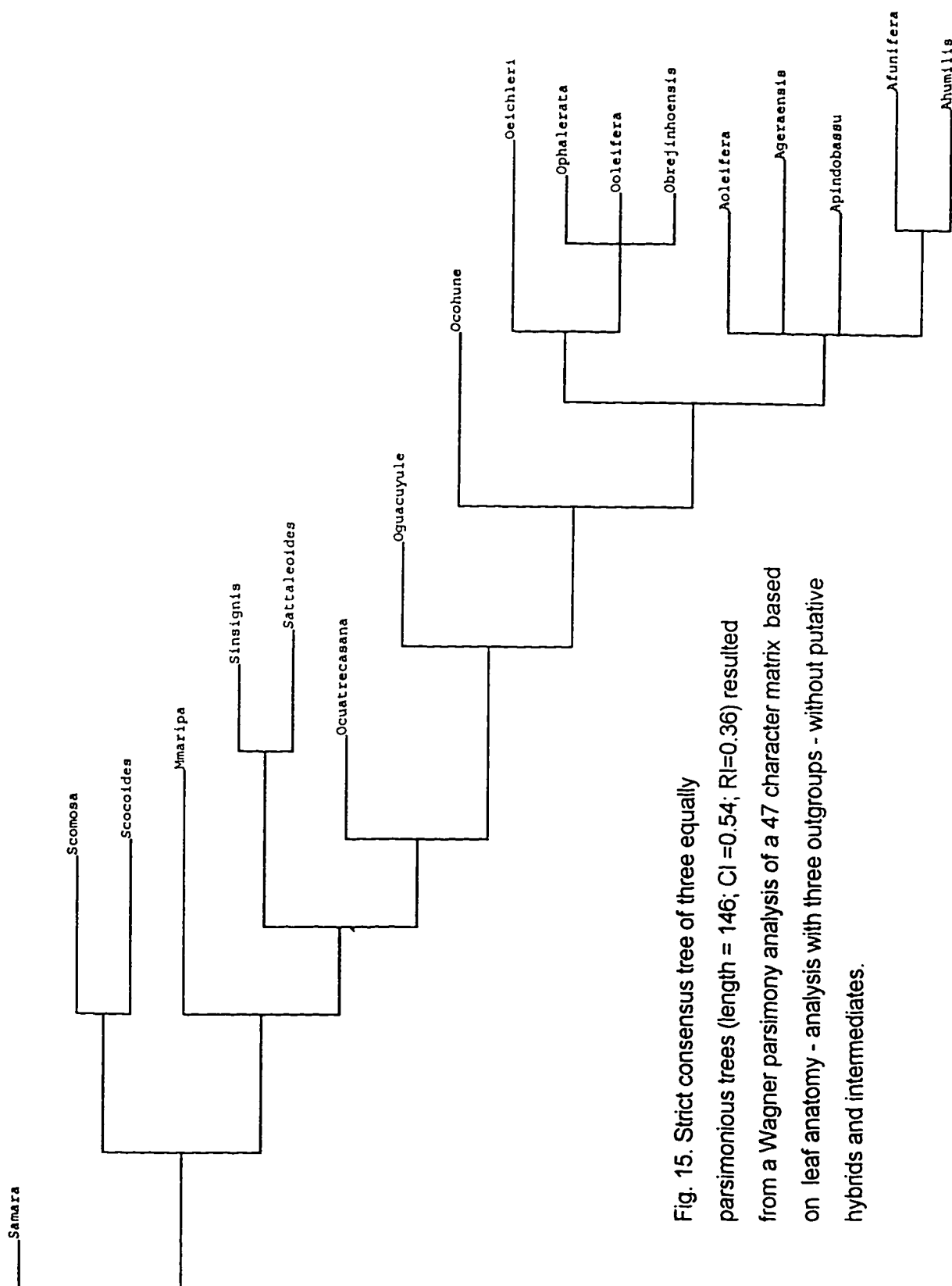


Fig. 15. Strict consensus tree of three equally parsimonious trees (length = 146; CI = 0.54; RI = 0.36) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with three outgroups - without putative hybrids and intermediates.

Selected Exclusion and Re-inclusion of Putative Hybrids and Intermediates - Effects on Cladogram

Since four putative hybrids were included in the study and a number of intermediates could be tentatively identified through the results of the different analyses performed (descriptive and multivariate), their exclusion and re-inclusion in the data matrix could easily be done. The following strategy was used to deal with the presence of a significant number of possible hybrids in this group of palms. After performing the analyses with all of them included and excluded, examining their overall effects on the cladograms, and the resulting evolutionary display with and without them (already discussed), they were taken out of the data matrix.

Subsequently, as shown below, individual or small group of putative hybrids and intermediates were re-included in the analysis and examined in relation to the expected effects on the cladograms. A data matrix including one possible hybrid at a time was submitted to *Nona*, with the 20 shortest trees retained, and replicated 1000 times. Swapping of these trees was performed when recommended by the program.

Markleya dahlgreniana

Twenty-two trees were retained by *Nona*. After swapping, 19 trees of 148 steps were retained. The strict consensus tree (shown in Figure 16) was 222 steps long (76 steps longer than the original strict consensus obtained without the inclusion of this hybrid), CI=0.36, and RI=0.26. M. dahlgreniana, as pointed out before, is a hybrid between O. phalerata and M. maripa, not sister taxa. The entire cladogram collapses to the basal node, and becomes polytomic, completely unresolved.

x Attabignya minarum

Ten trees of 148 steps were retained; the strict consensus (Figure 17) was 157 steps long; CI=0.50; RI=0.59. The presence of x A. minarum produced a similar effect as that observed with M. dahlgreniana, but to a lesser degree: only the clades formed by Orbignya and Attalea collapse, becoming a single polytomic clade. It does not cluster with any of the parents (O. oleifera or A. oleifera). This is probably due to the fact that Orbignya and Attalea are very closely related, and the clustering of the hybrid could be anywhere along the two groups, since they are anatomically very similar. To add to that, A. pindobassu and A. oleifera are very alike: morphologically they can only be separated on the basis of the number of stamens;

anatomically, the differences between the two species are minimal. Moreover, A. oleifera showed a high number of polymorphisms for some characters, which certainly contributed for the putative hybrid not clustering with it as expected. The majority of character states shown by the putative hybrid are characteristic of the Attalea group.

Attalea x piassabossu

Only two trees of 145 steps were retained; the strict consensus tree (Figure 18) was 146 steps long (CI= 0.54 ; RI= 0.65). The cladogram resulted as expected: the putative hybrid A. x piassabossu appears as sister taxon A. funifera (one of the putative parents), as it has been observed in all analyses performed. The tree is basically the same as that obtained in the analysis without any putative hybrid, and it has the same length. The hybrid status of A. x piassabossu, remains, therefore, doubtful.

Attalea colenda

One tree of 150 steps (CI= 0.53; RI= 0.64) was retained by *Nona* (Figure 19). The presence of A. colenda in the cladogram has an opposite effect compared to those observed in the other cases: it resolved within the Attalea clade, appearing as a

sister species to A. geraensis. However, this is not well supported and this clustering could have happened with any of the Attalea species, as indicated by the small number of steps required to change its position within the clade. This was also expected since anatomical signs of one of the putative parents (Orbignya) could hardly be distinguished in this species.

Attalea dubia

A. dubia has been switched back and forth between Attalea and Orbignya (see discussion on this species later). Although many Orbignya characters can be identified, the majority of the anatomical patterns are still from Attalea. Therefore, this intermediate, if a hybrid, would be expected to resolve with one of the parents without causing major effects on the topology of the original cladogram. Indeed, this was the result: only one tree (Figure 20) of 147 steps (only 1 step longer than the original tree; CI=0.54; RI=0.65) was retained by *Nona* after 1000 replications.

Attalea dubia resolved with A. pindobassu; they are sympatric species in the state of Bahia in northeastern Brazil. The other putative parent species (if A. dubia is indeed a hybrid) possibly is O. oleifera.

Attalea tessmannii

The presence of this species in the matrix collapses the entire cladogram. Five trees of 153 steps were retained; the strict consensus tree (Figure 21) is 214 steps long, with $CI=0.37$, and an $RI=0.33$. This is probably because the groups involved are not closely related; A. tessmannii possesses anatomical features that were polymorphic in the specimens studied, either close to one of the parent groups (Scheelea), or to the other (Attalea). Its relationship, therefore, could not be resolved with any of them. Moreover, this species has veins that uniquely form bumps on the lower surface of the lamina.

Attalea nucifera

The pattern observed in the descriptive and multivariate analysis is repeated in the cladistic analysis. Attalea nucifera joined the species of Scheelea without producing any major topological changes in the cladogram. Only two trees of 147 steps are generated; the strict consensus (Figure 22) was 148 steps long (just 2 steps longer than the original tree), with $CI=0.54$; $RI=0.68$. It formed a trichotomy with S. insignis and S. attaleoides, which is supported by one synapomorphy, and 10 other character states that occur independently in other groups.

Attalea racemosa

Six trees of 150 steps were retained by *Nona* (CI=0.54; RI=0.68). The strict consensus tree (Figure 23) however, was much longer (205 steps long; CI=0.39; RI=0.40) than the individual trees, and longer than the original strict consensus obtained without the presence of this species. The consensus cladogram is completely collapsed to the basal node, and A. racemosa sticks out as a sister taxon to the clade formed by Scheelea species. The separation of A. racemosa as a sister species to Scheelea within the collapsed cladogram is supported by only one synapomorphy (primary veins with an inner sheath formed by large fibers of thin walls, characteristic of the Scheelea group).

Scheelea phalerata

The nine trees retained after 1000 replications had 153 steps; the strict consensus tree (Figure 24) was 157 steps long (CI=0.51 ; RI=0.62). Scheelea phalerata splits the cladogram into two large clades, both mostly unresolved. The intermediate is placed into a polytomic clade as a sister species to M. maripa, O. cuatrecasana, and the two Scheelea species (these continue to be resolved as sister taxa). The clade has no synapomorphy to support it whatsoever, and it is built on 8 homoplastic character states.

Scheelea butyracea

The cladogram collapses to the basal node. Six trees of 147 steps were retained after 1000 replications; the strict consensus shown in Figure 25 is 204 steps long, with a CI=0.30, and RI=0.38. Scheelea butyracea formed a clade with Scheelea species, where it appears as a sister species to S. insignis and S. attaleoides (one of the two resolved clades; the other is A. funifera and A. humilis). Scheelea butyracea's position as a sister species to Scheelea is supported by one synapomorphy: the large fibers of thin walls that form the inner sheath of the primary veins.

Orbignya luetzelburgii

Two trees of 162 steps were obtained; the strict consensus (Figure 26) is 163 steps long, with CI=0.51, and RI=0.61. Orbignya luetzelburgii is inserted in the middle of the Orbignya-Attalea-related clade, in between O. guacuyule and O. cohune. The basic topology is not much affected, and O. luetzelburgii is differentiated as a sister species to O. cohune and the two clades formed by Orbignya and Attalea species. The idea of this species being a component of a large hybrid complex, which includes species of Scheelea, Orbignya, and Attalea is not supported by this result. Its separation from the rest of the Orbignya and Attalea

species is supported by only one synapomorphy (slightly sunken stomates, which is reversed in Attalea species). On the other hand, the number of autapomorphies in O. luetzelburgii is quite large, and includes four synapomorphies.

Orbignya crassispatha

Nine trees of 151 steps were obtained; the strict consensus tree (shown in Figure 27) was 153 steps long (just seven steps longer than the original strict consensus), with $CI=0.52$, and $RI=0.62$. No significant changes in the topology resulted from the presence of O. crassispatha in the data matrix, as it joins the polytomy originally formed by Attalea species.

Orbignya polysticha

Three trees of 150 steps were obtained; the strict consensus tree (Figure 28) had 151 steps ($CI=0.52$; $RI=0.65$). O. polysticha does not affect much of the original topology; it is placed as a sister species to Scheelea. The separation of this clade is, however, entirely homoplastic, but once more, the clade formed by S. insignis and S. attaleoides is supported by the type of fiber forming the primary veins (large, of thin walls).

Orbignya sagotii

Four trees of 150 steps were retained; a strict consensus (Figure 29) of 152 steps was obtained (six steps longer than the original strict consensus), with $CI=0.52$, and $RI=0.66$. Orbignya sagotii occupies the same position occupied by O. polysticha, but with the difference that the clade formed is now a trichotomy, supported by only one synapomorphy (large fibers of thin walls in primary veins). No other topological changes were produced by the re-inclusion of this putative hybrid.

Orbignya spectabilis

Three trees of 148 steps were retained; the strict consensus (shown in Figure 30) is 149 steps long (only 3 steps longer than the original consensus tree), with $CI=0.53$, and $RI=0.66$. Not surprisingly, O. spectabilis occupied the same position in the cladogram as the other two species (O. polysticha and O. sagotti) in the previous analyses: it formed a clade with Scheelea, the large fibers of thin walls in the inner sheath of primary veins being the only synapomorphy. The clade by S. insignis and S. attaleoides is not disrupted by the presence of O. spectabilis, and the two species remain as sister taxa to each other, with O. spectabilis as the sister species to both of them.

Re-inclusion of Orbignya polysticha, O. sagotii, and O. spectabilis at the same time

Nine trees of 157 steps were generated and retained by *Nona*. The strict consensus tree is shown in Figure 31 is 166 steps long, with a CI=0.48, and RI=0.65. Again, the results were unsurprising: the three species disrupt the Scheelea clade, taking the same position occupied individually, and formed a polytomy with S. insignis and S. attaleoides). Again, the polytomy is supported by the fibers in the inner sheath of primary veins (large of thin walls). These results support the suggestion that these three taxa are hybrids and conspecific.

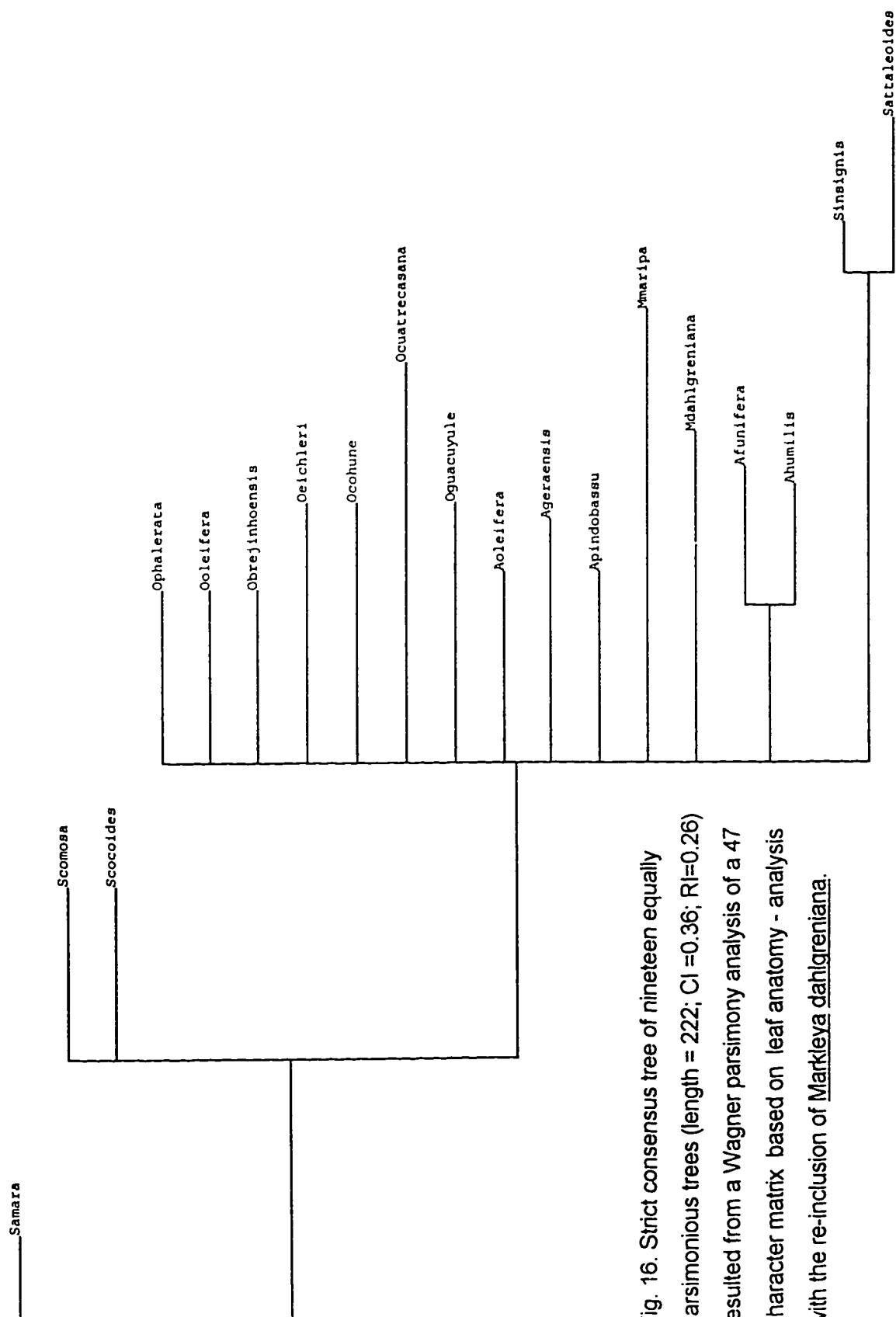


Fig. 16. Strict consensus tree of nineteen equally parsimonious trees (length = 222; CI = 0.36; RI = 0.26) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of Markleya dahlgreniana.

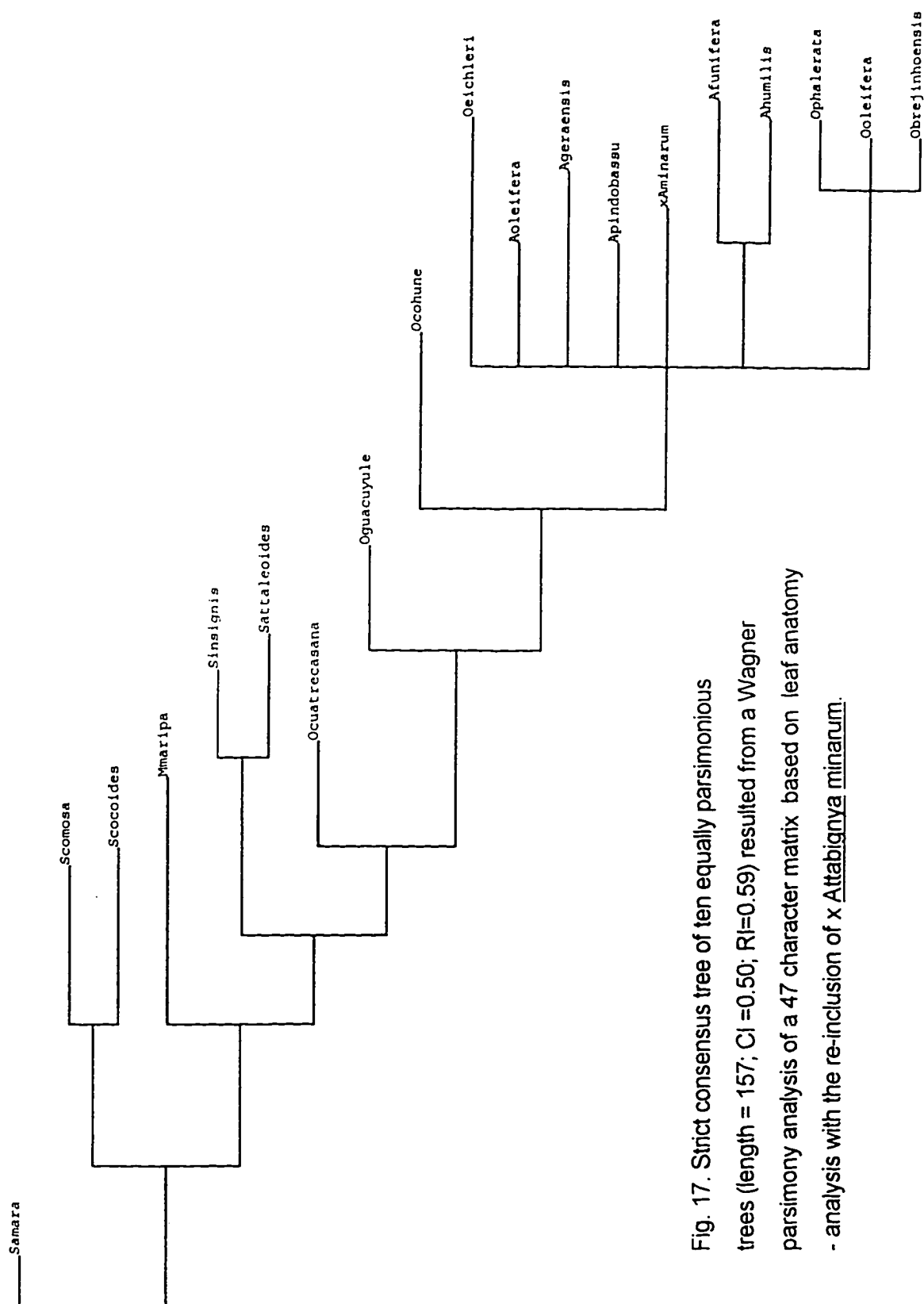


Fig. 17. Strict consensus tree of ten equally parsimonious trees (length = 157; CI = 0.50; RI = 0.59) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of x Attabignya minarum.

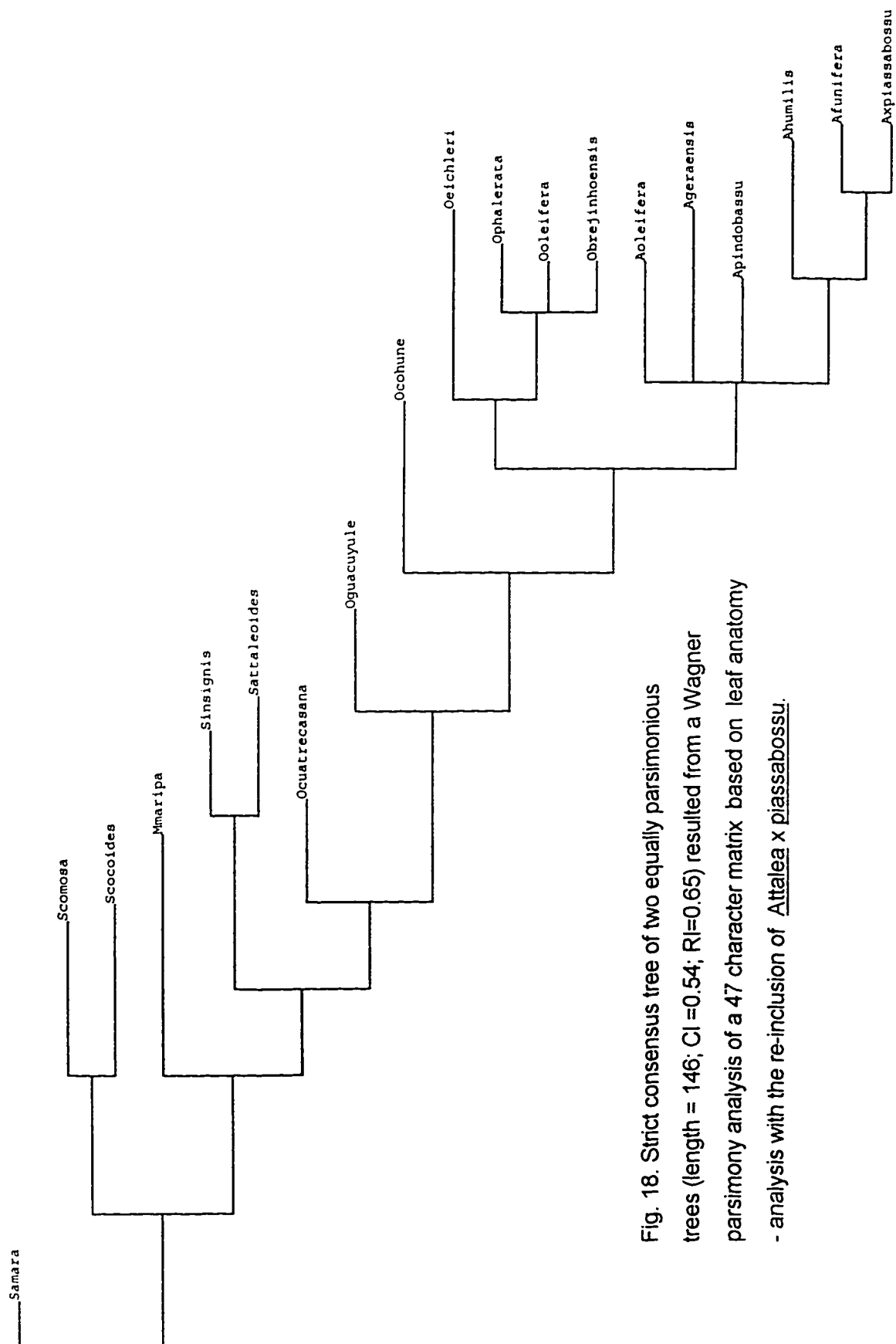


Fig. 18. Strict consensus tree of two equally parsimonious trees (length = 146; CI = 0.54; RI = 0.65) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of *Attalea* x *piassabossu*.

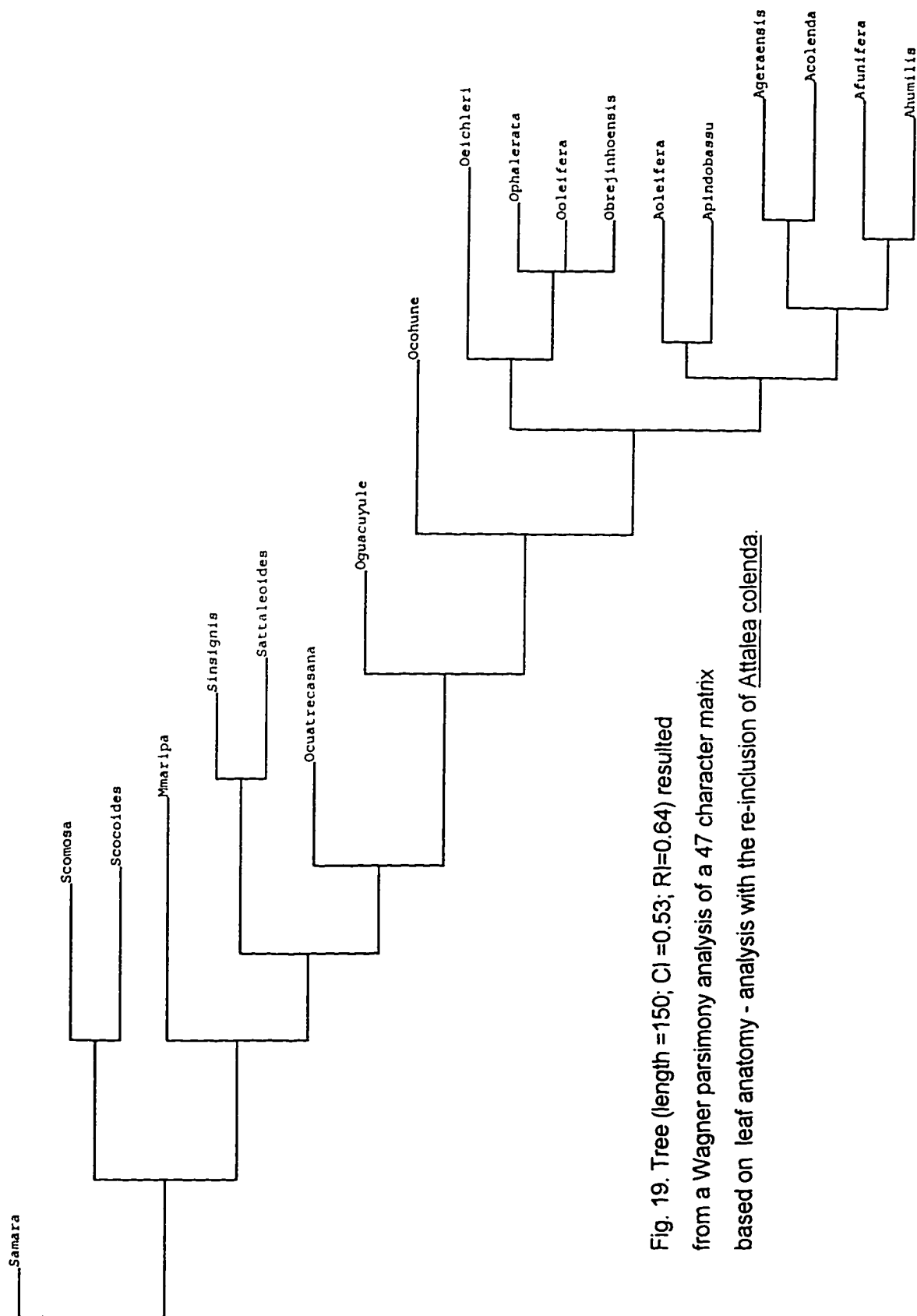


Fig. 19. Tree (length =150; CI =0.53; RI=0.64) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of *Attalea colenda*.

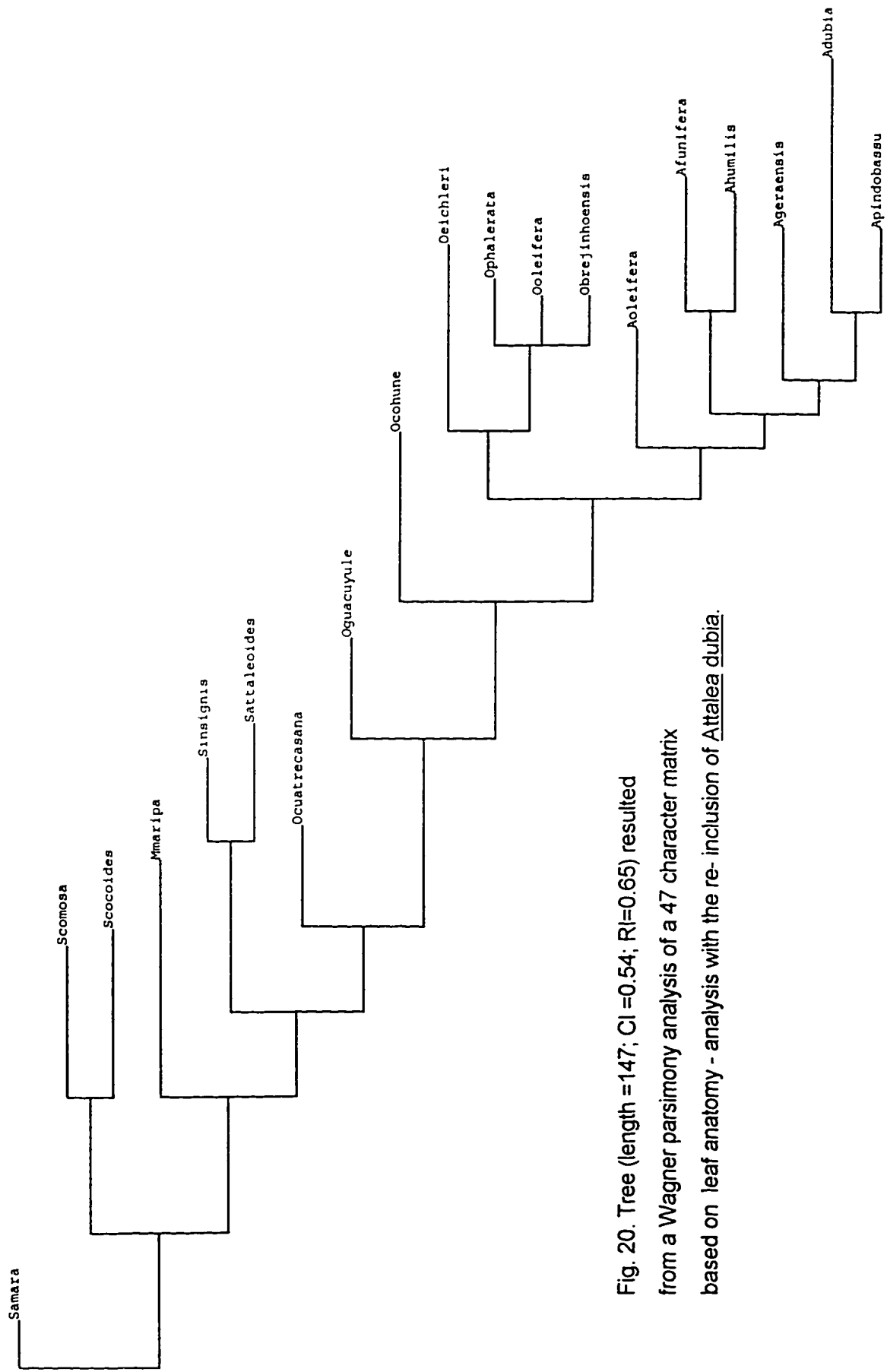


Fig. 20. Tree (length =147; CI =0.54; RI=0.65) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re- inclusion of Attalea dubia.

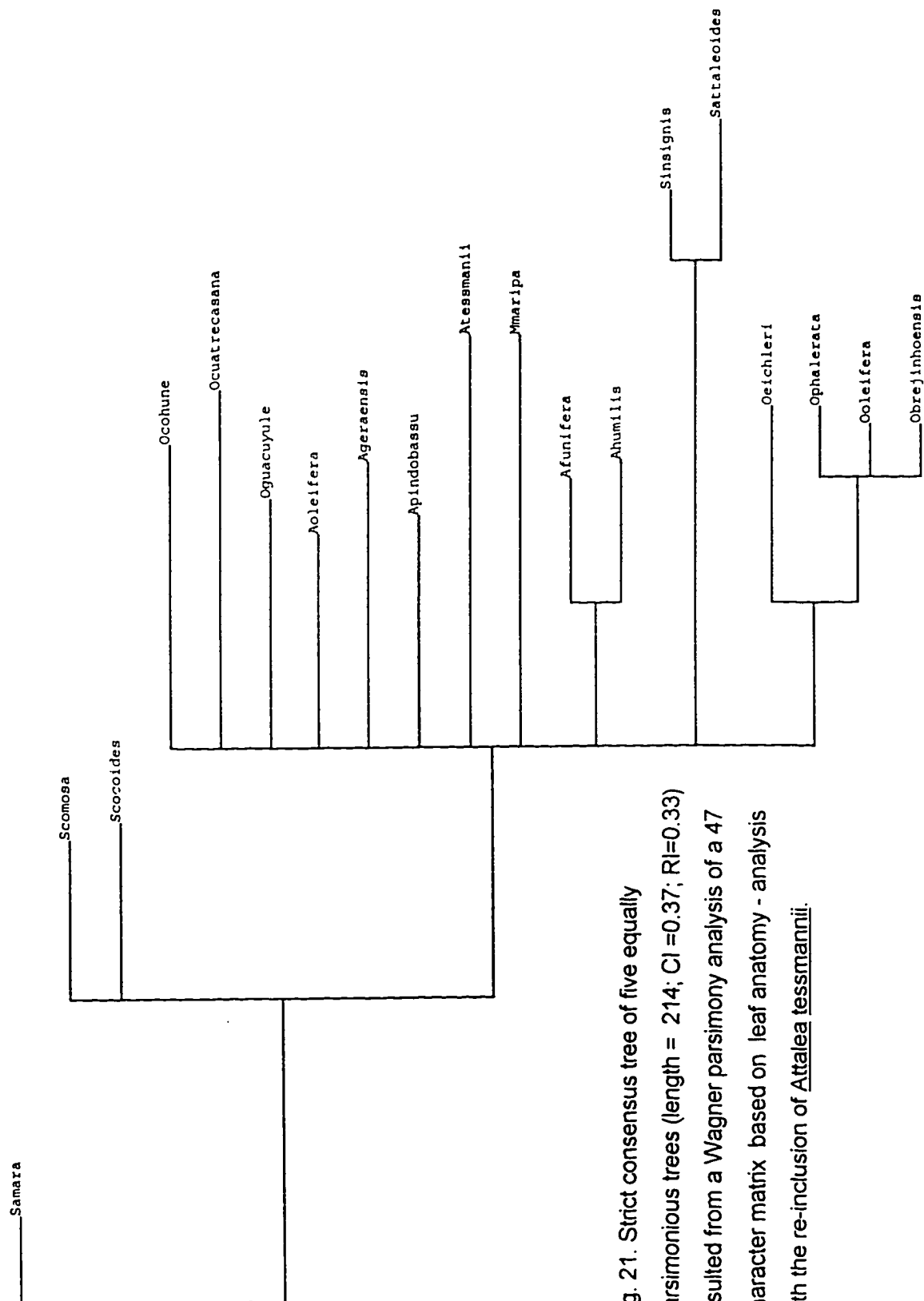


Fig. 21. Strict consensus tree of five equally parsimonious trees (length = 214; CI = 0.37; RI = 0.33) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of Attalea tessmannii.

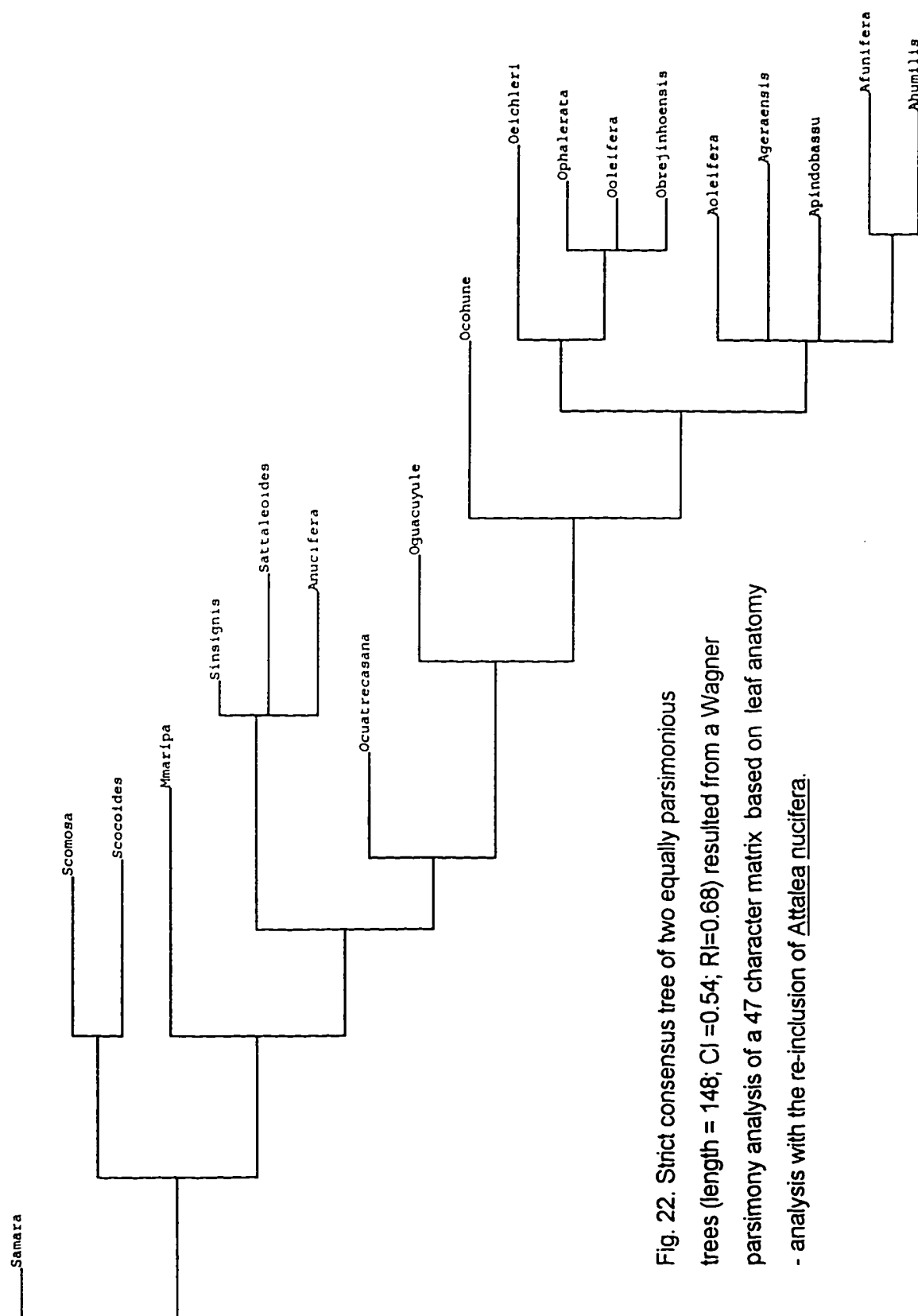


Fig. 22. Strict consensus tree of two equally parsimonious trees (length = 148; CI = 0.54; RI = 0.68) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of Attalea nucifera.

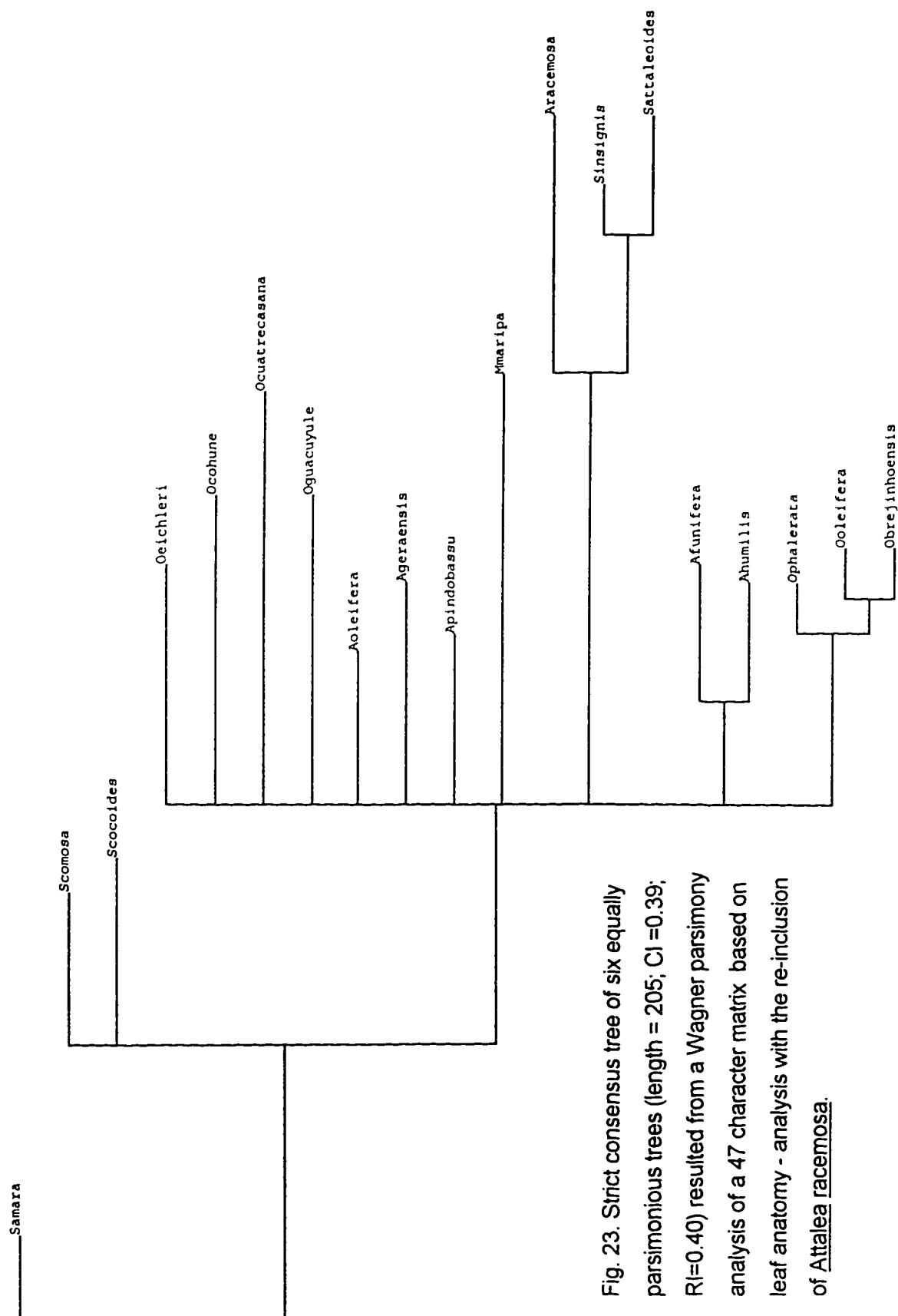


Fig. 23. Strict consensus tree of six equally parsimonious trees (length = 205; CI = 0.39; RI = 0.40) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of Attalea racemosa.

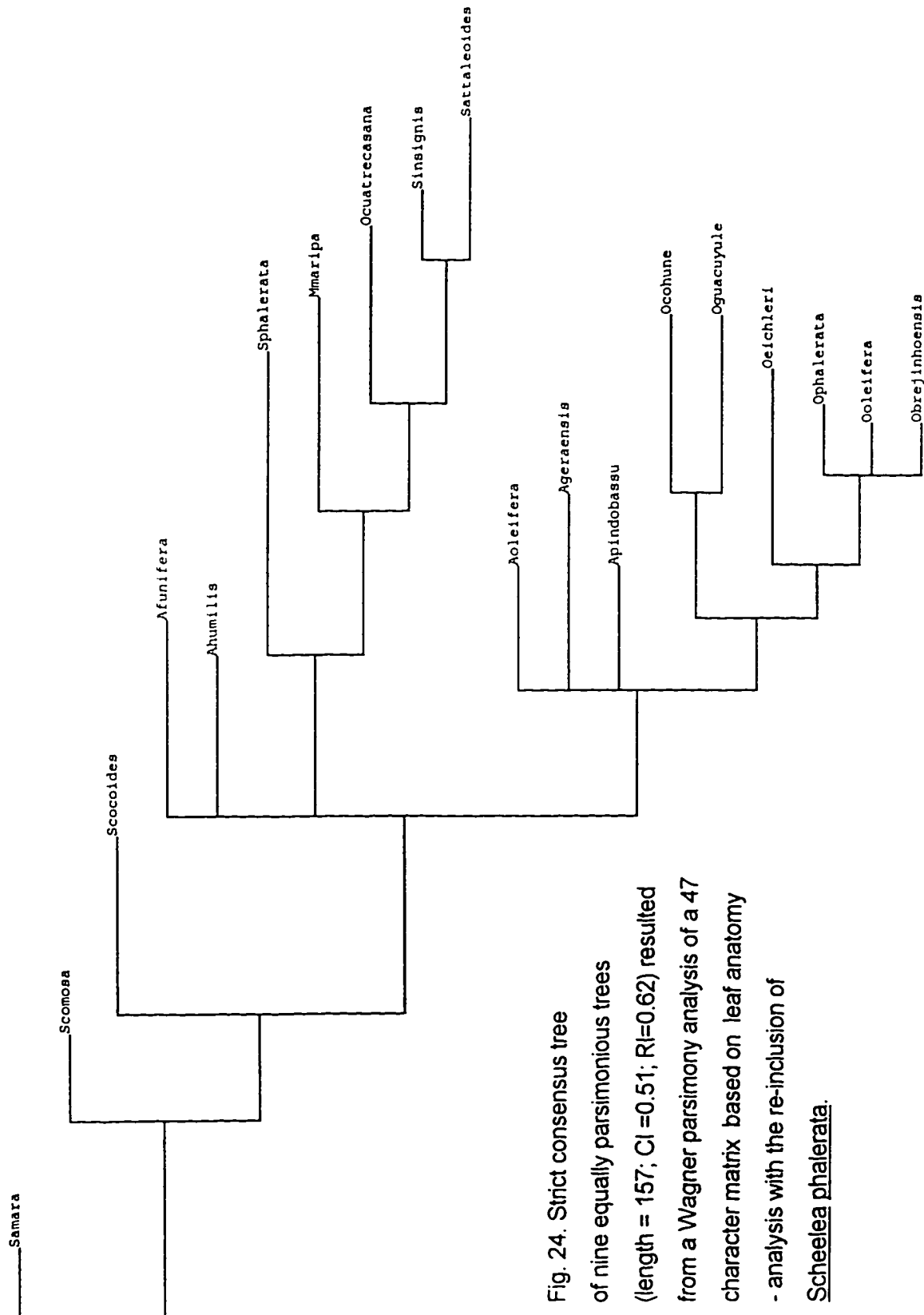


Fig. 24. Strict consensus tree of nine equally parsimonious trees (length = 157; CI = 0.51; RI = 0.62) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of Scheelea phalerata.

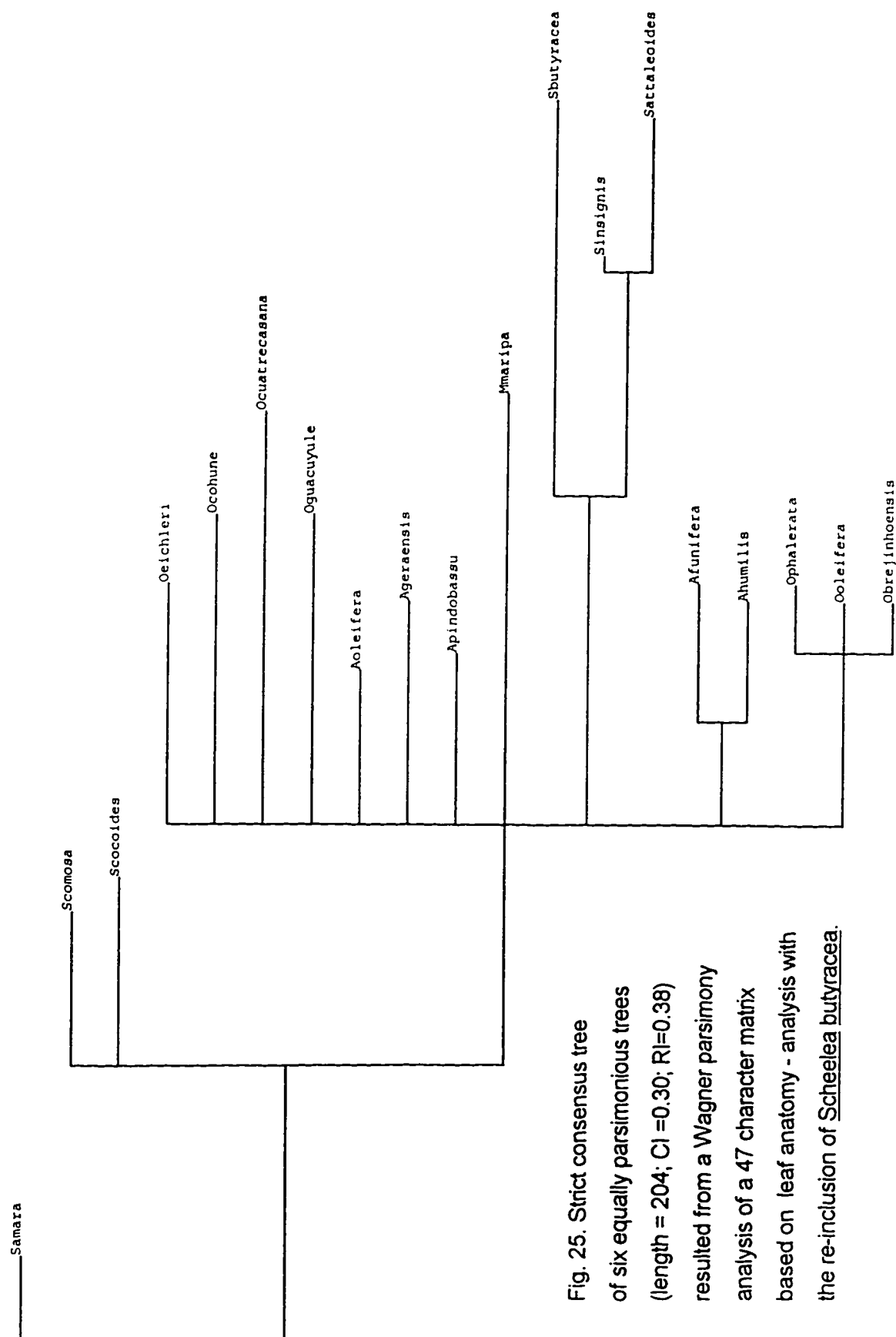


Fig. 25. Strict consensus tree of six equally parsimonious trees (length = 204; CI = 0.30; RI = 0.38) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of Scheelea butyracea.

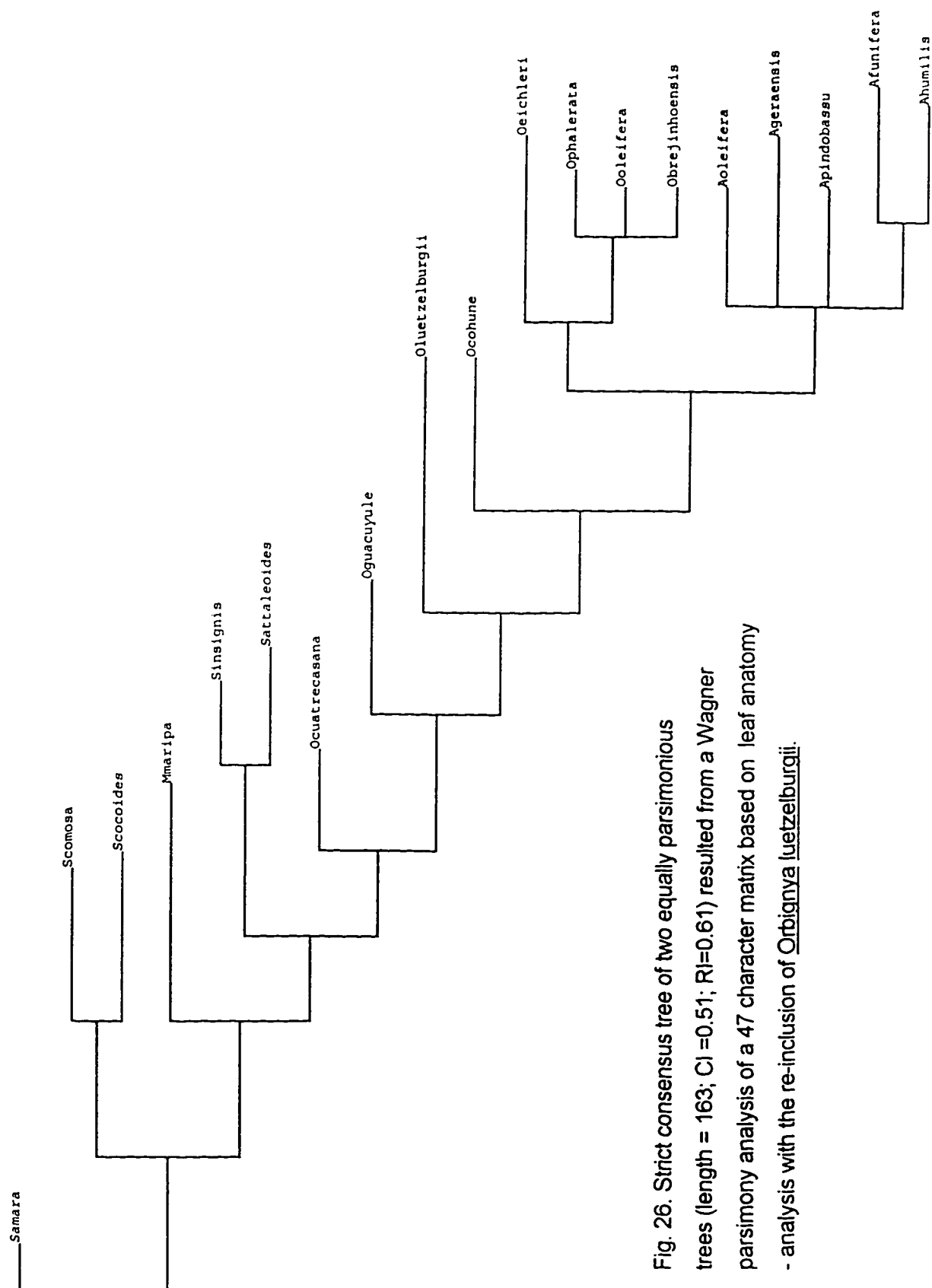


Fig. 26. Strict consensus tree of two equally parsimonious trees (length = 163; CI = 0.51; RI = 0.61) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of *Orbignya luetzelburgii*.

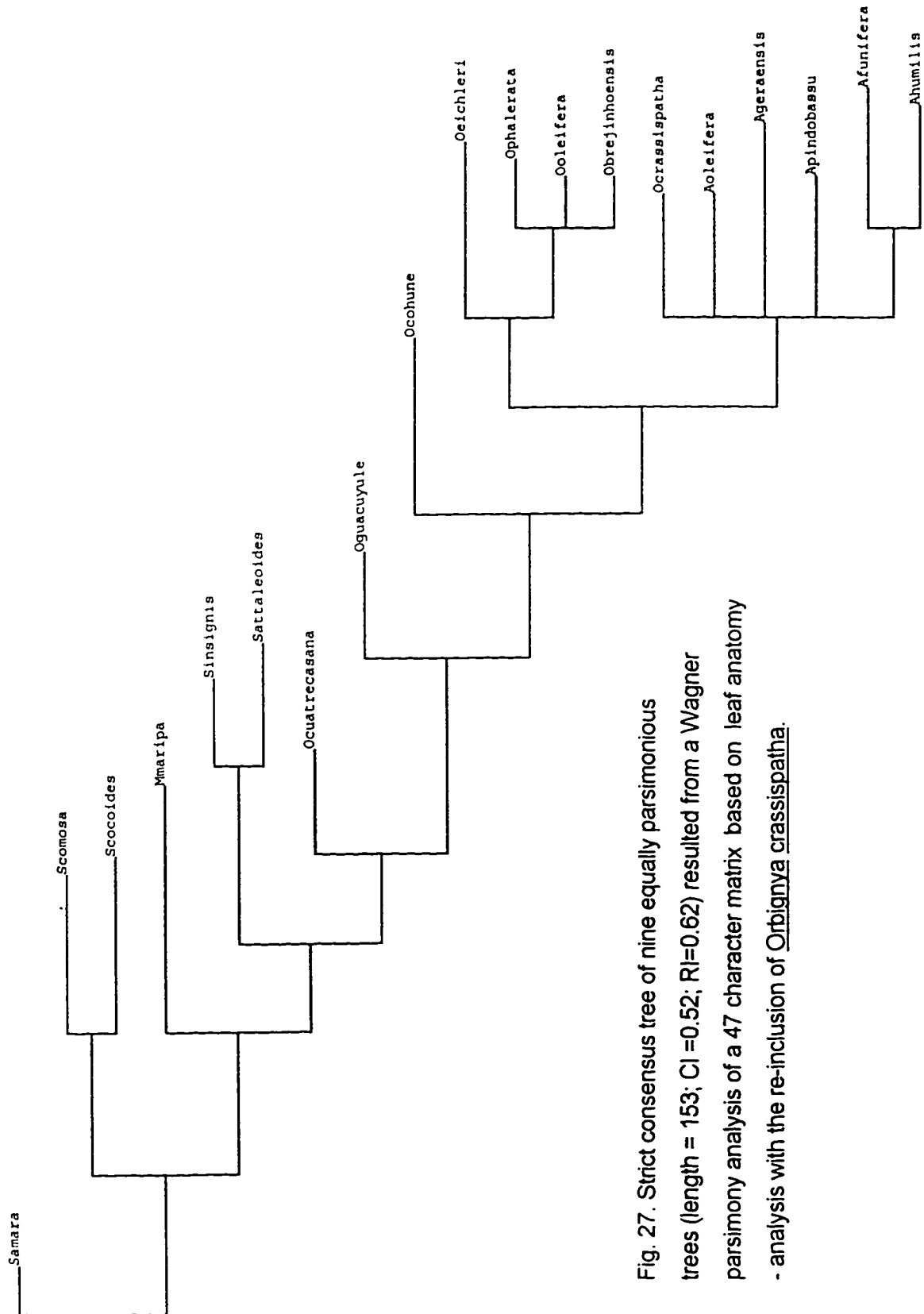


Fig. 27. Strict consensus tree of nine equally parsimonious trees (length = 153; CI = 0.52; RI = 0.62) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of Orbignya crassispatha.

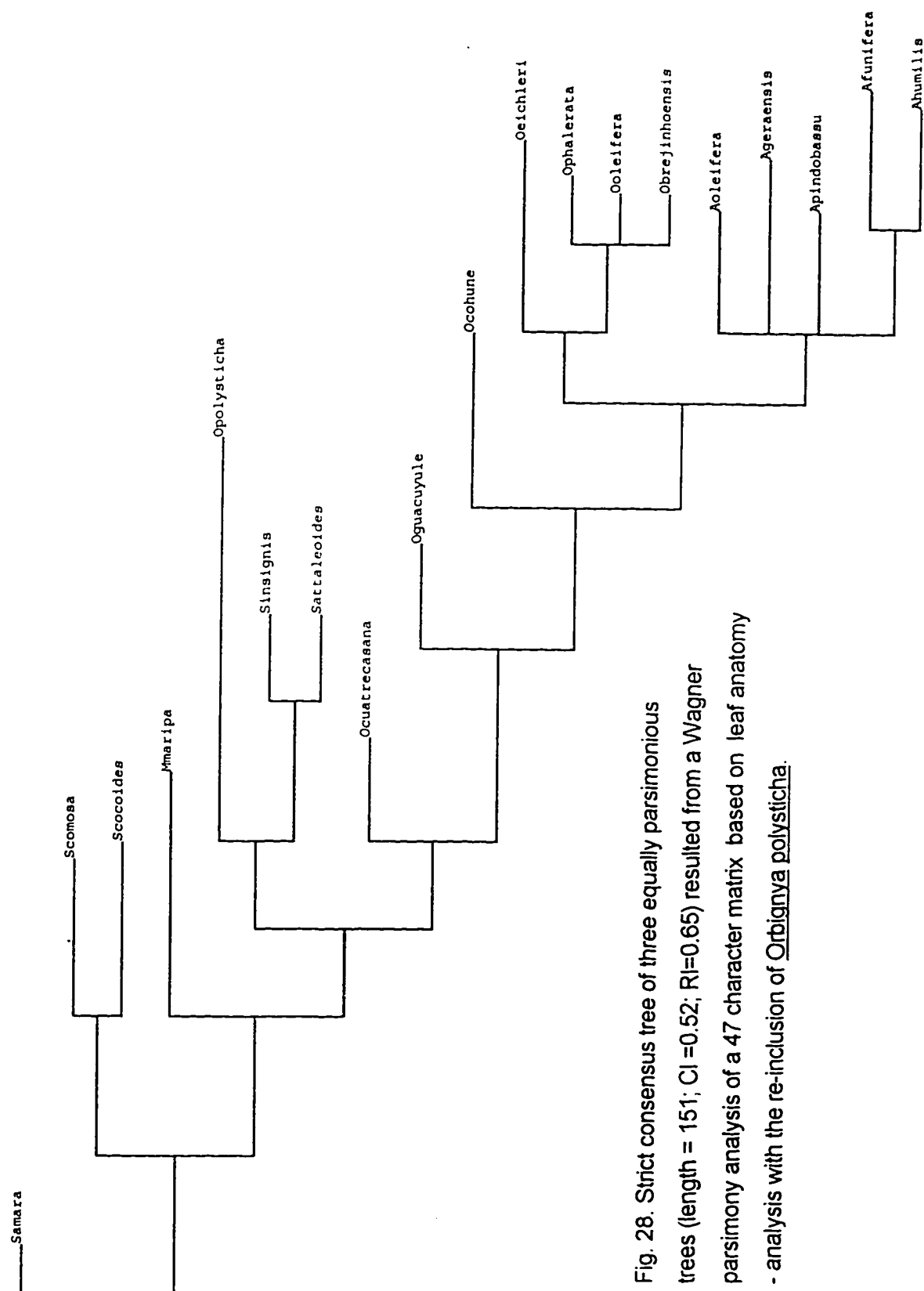


Fig. 28. Strict consensus tree of three equally parsimonious trees (length = 151; CI = 0.52; RI = 0.65) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of Orbignya polysticha.

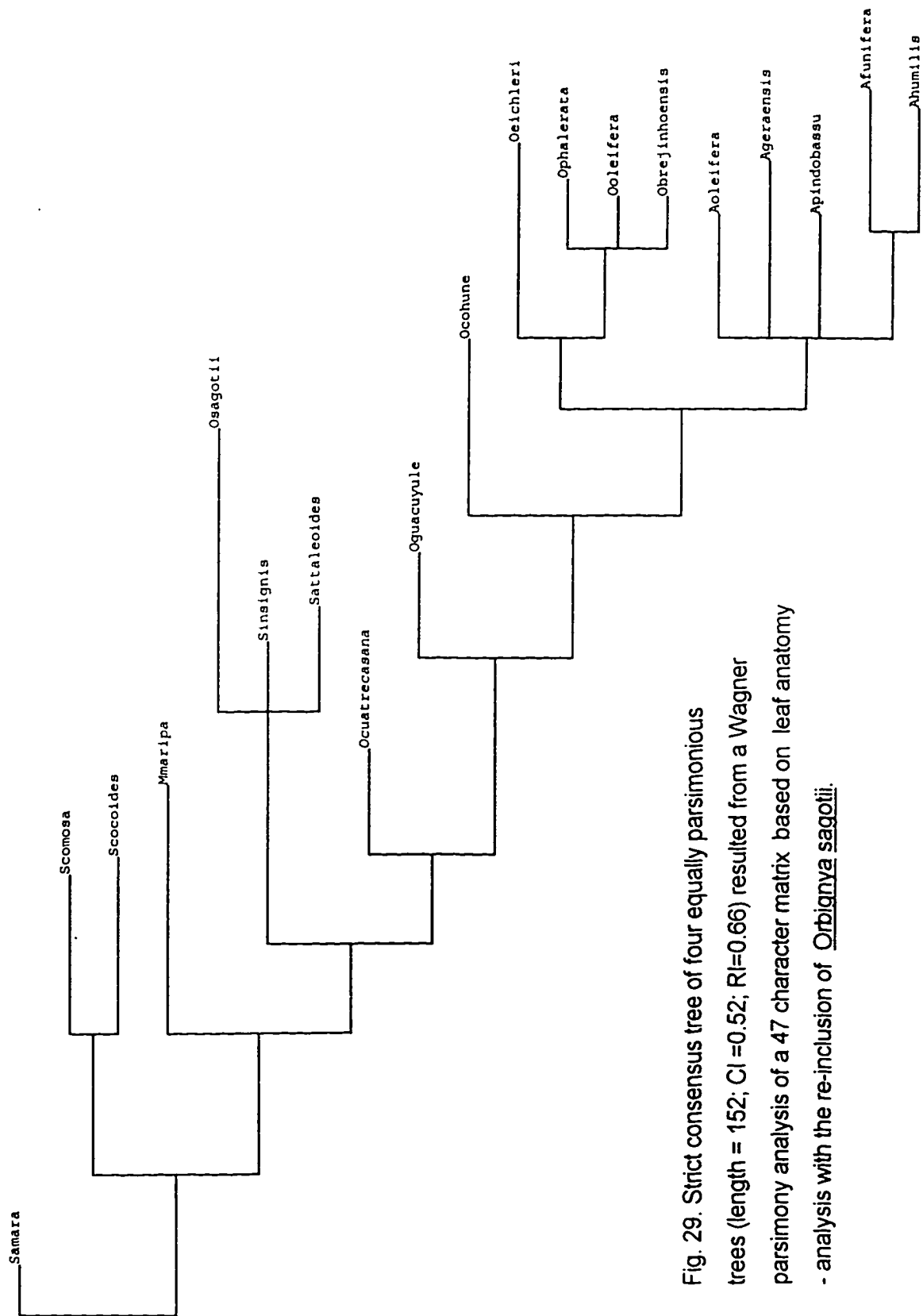


Fig. 29. Strict consensus tree of four equally parsimonious trees (length = 152; CI = 0.52; RI = 0.66) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of *Orbignya sagotii*.

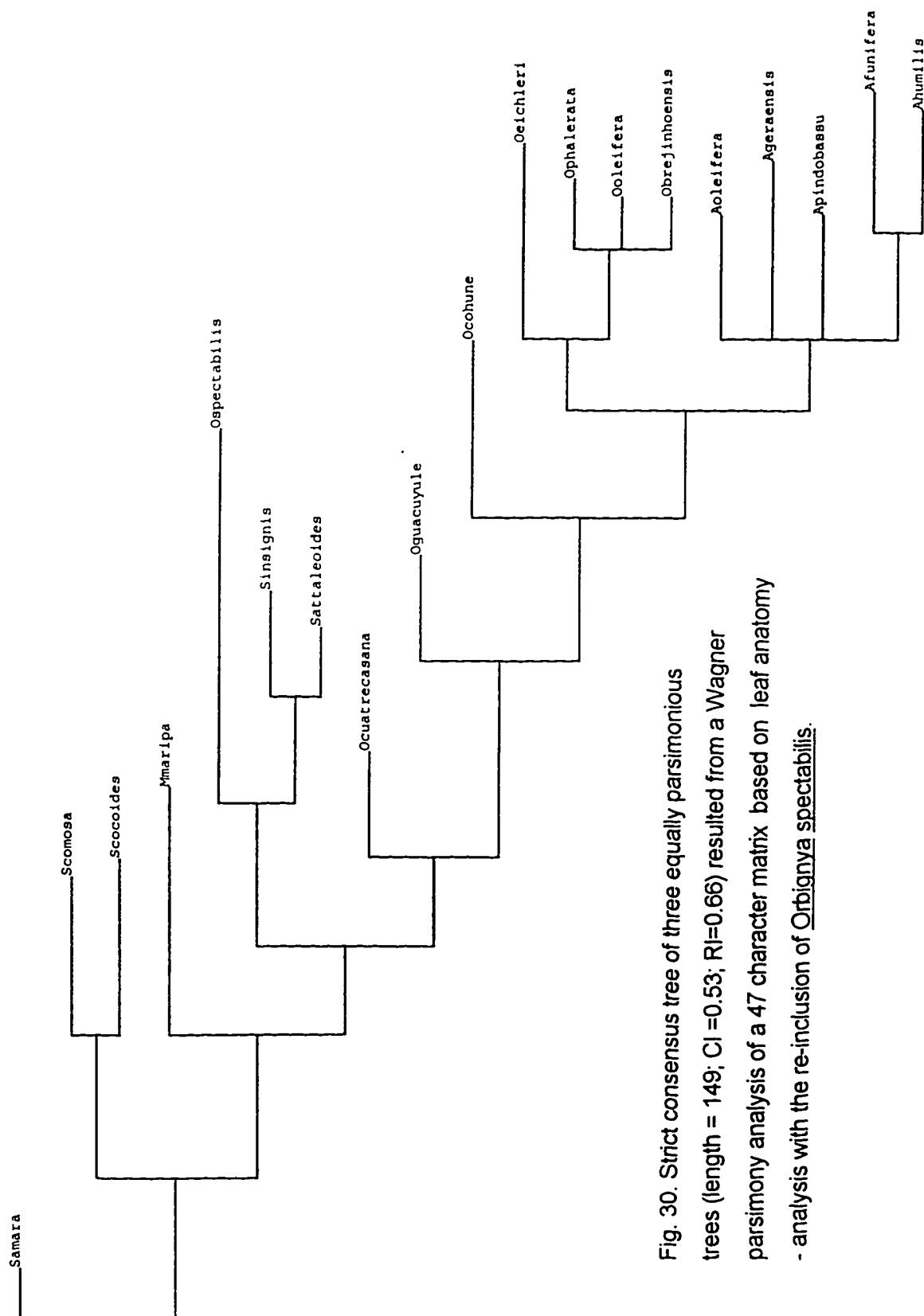


Fig. 30. Strict consensus tree of three equally parsimonious trees (length = 149; CI = 0.53; RI = 0.66) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of *Orbignya spectabilis*.

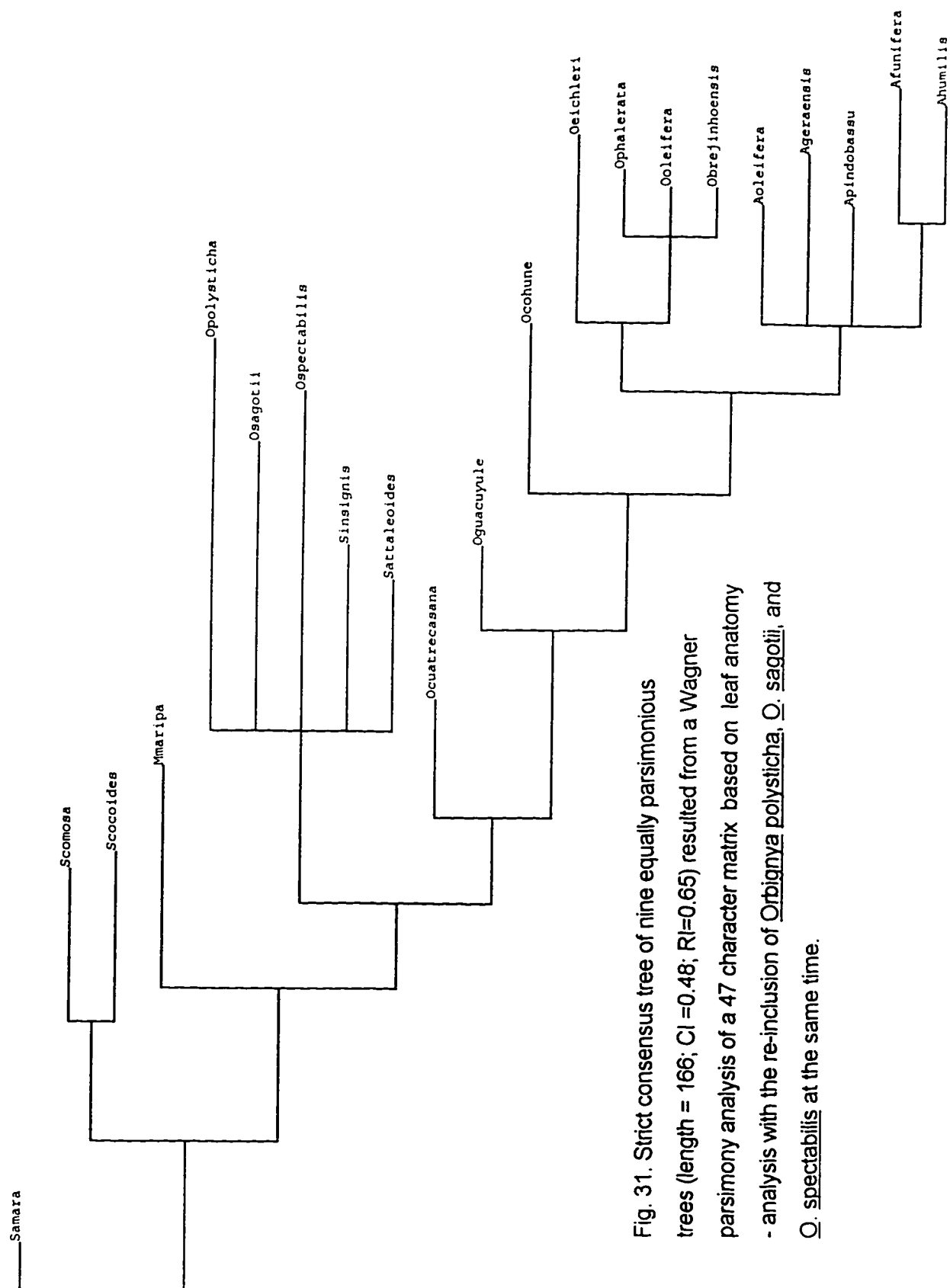


Fig. 31. Strict consensus tree of nine equally parsimonious trees (length = 166; CI = 0.48; RI = 0.65) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with the re-inclusion of *Orbignya polysticha*, *O. sagotii*, and *O. spectabilis* at the same time.

A final analysis re-included O. crassipatha, A. colenda, A. dubia, A. x piassabossu, O. luetzelburgii, and A. nucifera, which did not produce any major changes in the topology of the original tree. Only one tree of 179 steps (CI= 0.46; RI=0.65) was obtained after 1000 replications performed by *Nona*. The tree is shown in Figure 32 and its topology is basically the same (although 33 steps longer) as the strict consensus obtained without these species included (shown in Figure 15). Syagrus amara is separated from the other species of Syagrus and from the rest of the Attaleinae in the first dichotomy. Syagrus comosa and S. cocoides formed a clade of their own, as sister species in to each other, in the second dichotomy, where they are separated from the Attaleinae. Maximiliana maripa is separated in the third dichotomy, as a sister species to the rest of the subtribe. Scheelea insignis and S. attaleoides continued separated in the fourth dichotomy, but now forming a trichotomy with A. nucifera. Orbignya cuatrecasana is a sister species to O. guacuyule, O. luetzelburgii, O. cohune, and to all species of Orbignya and Attalea grouped into two inner clades. The composition of these clades is basically the same obtained before, except that A. dubia resolved with A. pindobassu, and A. colenda with A. geraensis; O. crassipatha is the sister species to A. humilis, A. funifera, and A. piassabossu; the latter two again formed the crown clade, sister species to each other.

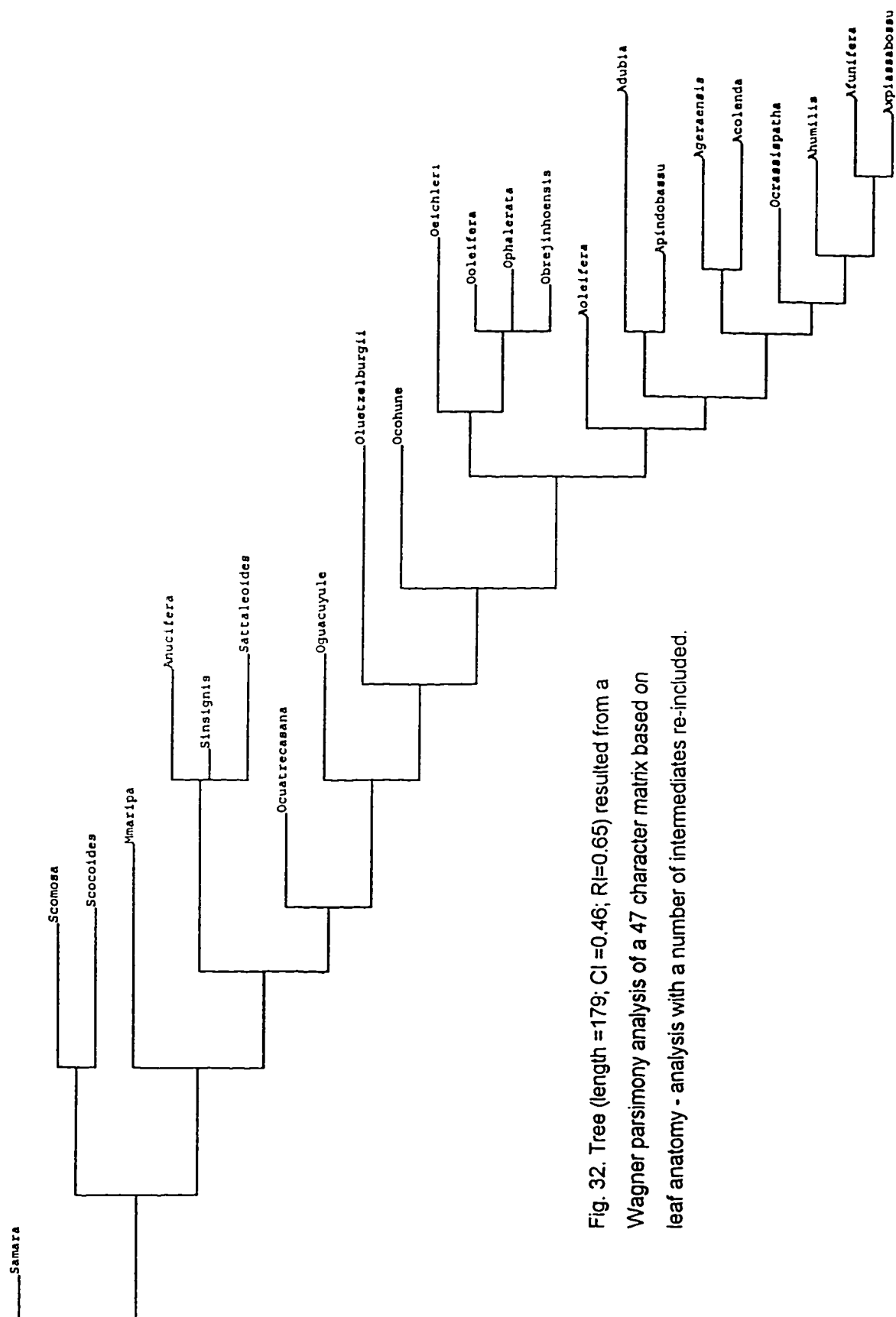


Fig. 32. Tree (length = 179; CI = 0.46; RI = 0.65) resulted from a Wagner parsimony analysis of a 47 character matrix based on leaf anatomy - analysis with a number of intermediates re-included.

4. Discussion

PCA and Cluster Analyses

The analysis including all taxa produced very similar results from both ordination and classification methods. In the PCA, where the patterns resulting from a character by character comparison over all taxa were the goal, correlation among characters was significant enough for groups to be delineated within the sample, as long as a number of specimens were excluded. In the cluster analysis, where the search was directed to more of a taxon by taxon comparison over all characters, the groups were confirmed.

Generic delimitation has been achieved using multivariate methods. Prance et al. (1969) using both PCA and cluster analysis, obtained taxonomically useful results to delimit the genera of the Hirtelleae, in the Chrysobalanaceae. Rogstad (1989) used PCA combined with other multivariate methods to support the delimitation of six species in the Polyalthia hypoleuca complex (Annonaceae). Crisp and Weston (1993) found both ordination and classification methods very useful in a study of morphological variation of Australian waratahs (Telopea, Proteaceae). Olivieri and Jain (1977) used the PCA to study hybridization in the Helianthus exilis-bolandieri complex (Asteraceae). Hassal (1976) used cluster analysis as evidence for generic

delimitation in Australian Euphorbieae. Introgression in Juniperus was studied by Flake et al. (1978) with the help of cluster analysis. Examples of the application of numerical methods for solving taxonomic problems are numerous, and demonstrate well the usefulness of the numerical approaches to taxonomy at both the generic and specific levels.

The clusters recognized here are differentiated by the possession of the greatest number of shared features, i.e. they are polythetic. None of these features are individually either necessary or sufficient to define the group, i.e. lack of any feature by a taxon does not exclude it from the group, although the majority of the most characteristic features were always present in the members of each group.

The double-layered hypodermis in the Brazilian Orbignya is a feature unique to that group, and absent in the non-Brazilian Orbignya. However, a few other character states common only to Orbignya (e.g., no buttresses in secondary and tertiary veins) link the two groups. The presence of O. cohune, O. guacuyule and O. cuatrecasana being close to Scheelea and Maximiliana, is therefore, surprising. It probably resulted from there being a great amount of variation in these species, especially the latter two. These species are, indeed, the least homogeneous group formed as a result of the analyses without the presence of the putative hybrids/intermediates. Except for O. cohune, which follows most of the Orbignya

patterns, the other two species showed noticeable variation in many character states.

Orbignya cuatrecasana is a distinctive species that still follows many of the characteristic patterns of the Orbignya group, such as short transverse veins, arrangement and size of fiber groups, and shape of secondary and tertiary veins. Based on these and other characters, its placement in Orbignya seemed to be reasonable; moreover, this is the group where it has traditionally been placed. It is indeed a strange species, however, which in certain regards resembles either Orbignya or Scheelea, and in others, does not resemble either of them. Orbignya cohune was the surprise in these results when clustering in the Scheelea group. Orbignya guacuyule (clustered with O. cohune) appeared to be the force driving O. cohune to the Scheelea group, mainly because of mesophylls features (i.e. well differentiated, with thick-walled cells), which resembled the Scheelea patterns. To test that, the specimen of O. guacuyule was excluded from the data matrix and the analysis rerun. As the result, O. cohune jumped up to the Attalea group and clustered with O. eichleri closer to the Brazilian-Orbignya.

Excluding the heterogeneity of the non-Brazilian species Orbignya, all other groups proved to be mostly homogeneous in terms of their membership. Given these results, it becomes imperative to re-visit the generic controversy in the Attaleinae. Although the groupings of taxa derived from the two multivariate methods

applied to the data are clear, and it mostly coincide with the traditional circumscription of the genera in the subtribe, resolution of this matter is still not easy. In numerical taxonomy, once phenotypic clusters are circumscribed, the application of taxon status is not yet straightforward, since no universally recognized criteria for that are available (Crisp and Weston, 1993). Davis and Heywood (1963) have applied the geographic-morphological method, but it is criticized for still not giving a clear criterion for determining rank because closely related allopatric taxa can be treated as species (Crisp and Weston, 1993). In the case of the Attaleinae, the problem goes beyond the ranking of the clusters found. The grouping derived from correlation of characters and taxa, which coincides with the circumscription of the old genera, seems to be unquestionable. The uncertainty that remains is whether "genus" is the taxonomic rank to be applied to the groups. Clear clusterings could be achieved only by excluding a number of specimens from both PCA and cluster analysis. These specimens revealed complex character variation, and the presence of any of them in any of the analyses performed was strong enough to cause the grouping patterns to collapse. Without them, the grouping results were very clear, and their suggestion as genera a natural choice. With them the variation is much more complex and grouping becomes difficult.

Phylogeny

Correlation of the evolutionary process in the subtribe *Attaleinae* with morphologically based patterns alone, considering the morphological information available, would probably prove to be as confusing as has been the application of the traditional taxonomic approach to this group. An attempt to combine morphological and anatomical data was frustrating and was given up, given the conditions under which data had to be collected. Incomplete collections with very restricted, sometimes non-existent, information for many characters provided unsatisfactory and/or unreliable results. The use of the existing descriptions of the species in the subtribe can be even more confusing, as they are often based on incomplete collections. To add to this, a great amount of subjectivity is involved in the way characters are interpreted and reported. In this group, it was established early that the distinction between species and genus (especially the latter) had to be based on a small number of features, and that became the rule to be followed. No other characters have ever been searched and used.

A cladistic analysis of the *Attaleinae* using morphological characters alone would be difficult to do. The anatomical approach used here seems more reliable, since data were collected from a large representative sample of the group, and much of the variation among and within groups could be gathered by using three specimens

from different geographic areas. The methodology used for gathering the data was applied uniformly to the sample, and the procedures followed to reduce subjectivity in the treatment of the data. This assured a mostly clean data set for the analyses performed.

Anatomical data have been used in the taxonomic treatment of palms, as discussed earlier in this document; a phylogenetic study, using only anatomical data, however, has no known precedent. Phylogenetic studies on palms are few. Dransfield and Ferguson (1990) studied patterns of variation and evolution in the coryphoid palms. Uhl and Dransfield (1995) included representatives of all tribes to study the phylogenetic relationships in the family using morphological, anatomical and chloroplast DNA restriction site variation. Although all tribes were represented in this study of 67 taxa, sampling at subtribal and generic levels was incomplete, and no member of the Attaleinae was included. The representatives of the subtribe Butiinae were Butia and Allagoptera; no Syagrus (the outgroup in the Attaleinae study) species was included in that analysis. The absence of Attaleinae members in one of the few phylogenetic studies in palms drastically restricts the comparison of the findings in this study with others.

The results confirmed the monophyletic status of the subtribe. The strength of the anatomical characters supporting the monophyly of the group was further tested by the increase in the number of outgroups. A greater proximity of at least one of the

outgroup taxa (S. cocoides) to the Attaleinae members reduced to seven the number of synapomorphies supporting the monophyly of the subtribe, in the three-outgroup analysis: 1) the presence of a thin abaxial epidermis; 2) round adaxial hypodermal cells; 3) abaxial groups of non-vascular fibers located between the hypodermis and epidermis; 4) secondary and tertiary veins formed by large thin-walled fibers; 5) long transverse veins; 6) sunken stomates; 7) clavate stomates. These are exactly the same character states that support the monophyly of the group in the one-outgroup-no-hybrid analysis, and in the final analysis with part of the intermediates re-included. Five character states lost their synapomorphy status with the inclusion of the other two outgroups.

In both analyses (one and three outgroups-no hybrids/intermediates), the topology was the same and the statistics for the two strict consensus trees were very close (Figures 13 and 15). In the final analysis, which re-included a number of the intermediates excluded in the previous analyses the topology was the same. In all three analyses, three major clades are indicated. Maximiliana maripa is resolved as a lineage separated from the groups; it is the sister species for the rest of the subtribe. The separation is supported by four character states present in the rest of Attaleinae, but not in M. maripa: 1) thin abaxial epidermis; 2) round primary veins; 3) primary veins located closer to the abaxial surface; 4) absence of bumps formed by the primary veins. Scheelea species are resolved as a second group, sister to the third line that encompasses O. cuatrecasana, O. guacuyule, O. cohune and the

remaining species of Orbignya and Attalea, which form two inner clades. With the intermediates re-included, O. luetzelburgii joined this group, as the sister species to O. cohune and the Orbignya-Attalea clades. The separation of O. luetzelburgii was, however, weakly supported by one synapomorphy, the presence of slightly sunken stomates in the group (O. luetzelburgii is superficial, or pseudo-sunken, according to the definition adopted in this study). The separation is, anyway, weakly supported, and it joins the Attalea clade if that character state is not considered.

The position of O. cuatrecasana in these analyses was somehow ambiguous. It was a species that, as pointed out before, regarding some characters, was closer to Scheelea, in others to Orbignya, but in many features it did not resemble either of them. This anatomical ambiguity was clearly reflected in the position occupied by that species on the cladograms derived from the different analyses performed.

Orbignya cuatrecasana was maintained as a member of the major Orbignya-Attalea, because its alternative presence in the Scheelea group, in some trees examined in several analyses, was also weakly supported. It clearly belongs to a separate lineage within the Orbignya-Attalea group: the only Orbignya in northwestern South America.

Another separate lineage within Orbignya is represented by O. cohune (and O. quacuyule). This species seems to have evolved in Central America, later reaching northwestern South America. On speculative grounds it may even be the line from

which O. cuatrecasana and the Brazilian species of Orbignya evolved. The separation of O. cuatrecasana from the rest of the Orbignya-Attalea group is very well supported: five synapomorphies (three, with the intermediates re-included) strengthen the suggestion that this species belongs to a separate evolutionary line. The presence of O. cohune (and O. guacuyule) within the Orbignya-Attalea group is better supported, and their separation could only be determined on the basis of homoplasies.

The Orbignya-Attalea group (excluding O. cuatrecasana) formed the best supported clade. Five synapomorphic character states separate the group, as follows: 1) spindle-shaped costal cells (5/1); 2) position of primary veins (30/2); 3) type of fibers in primary veins (31/3); 4) the presence of a mid-secondary vein (32/1), which is mostly characteristic of the Brazilian-Orbignya group; 5) midrib fibers located only on its upper portion (39). With the re-inclusion of the intermediates the number of synapomorphies is reduced to three (5/1; 30/2; 32/1).

The best defined lineage remained the Brazilian-Orbignya species, forming a clade with O. eichleri as a sister species to O. phalerata, O. oleifera, and O. breijinhoensis. Orbignya eichleri is separated from the rest of the Orbignya by its ovately shaped primary veins. The three species of Orbignya (O. phalerata, O. oleifera, and O. breijinhoensis) remained together (but unresolved) on the basis of their double-layered adaxial hypodermis, the two differently shaped types of cells,

the peculiar arrangement of fibers in between the two layers and, of course, the absence the buttresses. The characters in the Attalea clade are more weakly represented in terms of synapomorphic states. Attalea oleifera and A. pindobassu were joined by a homoplastic character state (infrequent present of tannins in the palisade mesophyll). Attalea funifera and A. humilis resolved forming a sister group, on the basis of arrangement of the groups of adaxial fibers, and location of these groups in relation to the adaxial hypodermis. The strong presence of tannins in the hypodermal cells, the replacement of some adaxial hypodermal cells by fibers, and the presence of hypodermal fibers all around the sclerotic sheath constitute synapomorphous autapomorphies in A. funifera. The Orbignya clade is separated from the Attalea group by only one synapomorphy: in Attalea the arrangement of abaxial fibers (when present) is irregular, as opposed to regular in Orbignya.

The re-inclusion of the intermediates produced slight changes in the Attalea clade (Figure 32). Attalea oleifera becomes the sister species to the rest of the clade; this separation is very weakly supported (one homoplasy). Attalea dubia resolved with A. pindobassu, forming a clade also supported only by homoplasies. These three species are separated within the Attalea clade because their adaxial fibers are not always located below the hypodermal layer (17/2). Attalea geraensis resolved with A. colenda, but this clade is also weakly supported. Orbignya crassispata and A. humilis did not resolve, and appear as the sister species to A. funifera and A. x

piassabossu, which still form the crown clade, supported by the presence of hypodermal fibers in the midrib, and replacing hypodermal cells as well (43/1; 44/1).

The Effects of Hybrids and Intermediates in the Cladistic Analysis

There are many aspects of hybridization and these can affect cladograms in various ways. Aspects involving hybrids, their role in the evolutionary process, and their treatment in phylogenetic analysis have been reviewed by some botanists (Stebbins, 1979; Bremer and Wanntorp, 1979; Wagner, 1969, 1983; Funk, 1981). Diploid hybridization can result in either hybrid speciation or the formation of hybrid swarms. In hybrid speciation, two of the species that hybridize can form an intermediate. Because this type of hybrid tends to be intermediate morphologically between its parents, it is said to have a predictable effect on the cladistic analysis (Funk, 1981). Additional complications by hybridization can include hybridization between hybrids, and more than two parent species can be involved. The expected effects of hybrids on cladograms, according to the literature cited above, can be described as follows:

- a. Hybrids between sister taxa will turn out as terminal trichotomies or, in the case of unbalanced character distributions, resolved with one or the other of the parents.

b. Hybrids of non-sister taxa can appear as unresolved basal taxa, as sister taxa to one of the parents, or fully or partially collapse the cladogram.

The most general suggestion about how to deal with hybrids in phylogenetic analysis has been *a priori* exclusion of them from the analysis and *a posteriori* inclusion on the cladogram (Wagner 1969, 1980; Funk, 1981). Nelson and Platnick (1980) suggested leaving the polytomies produced by the presence of hybrids in the cladogram because this display reflects the actual character information. However, plants often hybridize with non-sister taxa and the collapse of the cladogram is expected with their presence in the analysis (Funk, 1981). Individual inclusion of each putative hybrid in separate analyses performed produced a number of different effects on the cladogram.

The analyses including the putative hybrids/intermediates produced different results. The two analyses, with one and three outgroups, produced very similar patterns: 1) the topology is very similar; 2) the collapsing pattern is the same; 3) the species in each group are the same; 4) and the number of species in each group remained exactly the same as in the one-outgroup analysis: 12 in the Scheelea group; 19 in the Orbignya-Attalea group. The major difference is found in the length of each strict consensus tree produced (Figures 12 and 14). With one outgroup the consensus tree was 69 steps shorter, and a few clades were resolved, although some of them apparently did not make much sense. Maximiliana maripa joined S.

phalerata (also in the 3-outgroup tree) in a clade very weakly supported by homoplasious states only. An interesting result in both analyses was the clustering of O. polysticha, O. sagotii, and O. spectabilis, repeating previous results that have suggested the conspecificity of these three possible hybrids. Attalea funifera and A. x piassabossu remained the only well supported resolved clade in the entire cladograms of both analyses, as a result of the synapomorphies, already discussed, shown by these two species. The polymorphic states of some characters in the putative hybrids caused the collapse of even well-supported groups, such as the Brazilian-Orbignya species.

The monophyly of the subtribe was still well supported by four synapomorphic character states, when the two new outgroup-taxa were included (as opposed to eight in the one-outgroup analysis). Two of these characters (sunken and clavate trichomes) appeared in the first analysis at the basal node; the other three synapomorphies are the roundish groups of abaxial non-vascular fibers, located in between the hypodermis and epidermis, and the absence of bumps formed by primary veins on both surfaces of the lamina. The bumps formed on both surfaces of the lamina constitute a reversal in M. maripa and its hybrid M. dahlgreniana. The total number of synapomorphies for the Attaleinae was significantly different for the two analyses: with one outgroup the subtribe had 26 synapomorphies; with the three outgroups, this number was reduced to 19. These differences are even more significant when compared to the results obtained without the putative hybrids and

intermediates in the analyses: with one outgroup, 56 synapomorphies; with three outgroups 36 synapomorphies. These numbers indicate that putative hybrids and intermediates spread variation among characters and taxa, by possessing a high number of polymorphic character states.

Although the patterns may be mostly confusing and/or unresolved due to the extreme variation in character distribution brought about by the hybrids/intermediates, some of these patterns are indicative of the evolutionary lineage where they likely belong. Examination of some of the 108 trees of 232 steps retained by *Nona* after swapping in the hybrids/intermediates-in-three-outgroup analysis provided a better picture of the distribution of the species and a better evolutionary display of the groups in the middle of the apparent disarray produced by the possibly hybrid individuals. The tree is divided into two different clades: Orbignya-Attalea-related and Scheelea-related species. No synapomorphy supports the upper clade (Orbignya-Attalea); the lower clade (Scheelea), on the other hand, is distinguished by the long transverse veins characteristic of Scheelea and its related taxa. Although M. maripa has short transverse veins, it is placed inside the Scheelea-related clade because of its thin abaxial epidermis. Within the Orbignya-Attalea related group, the Brazilian-Orbignya taxa are grouped with their hybrids, x A. minarum (joined by the location of the adaxial fibers in between the two hypodermal layers), and with M. dahlgreniana (also on the basis of a hypodermal character state: the shape of cells). Attalea colenda and O. crassipatha join the

Attalea species. The relationships of individual hybrids/intermediates to their putative parents, species or groups and their effects on the cladograms are examined next.

Out of the sixteen putative hybrids/intermediates included singly in the data matrix, five produced the total collapse of the cladogram to the basal node: M. dahlgreniana, A. tessmannii, A. racemosa, S. phalerata, and S. butyracea. What these species may have in common (as putative hybrids) is the probability of being products of crossings between not closely related groups (non-sister groups), i.e., Maximiliana x Orbignya, Scheelea x Attalea, Scheelea x Orbignya, respectively for the first, second to fourth, and fifth putative hybrids. The major effect, therefore, was as expected. Partial collapse occurred within the clade where the putative parents were, i.e. x A. minarum (O. oleifera x A. oleifera) caused the collapse of the Orbignya and Attalea clades, producing a single polytomic clade; O. polysticha, O. sagotii, and O. spectabilis collapsed the Scheelea clade.

In the cases of hybridization between closely related groups (or sister-groups), this situation was observed: A. x piassabossu, A. colenda, O. crassispatha, and A. dubia resulted inconclusive. All these taxa were visibly closer to one of the possible parents (if hybrids), and that was reflected on the patterns that resulted from their inclusion in the analysis. Although the hypothesis of hybridity in these species cannot be supported by the results of the cladistic analysis, these do not eliminate

that possibility, since in cases of unbalanced character distribution, the putative hybrid may resolve with one of the parents.

A few cases deserve some separate considerations. Attalea nucifera formed a trichotomy with the two species of Scheelea, supported by one synapomorphy (31), large fibers of thin walls forming the inner sheath of primary veins). This species had to be labeled as doubtful in terms of its proper identification, since the great majority of anatomical patterns were those characteristics of the Scheelea group. It has been pointed out that it could either be a case of an incorrect identification of the specimens examined (both from the same area in Colombia), or even a case of a species mistakenly described in the wrong group. This doubt could not be morphologically clarified because the available collections are incomplete.

Orbignya luetzelburgii joined the evolutionary line of O. cuatrecasana, O. guacuyule, and O. cohune, as sister species to the rest of the Orbignya-Attalea clade. O. luetzelburgii is anatomically closer to Attalea than it is to any other group, and its separation from the group is based on just one synapomorphy (9): the fact that O. luetzelburgii has stomates with superficial guard-cells, as opposed to Orbignya and Attalea, more commonly with sunken and slightly sunken stomates, respectively. This weakly supported separation suggests that given the greater proximity to Attalea, this species could have resolved in that group. A strict consensus tree a few steps longer (3-6) was the major effect produced by its re-

inclusion in the analysis. The hypothesis of the hybridity of O. luetzelburgii was not supported by the results of the analyses.

Confirming the consistent pattern of similarities between O. polysticha, O. sagotii, and O. spectabilis they resulted in the same position in the cladogram either separately, or when included in the analysis as a group. A maximum of 4 trees were produced by these species, of approximately the same length. They always ended up in a clade with Scheelea: O. polysticha and O. spectabilis as the sister species to S. insignis and S. attaleoides. Orbignya sagotii on the other hand, disrupts the clade, forming a trichotomy. These species joined Scheelea mostly on the basis of their polymorphic states for characters such as round abaxial hypodermal cells, arrangement of adaxial fibers mostly in rows, abaxial fiber groups located in between hypodermal cells, and thick-walled palisade cells. This can be concluded as the case of hybrids between not closely related groups, in which distribution of characters is unbalanced. The similarity of evolutionary patterns reinforces the idea of the conspecificity in these taxa, and the suggestion of their being part of the same hybrid complex.

The large number of putative hybrids and specimens with conflicting patterns in this study restrained the possibility of a single viable hypothesis for their origin and for the patterns of character distribution shown by each of them, or each group. That could actually be easy if the hybrids followed the most general idea about them: that

they are intermediates between the parents. Intermediacy in hybridization, however, is not a rule that can be safely followed: 1) these individuals or even entire populations of them may inherit unique or derived characters from both parents (e.g., A. x piassabossu, if actually a hybrid shares at least 2 synapomorphies with A. funifera); 2) they may also undergo high intrapopulational segregation (difficult to determine in this sample since for the purpose of this study they were selected, supposedly, from different populations) and even produce abnormal characters (e.g. O. luetzelburgii, and its unique layer of hypodermal fibers, and a remarkable presence of cells inclusions); or 3) they may show nothing but conflict in character distribution (perhaps be the cases with regard to O. polysticha, O. sagotii, and O. spectabilis and others) when compared to the parents (Sanders, 1981; Humphries, 1983). Analysis of the data through different approaches, which focused on both character and taxa variation and their relationships, led to the conclusion that all possibilities discussed above can be considered for the sample studied. The complex character distribution among the putative hybrids and intermediates, plus a high number of polymorphic states for many characters, produced, at first, a huge polytomy, with the complete collapse of the cladogram to the basal node (supposedly to the node with the most recent ancestor for all species in the group). It was interesting, on the other hand, to see that in several cases the effect of including only one of these individuals was as devastating as that produced by the inclusion of all them.

Stebbins (1969) defined ways by which hybridization can stimulate evolutionary change: 1) increase in the size of the gene pool, by genetic recombination which takes place in fertile or semifertile progeny of hybrids; 2) increase in the frequency of morphological variants outside the normal range of the parental populations; 3) strengthening of the action of genes with a low degree of penetrance in the parental populations; 4) increase in the rates of mutation in the progeny of hybrids. Once they are able to overcome the barriers of segregation, genetic instability, and sterility, hybrids can play a very important role as catalysts of evolution. This role is considerably aided by favorable selective forces, such as the opening of new habitats, which allied to some degree of isolation from the parental populations, may change the course of natural selection and aid the hybrids in evolving in new directions (Anderson, 1948). Speciation, in these conditions, may only require cycles of hybridization and isolation, by which the gene pool is first enriched by hybridization (between adaptively different populations), followed by isolation of those stable derivatives originated in the hybrid swarms (Stebbins, 1969). These hybrid derivatives, once they become established, can give rise to more strongly isolated populations through continued genetic change and divergent evolution (Stebbins, 1969; Grant, 1981).

The above describes a scenario that could likely be related to the evolutionary events in the Attaleinae. The high number of mixed and/or conflicting anatomical patterns found in this study, allied to the great morphological plasticity consistently reported, and the distributional patterns of the members of the subtribe suggests

that hybridization may have played an important role in the evolutionary history of this group.

The Major Lineages

Maximiliana maripa is the most widespread species in the subtribe, occurring over an extensive area throughout northern and northwestern South America. As pointed out before, it is also a species that apparently does not hybridize often (only the case of M. dahlgreniana could be detected), although its range of distribution overlaps with those of Scheelea and Orbignya, as well as with that of the non-Brazilian Attalea (A. nucifera, and A. racemosa). Maximiliana maripa and the Brazilian Attalea are apparently allopatric, and it is uncertain whether that species has had any contact with O. cohune populations. Considering its extensive distributional range, the fact that it apparently only hybridizes with one group, and the results obtained as well, it could be suggested that Maximiliana, along with Scheelea, comprise the two major evolutionary lineages in the group that led the lineages of non-Brazilian South American members of the Attaleinae. These different evolutionary lineages may have followed different directions, raising the reproductive barrier that apparently exists between them. Scheelea seems to be the second most important lineage of the non-Brazilian South American Attaleinae, spread from west to north in South America, especially in the Amazon region.

Orbignya cohune probably represents another evolutionary lineage that probably arose in Central America and extended its range up to northern and northwestern South America. Its influence on evolutionary events within the group has been established by the detected crossings with Scheelea. It is not unlikely that the group of Orbignya distributed in northern and northwestern South America (the “messy” group formed by O. polysticha, O. sagotti, O. spectabilis, and possibly, O. luetzelburgii) could have had O. cohune as the Orbignya member of the complex, instead of one of the Brazilian species.

The Brazilian Orbignya and Attalea may comprise the same evolutionary line, considering the results of the phylogenetic analysis, and their remarkable resemblance both anatomical and morphological. The non-Brazilian Attalea did not show the same patterns as the Brazilian species, and in this study ended up as intermediate (A. racemosa) or doubtful regarding their proper identity (A. nucifera). The Brazilian Attalea seems to be the most allopatric of the groups in the subtribe; its only contact is apparently with the Brazilian species of Orbignya. The proposed anatomical phylogeny seems congruent with a possible evolutionary model justified by both morphological and distributional patterns.

Leaf Anatomy and Palm Taxonomy

Tomlinson (1961) stated that the major goal of systematic anatomy "is not to derive a classification of plants from their anatomical structure but to indicate in what way existing classification, based on traditional exomorphic vegetative and floral features, is supported by internal microscopic structures." Concurrence of opinion on the part of the taxonomist and the anatomist is achieved by the agreement of the evidence; a re-investigation of the problem by the taxonomist is suggested when the results do not agree. In this particular case, the results apparently do not agree, if the group of specific entities taken as a representative sample of the subtribe *Attaleinae* are to be seen as a major uniform unit, separated only by differences at the species level. The data gathered in this study showed that this uniformity does not exist at the level of subtribe; the pattern of variation is discontinuous and groups anatomically similar are formed, on the basis of several characters. Whether these anatomical groups are to be taken as genera or subgenera is the subject of further discussion.

The phenetic groups and the evolutionary lineages (which are basically the same) derived from the analysis of the data were defined mostly on a number of characters, which include: 1) number of hypodermal layers and shape of cells; 2) fiber groups, their shape, position and size; 3) differentiation of palisade and spongy

mesophylls; 4) primary veins, their shape, size, position and type of fibers forming their inner sheaths; 5) secondary and tertiary veins, especially their position in relation to the abaxial hypodermal layer, and the extension of their lower portions; 6) epidermal cells, both in cross section and surface view, in their arrangement, shape and type of walls; 7) stomates, the position of guard-cells in relation to the leaf surface; 8) venation, especially the patterns derived from the size of the transverse veins.

Some of them would automatically be considered plastic from a general point of view, and as such they were considered in this study, until proven consistent throughout the sample. One of the methodological concerns in this study was always to have replications of the species used, collected from different geographic areas, growing under different environmental conditions. That was to assure that the characters used did not alter as the environment changed, minimizing the use of such plastic features as much as reasonably possible. Some of these characters have traditionally been seen as plastic, associated with factors such as moisture and shading in the habitats where the plants grow. Some of the findings in this study, however, show that some of these associations cannot be taken as a general rule, and that some “plastic” characters can be as stable as those considered non-plastic, within the same group.

Stomates, and the position of their guard-cells in relation to the leaf can illustrate a case of these “plastic” characters. The number of stomates per leaf area unit was clearly related to habitat conditions (as much as environmental information could be gathered from the collecting labels of the specimens used). Their number was clearly lower in those specimens growing in drier conditions, but the position of these stomates in relation to the leaf surface (i.e., sunken or superficial) was quite stable within the same anatomical group, throughout their geographical range. Borchsenius and Bernal (1996) associated superficial stomates in Aiphanes with the height of the species (short, growing in forest understory) and habitat. It was suggested that superficial stomates are related to the need for increasing transpiration in such conditions; conversely, the species growing in open areas have sunken stomates. The results of my study do not agree with that. Depth of stomates was consistent in both tall and short species of Brazilian Orbignya (e.g., O. eichleri), throughout their range of distribution and in a variety of habitats. Scheelea species have superficial stomates no matter where they grow and the height of the palms (e.g., S. insignis, acaulescent vs. S. attaleoides, arborescent). Maximiliana always has superficial stomates, and it is a tall palm species, and all specimens examined in this study were collected in open, dry areas. Attalea always has slightly sunken stomates (except for a single species, A. funifera). Sunken stomates have always been considered a xeromorphic feature, but in this group, these assumptions do not hold. Barfod (1988) noted that some phytelephantoid species, which showed many “xeromorphic” anatomical features, do not grow in dry habitats, while others that

grow in areas subject to seasonal drought are not distinctly xeromophic. As Rudall (1987) suggested, the physiological bases for adaptive features in leaves are often assumed rather than proven. Special attention should be paid to the thickness of the cuticle in the examination of the position of stomates in relation to the leaf surface, when defining whether they are sunken or superficial. There are cases in which the stomates are apparently sunken because of a thick cuticle, but the guard-cells are at the same level as the normal adjacent epidermal cells. Stomate depth in this case, is being determined by the cuticle, not the actual position of the guard-cells in relation to the epidermal cells, and they should more accurately be classified as a pseudo-sunken (Figure 33A).

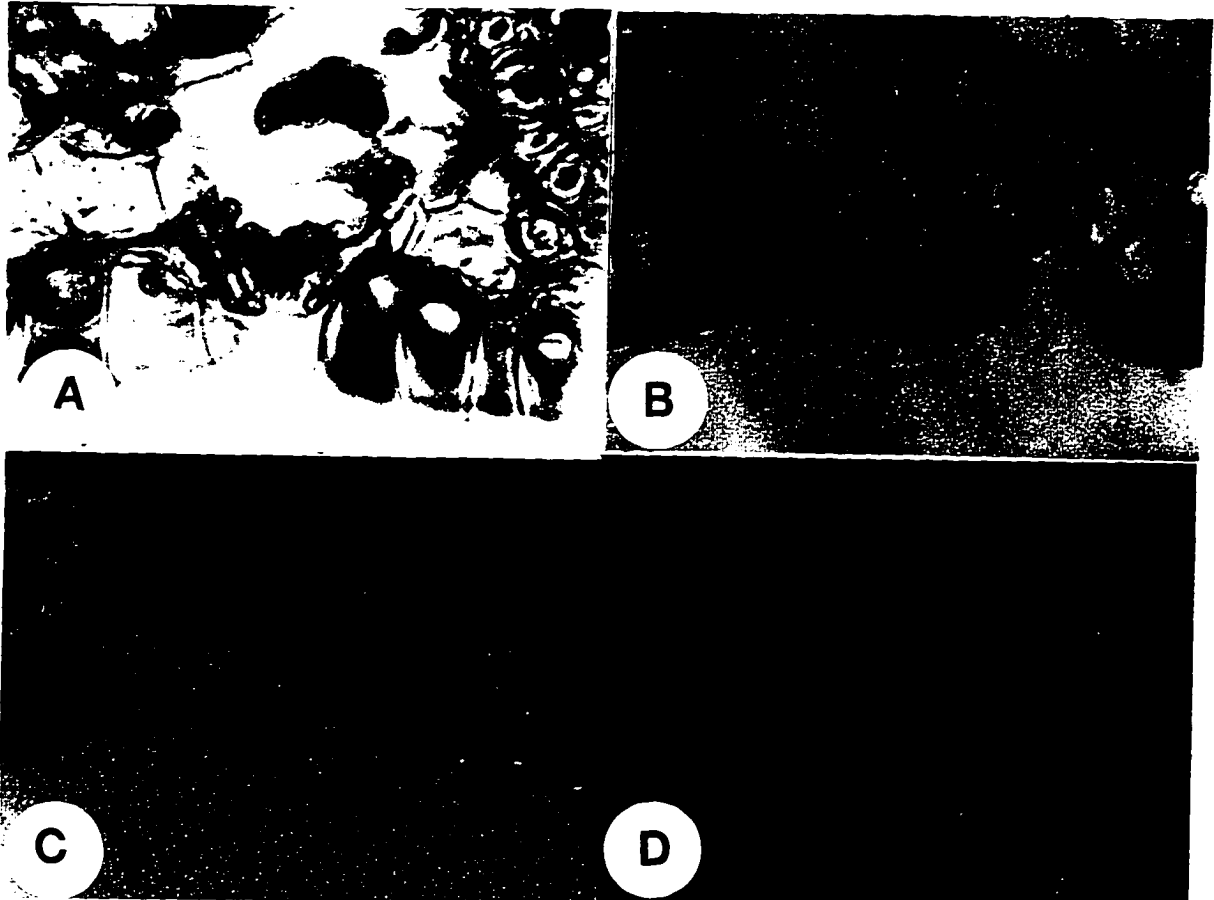
The definitions of sunken and slightly sunken stomates used in this study are based on the position of the guard-cells and the upper ends of the inner pair of lateral subsidiary cells in relation to the surrounding regular epidermal cells. Slightly sunken stomates are defined here as those cases in which the upper ends of the inner pair of subsidiary lateral subsidiary cells is at the same level or slightly below the normal epidermal cells (guard-cells in this case are also slightly below the normal epidermal cells). They are considered sunken when the upper ends of the inner pair of lateral subsidiary cells and guard-cells are below the normal epidermal cells (Figure 33B). Superficial stomates have lateral subsidiary cells and guard-cells usually above the normal epidermal cells (Figure 33C-D).

The hypodermis has also been defined as a xeromorphic feature; the presence of a thick hypodermis would function as a barrier to high amounts of light reaching the photosynthetic tissues. Based on that, it would be expected that all arborescent species growing in dry, light-intense conditions, would have two or more layers of hypodermal cells. This is not the case, and the only group showing more than one hypodermal layer was the Brazilian Orbignya, consistently 2-layered throughout its distribution range, from northern to eastern Brazil. This may reflect conditions under which the group evolved. The balance of the tall palm species in the other groups were consistently one-layered (e.g. Scheelea butyracea, Orbignya crassispata). No changes in the number of hypodermal layers could be observed in species growing in the understory of forests or in open areas; they were consistently the same within each group. Tomlinson (1961) suggested that the number of hypodermal layers may vary in different parts of a single leaf, but it is always constant for each species at any standard level. Two-layered specimens were observed only in the Orbignya group itself, and when there were crossings between species in that group and any other 1-layered species in another group (e.g. x Attabignya minarum, a case of hybridization discussed later).

The leaf mesophyll has been considered a restricted character for taxonomic use since its appearance may change in plants of the same species growing under different levels of exposure to sunlight (Tomlinson, 1961). In this study, however, some features in the palisade and spongy mesophylls turned out to be very stable

and useful characters. The differentiation of the mesophyll (seen here as related to the thickness of the cell walls) could consistently be used as one of the diagnostic characters, as its pattern was stable within each of the anatomical groups. Even the number of layers in the palisade and spongy mesophylls did not show strong variation within groups, or among specimens of the same species, collected from different locations. Henderson (1990) used the number of palisade layers to separate closely related genera in the subtribe Iriarteinae, but variation in the palisade mesophyll has been observed in some palm genera, including: Geonoma (Wessels Boer, 1968); Phytelephas (Barfod, 1988); and Aiphanes (Borchsenius & Bernal, 1996). In the Attaleinae, I could not find a correlation between differentiation of the mesophyll and growth habit of the species or ecological conditions. The patterns were consistent in relation to differentiation and thickness of both palisade and spongy mesophylls within each group, and conspicuously different between groups. To be safe, mesophyll features were used with some reservation until they were proven consistent for a given pattern or group. The analyses performed and the three replications of each specimen used in the sample provided relative certainty in using the features selected.

Fig. 33. Stomates in cross section: A - pseudo-sunken; B-sunken; C-superficial;
D-superficial, surface view;.



Groups, Taxa and Anatomical Characters

The Brazilian Orbignya (excluding O. eichleri) constituted the most anatomically homogeneous group (Figures 34 & 35A-D), easily distinguished from any other group by the presence of two layers of adaxial hypodermal cells. Another distinctive character is the position of secondary and tertiary veins always above the hypodermis – not forming buttresses ((Figures 34A, 34E & 35A). These three species occur mostly in Brazil (although O. phalerata is in Bolivia as well as in Surinam), from North to East, throughout a variety of habitats.

Orbignya phalerata Martius and O. oleifera Burret, both of which occur in Brazil, are considered to be the two principal members of the babassu palm complex. The first of these is most widely distributed; it was described from Bolivia and it is currently considered to be the true babassu (Anderson et al., 1986; Anderson and Balick, 1988); the second occurs in small populations in the São Francisco River Basin in the Brazilian states of Minas Gerais and Bahia. Orbignya breijinhoensis Glassman sp. nov. was recently described (but not published) from Bahia, Brazil, east of the Rio São Francisco. These are, if not the same, very closely related species. Exomorphically, distinction among them is made on the basis of a small number of characters. Orbignya breijinhoensis is felt to differ from the others mainly by its much longer petiole, longer staminate rachillae, shorter pistillate portion of

androgynous rachilla, smaller fruits, and the longer persistent perianth in relation to size of the fruit (Glassman, unpublished). The features used for distinction of these species seem to be questionable, except perhaps for the length of the leaf petiole, which is undoubtedly longer in O. breijinhoensis, and the fruit perianth, which is noticeably persistent and longer.

Anatomically, distinction could be made only using some quantitative features (e.g., number of groups of fibers, number and size of primary, secondary and tertiary veins, size of midrib). Most of these quantitative features ended up statistically insignificant, except for the size of primary veins: O. oleifera and O. breijinhoensis have larger primary veins (means= 0.199 mm, and 0.176 mm, respectively) compared to O. phalerata (0.128 mm); the difference between O. oleifera and O. breijinhoensis was not statistically significant. Qualitative characters were consistently similar among the three species, and separation was not possible on the basis of these characters. The multivariate analysis confirmed the grouping of these species on the basis of their character correlation; their positions were unresolved in the phylogenetic analysis, and these results may suggest conspecificity.

Orbignya eichleri showed some differences in relation to the other Brazilian species (Figure 35E-F): 1) number of hypodermal layers (1 in O. eichleri vs. 2 in the other three species); 2) the position of fiber bundles, always in between epidermis

and hypodermis vs. mostly located in between the two hypodermal layers, never above them, in the other species; 3) abaxial fibers lacking vs. regularly occurring in O. phalerata, O. oleifera, and O. breijinhoensis; 4) primary veins somewhat ovate vs. round, and the inner sheath mostly formed by large fibers of thick walls vs. small fibers in the other species; 5) a mid-secondary vein not distinguishable vs. distinguishable, mid way in between two large veins; 6) buttresses formed by secondary and tertiary veins, common and large in O. eichleri vs. absent in the other species; and 7) midrib is square in O. eichleri vs. rectangular in O. phalerata, O. oleifera, and O. breijinhoensis. Tables 17 - 24 provide a selective comparison of anatomical characters for the Brazilian species of Orbignya. Figure 36 shows the distribution of the specimens of the Brazilian Orbignya used in this study. Orbignya eichleri clustered with the Attalea species in both PCA and cluster analysis; in the cladistic analysis, it resolved as the sister species of the other Brazilian Orbignya.

Table 17. Selective anatomical comparison of Orbignya phalerata, O. oleifera, O. breijinhoensis, and O. eichleri - Adaxial epidermis.

Group	Adaxial Cuticle (mm)	Epidermis - Size Cross Section View	Adaxial Epidermis Thickness	Adax.Epid. Cell Extension	Adaxial Epidermis - Cell Shape	Adaxial Epidermis - Cell Walls
<i>O. phalerata</i>	0.008	adaxial smaller than abaxial	thick	longitudinal oblique	rectangular rhombohedral	undulate linear
<i>O. oleifera</i>	0.008	adaxial smaller than abaxial	thick	oblique longitudinal	rhomboidal rectangular	linear slightly undulate(?)
<i>O. breijinhoensis</i>	0.006 - 0.010	adaxial smaller than abaxial	thick	oblique longitudinal	rhomboidal rectangular	linear slightly undulate(?)
<i>O. eichleri</i>	0.004 - 0.006	adaxial smaller than abaxial	thick	oblique longitudinal	rhomboidal rectangular	slightly undulate

Table 18. Selective anatomical comparison of Orbignya phalerata, O. oleifera, O. breijinhoensis, and O. eichleri - Abaxial epidermis.

Group	Abaxial Cuticle (mm)	Abaxial Epidermis Costal Cells - Orientation	Abaxial Epidermis Costal Cells Shape	Abaxial Epidermis Costal Cells - Walls	Abaxial Epidermis Intercostal Cells Walls	Stomates Guard-Cells	Stomates Arrangement
<i>O. phalerata</i>	0.008	longitudinal	spindle-shaped	linear	linear	sunken	not in def. files
<i>O. oleifera</i>	0.003 - 0.008	longitudinal	spindle-shaped	linear	linear	sunken	not in def. files
<i>O. breijinhoensis</i>	0.008 - 0.010	longitudinal	spindle-shaped	linear	linear	sunken	not in def. files
<i>O. eichleri</i>	0.004 - 0.007	longitudinal	spindle-shaped	linear	linear	sunken	not in def. files

Table 19. Selective anatomical comparison of Orbignya phalerata, O. oleifera, O. brejinhoensis, and O. eichleri - Hypodermis.

Groups	Adaxial Hypod. # layers	Adaxial Hypodermis Shape - Cells
<u>O. phalerata</u>	2	rectangular round
<u>O. oleifera</u>	2	rectangular round
<u>O. brejinhoensis</u>	2	rectangular round
<u>O. eichleri</u>	1	rectangular

Table 20. Selective anatomical comparison of Orbignya phalerata, O. oleifera, O. brejinhoensis, and O. eichleri - Non-vascular fibers.

Groups	Adaxial Fibers - Number of Groups(x)	Adaxial Fibers - Size of Groups	Adaxial Fibers - Lignin	Adaxial Fibers - Position	Abaxial Fibers - Distribution	Abaxial Fibers - Number of Groups	Abaxial Fibers - Size of Groups	Abaxial Fibers - Position
<u>O. phalerata</u>	260-375	8-10	non-lignified slightly lignified	in between hypodermal layers	regular	75-80	1-4	in between hypodermis & epidermis
<u>O. oleifera</u>	345-390	6-12	non-lignified slightly lignified	in between hypodermal layers	regular	110-187	1-4	in between hypodermis & epidermis
<u>O. brejinhoensis</u>	215-390	3-10	non-lignified slightly lignified	in between hypodermal layers	regular	65-95	2-4	in between hypodermis & epidermis
<u>O. eichleri</u>	110-170	5-8	non-lignified lignified	in between epidermis and hypodermis	no fibers	no fibers	no fibers	no fibers

Table 21. Selective anatomical comparison of Orbignya phalerata, O. oleifera, O. brejinhoensis, and O. eichleri - Chlorenchyma.

Group	Palisade Differentiation	Palisade Number of layers	Palisade Width(μ)	Spongy Differentiation	Spongy Number of layers	Spongy Width (μ)
<i>O. phalerata</i>	poorly differentiated	2	50 -60	poorly differentiated	5-7	80-100
<i>O. oleifera</i>	poorly differentiated	2	90-120	poorly differentiated	5-8	150-190
<i>O. brejinhoensis</i>	poorly differentiated	2	60-80	poorly differentiated	6-8	130-160
<i>O. eichleri</i>	poorly differentiated	2	60-70	poorly differentiated	5-6	80-100

Table 22. Selective anatomical comparison of Orbignya phalerata, O. oleifera, O. brejinhoensis, and O. eichleri - Venation.

Group	Prim. Veins Position	Prim. Veins Type of Fibers	Prim. Veins Shape	Mid-secondary Vein	Sec/Tert Veins Buttresses	Sec/Tert Veins Position	Sec/Tert. Inner Sheath	Transverse Vein - Pattern
<i>O. phalerata</i>	centered	small-thick walls	round	distinguishable	absent	above hypodermis	incomplete	short
<i>O. oleifera</i>	centered	small- thick walls	round	distinguishable	absent	above hypodermis	incomplete	short
<i>O. brejinhoensis</i>	centered	small-thick walls	round	distinguishable	absent	above hypodermis	incomplete	short
<i>O. eichleri</i>	centered	large-thick walls	ovate	not distinguishable	present	through hypodermis	incomplete	short

Table 23. Selective anatomical comparison of Orbignya phalerata, O. oleifera, O. brejinhoensis, and O. eichleri - Midrib.

Group	Midrib Cuticle (mm)	Midrib Shape	Midrib - Size (mm)	Midrib Number of VBs	Midrib Expansion Cells # layers	Midrib Expansion Cells - Confluence	Fibers Bundles on Midrib
<i>O. phalerata</i>	0.006 - 0.008	rectangular	2.20-2.72	18-20	3-4	confluent	upper portion only
<i>O. oleifera</i>	0.010 - 0.020	rectangular	2.70-3.10	18-20	3-5	confluent	upper portion only
<i>O. brejinhoensis</i>	0.010 - 0.014	rectangular	1.60-2.60	16-22	4-6	confluent	upper portion only
<i>O. eichleri</i>	0.004 - 0.006	square	0.64-0.84	4-12	3	confluent	upper portion only

Fig. 34. Cross sections, adaxial and abaxial epidermal peels, and clearings: A, B, C, D - Orbignya phalerata (OPH-02 & OPH-03); E, F, G, H - O. oleifera (OO-04, OO-05 & OO-06).

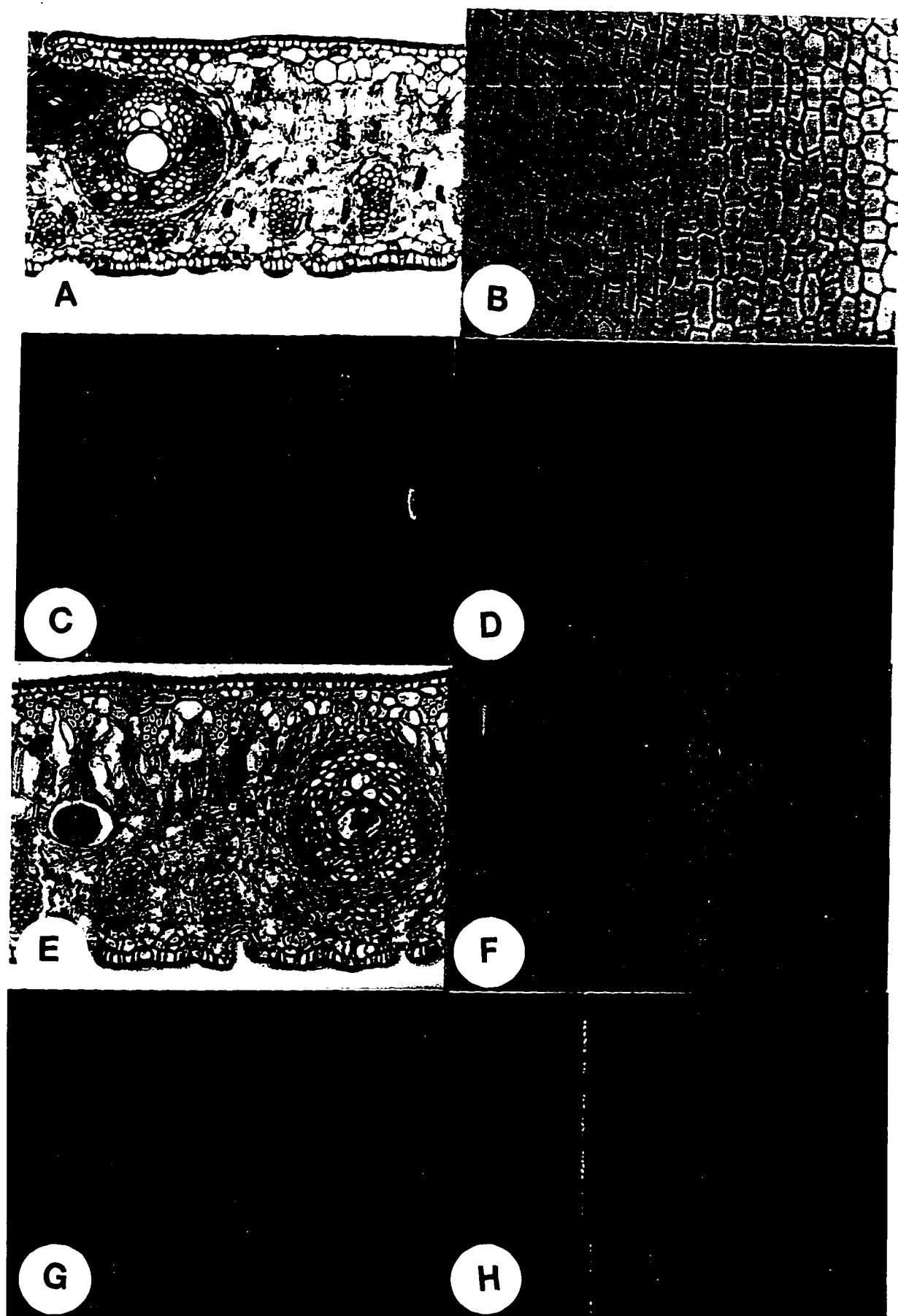


Fig. 35. Cross sections, adaxial and abaxial epidermal peels, and clearings: A, B, C, D - Orbignya brejinhoensis (OB-07 & OB-09); E, F, G, H - O. eichleri (OE-11 & OE-12).

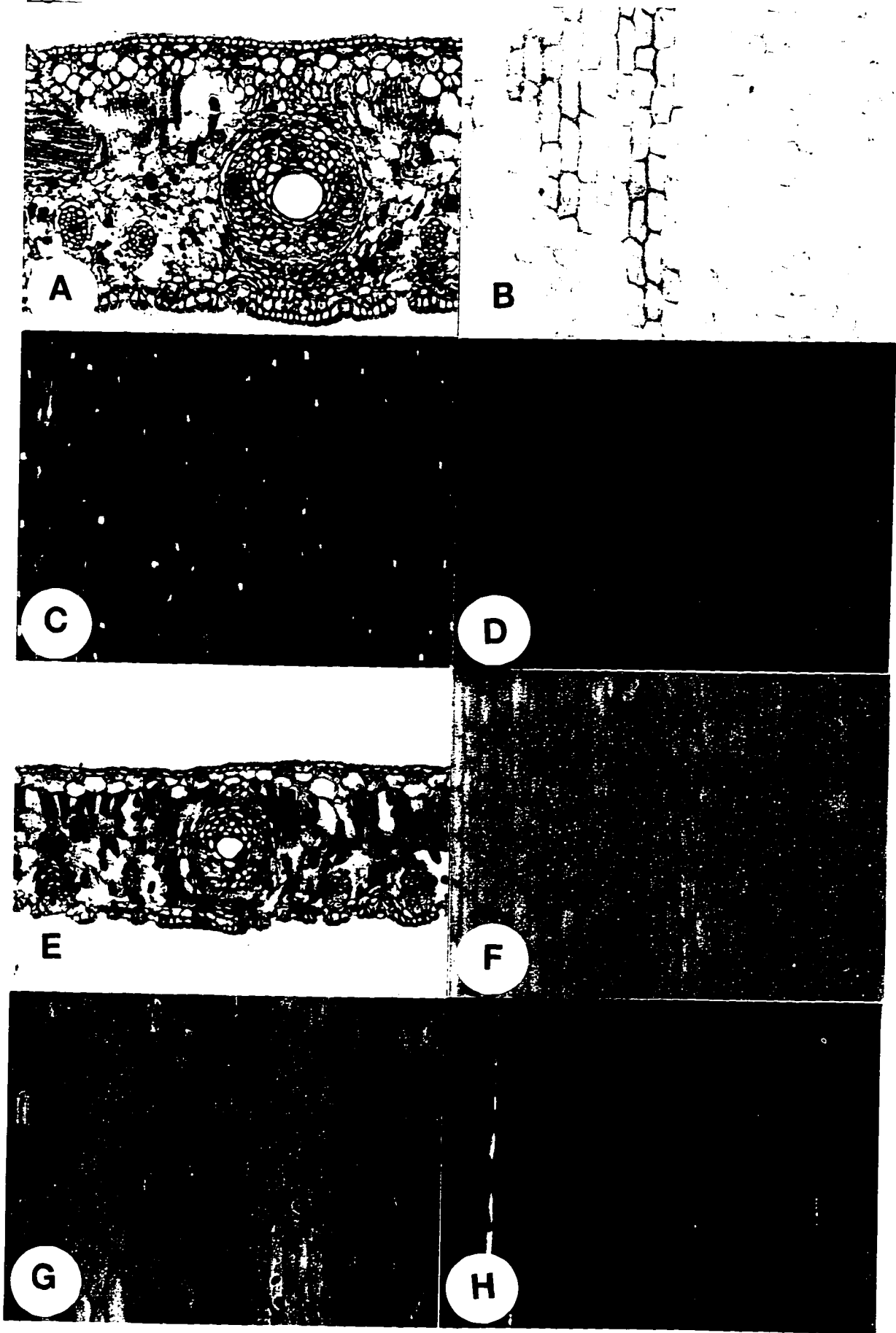
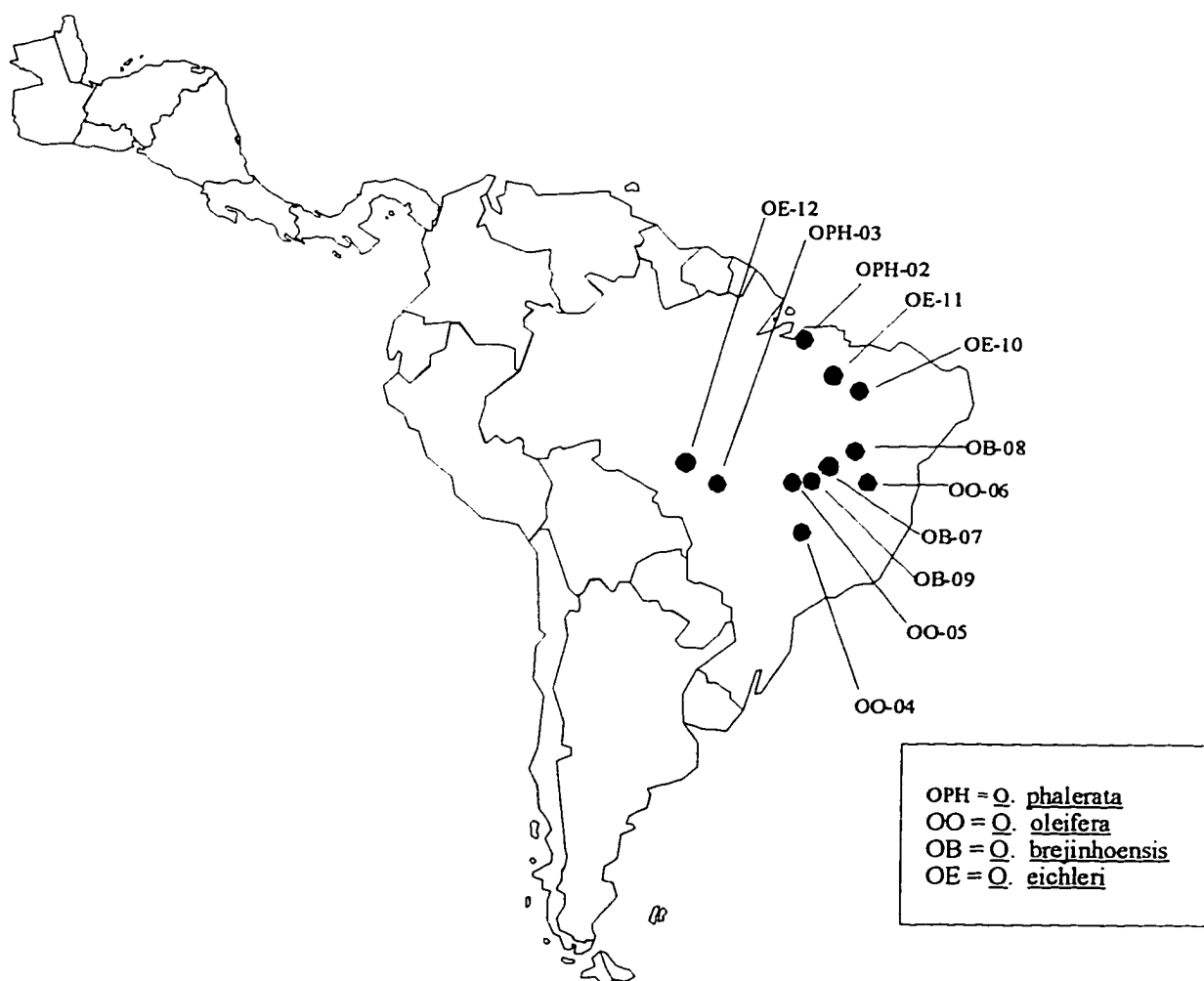


Fig. 36. Distribution of the Brazilian specimens of Orbignya studied.



In general, the “non-Brazilian Orbignya” completely lacked anatomical homogeneity, and mixed patterns characterized this group of species. Orbignya crassispatha could easily be included in the Attalea group, if a few features only common to Orbignya were not present. Orbignya crassispatha ((Martius) Glassman (= Maximiliana crassipatha Martius; = Attalea crassispatha (Martius) Burret) is an endangered palm native and endemic to Haiti, (Figure 39) with only about 25 individual trees known to exist (Henderson and Balick, 1991). Orbignya crassispatha is the only species in the subtribe Attaleinae found outside of Central and South America (Henderson and Aubry, 1989). It has attracted botanical attention for the unique structure of its staminate flower, which does not fit the patterns described for the other genera in the Attaleinae. It is somehow intermediate between Attalea and Orbignya although closer to Orbignya, especially the coiled anthers (Uhl and Dransfield, 1987). Because of a number of additional morphological characters distinguish O. crassispatha from any other genus in the subtribe, this Haitian palm was once placed in its own genus, Bornoa (Cook, 1939), but this was not validly published.

The leaf anatomical structure of O. crassispatha conforms mostly to the Attalea pattern (Figure 37A-D), which is very distinctive due to its large pear-shaped primary veins with top buttresses; nearly equally sized secondary and tertiary veins with fibrous lower portions which go through the hypodermis, forming usually large buttresses; rhombohedral (adaxial) and spindle-shaped (abaxial-costal) epidermal

cells; and large bundles of adaxial fibers, regularly distributed and arranged in bunches below an one-layered hypodermis, formed by regularly rectangular hypodermal cells of approximately the same size. These characters are all clearly present in Q. crassispatha, and a less careful examination would immediately result in the placing of this species in the Attalea group. Orbignya crassispatha has been the subject of extensive controversy, however, mostly because of its stamens with coiled and twisted anthers. Only a very small number of the anatomical features characteristic of the Orbignya group could be found: the number of abaxial fiber groups (90-100) and their position (in between hypodermis and epidermis), and stomates with sunken guard-cells. As in Attalea, the groups of abaxial fibers are usually lacking, or otherwise occur in very small number (up to 20), and are always located above the hypodermal layer in the spongy mesophyll; guard-cells are slightly sunken, as opposed to completely sunken in the Orbignya group (as in Q. crassispatha). Mixed patterns involving these two groups are more difficult to detect because of their anatomical proximity. Because of the controversy that has surrounded this species, the possibility of hybridity was tested. The results from both multivariate and cladistic analyses, however, did not support Q. crassispatha as a hybrid or as belonging in Orbignya. PCA, cluster and cladistic results placed this species in the Attalea group. Tables 25 - 29 provide a comparison of quantitative characters of Q. crassispatha with the Brazilian Orbignya group, the Attalea group, and Q. cohune, which could be hypothesized as the most likely potential Orbignya parent if this was indeed a case of hybridization between Orbignya and Attalea.

Table 24. Selective comparison of *O. crassipatha*, *Attalea* spp. and *Orbignya* spp.

- Quantitative characters - Non-vascular fibers.

Groups	Adaxial Fibers - Number of Groups			Adaxial Fibers - Number/Fibers/Group			Abaxial Fibers - Number of Groups			Abaxial Fibers - Number/Fibers/Group		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	215-390	329.3	64.7	4-9	7	2.32	65-187	102.1	38.2	3-4	3.4	0.51
<i>Attalea</i>	152-360	227.4	63.8	4-14	8.2	2.52	0-60	25.2	21.9	0-5	2.5	1.80
<i>O. crassipatha</i>	300-360	330	42.42	9-11	10	1.41	95-100	97.5	3.53	3-9	6	4.24
<i>O. cohune</i>	400-490	445	63.6	3-4	3.5	0.70	80-85	82.5	3.5	3	3	-

Table 25. Selective comparison of *O. crassipatha*, *Attalea* spp. and *Orbignya* spp.

Quantitative characters - Chlorenchyma.

Groups	Palisade - Thickness			Spongy Mesophyll - #layers			Spongy Mesophyll - Thickness		
	range	mean	SD	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	50-120	79	24.88	6-8	7	0.75	80-190	138.7	34.91
<i>Attalea</i>	50-120	81.5	19.08	6-10	6.9	1.11	90-240	116.1	39.90
<i>O. crassipatha</i>	50-60	55	7.07	7	7	0.00	90	90	0.00
<i>O. cohune</i>	40-50	45	7.07	8	8	-	100	100	-

Table 26. Selective comparison of *O. crassispatha*, *Attalea* spp. and *Orbignya* spp.
Quantitative characters - Primary veins.

Groups	Primary Veins - Number			Primary Veins - Height (μ)			Primary Veins - Width (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	8-13	10.5	2.26	120.7-211.7	173.3	33.20	112.8-182.8	155.2	26.89
<i>Attalea</i>	8-13	10.7	1.64	154.4-306.0	194.4	41.75	110-219	149.6	29.02
<i>O. crassispatha</i>	12	12	0.00	161.6-175	168.3	9.47	110-116.2	113.1	4.38
<i>O. cohune</i>	12-13	12.5	0.70	105.9-115.8	110.8	7	100-125	112.5	17.67

Table 27. Selective comparison of *O. crassispatha*, *Attalea* spp. and *Orbignya* spp.
Quantitative characters - Secondary veins.

Groups	Sec./Tert. Veins - Number			Sec./Tert. Veins - Number/Between L. V.			Secondary Veins - Height (μ)			Tertiary Veins - Height (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	92-138	116.5	16.14	13-16	14.8	1.12	62.8-112	82.5	14.94	41.6-63.1	50.8	6.85
Scheelea	38-119	81.3	28.45	7-15	11.3	3.38	41.2-50.8	41.5	3.83	31.4-38.7	34.5	2.95
<i>Attalea</i>	66-127	90.1	20.09	7-14	9.9	2.84	62.5-106.1	85.6	13.20	51.7-85.2	68.1	9.27
<i>O. crassispatha</i>	96-127	111.5	21.92	14	14	0.00	62.5-68.8	62.6	0.21	55.3-58	56.6	1.90
<i>O. cohune</i>	88-132	110	31.11	8-14	11	4.24	55.2-69.8	62.5	10.32	42-50.8	46.4	6.22

Table 28. Selective comparison of *O. crassipatha*, *Attalea* spp. and *Orbignya* spp.
Quantitative characters - Midrib.

Groups	Midrib - Size			Midrib - Number of VBs		
	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	1.7-3.1	2.47	0.52	18-22	20	1.06
<i>Scheelea</i>	0.78-1.84	1.31	0.36	8-20	12.5	4.08
<i>Attalea</i>	0.94-2	1.27	0.30	6-22	11.3	4.98
<i>O.</i> <i>crassipatha</i>	1.20	1.20	0.00	20-22	21	1.41
<i>O. cohune</i>	1.28-1.88	1.58	0.42	18	18	0.00

Orbignya cohune was separated from the Brazilian species on the basis of one major difference: it has a one-layered hypodermis. Position of secondary and tertiary veins basically follow the overall Orbignya pattern (above hypodermis); tertiary veins, however, are closer to the hypodermal layer, sometimes pressing it down, but rarely forming small buttresses (Figure 37E-H). Overall, there is no doubt about the anatomical patterns in O. cohune as being characteristic of the Orbignya group. The anatomical similarity between O. guacuyule (Figure 38A-D) and O. cohune supports the view of these two taxa being conspecific, or very closely allied (Dahlgren, 1959). Morphologically, these two species have been separated by differences in the staminate flowers, particularly size, consistency, and color of petals, and in the number of stamens as well. They both have the same distribution range – from Mexico to most of the Central American countries (Figure 39). Results from the multivariate and cladistic analyses, however, did not confirm this conspecificity. Tables 30 - 34 provide an anatomical comparison of these two species and O. cuatrecasana.

A different story is found in the leaf anatomy of O. cuatrecasana, the third species of the non-Brazilian Orbignya. Although many of the Orbignya patterns are present (e.g., shape and location of abaxial fibers, differentiation of mesophylls, shape of midrib), there is a confusing mixture of patterns closer to the Scheelea group (Figure 38E-H). These characters include epidermal cells of approximately the same size, shape and orientation in both surfaces, and more importantly, long transverse veins.

This species is the only Orbignya known from Colombia (Glassman, 1977b) (Figure 39). It is an acaulescent species that, like other acaulescent species in this sample, showed a strong presence of tannins in the mesophyll (e.g. O. eichleri, A. geraensis). Unlike the others, it does not grow in dry areas with sandy soils, but rather in very wet lowland rain forest (Henderson et al., 1995).

Table 29. Selective comparison anatomical characters in O. guacuyule, O. cohune, and O. cuatrecasana - Quantitative characters: Non-vascular fibers.

Groups	Adaxial Fibers - Number of Groups			Adaxial Fibers - Number/Fibers/Group			Abaxial Fibers - Number of Groups			Abaxial Fibers - Number/Fibers/Group		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. guacuyule</i>	490	490.0	-	4	4	-	80	80	-	3	3	-
<i>O. cohune</i>	400-490	445	63.6	3-4	3.5	0.70	80-85	82.5	3.5	3	3	-
<i>O. cuatrecasana</i>	300-320	311.6	10.4	4-6	4.6	1.15	60-75	68.3	7.6	6-9	7	1.73

Table 30. Selective comparison anatomical characters in O. guacuyule, O. cohune, and O. cuatrecasana - Quantitative characters: Chlorenchyma.

Groups	Palisade - Thickness			Spongy Mesophyll - #layers			Spongy Mesophyll - Thickness		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. guacuyule</i>	50	50.0	-	8	8	-	100	100	-
<i>O. cohune</i>	40-50	45	7.07	8	8	-	100	100	-
<i>O. cuatrecasana</i>	60-70	63.3	5.77	5-6	5.6	0.57	80-100	90	10

Table 31. Selective comparison anatomical characters in O. guacuyule, O. cohune, and O. cuatrecasana - Quantitative characters: Primary veins.

Groups	Primary Veins - Number			Primary Veins - Height (μ)			Primary Veins - Width (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. guacuyule</i>	13	13.0	-	115.8	115.8	-	125	125.0	-
<i>O. cohune</i>	12-13	12.5	0.70	105.9-115.8	110.8	7	100-125	112.5	17.67
<i>O. cuatrecasana</i>	11-16	13.3	2.51	122-132.5	125.7	5.87	133.1-144	139.4	5.66

Table 32. Selective comparison anatomical characters in O. guacuyule, O. cohune, and O. cuatrecasana - Quantitative characters: Secondary and tertiary veins.

Groups	Sec./Tert. Veins - Number			Sec./Tert. Veins - Number/Between L. V.			Secondary Veins - Height (μ)			Tertiary Veins - Height (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. guacuyule</i>	132	132.0	-	14	14.0	-	69.8	69.8	-	50.8	50.8	-
<i>O. cohune</i>	88-132	110	31.11	8-14	11	4.24	55.2-69.8	62.5	10.32	42-50.8	46.4	6.22
<i>O. cuatrecasana</i>	91-138	108.3	25.81	14	14	-	70-73.2	71.1	1.79	51.2-58	53.7	3.71

Table 33. Selective comparison anatomical characters in O. guacuyule, O. cohune, and O. cuatrecasana - Quantitative characters - Midrib.

Groups	Midrib - Size			Midrib - Number of VBs		
	range	mean	SD	range	mean	SD
<i>O. guacuyule</i>	1.8	1.8	-	18	18.0	-
<i>O. cohune</i>	1.28-1.88	1.58	0.42	18	18	-
<i>O. cuatrecasana</i>	1.68-2.20	2	0.28	18-20	19.3	1.15

Fig. 37. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D
- Orbignya crassispata (OCR-22); E, F, G, H - O. cohune (OCO-21).

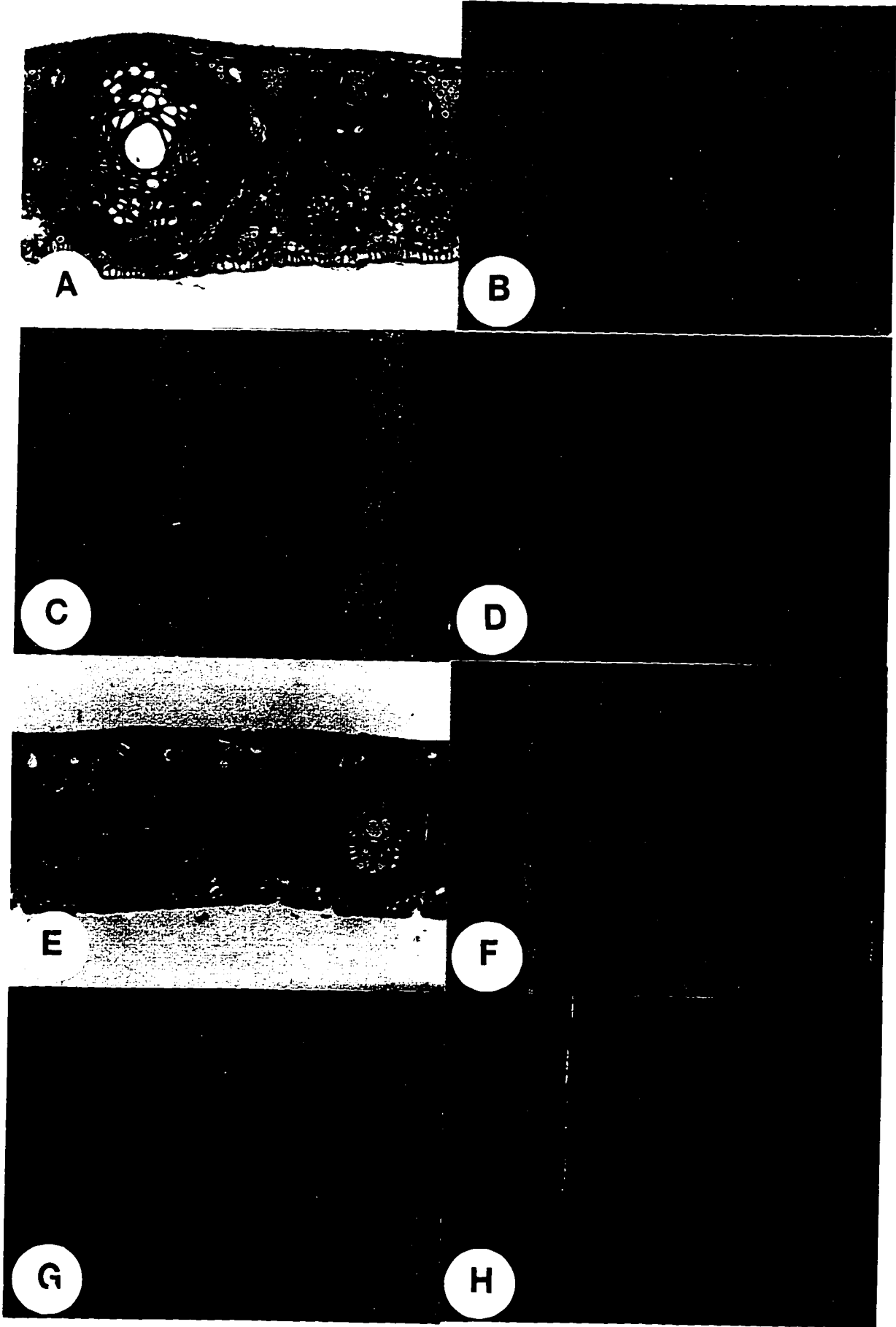


Fig. 38. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Obignya guacuyule (OG-27); E, F, G, H - O. cuatrecasana (OCU-24 & OCU-26).

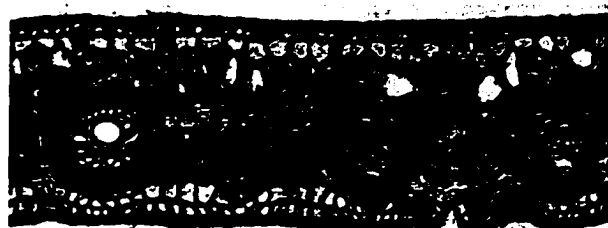
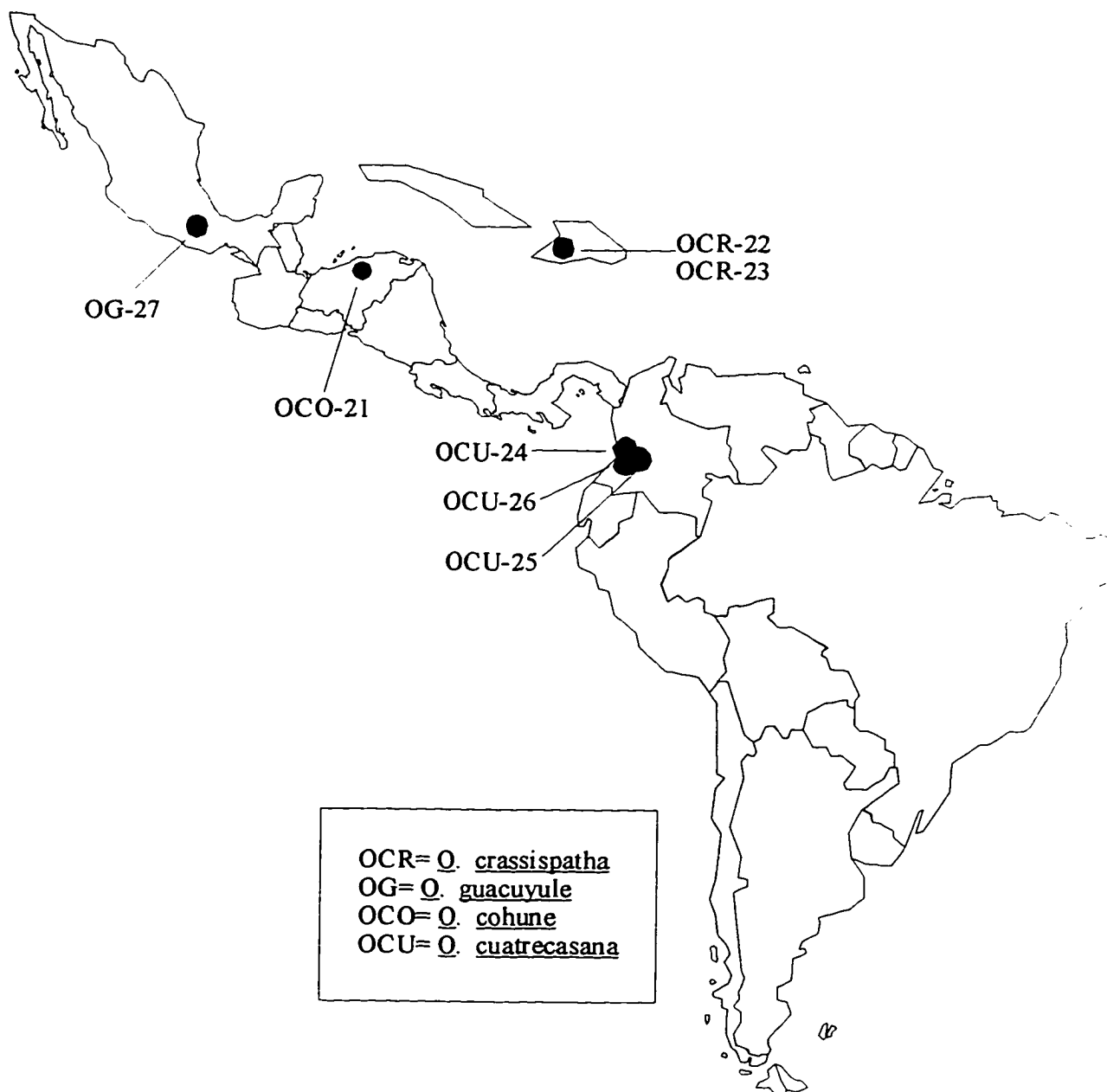
**A****B****C****D****E****F****G****H**

Fig. 39. Distribution of the specimens of Orbignya crassispatha, O. cohune, O. guacuyule, and O. cuatrecasana studied.



The other species of Orbignya included in this study constituted the most confusing taxa in the group. That is not surprising, considering that at the morphological level they have also been a source of controversy and confusion. Orbignya polysticha and O. sagotii are both acaulescent species that share the same range: the Guianas, and northern Amazon region in Colombia, Venezuela (Amazonas), Peru (Loreto), and Brazil (Amapá, Amazonas) (Henderson, 1995). These two species have recently been reduced to synonymy with O. microcarpa (Mart.) Burret, under the name Attalea microcarpa Mart. by Henderson et al. (1995) who also suggested they form hybrids with A. speciosa (Orbignya spp.), but the anatomical evidence did not support this suggestion. Scheelea is likely to be involved in crossings with these Orbignya species, given a number of anatomical characters common to that group, present in O. polysticha and O. sagotii specimens (Figure 40A-D & 40-E-H).

Epidermal cells of same shape, size and orientation on both surfaces are characteristic of the Scheelea group; the shape (somewhat square) and location (between hypodermal cells) of abaxial fiber groups is also closer to Scheelea. Primary veins show a mixture of both Orbignya and Scheelea patterns: a number of veins formed by large thin walled fibers, located closer to the abaxial surface (like Scheelea), or centered (like Orbignya). The shape of the secondary and tertiary veins is mostly roundish; these veins are small, formed by large fibers of thin walls,

and small buttresses are formed (all closer to the Scheelea pattern). The adaxial epidermis is basically a mixture of rectangular (from Scheelea) and rhombohedral cells (from Orbignya), of usually undulate walls (more common in Scheelea). The abaxial epidermis has spindle-shaped (Orbignya type) or rectangular (Scheelea type) costal cells, also of undulate walls. The shape of midrib, although somewhat irregular (a common phenomenon in cases of hybridization), is mostly rectangular like in Orbignya. The stomates have guard-cells sunken (Orbignya), slightly sunken, (Attalea) or superficial (Scheelea) in different specimens. Finally, the long transverse veins, characteristic of the Scheelea group.

One of the specimens studied (OPO-17), however, added more confusion to this group, showing no signs of Scheelea characters but rather features that are found only in the Attalea group, opening the way for the assumption that an Attalea may also be involved in another part of the range of this species. This specimen shows a layer of hypodermis which is a mixture of rectangular and roundish cells, with large bunches of fibers below it; the abaxial fibers are irregularly distributed; mesophyll (both palisade and spongy) is poorly differentiated (meaning thin-walled cells) and it has features that are present to both Orbignya or Attalea, such as 2 palisade and 5-6 spongy cells layers; adaxial epidermal cells of rhombohedral shape; spindle-shaped abaxial costal cells; both with linear walls; and a mixture of long and short transverse veins.

An examination of the area of occurrence of these species shows that they overlap with Scheelea attaleoides in the easternmost portion of their range, which includes Brazil (Amazonas and Pará), and the Guianas. In the southwestern portion of the range they overlap with Scheelea insignis (in the Brazilian state of Amazonas, southern Colombia, and northern Peru). The specimens of O. polysticha used in this study were collected in Peru, the Brazilian state of Amazonas, and Venezuela. Orbignya sagotii specimens came from French Guiana, Brazil (Pará), and Surinam (Figure 42). The specimens collected in Peru, Brazil, French Guiana and Surinam are those that show signs of hybridization involving Scheelea, which occurs in those areas. The other specimen of O. polysticha (OPO-17) was collected in southern Venezuela (territorio Amazonas), and it is exactly in that specimen that no signs of Scheelea were found: the hybridization shows signs of Attalea, and at least one species of Attalea has been collected in that region: A. racemosa Spruce. These varying patterns within the same species suggest changes of crossing partners according to the region where they grow.

Orbignya spectabilis shows also a mixture of patterns, but less confusing as only Orbignya and Scheelea characters can be distinguished (Figure 41A-D). This is a poorly known species that has been suggested to be a hybrid between O. microcarpa (= O. polysticha and O. sagotii) and an Orbignya species (Henderson et al., 1995). Glassman (1977) treated O. spectabilis as a species dubia because of the ambiguous description of the staminate flowers. It grows in a very restricted

range (north of Pará State, Brazil), an area that overlaps with the distribution range of the other two species previously discussed. Crossings between Orbignya and Scheelea species are quite possible, at least from a geographical point of view: O. spectabilis' restricted area of occurrence coincides with the southern portion of the distribution range of S. attaleoides. Since O. polysticha, O. sagotii, and O. spectabilis have overlapping distributions, it can be hypothesized that all are part of the same hybrid complex. Indeed, they have a very similar anatomical structure that mixes Orbignya and Scheelea characters, with a slight predominance of the latter. For most of the characters, the variation occurs just in the way the dominance of a certain character state is expressed: changing from one specimen to another, but keeping the major patterns that come from Scheelea and Orbignya. For instance, in one specimen, adaxial epidermal cells can show an overall pattern of mostly rectangular cells with a mixture of rhombohedral cells, and in another specimen the major pattern can be the opposite: mostly rhombohedral with a mixture of rectangular cells. Figure 42 shows the distribution of the specimens of O. spectabilis studied.

The complexity of character variation in these three species was reflected in the results of the analyses performed. In the PCA, although the overall pattern revealed most of the specimens used to be closer to the Scheelea pattern, at least one specimen of each species showed some sort of character conflict or polymorphism. These resulted in being satellite specimens, away from the group (Scheelea) where

the others clustered. The same pattern was observed in the cluster analysis. In the cladistic analysis, they all showed exactly the same pattern: either collapsing the clade, or ending up as sister species to the Scheelea species. When all three species are included in the analysis at the same time, the Scheelea clade collapses, becoming a polytomy.

Orbignya luetzelburgii was first described by Burret (1930), and later transferred to its own genus Parascheelea by Dugand (1940). More recently, Uhl and Dransfield (1987) subsumed Parascheelea under Orbignya; finally, it was treated as a species of Attalea by Henderson et al. (1995). It is known from a very small distribution range in northwestern Brazil (state of Amazonas), southeastern Colombia (Vaupés), and southwestern Venezuela (territory of Amazonas) (Henderson et al., 1995). This taxon apparently combines morphological features of Orbignya (coiled anthers) and Scheelea (plano-convex petals) (Glassman, 1977b).

A number of very distinctive (some of them unique) characters make O. luetzelburgii anatomically one of the most easily recognizable species among those studied (Figure 41E-H). The examination of its leaf anatomical structure makes it easy to understand why it was transferred to its own genus. The most distinctive and unique character in O. luetzelburgii is the complete replacement of the abaxial hypodermis by a continuous layer of large fibers (here termed hypodermal fibers). This type of fiber was observed only in A. funifera, as discussed later, but in that

species these fibers only replace a few adaxial hypodermal cells, or are accumulated on upper portions of primary veins and around the midrib. Orbignya luetzelburgii showed the highest number and variety of cell inclusions: oil globules, especially on hypodermal cells, and tanniniferous and mucilage cells, as well as sclereids, make the mesophyll of this species very distinctive. Most of the features are divided between the Orbignya-Attalea and Scheelea patterns. Primary veins in O. luetzelburgii are mostly slightly pear-shaped with a tendency toward accumulation of fibers on the upper portions of veins, forming, in this case, slight, top buttresses. The other most important characters are a combination of patterns identifiable in the three groups, which complicates any attempt of an explanation for such unusual leaf anatomy in this species.

The small region where O. luetzelburgii occurs is enclosed in the distribution range of several species in all groups: O. polysticha, O. sagotii, O. spectabilis, A. racemosa, and S. insignis. Crossings and back crossings among different species growing in the same or adjacent regions could be an explanation for such a variety of anatomical patterns in O. luetzelburgii. The dominance, however, at least at the anatomical level, seems to be Scheelea's, which correlates with the external morphology of the plant (more Scheelea-like). PCA results, however, showed O. luetzelburgii closer to Attalea group; clustering proved inconclusive since the two specimens formed a cluster of their own, probably defined by the uniqueness of a few characters, as pointed out before. Cladistic results placed O. luetzelburgii as a

sister species to O. cohune and to the clade formed by the Orbignya-Attalea species. Its hybrid status, hypothesized and tested, was not supported by the results of the analyses. Table 35- 39 compares quantitative characters in O. luetzelburgii with the Brazilian Orbignya, Attalea, Scheelea, and O. cohune. Figure 42 shows the local of collection of specimens of O. polysticha, O. sagotii, O. spectabilis, and O. luetzelburgii studied.

Table 34. Selective comparison of anatomical characters in O. luetzelburgii, Orbignya spp., O. cohune, Scheelea spp., and Attalea spp.

Quantitative characters - Non-vascular fibers.

Groups	Adaxial Fibers - Number of Groups			Adaxial Fibers - Number/Fibers/Group			Abaxial Fibers - Number of Groups			Abaxial Fibers - Number/Fibers/Group		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	215-390	329.3	64.7	4-9	7	2.32	65-187	102.1	38.2	3-4	3.4	0.51
<i>O. luetzelburgii</i>	190-285	237.5	67.17	7	7	0.00	layer	layer	layer	layer	layer	layer
<i>O. cohune</i>	400-490	445	63.6	3-4	3.5	0.70	80-85	82.5	3.5	3	3	-
<i>Scheelea</i>	260-545	344.5	105.7	2-3	2.8	0.40	70-230	119.8	57.7	3-6	3.8	1.16
<i>Attalea</i>	152-360	227.4	63.8	4-14	8.2	2.52	0-60	25.2	21.9	0-5	2.5	1.80

Table 35. Selective comparison of anatomical characters in O. luetzelburgii, Orbignya spp., O. cohune, Scheelea spp., and Attalea spp.

Quantitative characters - Chlorenchyma.

Groups	Palisade - Thickness			Spongy Mesophyll - Number of layers			Spongy Mesophyll - Thickness		
	range	mean	SD	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	50-120	79	24.88	6-8	7	0.75	80-190	138.7	34.91
<i>O. luetzelburgii</i>	50	50	0.00	6-8	7	1.41	90-100	95	7.07
<i>O. cohune</i>	40-50	45	7.07	8	8	-	100	100	-
<i>Scheelea</i>	30-50	40	6.32	4-5	4.2	0.40	50-70	61.6	7.52
<i>Attalea</i>	50-120	81.5	19.08	6-10	6.9	1.11	90-240	116.1	39.90

Table 36. Selective comparison of anatomical characters in O. luetzelburgii, Orbignya spp., O. cohune, Scheelea spp., and Attalea spp.
Quantitative characters - Primary veins.

Groups	Primary Veins - Number			Primary Veins - Height (μ)			Primary Veins - Width (μ)		
Groups	range	mean	SD	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	8-13	10.5	2.26	120.7-211.7	173.3	33.20	112.8-182.8	155.2	26.89
<i>O. luetzelburgii</i>	5-8	6.5	2.12	136-160	148.1	16.82	127-157	142.1	21.07
<i>O. cohune</i>	12-13	12.5	0.70	105.9-115.8	110.8	7	100-125	112.5	17.67
<i>Scheelea</i>	6-12	8.66	2.42	82.5-115.7	103.0	12.70	102.8-126.7	112.9	8.40
<i>Attalea</i>	8-13	10.7	1.64	154.4-306.0	194.4	41.75	110-219	149.6	29.02

Table 37. Selective comparison of anatomical characters in O. luetzelburgii, Orbignya spp., O. cohune, Scheelea spp., and Attalea spp.
Quantitative characters: Secondary and tertiary veins.

Groups	Sec./Tert. Veins - Number			Sec./Tert. Veins - Number/Between L.V.			Secondary Veins Height (μ)			Tertiary Veins Height (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	92-138	116.5	16.14	13-16	14.8	1.12	62.8-112	82.5	14.94	41.6-63.1	50.8	6.85
<i>O. luetzelburgii</i>	118-122	120	2.82	16-18	17	1.41	56-59	57.6	1.97	39-44.5	41.8	3.87
<i>O. cohune</i>	88-132	110	31.11	8-14	11	4.24	55.2-69.8	62.5	10.32	42-50.8	46.4	6.22
<i>Scheelea</i>	38-119	81.3	28.45	7-15	11.3	3.38	41.2-50.8	41.5	3.83	31.4-38.7	34.5	2.95
<i>Attalea</i>	66-127	90.1	20.09	7-14	9.9	2.84	62.5-106.1	85.6	13.20	51.7-85.2	68.1	9.27

Table 38. Selective comparison of anatomical characters in O. luetzelburgii, Orbignya spp., O. cohune, Scheelea spp., and Attalea spp.

Quantitative characters - Midrib.

Groups	Midrib - Size			Midrib - Number of VBs		
	range	mean	SD	range	mean	SD
Brazilian <i>Orbignya</i>	1.7-3.1	2.47	0.52	18-22	20	1.06
<i>O. luetzelburgii</i>	0.6-0.72	0.66	0.08	8-10	9	1.41
<i>O. cohune</i>	1.28-1.88	1.58	0.42	18	18	0.00
<i>Scheelea</i>	0.78-1.84	1.31	0.36	8-20	12.5	4.08
<i>Attalea</i>	0.94-2	1.27	0.30	6-22	11.3	4.98

Fig. 40. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Orbignya polysticha (OPO-15 & OPO-16); E, F, G, H - O. sagotii (OSA-18 & OSA-19).

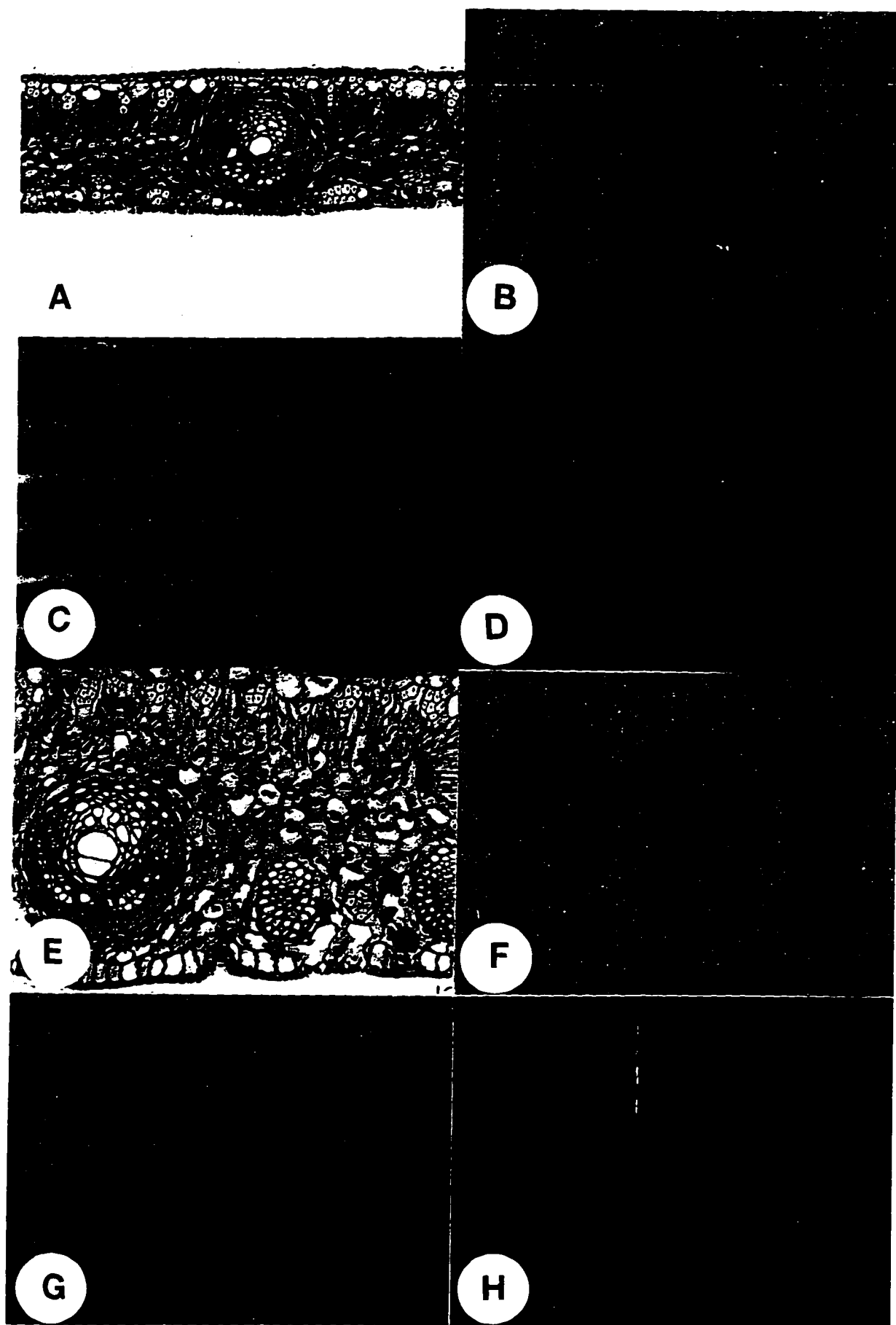


Fig. 41. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Orbignya spectabilis (OSP-28 & OSP-30); E, F, G, H - O. luetzelburgii (OL-13 & OL-14).

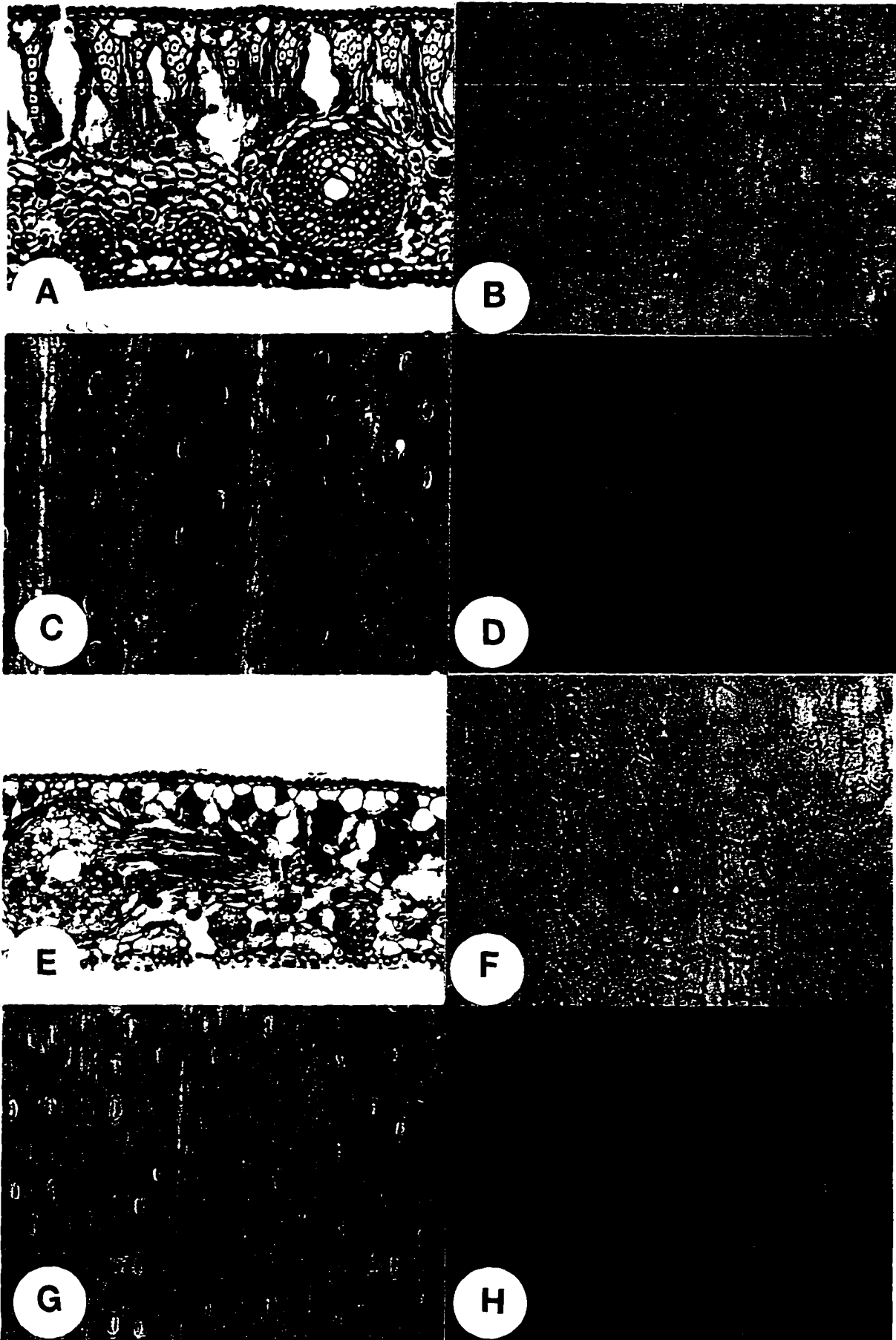
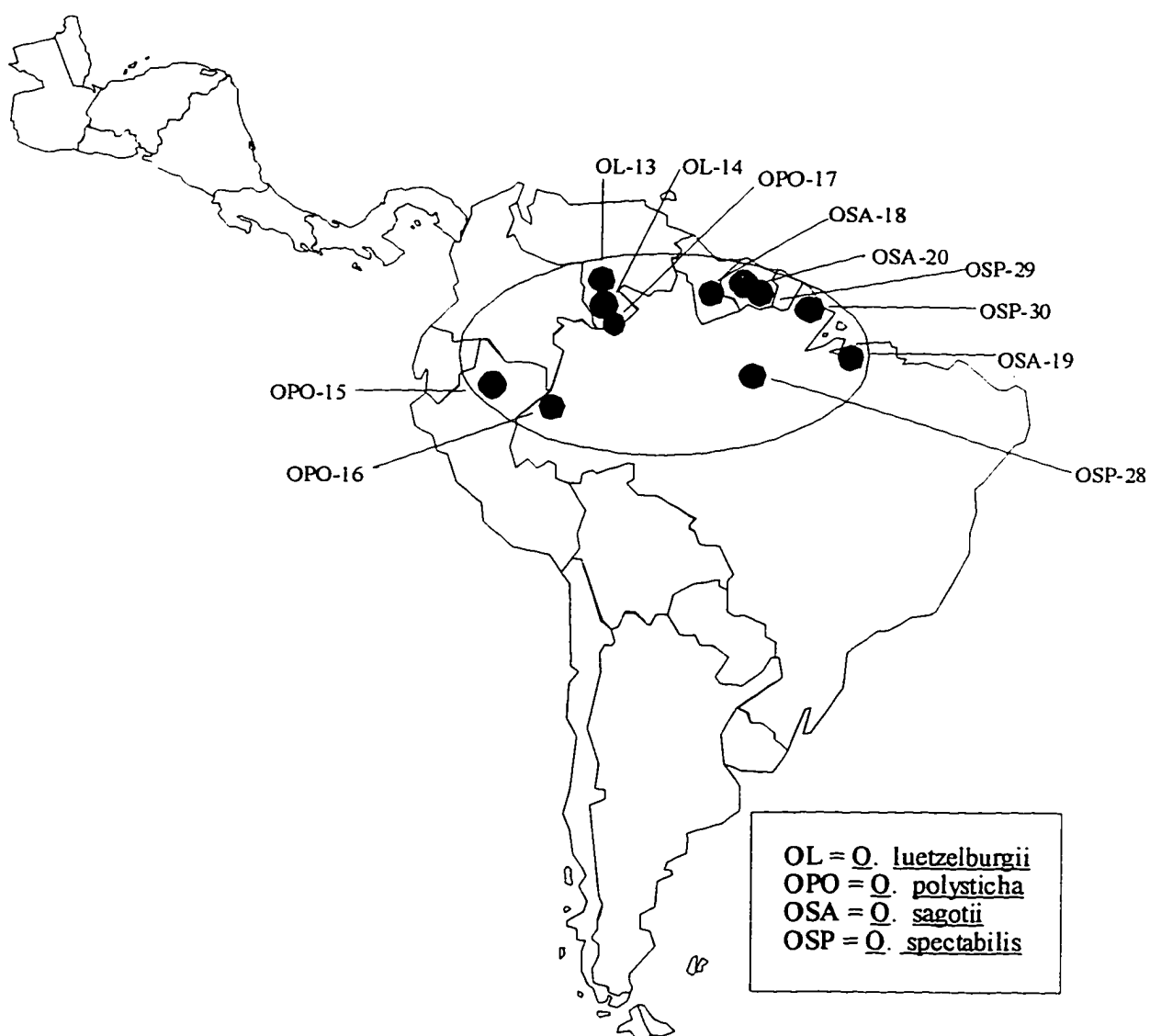


Fig. 42. Distribution of specimens of O. polysticha, O. sagotii, O. spectabilis, and O. luetzelburgii studied.



One of the first observations in relation to epidermal features was made during the preparation of samples for epidermal peels. I noticed that there were a number of samples for which handling of the separated epidermis was much more difficult than for the rest of the samples. I recorded the numbers of this group of samples at the time; later, by comparing the numbers, it was revealed that all of them were from specimens in the Scheelea group, or intermediates in which there were signs of Scheelea's parentage. Those peels were the most difficult to handle because the epidermis is very thin (both adaxially and abaxially). The short height of the epidermal cells and their longitudinal orientation, makes the peels wrinkle easily, and difficult to mount flat on the slides. Indeed, the thickness of the epidermis ended up being one distinctive character in Scheelea in relation to the other groups. That is very easy to observe both in cross section and surface view: in the first, epidermal cells look small (compared to the other groups), and show uniformity of shape and orientation on both surfaces; in the second, a thin, almost transparent epidermis shows mostly elongate rectangular cells with thin anticlinal walls.

A number of other characters make the leaf anatomical structure of the Scheelea group very distinctive and relatively easy to recognize. The most distinctive include the arrangement of abaxial fibers in essentially squared groups, always located in between hypodermal cells; large, thin-walled fibers in the inner sheath of primary veins that give the veins a "chain" appearance, especially on the upper portions; a

mesophyll always composed of thick-walled cells, with usually 1 layer of palisade cells and 4 layers of spongy cells, with a “brick wall” appearance; roundish, small secondary veins forming small buttresses; stomates with superficial guard-cells; usually a very pointed sclerotic sheath, and small fiber groups surrounding it in the spongy mesophyll, making Scheelea’s midrib distinctive; and always long transverse veins connecting many primary veins.

Since the establishment of Scheelea by Karsten (1857), it has been treated many times; numerous additions and subtractions, and transfers of species from this genus to others were made (Barbosa Rodrigues, 1891-1907; Hooker (1897); Beccari (1916); Burret (1929, 1934, 1940), Bailey (1933, 1947); Bartlett (1935); Dugand (1959); and Boer (1965, 1972). More recent accounts of the genus recognized 28 species of Scheelea (Glassman, 1977c; Uhl and Dransfield, 1987); Henderson et. al. (1995) not only lumped the genus into Attalea, but drastically reduced the number of valid species to four (the ones used in this study).

Scheelea species often grows in a wide variety of habitats, from open savannas in dry areas to tropical rain forests (Uhl and Dransfield, 1987). Their separation from the other genera has traditionally been on the basis of their stamens being shorter than the petals, and with straight anthers. They are more easily recognizable using anatomical evidence as compared to their morphology; this recognition, however, may be obscured by the existence of intermediate or mixed patterns. Of the four

specimens of Scheelea, S. insignis and S. attaleoides showed “pure” patterns (Figures 43E-H & 44-E-H), and S. butyracea, and S. phalerata showed mixed patterns (Figures 43A-D & 44-A-D), readily distinguishable from the other groups. The latter two, given the crossed patterns observed were marked as intermediates, and tested as such. The local of collection of the Scheelea specimens studied are shown in Figure 45.

The Scheelea attaleoides examined in this study is the species considered by Wessels Boer (1965) to be a species of Maximiliana; the differentiation from the S. attaleoides described by Karsten, was made on the basis of the difference between the arrangement of pinnae in the two species. This view was followed by Henderson (1995), who interpreted this species as being a “Maximiliana” rather than a “Scheelea”, in his subgeneric division of the genus Attalea. Glassman (1978), based on the type of petals of the male flower, decided that S. attaleoides is a true Scheelea. However, since another S. attaleoides already existed, he designated it a species confusum. The anatomical results fully support S. attaleoides (Figure 44E-H) as a being a true Scheelea. The specimens of S. attaleoides studied were collected in Brazil (Prance 17572, Henderson 1170; and Surinam: Wessels Boer 1431).

Scheelea phalerata (Mart. ex Spreng) Burret, as placed by Henderson et al. (1995) under Attalea phalerata Mart. ex Spreng, includes as synonymy and based

on the taxonomic opinion of other specialists, 5 taxonomic names of Scheelea: S. weberbaueri Burret, S. princeps (Mart.) H. Karst., S. blepharopus Mart., S. microspadix Burret, S. martiana Mart. ex Spreng, and at least one species of Attalea (A. hoehnei Burret). With these additions, from a narrow range of distribution in Brazil (states of Goiás and Mato Grosso), S. phalerata became a widespread species, occurring in Brazil (Amazon region and Brazilian central plateau), Peru, Bolivia, and Paraguay (Henderson et al., 1995). From the specimens used in the study, two were collected in Brazil (one in the Amazon region, state of Pará; the other from the *planalto* region, state of Goiás), and one in Peru (Figure 45).

The three specimens showed anatomical variation, which ranges from the Scheelea to the Attalea patterns. The overall anatomical structure shows a clear predominance of Scheelea (Figure 44A-D); however, a few important features characteristic of the Attalea group were discerned: 1) dissimilarity in shape, size and orientation of adaxial vs. abaxial epidermal cells; 2) abaxial fiber groups located above lower hypodermis - even though the number of groups (70-90) is more typical of Scheelea; one of the specimens lacked abaxial fibers; 3) pear-shaped primary veins, forming small top buttresses in 2 specimens, and not forming them in one specimen; 4) the type of fibers in these veins (small or large, with thick walls) and their position in relation to the surfaces (centered); 5) shape and location of secondary and tertiary veins, forming large buttresses; adaxial epidermal cells of rhombohedral shape and linear walls (although the costal cells of the abaxial

epidermis are rectangular, as is typical of Scheelea, versus always spindle-shaped in Attalea); and finally, at least one specimen has short transverse veins, with the two other showing mixed patterns: short and long transverse veins.

For some of the characters the intermediacy of patterns is clear. A hypodermal layer that mixes roundish with regularly rectangular cells; or regularly distributed abaxial fiber groups (common in Scheelea, uncommon in Attalea) located above the hypodermis in spongy mesophyll (common in Attalea when abaxial fibers are not completely lacking, but atypical in Scheelea, which has these fibers located in between hypodermal cells, close to the epidermis); or a mixture of short and long transverse veins (always short in Attalea, as opposed to always long in Scheelea).

This evidence suggests that S. phalerata could be a hybrid between species of Scheelea and Attalea, although the determination (or even the guessing) as to the identity of the parent species would be quite difficult, given its wide range. A useful taxonomic finding, however, would be the confirmation of the lumped species as a single one, since the anatomical structure of the three specimens was basically the same in the three specimens examined, which were collected at the extremes and in the middle of its range. The confirmation of this species as a hybrid would correlate with the morphological variability observed in some characters, such as having leaflets irregularly arranged and spreading in different planes in some cases, and in others, regularly arranged with only the tips spreading in different planes

(Henderson et al., 1995). It also correlates with the uncertainty in placing this species in one of those genera: one of the Scheelea names included in synonymy by Henderson (1995) is S. martiana Burret (under the name Attalea excelsa Mart. ex Spreng.). The author apparently doubted that this species was really a "Scheelea", implying that it probably was an "Attalea". Scheelea martiana was transferred by Burret (1929) from Attalea to Scheelea, on the basis of the presence of fiber clusters in the endocarp of the fruit. Glassman (1977c), considered S. martiana a species dubia, since the species definition was mostly based on fruit characters, especially the fiber clusters in the endocarp, which are also present in many species of Attalea and Orbignya. The uncertainty in relation to the proper identity of this species correlates with the mixed anatomical patterns and with the morphological variations reported, leaving this species half way between a Scheelea and an Attalea.

Scheelea butyracea (Mutis ex L.f.) H. Karsten, also has a history of taxonomic changes. Henderson et al. (1995) listed 37 names included as synonym for S. butyracea (under A. butyracea (Mutis ex L.f.) Wess. Boer): 25 as a Scheelea; 2 as Cocos; and 10 as an Attalea. It is also a widely distributed species: it grows from most of Central America to parts of South America and southern Mexico. From the three specimens used in this study, one was collected in Venezuela, one in Ecuador, and one in the southwestern Brazilian Amazon, in the state of Acre (Figure 45).

The results in the anatomical study revealed two different situations: one specimen (Henderson et al. 821) from Acre, Brazil fit the Scheelea pattern mostly; the other two specimens (Wessels Boer 1990, and Balslev 4339), from Venezuela and Ecuador, respectively, showed unquestionable mixture of anatomical patterns involving Scheelea and Orbignya. The anatomical structure is primarily from Scheelea (Figure 44A-D), and this predominance is reflected in the external morphology of the plant. However, two major anatomical characters undoubtedly come from the Orbignya group. Epidermal cells do not follow the Scheelea pattern of similarity in shape, size and orientation between adaxial and abaxial surfaces; they are smaller and differently sized and oriented on the adaxial epidermis compared to the abaxial; the adaxial epidermis is thick, with rhombohedral cells, with linear walls (not a Scheelea pattern); costal cells of the abaxial epidermis are spindle-shaped, with linear walls (these cells would normally be rectangular, of undulate walls in Scheelea); the abaxial hypodermal layer is formed by square cells (not roundish as in the typical Scheelea); primary veins are round, but centered, which is an Orbignya (or Attalea) pattern, as opposed to closer to the abaxial surface in Scheelea; a mid-secondary vein is distinguishable, a characteristic of Orbignya; secondary and tertiary veins are located above the lower hypodermis, a situation only observed in the Orbignya group, in which no buttresses are ever formed; the stomates have sunken guard-cells, not in definite files (as opposed to superficial and arranged in

files in Scheelea); and finally, small fiber groups in the midrib are located on its upper portion (in Scheelea these fibers surround the sclerotic sheath of the midrib).

The specimens were collected in two geographically disjunct countries, Ecuador and Venezuela. In the case of Ecuador, there is at least one report of a putative hybrid involving an Orbignya species, Attalea colenda later discussed. Glassman (1977c), citing Standley & Steyermark (1958), stated "S. butyracea (as S. lundelii Bartlett) grows in the same forests in Petén (Guatemala) as Orbignya cohune, which it resembles very closely in appearance." Henderson et al. (1995) reported that in Central America and in the Magdalena valley of Colombia, S. butyracea and Orbignya cohune (as Attalea cohune), grow together in mixed stands. There is, therefore, distributional evidence of the involvement of S. butyracea with a species of Orbignya, and it happens throughout the narrow geographic channel which is Central America down to South America. Orbignya cohune can indeed be the mixing species in this case, particularly if we consider that it belongs to the one-layered hypodermis group of Orbignya, as opposed to two layers in the Brazilian group of Orbignya. The anatomically-mixed specimens of S. butyracea both have an one-layered adaxial hypodermis.

Results from PCA and cluster analysis confirmed what I observed and was reported in the descriptions: one specimen of S. butyracea (SB-38) joins the Scheelea group; the other two specimens join a group in between Scheelea and Orbignya, and this group is joined by all specimens of S. phalerata. Inclusion of S.

butyracea and S. phalerata, together or separately, in the cladistic analysis, causes the collapse of the cladogram to the basal node. The results support the hypothesis of the hybrid status of these two species.

.

Fig. 43. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Scheelea phalerata (SP-31 & SP-32); E, F, G, H - S. insignis (SI-34, SI-35 & SI-36).

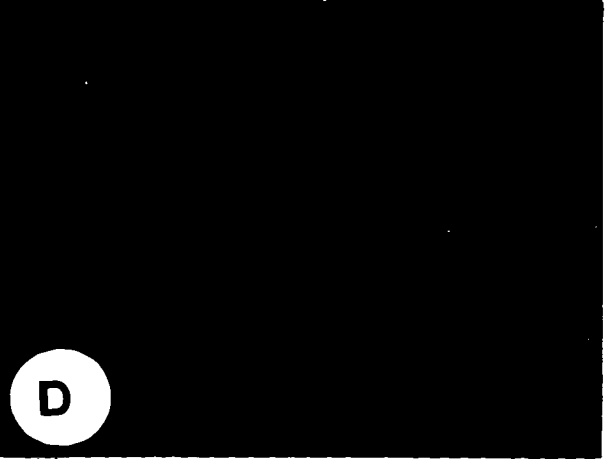
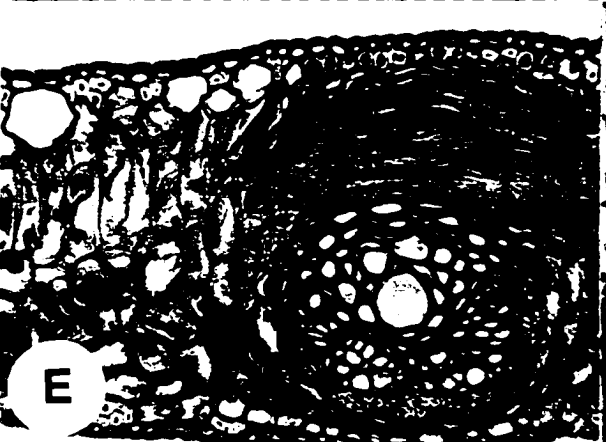
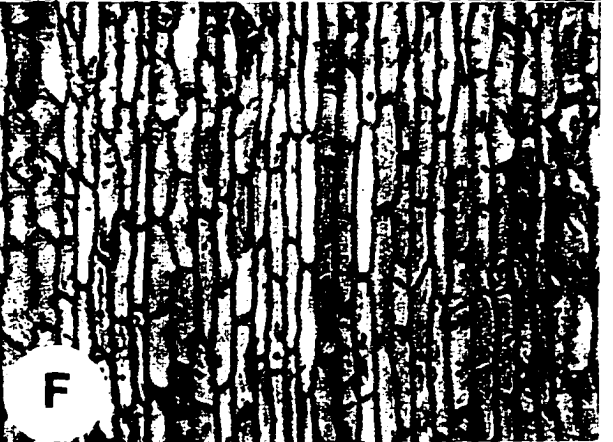
**A****B****C****D****E****F****G****H**

Fig. 44. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Scheelea butyracea (SB-38 & SB-39); E, F, G, H - S. attaleoides (SA-40 & SA-42).

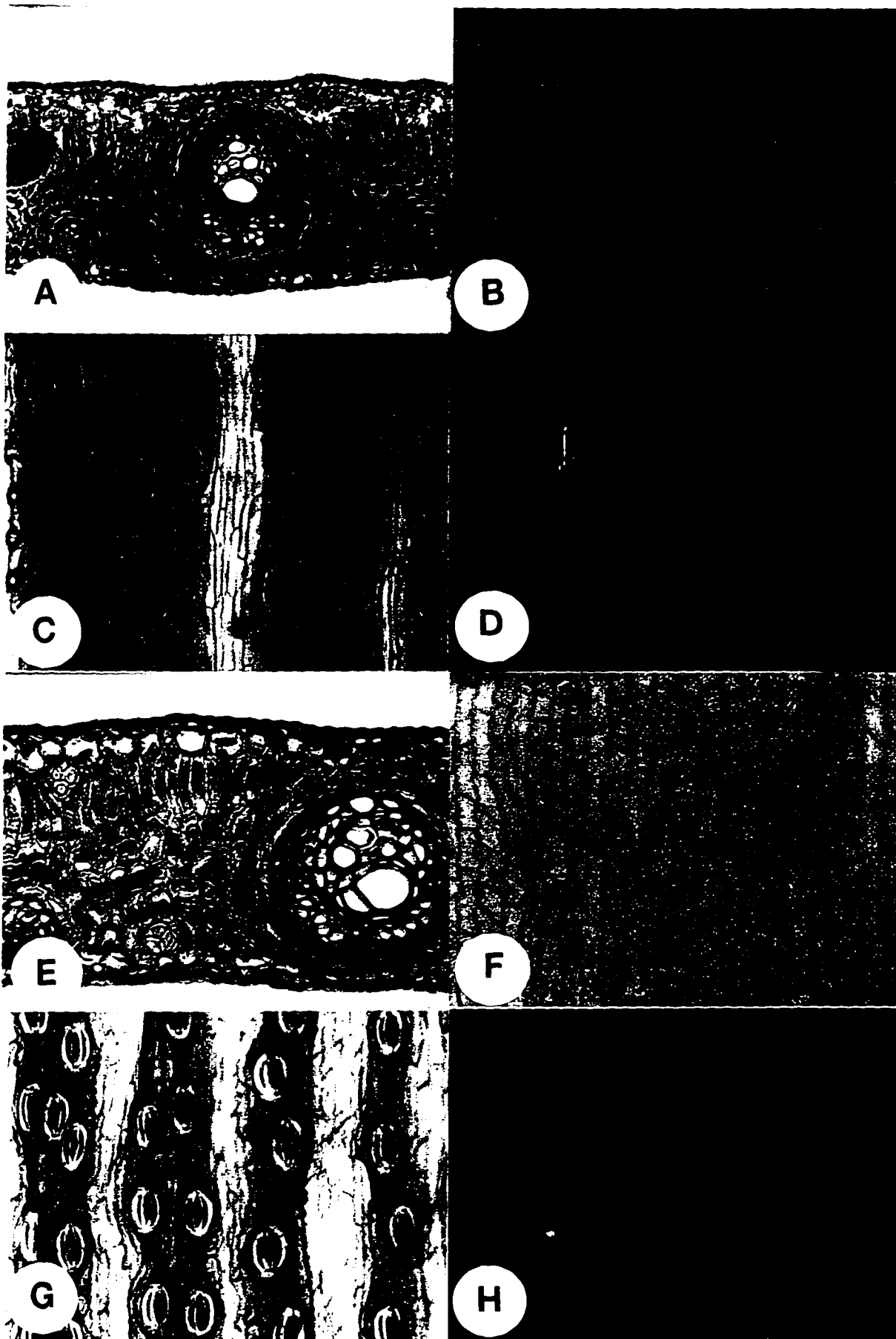
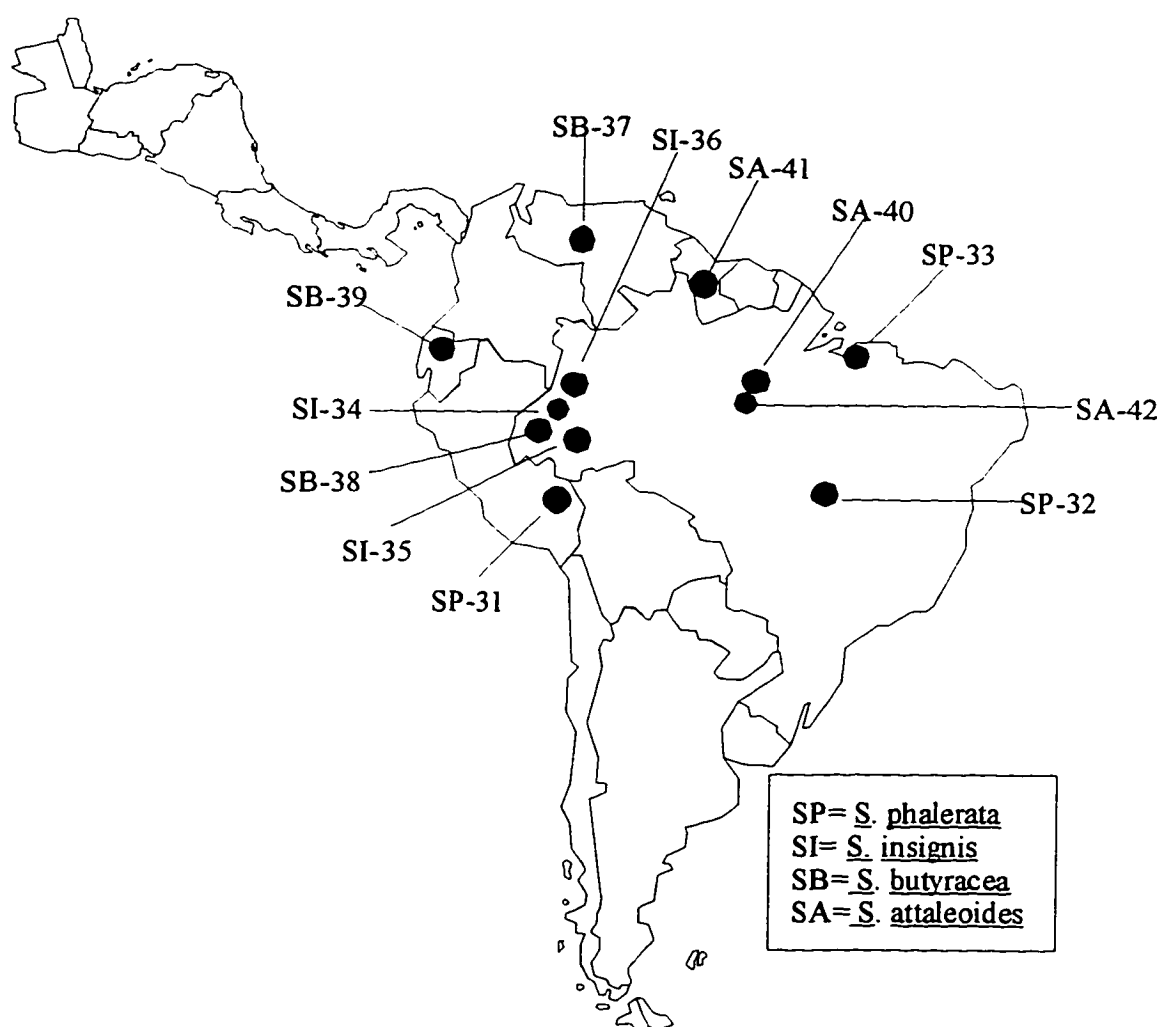


Fig. 45. Distribution of specimens of Scheelea studied.



The genus Attalea (the first in the subtribe) was created by Humboldt, Bonpland and Kunth in 1816, with the description of A. amygdalina. Since then, ca. 16 taxonomic treatments have been produced on the genus (see Glassman, 1977a for the taxonomic history of the genus), including Wessels Boer's (1965) controversial lumping of the other genera in the subtribe into this genus, and Henderson (1995), who followed his thinking. The more recent accounts of the genus (before the lumping) recognize 21 and 22 species (Glassman, 1977a; Uhl and Dransfield, 1977, respectively). The genus Attalea as seen by Henderson (1995) includes 27 species, a very small number, considering that it encompasses species from the other four lumped genera.

The species in the genus Attalea sensu stricto, occur from Panama southwards to Brazil, Peru, Colombia, Paraguay (Uhl and Dransfield, 1987; Glassman 1977a), with the greatest concentration of species in Eastern Brazil (Glassman, 1977a). The species in this genus, as in the other genera of the subtribe, grow in a wide variety of habitats, ranging from mesic conditions of rain and coastal forests to drier habitats, such as cerrados and savannas.

For this study, nine of the mostly accepted species of Attalea were taken as representatives of the traditional genus (Figures 46-50). Five of them showed "pure" anatomical patterns (Figures 46A-D, 47A-H & 48A-H,). The remaining four species

were those that in one way or another showed anatomical features characteristics of any of the other groups (Figures 46E-H, 49A-H & 50A-D). From these four, two showed anatomical signs of Scheelea (A. tessmannii and A. racemosa; Figures 49E-H & 50A-D), one of Orbignya (A. dubia; Figure 46E-H) and the last one (A. nucifera; Figure 49A-D) may be a case of mistaken identification, since it completely fits the Scheelea pattern, having little or nothing in common, anatomically, with Attalea.

Attalea is, anatomically, very closely related to the Orbignya group, especially to the Brazilian group of species. These two groups share many similar anatomical characters, making their separation most difficult. However, a few distinctive characters can be used for separating Attalea from the Orbignya group: 1) the hypodermis in Attalea is formed by only one layer of rectangular cells; 2) adaxial fibers are arranged in medium to large bunches, always located below the hypodermis; 3) abaxial fiber groups are lacking, or when present, they occur in very small number, located above hypodermis in the spongy mesophyll; 4) primary veins are large and pear-shaped; and 5) secondary and tertiary veins are large, with fibrous lower portions always forming buttresses. The other characters, as can be seen from the description of the groups, and from comparison in tables, although very distinctive in relation to the other groups, are basically very similar in Attalea and Orbignya. Mixed anatomical patterns were observed in A. dubia, A. racemosa, A. tessmannii, and A. nucifera, and are discussed below.

The name given to A. dubia (Mart.) Burret is easily understood by examining its anatomical structure. A mixture of two patterns could be discerned: Attalea and Orbignya share several of their most distinguishable characters in this species. Only two specimens were available in the NYBG herbarium, both collected in the same area: eastern Brazil, state of São Paulo. One of the specimens shows clear signs of crossings between species of Attalea and Orbignya in its leaf anatomy; the other specimen is more of the Attalea type, but still with some mixture. The major anatomical signs of Orbignya in A. dubia (Figure 46E-H) include: 1) a second hypodermal layer (although intermittent, broken at several points), with more roundish cells, below Attalea's characteristic rectangular cells in one specimen (in the other specimen, only one layer); 2) presence of a distinguishable mid-secondary vein; 3) secondary and tertiary veins with their fibrous lower portions above hypodermis, not forming buttresses in one specimen (in the other, large buttresses characteristics of Attalea are formed); and 4) stomates with completely sunken guard-cells (second specimen only slightly sunken, typical of Attalea).

Attalea dubia is an arborescent palm, 5-7 (-25) m tall, distributed along the Atlantic coast of Brazil (states of Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina), in disturbed areas or in lowland rain forest (Henderson et al., 1995). In some of its areas of occurrence this species is locally called babassu; it is also a synonym for Orbignya dubia Martius. Glassman (1977b), in his preliminary

taxonomic studies in the genus, concluded that O. dubia was definitely not an Orbignya, and transferred it to Attalea, on the basis of the morphology of the male flowers. In terms of geographical distribution, this possible case of crossed patterns is not difficult to understand, since there are some populations of Orbignya oleifera Burret in the neighboring state of Minas Gerais, and it is known that in the past, the extreme southern range of that species was the state of São Paulo (Markley, 1971), where these two specimens of A. dubia were collected (Figure 51).

Because of the greater proximity of A. dubia to the Attalea group, and of this group to the Orbignya group, if A. dubia is indeed a hybrid, it could not be demonstrated from the results of the analyses. PCA and cluster analysis both placed the two specimens in the Attalea group; cladistic analysis resolved A. dubia with A. pindobassu. The results from the multivariate and cladistic analyses could not confirm the hybrid status suggested by the mixed patterns observed and reported in the descriptions.

The three specimens of Attalea racemosa Spruce taken for this study showed quite a confusing mixture of patterns. The overall pattern is that shown by Scheelea, and only a small number of anatomical signs of Attalea could be seen. One of the specimens (Vásquez 14323) was collected in Peru; the second (Wessels Boer 1894) came from Venezuela; and the third specimen (Torres 3206) was collected in Colombia (Figure 51). The specimen from Venezuela is the one which shows the

Attalea type of anatomy, such as centered, slightly pear-shaped primary veins, formed by large fibers of thick walls, and secondary-tertiary veins with fibrous lower portions forming large buttresses. An examination of the herbarium specimens showed a significant difference in terms of staminate flowers: those in the specimen from Venezuela, visibly differ from the Peruvian specimen's flowers. The Venezuelan flowers are bigger, with big petals enclosing a great number of stamens (33); the Peruvian flowers are much smaller, of narrower petals, enclosing only 16 stamens. The Colombian specimen was sterile and it probably was identified on the basis of its area of collection. The Peruvian and Colombian specimens were collected in more adjacent areas of the Amazon region close to the border between the two countries, within the distribution range of S. insignis; the Venezuelan specimen also came from the Amazon region, southwestern Venezuela, near the Colombian border.

Henderson (1995) reported considerable variation in fruit size and endocarp fiber arrangement, with smaller fruits and scattered endocarp fibers in Venezuela; and on the other extreme, in Peru, larger fruits and large clusters of endocarp fibers. Anatomical variation is also observed in the extremes of the distribution range. On one side, Peruvian and Colombian specimens with an anatomical structure which includes most of Scheelea's patterns; on the other side, the Venezuelan specimen shows features closer to the Attalea-Orbignya patterns (in this case, hard to separate, since the most distinctive characters in these groups are not clearly

expressed). Orbignya-Attalea characters in the Venezuelan specimen include: adaxial hypodermis formed mostly by roundish cells, but with some portions of rectangular cells; an abaxial hypodermis of mostly square cells; shape and position of primary veins; shape and position of secondary and tertiary veins, with formation of large buttresses; adaxial epidermal cells smaller than abaxial, of linear walls; costal cells spindle-shaped mostly, but mixed with rectangular cells, of linear walls; and it is the only specimen with short transverse veins, although mixed with a few long ones, connecting up to 3 large veins; technically, still in the short pattern (Figure 50A-D).

The specimens of A. racemosa showed strong conflict in terms of their character variation and correlation. This was reflected on the results obtained from the analyses performed. PCA and cluster analysis placed all three specimens of this species in the Scheelea group. Cladistic results, on the other hand, were characteristic of hybrid effects: the cladogram completely collapsed with the inclusion of A. racemosa in the analysis, which ended up as a sister species to S. insignis and S. attaleoides.

Attalea tessmannii Burret is an arborescent palm (up to 19 m tall) that grows in the state of Acre (western Brazilian Amazon) and in Peru (regions of Madre de Dios, Ucayali, and Loreto), common in lowland rain forest (Henderson et al., 1995). Three specimens were taken for the study: two from Acre, Brazil (Jangoux 85-027;

Henderson 1656), and one from Loreto, Peru (Nuñez 14976), as shown in Figure 51. The Peruvian specimen, however, turned out to be a case of misidentification, because of mixed plant parts in the herbarium specimen. The leaf parts of the specimen could, first anatomically, and then morphologically, be identified as belong to a Syagrus species. Therefore, only two specimens of A. tessmannii were used in the study.

Attalea tessmannii (along with O. luetzelburgii, A. funifera, and M. maripa), turned out to be, anatomically, one of the most easily recognizable species in the subtribe, because of the bumps formed on the lower surface of the leaf blade, below each primary, secondary and tertiary vein (Figure 49E). This results in a unique sinuous lower surface. Most of the anatomical patterns are those common to the Attalea group, but not in a “pure” way. A few, but important features, recognizable as characteristics of the Scheelea group could be observed, especially in the specimen collected along the Juruá river (Henderson 1656), as opposed to the other specimen, which is almost totally of the Attalea type (Jangoux 85-027, collected near the city of Cruzeiro do Sul, closer to the Peruvian border).

Scheelea-like features recognized in the specimens of A. tessmannii (Figure 49E-H) include: 1) shape (round), and location (closer to abaxial surface) of primary veins; 2) this is the only specimen of Attalea, having its characteristic rhombohedral (adaxial) and spindle-shaped (abaxial -costal) epidermal cells of undulate (although

only slightly) walls; 3) transverse veins are long, connecting 3–8 large veins. Some characters are clearly intermediate between the two groups of patterns, or just mixed in the specimens. Characters such as the epidermal cells, mentioned above, which mix the shape of one group with the type of walls of the other; or roundish and rectangular cells in the hypodermal layer are a couple of examples. Some other characters were only inverted in different specimens: the palisade mesophyll is poorly differentiated in one specimen, but it is well differentiated in the other; one specimen has small fiber groups only on the upper portion of the midrib (Attalea type), while the other has these fibers all the way around the midrib (Scheelea type).

Additional information was obtained from the morphological description of this species, from the collection label, as well as from Henderson (1995), and Henderson et al. (1995). In one of the labels (Jangoux 85-027), the specimen is described as having its pinnae irregularly grouped only in the first fourth of the rachis, and then regularly arranged; the other specimen (Henderson 1656) is said to be clustered with leaflets in different planes. One of the descriptions in the literature (Henderson 1995), defines this species as having leaflets more or less clustered, and the other (Henderson et al., 1995) says the leaflets are definitely clustered, spreading in different planes. The specimens used in this study, however, have regularly arranged leaflets which spread in the same plane. The flowers in the specimens have narrow, free petals, which do not completely enclose the stamens,

and they seem to be somehow intermediate between Attalea and Scheelea. All these facts lead to the suggestion of another case of hybridization.

Three species of Scheelea occur in Acre and in Peru: S. insignis, S. butyracea, and S. phalerata, the last two with mixed anatomical patterns, as shown and discussed before. Scheelea insignis is acaulescent (we may be looking for an arborescent species), and it probably does not reach the distribution range of A. tessmannii. Scheelea butyracea has leaflets regularly arranged and spreading in the same plane, and we would want a species with clustered leaflets, given the uncertainty in relation to this character in A. tessmannii. Scheelea phalerata (the “false” Scheelea), is widespread in most of Peru and Acre, is an arborescent species, and just like A. tessmannii has been described as having clustered leaflets irregularly or regularly arranged leaflets, spreading in the same or in different planes. Although the crossing species in this case can only be guessed, this is undoubtedly, a case of mixed anatomical patterns, with predominance of the Attalea pattern.

The possibility of hybridization in A. tessmannii was tested as part of this study. In the all-taxa PCA both specimens used in the study ended close, but outside the Attalea-related group; in the cluster analysis, probably due to some of its unique characteristics, it ended up forming its own cluster, separated from Attalea. The cladistic results were more supportive of the possibility of A. tessmannii being a

hybrid: its inclusion in the analysis provoked the collapse of the entire cladogram to the basal node. The cladogram becomes almost entirely polytomic, and A. tessmannii does not resolve in the Attalea group.

Attalea nucifera Karsten was first described in 1816. It is a short-stemmed or acaulescent palm, growing in a restricted area along the Rio Magdalena valley in Colombia, reported as scarce in most of its distribution range (Henderson et al., 1995). Only two specimens of A. nucifera from the NYBG herbarium were available for this study, both from Santander, Colombia (Figure 51), and both sterile.

Apparently little or no controversy has surrounded the botanical identity of this species. However, it must be noted that only a few specimens of A. nucifera seem to have been collected and examined. Glassman (1977a) cited Dugand (1953), who supposedly examined two specimens, one from the Dept. Santander and the other from Dept. Bolivar, both from Colombia, which corresponded to A. nucifera. Henderson et al. (1995) do not list the specimens examined for the establishment of their field characters for this species, but probably the specimens examined were that sterile material at the NYBG herbarium along with the original description by Karsten.

Attalea nucifera is definitely the most intriguing species included in this study. The anatomical patterns completely fit those defined as characteristic of the Scheelea

group, and no signs of other patterns could be observed (Figure 49A-D). The fact is that, technically, A. nucifera can be considered a Scheelea: it grows in an area close to where other Scheelea are known to grow (at least S. butyracea), and it has 6 stamens, one of the requirements that, traditionally, have separated Scheelea from the other genera. PCA and cluster analyses placed this species in the Scheelea group. In the cladistic analysis, it forms a trichotomy with S. insignis and S. attaleoides, without causing any other significant topological change in the cladogram; even the number of steps is only increased by a few (2) for its placement in that position. Attalea nucifera is, indeed, a case for further study.

Fig. 46. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Attalea
oleifera (AO-43 & AO-44); E, F, G, H - A. dubia (AD-46 & AD-47).

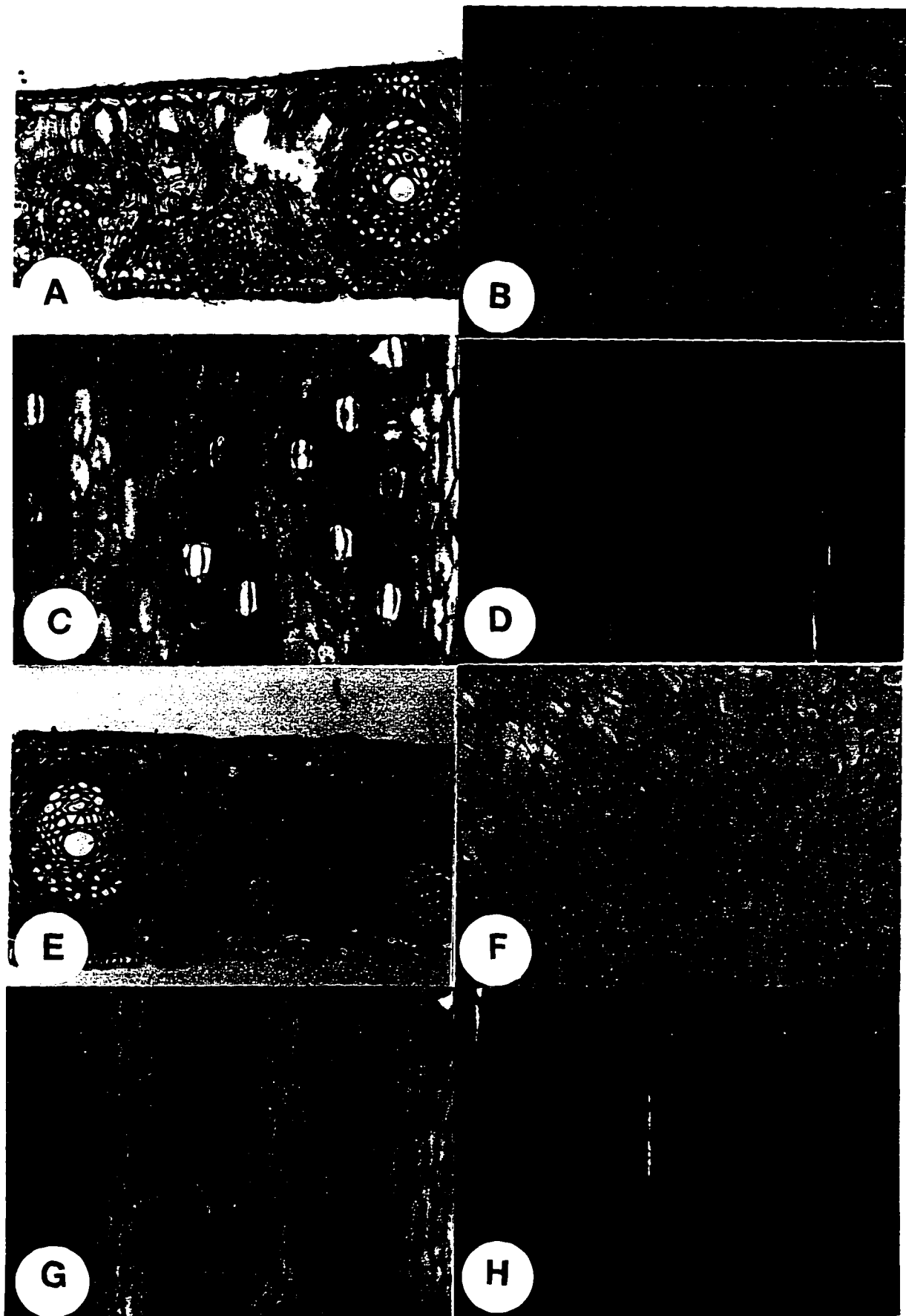


Fig. 47. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Attalea
funifera (AF-48, AF-49 & AF-50); E, F, G, H - A. geraensis (AG-52 & AG-53).

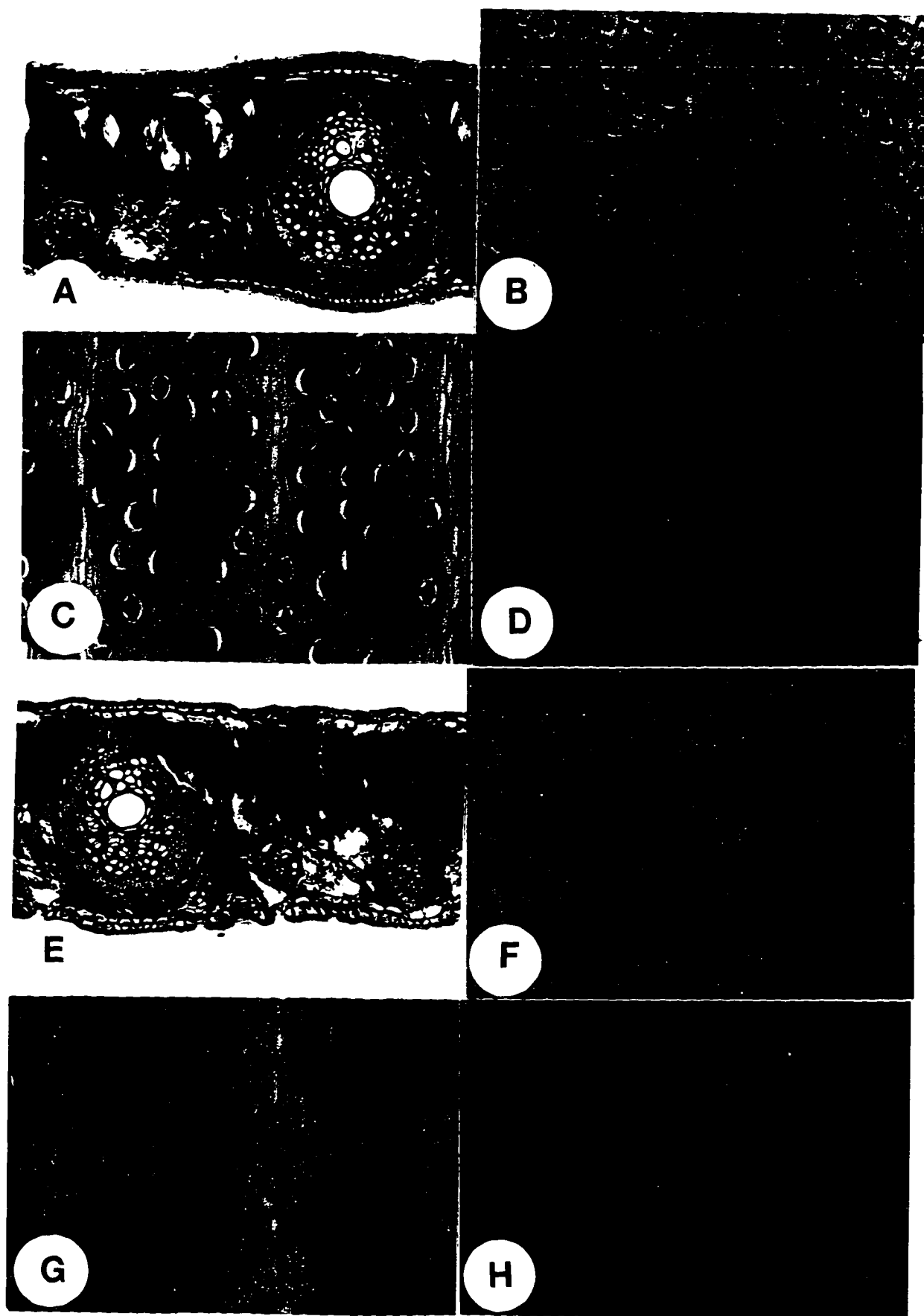


Fig. 48. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Attalea humilis (AH- 54); E, F, G, H - A. pindobassu (AP-56 & AP-57).

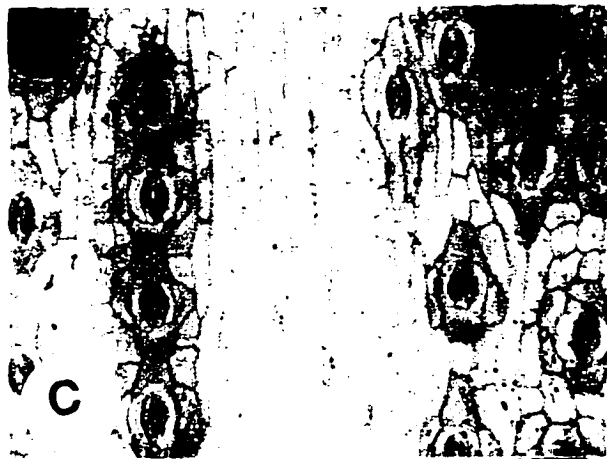
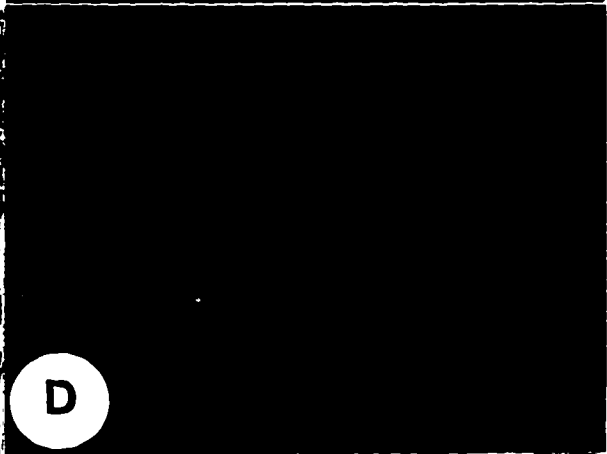
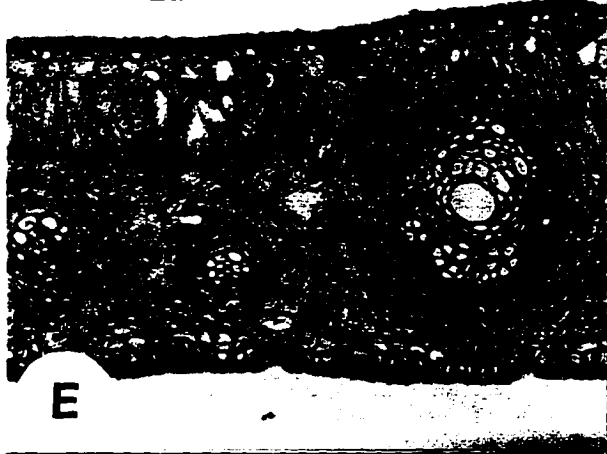
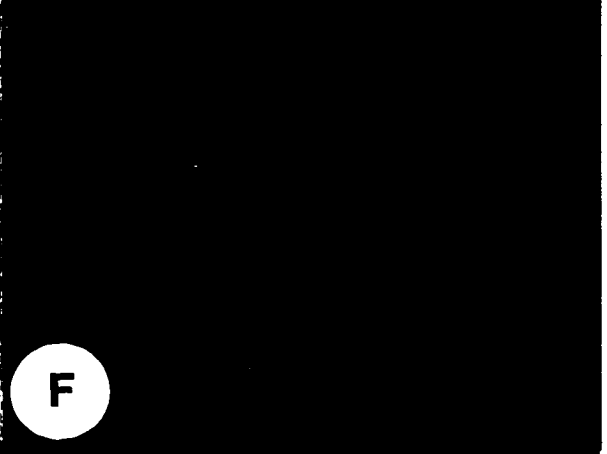
**A****B****C****D****E****F****G****H**

Fig. 49. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Attalea
nucifera (AN-58 & AN-59); E, F, G, H - A. tessmanni (AT-60 & AT-62).

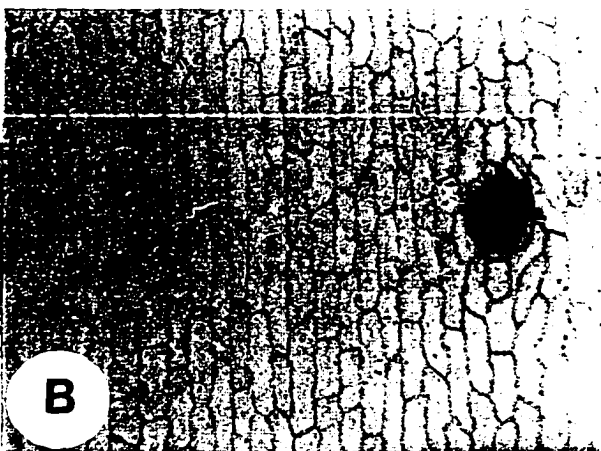
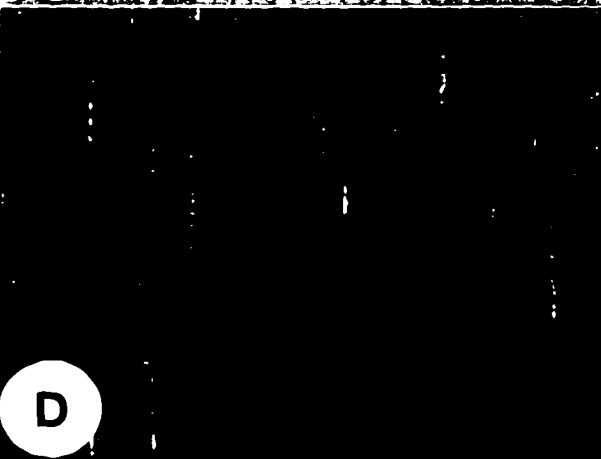
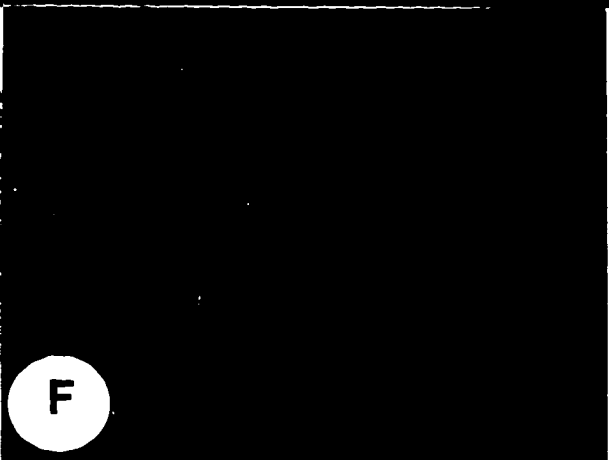
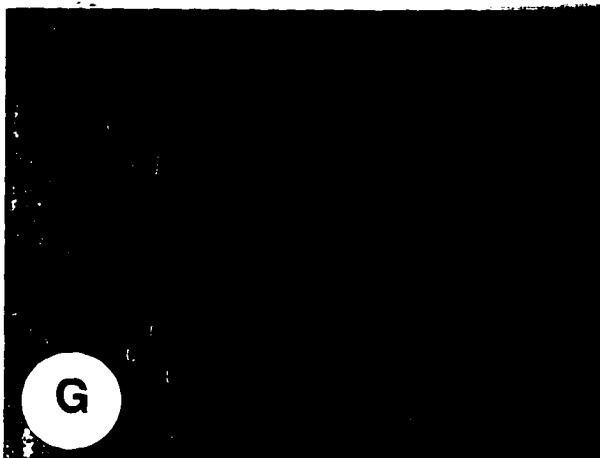
**A****B****C****D****E****F****G****H**

Fig. 50. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Attalea racemosa (AR-63, AR-64 & AR-65).

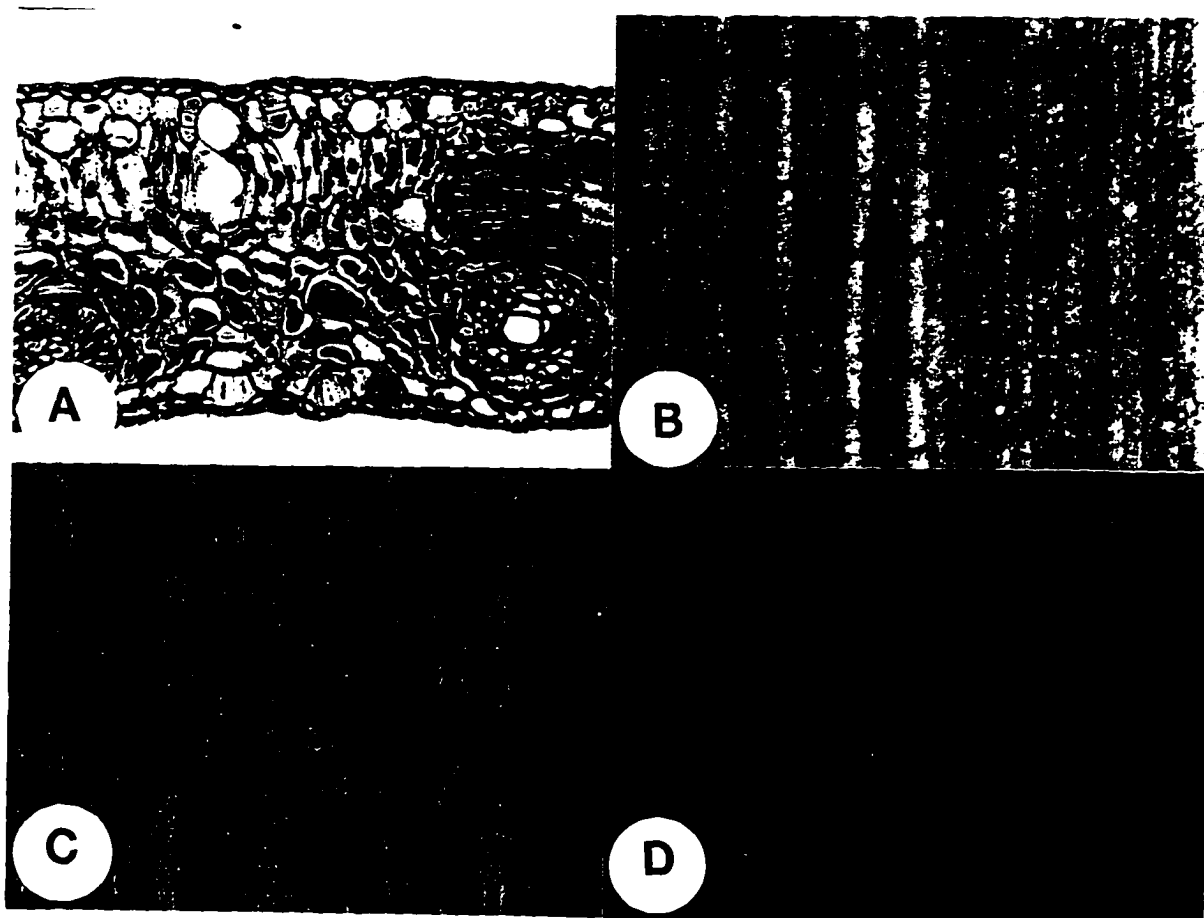
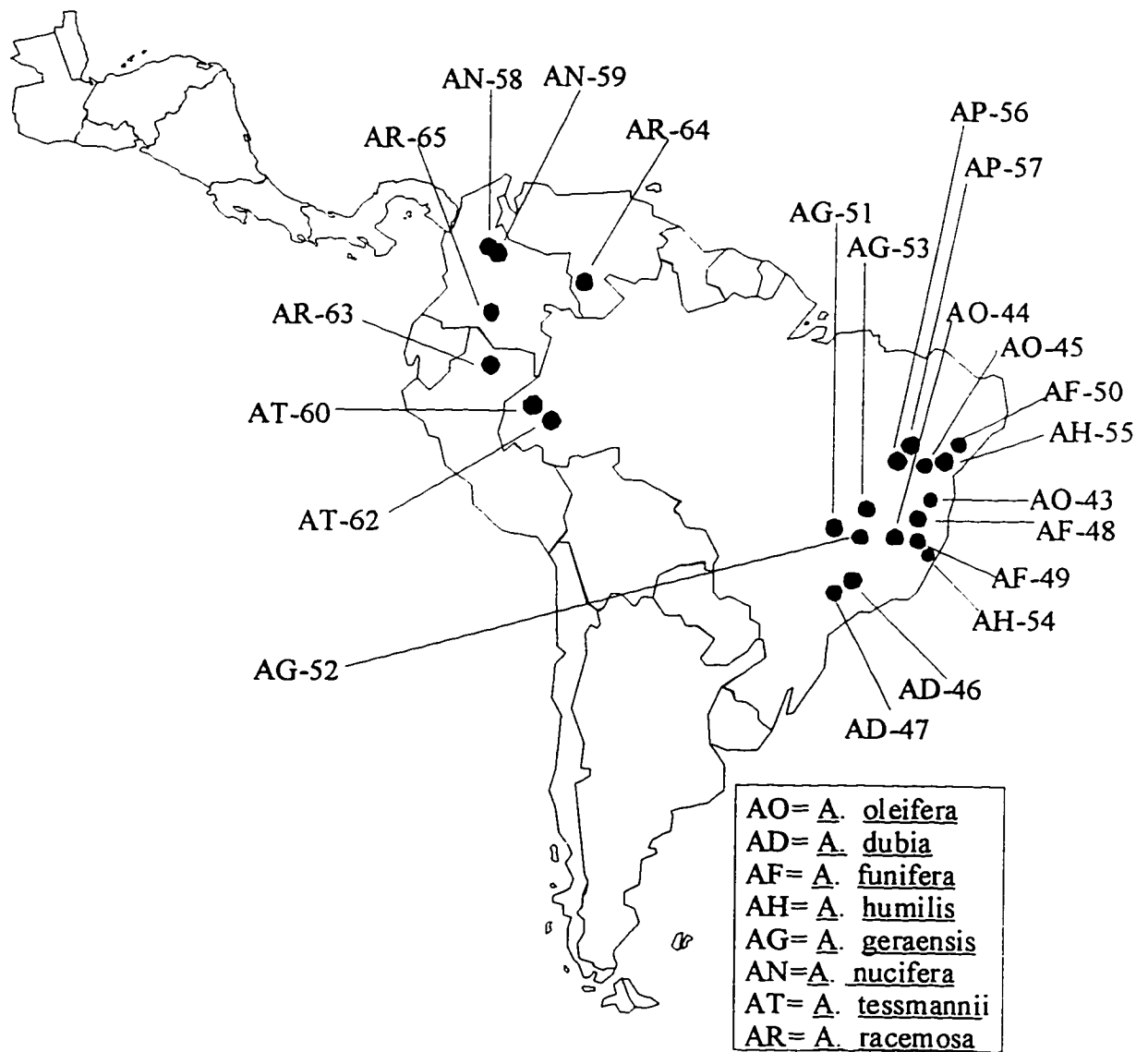


Fig. 51. Distribution of specimens of *Attalea* studied.



Maximiliana maripa (Corrêa) Drude has a very widespread distribution in northern South America, where it grows in ca. 10 countries, in a variety of habitats, from lowland forests to secondary forests, and in open, disturbed areas as well. Taxonomically, M. maripa has a long record of changes and controversy; Henderson et al. (1995) list 23 names as synonyms for this species, under four other genera, which include Attalea, Englerophoenix, Scheelea, and Palma. The shrinking of the genus started with Glassman (1978), who reduced most of the names in Maximiliana to synonymy, leaving only two valid species (M. macropetala Burret, and M. martiana Karsten); later, Uhl and Dransfield (1987) considered the genus to be monotypic, and M. maripa as its only species.

Maximiliana can be readily distinguished from the other groups on the basis of some distinctive anatomical characters (Figure 52A-D): 1) spindle-shaped adaxial epidermal cells, of linear walls, could only be found in this group; 2) both adaxial and abaxial hypodermal cells are smaller than in the other groups; 3) it has the biggest primary veins among all groups – they are so big they form bumps on both surfaces of the lamina below and above each primary vein; 4) hairs are very infrequent on both surfaces; 5) and silica bodies are unusually big.

Maximiliana seems, anatomically, more related to the Scheelea group. Many character states are similar in these two groups; however, the differences are also very clear. Besides those mentioned above, Maximiliana also has these

distinguishing features(Figure 52A & 52D): 1) primary veins are pear-shaped, formed by small fibers of thick walls; 2) secondary and tertiary veins are elongate, with only the tip of the fibrous lower portions going through the hypodermis, technically forming buttresses, although not much contact is made with the epidermis; 3) transverse veins are short.

Henderson et al. (1995) considered Maximiliana maripa (as Attalea maripa) one of the most distinct species in the subtribe, which in some respects resembles Syagrus in the subtribe Butiinae; they consider the possibility of M. maripa to be eventually recognized at generic level. This potential taxonomic proximity of M. maripa to the genus Syagrus was also one of the reasons to include three species of Syagrus in this study. Like Henderson et al. (1995), I had also noticed the morphological resemblance between M. maripa and some species in the genus Syagrus; this resemblance seemed to be a worth anatomical investigation. The separation of the genera in the subtribe Butiinae from those in the Attaleinae is made mostly on the basis of the type of inflorescences produced in the two groups: the Attaleinae is bisexual (staminate and pistillate inflorescences), and the Butiinae is unisexual (inflorescences with both staminate and pistillate flowers). Maximiliana maripa, besides the usual staminate and pistillate inflorescences, also produces inflorescences with both staminate and pistillate flowers, which brings it closer to the Butiinae. Figure 53 shows the locals of collections of the specimens of M. maripa studied.

Fig. 52. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D -
Maximiliana maripa (MM-66, MM-67 & MM-68).

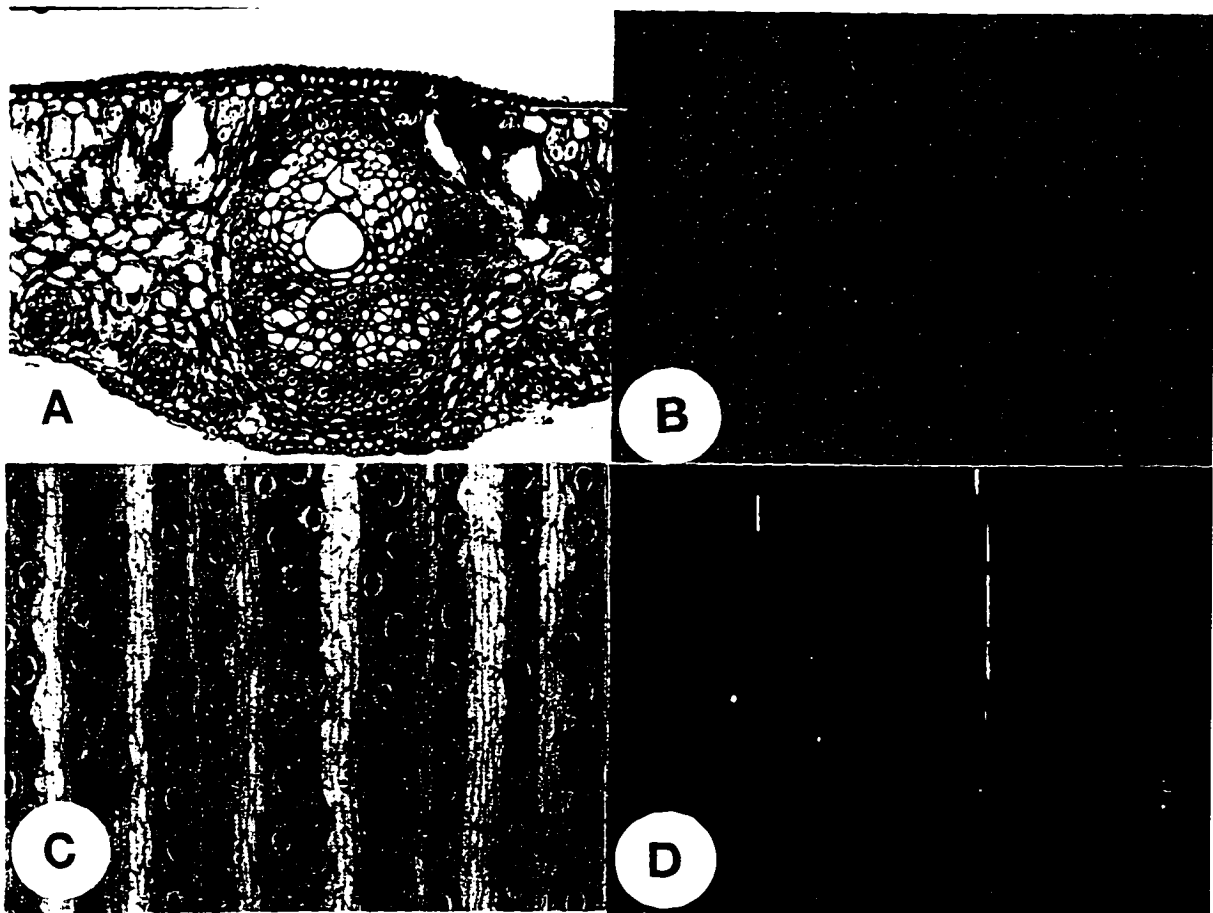


Fig. 53. Distribution of specimens of Maximiliana maripa studied.



The anatomical structure of the three specimens of Syagrus suggested this to be a more anatomically heterogeneous genus than those in the Attaleinae. The three species of Syagrus examined appeared to be less closely allied to one another than the species in the Attaleinae. Conspicuous anatomical differences from one species to another make them easily separable. The locals of collection of the specimens of Syagrus studied are shown in Figure 57.

Syagrus can be anatomically separated from the Attaleinae by several features (Figure 54 & 55). The most distinctive and common in the three species studied, were: 1) trichomes: while clavate and sunken in the Attaleinae, they are shorter, flask-shaped, and only partially sunken in Syagrus (Figure 56); 2) a hypodermal layer usually of octagonally shaped cells, bigger than the Attaleinae type; 3) the arrangement of fibers on the adaxial surface, although variable among species, sometimes in straight horizontal rows (not seen in the Attaleinae), or large, square groups of fibers; 3) characteristic flat buttresses formed by lower portions of secondary and tertiary veins; 4) although the transverse vein patterns are variable from one species to another, they showed strong differences as compared to the Attaleinae: transverse are always short, but sometimes very few, or very thick, or connecting mostly secondary and tertiary veins, and just a few large veins. Some other differences exist, but they vary from species to species, and that makes it difficult to define them as common feature for the genus.

The anatomical study showed some similarity between Maximiliana maripa and Syagrus. The most striking of them is the formation of bumps on both sides of the leaf blade, below each primary vein. These veins are large, widely spaced, and pear-shaped, just like in Maximiliana; the type of fibers forming them is, however, different: Maximiliana's primary veins are always formed by small fibers, of thick walls, while in Syagrus fibers are large. As in Maximiliana, trichomes are very infrequent in Syagrus, although the shape is completely different in the two groups, as pointed out before. Syagrus cocoides (Figure 55) showed, overall, the most similar leaf anatomy compared to M. maripa, including those conspicuous bumps on the lamina formed by the primary veins.

The results indicated that Maximiliana maripa is anatomically closer to Scheelea than to Syagrus. Cladistic results showed four synapomorphies separating M. maripa and the outgroups from the rest of the Attaleinae; separation from Scheelea, on the other hand, was not well supported.

Fig. 54. Cross sections, adaxial and abaxial epidermis, and clearings: A, B, C, D - Syagrus amara (SYA-76); E, F, G, H - S. comosa (SYC-77).

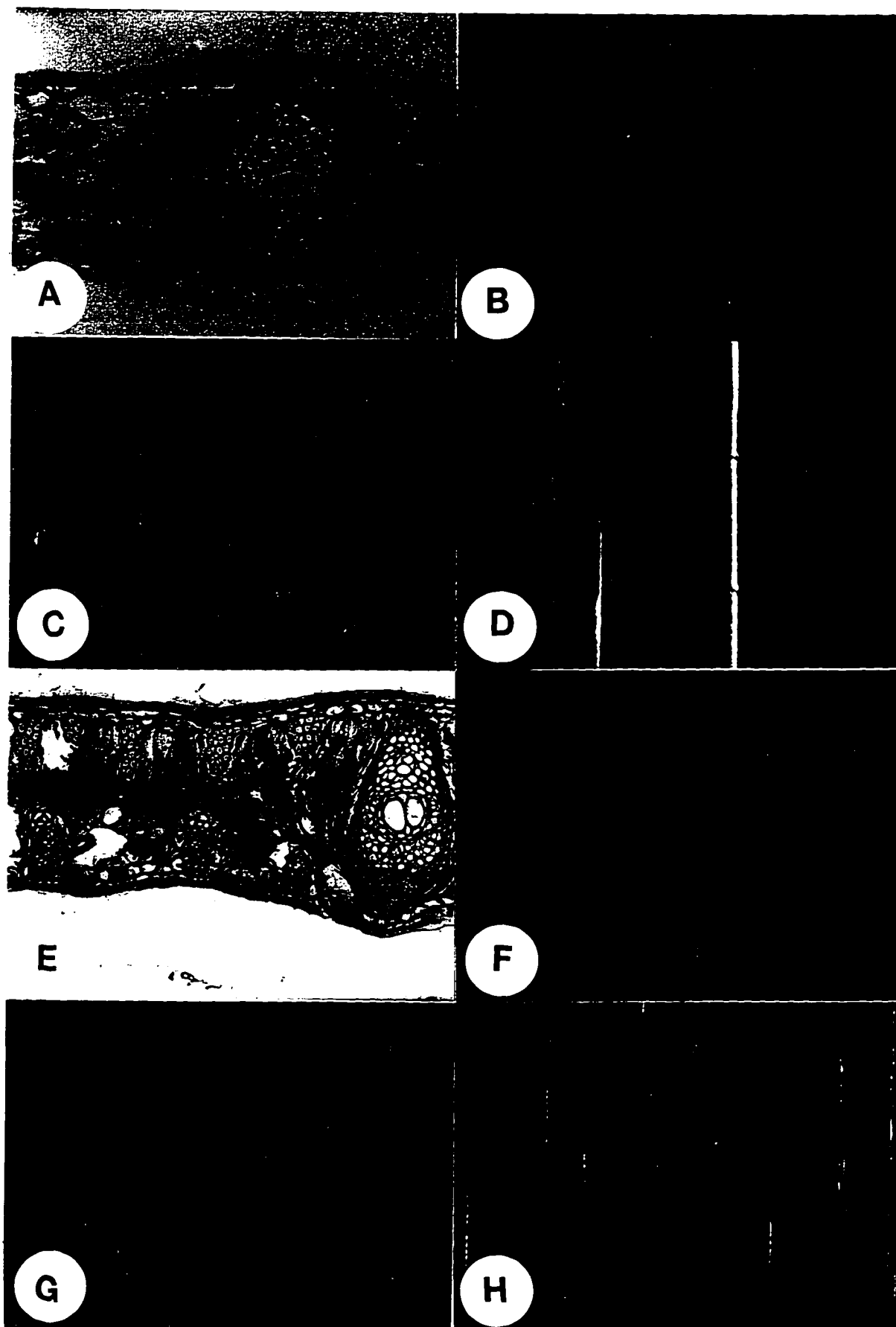


Fig. 55. Cross sections, adaxial and abaxial epidermis, and clearing: A, B, C, D - Syagrus
cocooides (SC-78)

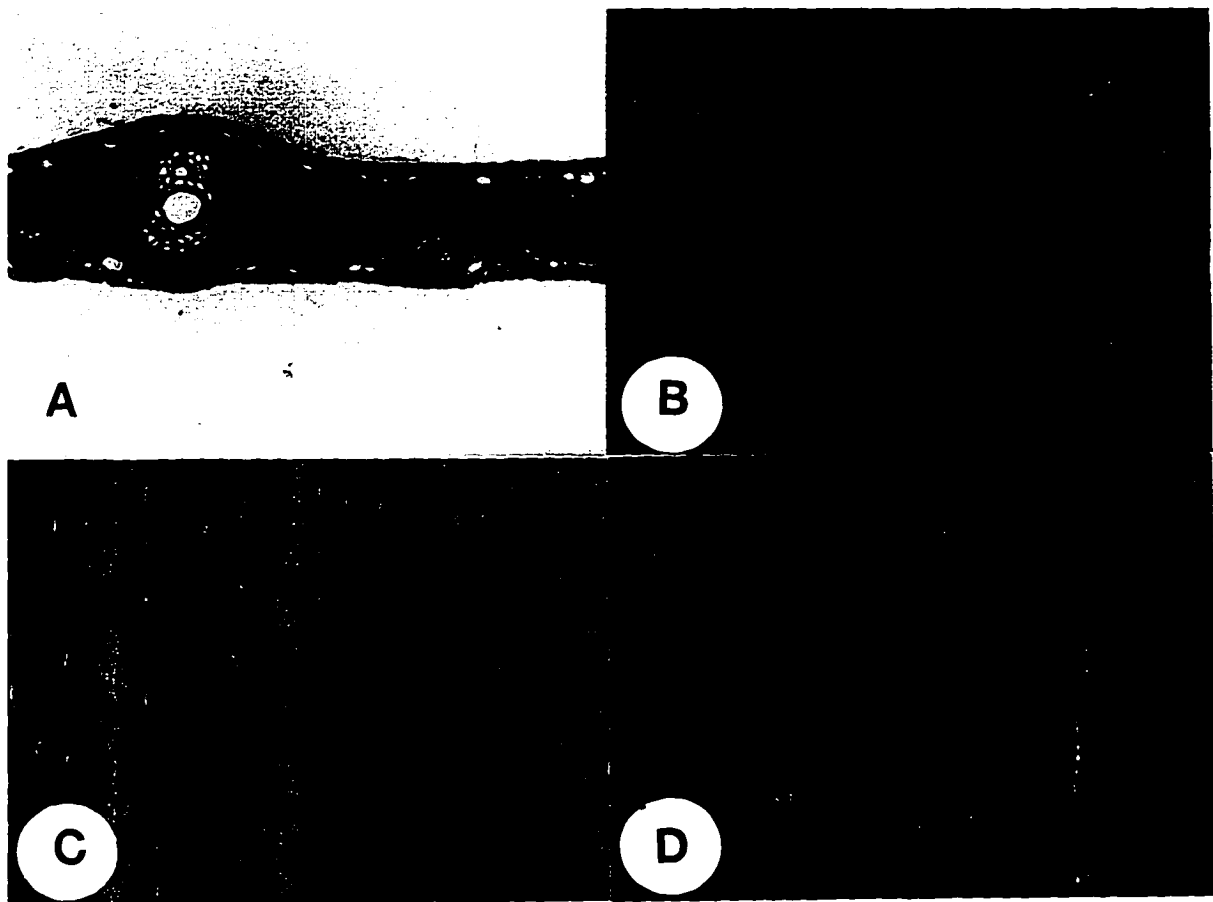
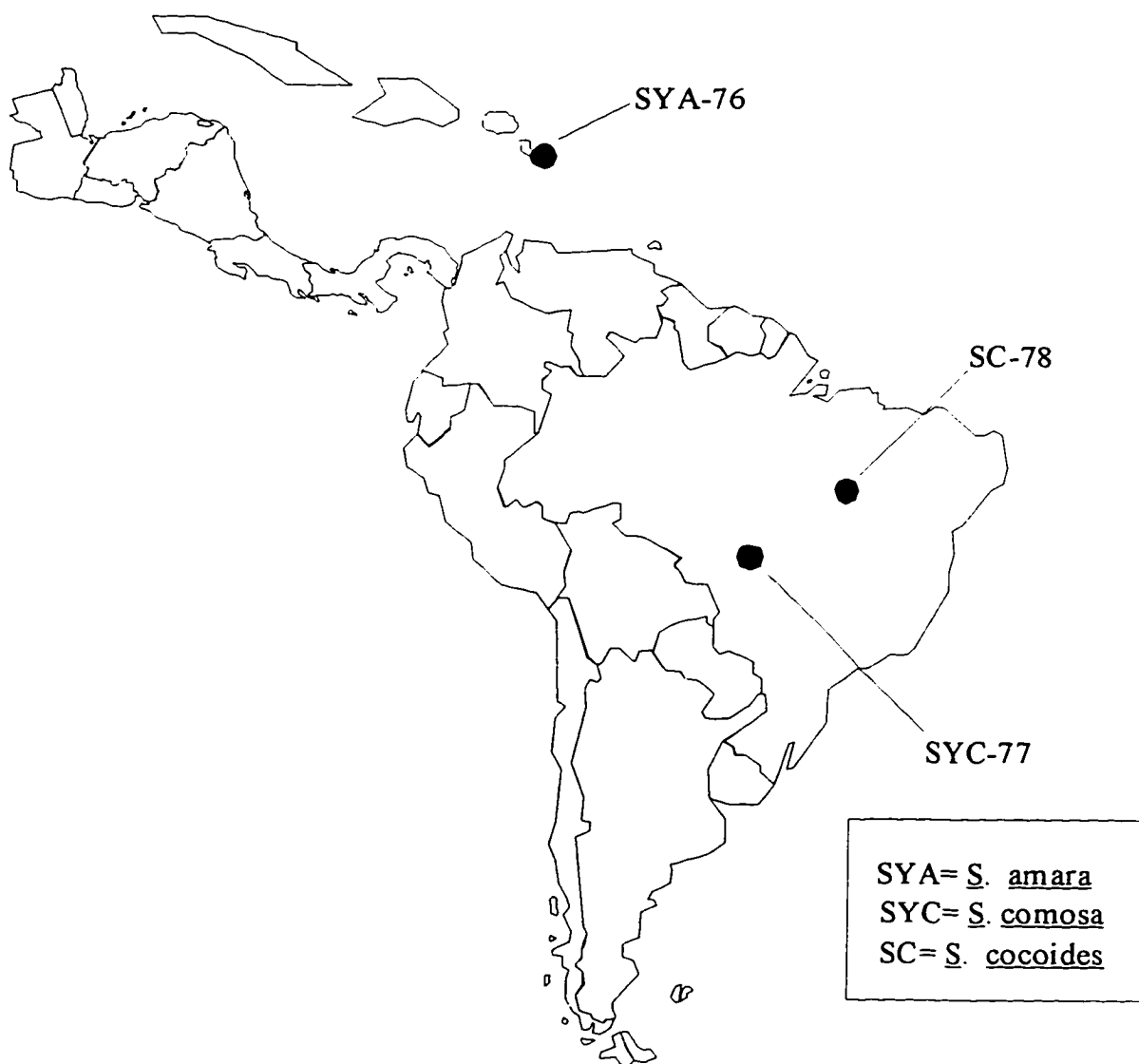


Fig. 56. Trichomes: A - Clavate, sunken in the *Attaleinae*; B - flask-shaped, partially sunken in *Syagrus*.



Fig. 57. Distribution of the specimens of Syagrus studied.



Hybridization in the Attaleinae - Case Studies

The propensity of the species in this subtribe to hybridize seems to be a major contribution to their high morphological variability, and hence, to the taxonomic confusion that has been characteristic of this group. Determining the status of purported hybrids in palms has most frequently been based on morphology as discussed later, but this study confirmed the usefulness of leaf anatomical characters in the identification of hybridization cases in palms. It is known and reported (but not studied) that all “genera” of the subtribe are involved in hybridization, producing both intergeneric (if these groups are to be considered different genera) and interspecific hybrids. The cases reported are:

1. Markleya dahlgreniana Bondar. (Orbignya phalerata Martius x Maximiliana maripa (Corrêa) Drude).
2. Attalea colenda (O. F. Cook) Balslev & Henderson (according to Glassman (unpublished) unknown species of Attalea and Orbignya or Maximiliana).
3. x Attabignya minarum Balick, Anderson & Medeiros-Costa (Orbignya oleifera Burret x Attalea oleifera Barb. Rodr.).
4. Attalea x piassabossu Bondar (A. funifera Mart. ex Spreng. X A. oleifera Barb. Rodr.)
5. Orbignya x teixeirana (Bondar) Balick, Pinheiro & Anderson (Orbignya phalerata Martius x Orbignya eichleri Drude).

From these cases, O. x teixeirana is the only one that has been studied, both morphologically and anatomically, and its hybrid status formally established (Balick et al., 1987). The determination of the hybrid status of O. x teixeirana using leaf anatomy was relatively easy. As it could be seen from the anatomical descriptions of O. phalerata and O. eichleri, they are not anatomically similar, and it constitutes one of the few cases of easy anatomical separation at the species level within the Attaleinae. At the descriptive level, the hybridization could be characterized on the basis of characters such as the number of hypodermal layers: two in O. phalerata, one in O. eichleri, and basically one continuous layer in O. x teixeirana, but with a second lower layer, intermittent, often broken in many points. Orbignya phalerata does not form buttresses, but O. eichleri does form large buttresses, and the hybrid was found to be intermediate, with most of the secondary and tertiary veins above the hypodermis, but with some of them forming medium-size buttresses.

Arrangement, frequency and size of non-vascular fibers was also a useful feature in the characterization of this hybridization case. Morphologically, a number of quantitative and qualitative characters were intermediate in the hybrid. Field observations revealed that the hybrid is limited to areas where both O. phalerata and O. eichleri occur, providing further support for its hybrid status (Balick et al., 1987).

In the present study, possibilities of hybridization could only be supported by the anatomical evidence in the cases of crossings between species of different groups. Between species of the same group (e.g., *A. x piassabossu*, discussed later), the characterization could not be satisfactorily done, because most of the distinctive characters were closer to one of the putative parents. Another problem for the study of these cases of hybridization is the frequent formation of hybrid swarms, with backcrossings between intermediates and the parent species, where remarkable variation in the morphotypes can be observed. The results from this study showed that at least seven new cases must be considered for further study. The anatomical evidence supporting most of the cases of the reported hybrids, convinced me that a considerable proportion of the pronounced morphological variability in the subtribe Attaleinae can be attributed to their propensity to hybridize freely in the wild. The results for each “old” case of purported hybridization in the Attaleinae, are discussed below.

Case Study 1. *Markleya dahlgreniana* Bondar

This taxon occurs in the eastern portion of the Amazon region, in Surinam and Brazil (states of Maranhão and Pará). *Markleya dahlgreniana* was first described by Bondar (1957), who speculated on the possibility of it being a hybrid between *O. phalerata* and *Maximiliana maripa*. Its hybrid status was, however, questioned by Wessels Boer (1965), based on the uniformity of the populations of this species

observed in Surinam. Although most of the palm taxonomists (Moore, 1973; Uhl and Dransfield, 1987; Henderson and Balick, 1987) have been treating M. dahlgreniana as an intergeneric hybrid, its status as such has never been formally changed. The specimens of M. dahlgreniana were collected in three distinct points of its distribution range: one from Surinam (Wessels Boer 805); and two from Brazil (Pará State: Balick 1305; Maranhão State: Pinheiro 89-9) (Figure 62). The specimen from Surinam showed an anatomical structure closer to Maximiliana in many regards, while the Brazilian specimens were closer to Orbignya in most of the characters. The strongest anatomical signs of hybridization in M. dahlgreniana (Figure 58) were:

1. A two-layer hypodermis, with the upper layer of regularly shaped rectangular cells, and the lower layer of more roundish cells (as in Orbignya); the specimen from Surinam was one-layered (as in Maximiliana).
2. A poorly differentiated palisade mesophyll of thin-walled cells (as in Orbignya; Maximiliana has thick-walled palisade cells), and a well differentiated spongy mesophyll of thick walled cells (as in Maximiliana; Orbignya has thin-walled spongy cells).
3. Primary veins pear-shaped (as in Maximiliana) or round (as in Orbignya), forming slight bumps on lamina, below and above veins (not as pronounced as in Maximiliana).

4. Location of lower portions of secondary and tertiary veins: a) going through hypodermis, and slightly touching the hypodermis (as in Maximiliana); b) above hypodermis, with no buttresses formed (as in Orbignya); and c) in a mixed pattern, with most of the veins above, but close to hypodermis, with some forming small buttresses.
5. Stomates with guard-cells sunken (as in Orbignya) or superficial (as in Maximiliana).
6. Adaxial epidermal cells longitudinally extended, spindle-shaped (as in Maximiliana), or obliquely extended, rhombohedral (as in Orbignya); spindle-shaped costal cells, or a mixture of rectangular (as in Maximiliana) and spindle-shaped cells (as in Orbignya).
7. Small fiber bundles all the way around midrib (as in Maximiliana), or only on its upper portion (as in Orbignya).

Anderson and Balick (1988) provided a morphological comparison of the three taxa, showing the intermediate nature of the hybrid. The anatomical evidence supports the speculated hybrid status of M. dahlgreniana, and also supports Orbignya phalerata and Maximiliana maripa as the most likely parent species. In the PCA and clusteranalyses M. dahlgreniana joined the Orbignya group, because of its resemblance to Orbignya. The cladistic analysis produced the most striking results from the analyses performed: the collapse of the entire cladogram to the basal node by simply including M. dahlgreniana in the analysis.

The variation found from one specimen to another, may again be the result of backcrossings, and/or segregation in the hybrid derivatives. In hybrid swarms with frequent backcrossing, the characters tend to be one-sided, especially if introgression occurs (Anderson, 1949). Wagner (1983) says that some or all of the backcross hybrids may be so close to one or the other of the parents that their hybrid origin may be undetected. In Brazil, no populations of M. dahlgreniana have been reported to be seen; this species occurs mostly as isolated individuals, or in very small groups, always in areas where both O. phalerata and M. maripa also occur. Individuals of M. dahlgreniana are easily spotted, for they resemble a babassu palm in overall appearance, but at the same time, different, because of the clustered pinnae. Tables 40 through 50 provide comparison of many anatomical in M. dahlgreniana with the parents O. phalerata and M. maripa.

Table 39. Comparison of anatomical characters in Orbignya phalerata, Markleya dahlgreniana and Maximiliana maripa - Adaxial Epidermis.

Taxa	Epidermis - Size Cross Section View	Adaxial Epidermis Thickness	Adax. Epid. Cell Extension	Adaxial Epidermis -Cell Shape	Adaxial Epidermis - Cell Walls
<i>O. phalerata</i>	Adaxial cells smaller than abaxial	thick	longitudinal oblique	rectangular rhombohedral	undulate linear
<i>M. dahlgreniana</i>	Adaxial cells smaller than abaxial	thick	longitudinal oblique	spindle-shaped rhombohedral	linear
<i>M. maripa</i>	Adaxial cells are bigger than abaxial	thick	longitudinal	spindle-shaped	linear

Table 40. Comparison of anatomical characters in Orbignya phalerata, Markleya dahlgreniana and Maximiliana maripa - Abaxial Epidermis.

Taxa	Abaxial Epidermis Thickness	Abaxial Epidermis Costal Cells Orientation	Abaxial Epidermis Costal Cells Shape	Abaxial Epidermis Costal Cells - Walls	Abaxial Epidermis Intercostal Cells Walls	Stomates Guard-Cells	Stomates Arrangement
<i>O. phalerata</i>	thick	longitudinal	spindle-shaped	linear undulate	linear	sunken	not in def. files
<i>M. dahlgreniana</i>	thick	longitudinal	spindle-shaped rectangular	linear	linear	superficial sunken	not in def. files
<i>M. maripa</i>	thick	longitudinal	rectangular	linear	linear	superficial	files

Table 41. Comparison of anatomical characters in Orbignya phalerata,
Markleya dahlgreniana and Maximiliana maripa - Hypodermis.

Taxa	Adaxial Hypodermis Number of layers	Adaxial Hypodermis Shape - Cells
<i>O. phalerata</i>	2	rectangular roundish
<i>M. dahlgreniana</i>	1-2	rectangular roundish
<i>M. maripa</i>	1	roundish

Table 42. Comparison of anatomical characters in Orbignya phalerata,
Markleya dahlgreniana and Maximiliana maripa - Non-vascular fibers.

Taxa	Adaxial Fibers Lignification	Adaxial Fibers Position	Abaxial Fibers Position
<i>O. phalerata</i>	slightly lignified	mostly in between two hypodermal layers	in between hypodermis and epidermis
<i>M. dahlgreniana</i>	slightly lignified	mostly in between the two layers & above single layer	in between hypodermis and epidermis
<i>M. maripa</i>	slightly lignified	above single hypodermal layer	in between hypodermis and epidermis

Table 43. Comparison of anatomical characters in Orbignya phalerata,
Markleya dahlgreniana and Maximiliana maripa.

Quantitative characters - Non-vascular fibers.

Taxa	Adaxial Fibers - Number of Groups			Adaxial Fibers Number of Fibers per Group		Abaxial Fibers - Number of Groups			Abaxial Fibers - Number/Fibers/Group			
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	260-275	317.5	81.31	4-9	6.5	3.53	75-80	77.5	3.53	3	3	-
<i>M. dahlgreniana</i>	190-526	390	176.9	3-6	4.3	1.52	25-273	147	124.1	2-5	3.3	1.52
<i>M. maripa</i>	289-352	324	32.1	2-3	2.3	0.57	94-104	98.3	5.1	4-6	4.6	1.15

Table 44. Comparison of anatomical characters in Orbignya phalerata,
Markleya dahlgreniana and Maximiliana maripa - Chlorenchyma.

Taxa	Palisade Differentiation	Palisade Number of layers	Spongy Differentiation
<i>O. phalerata</i>	poorly differentiated	2	poorly differentiated
<i>M. dahlgreniana</i>	well differentiated or not	1	well differentiated
<i>M. maripa</i>	well differentiated	1	well differentiated

Table 45. Comparison of anatomical characters in Orbignya phalerata,Markleya dahlgreniana and Maximiliana maripa.

Quantitative characters - Chlorenchyma.

Taxa	Palisade - Thickness(μ)			Spongy Mesophyll Number of layers			Spongy Mesophyll Thickness(μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	50	50	-	6-7	6.5	0.70	80-100	90	14.14
<i>M. dahlgreniana</i>	40-60	53.3	11.54	5-7	6	1	90-120	110	17.32
<i>M. maripa</i>	50-60	56.6	5.77	6	6	-	90-120	100	17.32

Table 46. Comparison of anatomical characters in Orbignya phalerata,Markleya dahlgreniana and Maximiliana maripa - Venation.

Taxa	Primary Veins Position	Prim. Veins Type of Fibers	Prim. Veins Shape	Mid- secondary	Sec/Tert Veins Buttresses	Sec/Tert Veins Position	Sec/Tert Inner Sheath	Transverse Vein - Pattern
<i>O. phalerata</i>	Centered	Small - thick walls	round	present	absent	above hypodermis	incomplete	short
<i>M. dahlgreniana</i>	Centered	small - thick walls	pear- shaped round	present or not	present or not	above and through hypodermis	complete or incomplete	short
<i>M. maripa</i>	Centered	Small - thick walls	pear- shaped	not present	present	through hypodermis	complete	short

Table 47. Comparison of anatomical characters in Orbignya phalerata,
Markleya dahlgreniana and Maximiliana maripa.

Quantitative characters - Primary veins.

Taxa	Primary Veins - Number			Primary Veins - Height (μ)			Primary Veins - Width (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	10-13	11.5	2.12	120.7-136.6	128.6	11.24	112.8-131.5	122.1	13.22
<i>M. dahlgreniana</i>	8-14	10.6	3.05	165.7-186.2	173.4	11.16	150-161.4	156.3	5.80
<i>M. maripa</i>	5-7	6	1	263.3-316.0	293.9 3	27.37	211.6-242.5	228.7	15.71

Table 48. Comparison of anatomical characters in Orbignya phalerata,
Markleya dahlgreniana and Maximiliana maripa.

Quantitative characters - Secondary and tertiary veins.

Taxa	Sec./Tert. Veins - Number			Sec./Tert. Veins - Number/Between L.V.			Secondary Veins - Height (μ)			Tertiary Veins Height (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	115-132	123.5	12.12	14	14.0	-	62.8-80	71.4	12.16	45.0-55.0	51.5	-
<i>M. dahlgreniana</i>	77-162	120.3	42.52	7-12	10	2.64	65-82	75.7	8.90	48.7-67	60.4	10.16
<i>M. maripa</i>	98-145	119.6	23.71	24-32	27.6	4.04	63-67.7	65.2	2.36	41.1-43.2	42.3	1.09

Table 49. Comparison of anatomical characters in Orbignya phalerata,
Markleya dahlgreniana and Maximiliana maripa - Midrib.

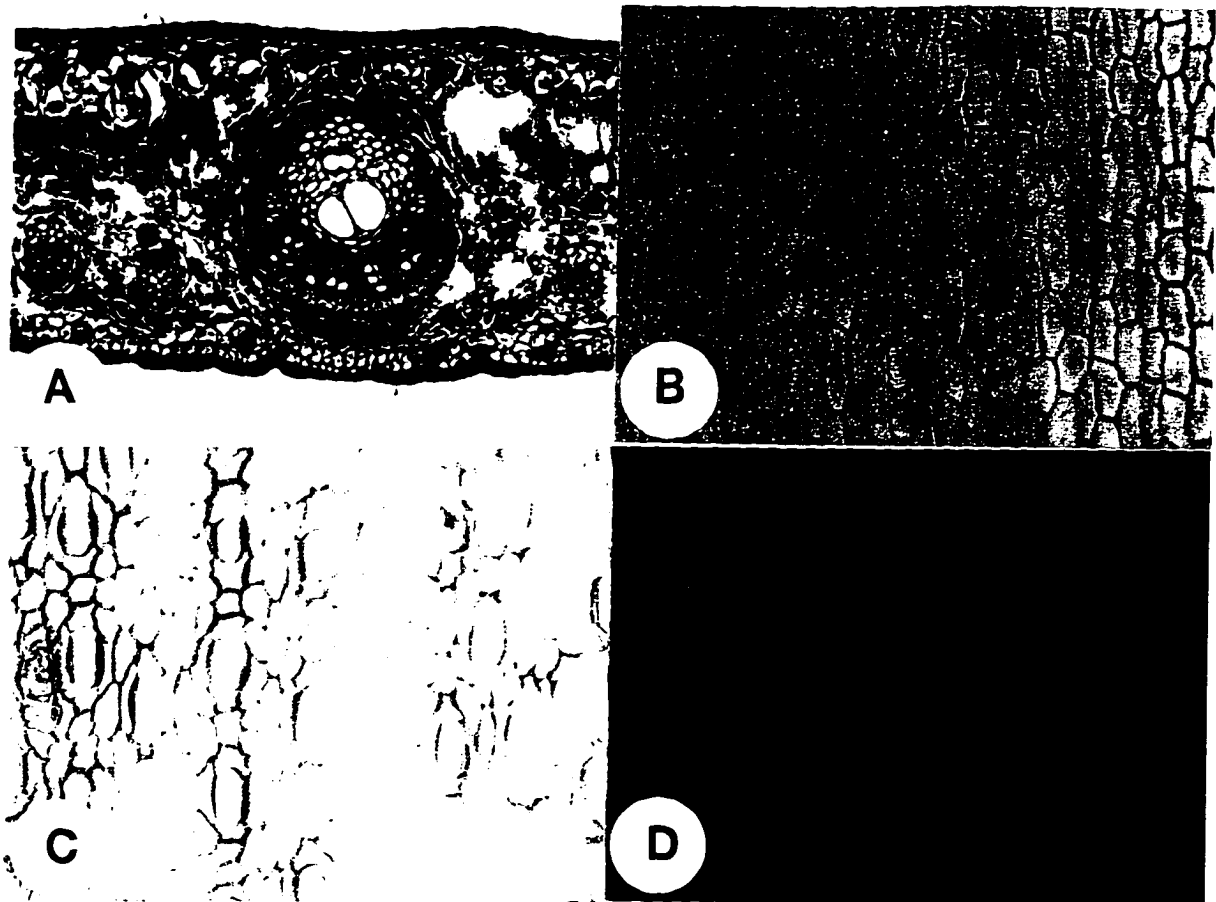
Taxa	Midrib Shape	Midrib Expansion Cells # layers	Midrib Expansion Cells - Confluence	Fibers Bundles on Midrib
<i>O. phalerata</i>	Rectangular	3-6	confluent	upper portion only
<i>M. dahlgreniana</i>	Rectangular	3-5	confluent or not	around midrib or on upper portion only
<i>M. maripa</i>	Triangular	3-4	not confluent	around midrib

Table 50. Comparison of anatomical characters in Orbignya phalerata,
Markleya dahlgreniana and Maximiliana maripa.

Quantitative Characters - Midrib.

Taxa	Midrib - Size			Midrib - Number of VBs		
	range	mean	SD	range	mean	SD
<i>O. phalerata</i>	1.7-3.1	2.47	0.52	18-22	20	1.06
<i>M. dahlgreniana</i>	1.46-2.5	2.0	0.52	8-24	18	8.71
<i>M. maripa</i>	2.1-2.8	2.36	0.37	18-20	18.6	1.15

Fig. 58. Cross section, adaxial and abaxial epidermis, and clearing: A, B, C, D -
Markleya dahlgreniana (MD-70 & MD-71).



Case Study 2. Attalea colenda (O. F. Cook) Balslev & Henderson

Attalea colenda is an arborescent palm (up to 30 m tall), endemic to western Ecuador and southern Colombia (Pedersen and Balslev, 1992). It grows in the rain forest, as well as in the drier areas. Balslev and Blicher-Mathiesen (1991) suggested that this palm species is endangered in Ecuador, because of habitat destruction, and its deficient regeneration in areas of open pastures, where the palm is left after forest lands are cleared for agriculture. This species was first described as a new genus (Ynesa) by O. F. Cook (1942), and only recently it was definitely transferred to the genus Attalea by Balslev and Henderson, 1987, although they concede that A. colenda differs from most of Attalea species in characters such as arrangement and size of staminate flowers, number of stamens, length of anthers, and its one-seeded fruit. Its placement in the genus Attalea sensu stricto was based on the long, flattened petals and straight anthers of the staminate flowers. (see Balslev and Henderson, 1987, for historical background and taxonomic description of A. colenda). The suggestion by Glassman (unpublished) that this taxon could be the product of crossings between unknown species of Attalea and Orbignya or Maximiliana motivated the investigation of this possibility in this study.

Two specimens of Attalea colenda were anatomically examined, both from Ecuador (Figure 62), both from the province of Manabi, both collected in pasture

lands, the major habitat of this palm, nowadays (Balslev 6027; Blicher-Mathiesen 62617); no specimens from Colombia were available. Most of the anatomical characters in this species are those common to the Attalea group; if this is in fact a hybrid, Attalea is certainly one of the parents; the other parent, however, can only be an Orbignya species, since no anatomical signs of Maximiliana or Scheelea could be found. As pointed out before, Attalea is anatomically closely related to Orbignya, which makes separation of features difficult since many characters are shared by both groups. However, the position of secondary and tertiary veins above the hypodermal layer (Figure 58A), with consequent absence of buttresses, is unique to Orbignya, and that makes Orbignya the only possible second parent in this putative case of hybridization. The depth of guard-cells is more evidence of a possible involvement of Orbignya in this case (Figure 58A). Attalea usually has just slightly sunken stomates. The location of the abaxial fiber groups, in between the hypodermis and epidermis, is more characteristic of Orbignya (in Attalea, when these fibers are not lacking completely, they occur in very small number, located above the hypodermis, embedded in the spongy mesophyll). Figure 58A-D provides a view of cross section, epidermis, and venation patterns in A. colenda. Tables 52 - 63 provide a selective comparison of A. colenda, O. cohune, and Attalea as a group, since a putative species of Attalea as one of the parents could not be hypothesized.

Some facts contributed to considering the possibility of hybridization in the case of Attalea colenda. Earlier in this paper, anatomical evidence of crossings between a

Scheelea and an Orbignya species, was shown when S. butyracea was discussed.

It was then hypothesized, on the basis of geographical distribution, and from the anatomical signs of Orbignya observed in that species as well, that O. cohune could technically be one of the species involved. One of the specimens of S. butyracea studied was also collected in Ecuador, and like A. colenda it showed the one of the most characteristic anatomical characters of an Orbignya: the location of secondary and tertiary veins above the hypodermal layer, with no buttresses formed. Moreover, in S. butyracea, as in A. colenda, there was no sign of a second adaxial hypodermal layer, which increases the likeliness of a species with an one-layered hypodermis to be involved (O. cohune is one-layered), and reduces the possibility of considering the involvement of a Brazilian Orbignya (with a two-layered hypodermis). The distribution range of O. cohune, which reaches up to Colombia, may provide further support for the hypothesis that Orbignya is the parent of A. colenda. Reaching Ecuador, from Central America, is not difficult; on the Pacific side of the Cordillera Central there is an extensive lowland corridor which links northern Ecuador to Panama. Several plant species are known to have been dispersed through this corridor from Central America to Ecuador; O. cohune could very likely have been one of these. Additionally, the presence of Mystrops sp. (Nitidulidae), well-known pollinators of Orbignya phalerata (Anderson et. al., 1988) was observed in staminate inflorescences of A. colenda by Balslev and Henderson (1987), who suggested the possibility that the pollination system in A. colenda is similar to that in Orbignya species, which is pollinated by the same insect. Another interesting fact, that adds to

the possibility of hybridization, is that some morphological characters of A. colenda do not fit in the description of Attalea, i.e. arrangement and size of staminate flowers, number of stamens, length of anthers, and its one-seeded fruit. The anthers of A. colenda are described as “more or less straight, and not coiled or twisted”. The drawings shown by Balslev and Henderson (1987) clearly show anthers with some degree of twisting.

The results from the PCA, cluster and cladistics analyses could not characterize the case of hybridization in Attalea colenda. In the PCA and cluster analyses, A. colenda clustered in the Attalea group. Its inclusion in the cladistic analysis did not produce any major changes in the strict consensus tree, which was increased by just a few more steps (4); A. colenda resolved with A. geraensis (weakly supported) in the Attalea clade. This result, however, does not eliminate the possibility of hybridization, since as often happens in cases of crossings between sister taxa (in this case, sister groups), and unbalanced character distribution (definitely the case, as anatomical characters potentially coming from Orbignya were in very small number), it is resolved with one of the parents (in this case, the parent-group, Attalea).

Table 51. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda - Adaxial Epidermis.

Taxa	Epidermis - Size Cross Section View	Adaxial Epidermis Thickness	Adax. Epid. Cell Extension	Adaxial Epidermis Cell Shape	Adaxial Epidermis Cell Walls
<i>O. cohune</i>	adaxial smaller than abaxial	thick	oblique	rhombohedral	slightly undulate
<i>A. colenda</i>	adaxial smaller than abaxial	thick	oblique	rhombohedral	linear
<i>Attalea</i>	adaxial smaller than abaxial	thick	oblique	rhombohedral	linear

Table 52. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda - Abaxial Epidermis.

Taxa	Abaxial Epidermis Thickness	Abaxial Epidermis Costal Cells Orientation	Abaxial Epidermis Costal Cells Shape	Abaxial Epidermis Costal Cells - Walls	Abaxial Epidermis Intercostal Cells Walls	Stomates Guard-Cells	Stomates Arrangement
<i>O. cohune</i>	thick	longitudinal	spindle-shaped	slightly undulate	slightly undulate	sunken	not in def. files
<i>A. colenda</i>	thick	longitudinal	spindle-shaped	linear	linear	sunken	not in def. files
<i>Attalea</i>	thick	longitudinal	spindle-shaped	linear	linear	slightly sunken	not in def. files

Table 53. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda - Hypodermis.

Taxa	Adaxial Hypodermis # layers	Adaxial Hypodermis Shape of Cells
<i>O. cohune</i>	1	rectangular & roundish
<i>A. colenda</i>	1	rectangular
<i>Attalea</i>	1	rectangular

Table 54. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda - Non-vascular fibers.

Taxa	Adaxial Fibers Lignification	Adaxial Fibers Position	Abaxial Fibers Position
<i>O. cohune</i>	slightly lignified	in between or below hypodermal cells	in between hypodermis and epidermis
<i>A. colenda</i>	non-lignified	below hypodermal layer	in between hypodermis and epidermis
<i>Attalea</i>	lignified	below hypodermal layer	above hypodermis

Table 55. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda - Quantitative Characters: Non-vascular fibers.

Taxa	Adaxial Fibers - Number of Groups			Adaxial Fibers - Number/Fibers per Group			Abaxial Fibers - Number of Groups			Abaxial Fibers - Number/Fibers per Group		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. cohune</i>	400	400	-	3	3	-	85	85	-	3	3	-
<i>A. colenda</i>	245-283	264	26.8	18-20	19	1.41	0-15	7.5	10.6	0-2	1	1.41
<i>Attalea</i>	152-360	227.4	63.8	4-14	8.2	2.52	0-60	25.2	21.9	0-5	2.5	1.80

Table 56. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda - Chlorenchyma.

Taxa	Palisade Differentiation	Palisade - Number of layers	Spongy - Differentiation
<i>O. cohune</i>	poorly differentiated	1-2	poorly differentiated
<i>A. colenda</i>	poorly differentiated	2-3	poorly differentiated
<i>Attalea</i>	poorly differentiated	1-2	poorly differentiated

Table 57. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda. Quantitative characters - Chlorenchyma.

Taxa	Palisade - Thickness			Spongy Mesophyll - #layers			Spongy Mesophyll - Thickness		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. cohune</i>	40	40.0	-	8	8	-	100	100	-
<i>A. colenda</i>	100-110	105	7.07	9-10	9.5	0.70	140-150	145	7.07
<i>Attalea</i>	50-120	81.5	19.08	6-10	6.9	1.11	90-240	116.1	39.90

Table 58. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda - Venation.

Taxa	Prim. Veins Position	Prim. Veins Type of Fibers	Prim. Veins Shape	Mid-secondary	Sec/Tert Veins Buttresses	Sec/Tert Veins Position	Sec/Tert Inner Sheath	Transverse Vein - Pattern
<i>O. cohune</i>	Centered	Small - thick walls	round	present	absent	above hypodermis	incomplete	short
<i>A. colenda</i>	Centered	Small - thick walls	pear-shaped	present	absent	above hypodermis	incomplete	short
<i>Attalea</i>	Centered	Small - thick walls	pear-shaped	not present	present	through hypodermis	incomplete	short

Table 59. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda. Quantitative characters - Primary veins.

Taxa	Primary Veins - Number			Primary Veins - Height (μ)			Primary Veins - Width (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. cohune</i>	12	12.5	0.70	105.9	105.9	-	100	100.0	-
<i>A. colenda</i>	14	14	-	175.4-214.3	194.8	27.50	158.4-172.1	165.2	9.68
<i>Attalea</i>	8-13	10.7	1.64	154.4-306.0	194.4	41.75	110-219	149.6	29.02

Table 60. Comparison of anatomical characters in Orbignya cohune, Attalea spp., and A. colenda. Quantitative characters - Secondary and tertiary veins.

Taxa	Sec./Tert. Veins - Number			Sec./Tert. Veins - Number/Between L.V.			Secondary Veins - Height (μ)			Tertiary Veins Height (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>O. cohune</i>	88	88.0	-	8	8.0	-	55	55.0	-	42	42.0	-
<i>A. colenda</i>	143-158	150.5	10.60	9-15	12	4.24	96.2-107.7	101.9	8.13	74.7-75.1	74.9	0.28
<i>Attalea</i>	66-127	90.1	20.09	7-14	9.9	2.84	62.5-106.1	85.6	13.20	51.7-85.2	68.1	9.27

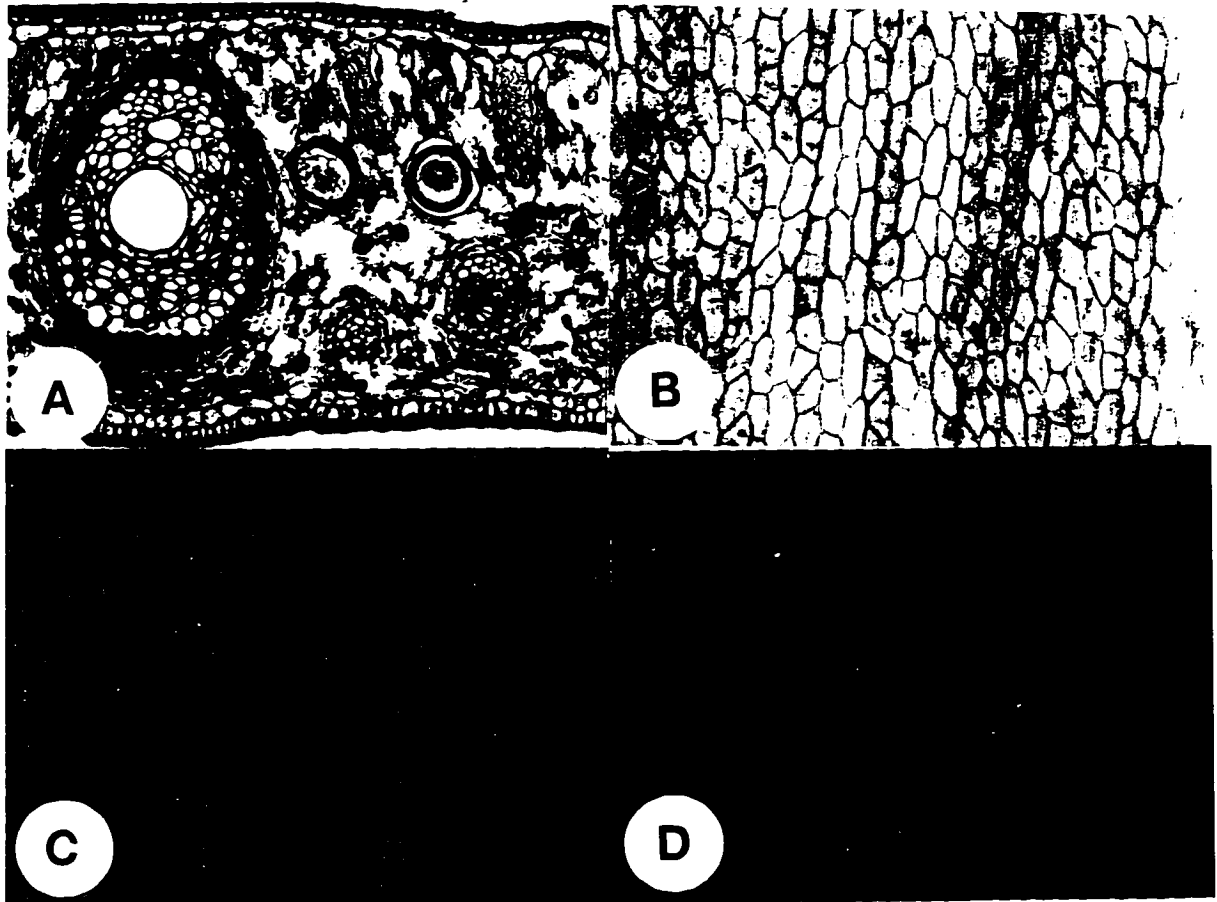
Table 61. Comparison of anatomical characters in Orbignya cohune,
Attalea spp., and A. colenda - Midrib.

Taxa	Midrib Shape	Midrib Expansion Cells - # layers	Midrib Expansion Cells - Confluence	Fibers Bundles on Midrib
<i>O. cohune</i>	Rectangular	3-6	confluent	upper portion only
<i>A. colenda</i>	Rectangular	4	not confluent	upper portion only
<i>Attalea</i>	Rectangular Round	3-5	confluent or not	upper portion only

Table 62. Comparison of anatomical characters in Orbignya cohune,
Attalea spp., and A. colenda. Quantitative characters - Midrib.

Taxa	Midrib - Size			Midrib - Number of VBs		
	range	mean	SD	range	mean	SD
<i>O. cohune</i>	1.28-1.88	1.58	0.42	18	18	-
<i>A. colenda</i>	2.38-2.44	2.4	0.04	20	20	-
<i>Attalea</i>	0.94-2	1.27	0.30	6-22	11.3	4.98

Fig. 59. Cross sections, adaxial and abaxial epidermis, and clearing: A, B, C, D -
Attalea colenda (YC-72 & YC-73).



Case Study 3. x Attabignya minarum Balick, Anderson & Medeiros-Costa

This the first documented case of hybridization between species of Orbignya and Attalea. It was discovered in 1984, growing among intermingled stands of A. compta Mart. (= A. oleifera Barb. Rodr.) and O. oleifera Burret, in the Rio São Francisco Valley of Minas Gerais State, eastern Brazil (Balick et. al., 1987) (Figure 62). Comparisons of several morphological characters showed most of them to be intermediate between those of the parent species, although the hybrid group was reported as a swarm of individuals with much morphological variation. This anatomical study supports the morphological evidence of the hybridization, showing qualitative and quantitative characters that are intermediate between the parent species, or closer to one another. In the PCA x A. minarum, joins the major group formed by Attalea species, although at some distance from the “good” species; in the cluster analysis, it forms a cluster of its own, close to the Attalea group. The cladistic analysis provided stronger evidence on the hybridity of xA. minarum: the Orbignya-Attalea clade collapsed as it was included in the analysis. Tables 64 -75 provide a selective comparison of the most important anatomical characters in the hybrid and parent species.

Four major anatomical character states discussed before provide the most striking evidence in support of the hybridization between these species of Orbignya and Attalea (Figure 60A-D):

1. The presence of a second hypodermal layer in x A. minarum, which is definitely a feature inherited from O. oleifera, a two-layered species, as opposed to A. oleifera, which is one-layered. The hybrid keeps the regularly sized and rectangular cells in the continuous upper layer (characteristic of Attalea) and adds a lower layer of more roundish, less regularly shaped and sized cells (from Orbignya), frequently interrupted by fiber bundles (Figure 60A).

2. Adaxial fiber bundles are intermediate between the two groups, in shape, size and location in relation to the adaxial hypodermis. The arrangement in bunches from Attalea, mixes with the more square arrangement of medium-size groups of Orbignya; it is interesting that the location of the fiber bundles right below the upper hypodermal layer (as in Attalea) is maintained, hanging in between hypodermal cells of the lower layer (Figure 60A).

3. Primary veins are either pear-shaped (as in Attalea), or round (as in Orbignya), well centered, inner sheath complete, and formed by small fibers of thick walls (Figure 60A).

4. Secondary veins are bigger than tertiary veins, but they are positioned nearly at the same level, above the abaxial hypodermal layer, and no buttresses are formed (features common in Orbignya; Figure 60A).

Most of the quantitative characters also showed intermediacy in the hybrid (e.g., number of fiber bundles, number of fibers per group, size of midrib, number of vascular bundles inside sclerotic sheath of midrib, etc.), and are compared to the parent species in Tables 64 through 75. The persistence of the two-layer hypodermis character is confirmed in at least two cases of hybridization (i.e., A. minarum, and M. dahlgreniana) when involving the Brazilian Orbignya (two-layered).

Table 63. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum - Adaxial epidermis.

Taxa	Adaxial Cuticle (mm)	Epidermis - Size Cross Section View	Adaxial Epidermis Thickness	Adax. Epidermis Cell Extension	Adaxial Epidermis - Cell Shape	Adaxial Epidermis - Cell Walls
<i>A. oleifera</i>	0.022	adaxial smaller than abaxial	thick	oblique	rhombohedral	linear
x <i>A. minarum</i>	0.020	adaxial smaller than abaxial	thick	oblique	rhombohedral	linear
<i>O. oleifera</i>	0.010	adaxial smaller than abaxial	thick	oblique	rhombohedral	linear

Table 64. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum - Abaxial epidermis.

Taxa	Abaxial Cuticle (mm)	Abaxial Epidermis Costal Cells - Orientation	Abaxial Epidermis Costal Cells Shape	Abaxial Epidermis Costal Cells - Walls	Abaxial Epidermis Intercostal Cells Walls	Stomates Guard-Cells	Stomates Arrangement
<i>A. oleifera</i>	0.010	longitudinal	spindle-shaped	linear	linear	slightly sunken	not in def. files
x <i>A. minarum</i>	0.010	longitudinal	spindle-shaped	linear	linear	sunken	not in def. files
<i>O. oleifera</i>	0.008	longitudinal	spindle-shaped	linear	linear	sunken	not in def. files

Table 65. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum - Hypodermis.

Taxa	Adaxial Hypodermis Number of layers	Adaxial Hypodermis - Shape of Cells
<i>A. oleifera</i>	1	rectangular
x <i>A. minarum</i>	2	rectangular round
<i>O. oleifera</i>	2	rectangular round

Table 66. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum - Non-vascular fibers.

Taxa	Adaxial Fibers - Lignin	Adaxial Fibers Position	Abaxial Fibers - Distribution	Abaxial Fibers Position
<i>A. oleifera</i>	slightly lignified	below hypodermis	irregular	above hypodermis
x <i>A. minarum</i>	slightly lignified	below upper layer, in between lower layer	irregular	above hypodermis
<i>O. oleifera</i>	slightly lignified	in between hypodermal layers	regular	in between hypodermis & epidermis

Table 67. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum. Quantitative characters - Non-vascular fibers.

Taxa	Adaxial Fibers - Number of Groups			Adaxial Fibers - Number/Fibers per Group			Abaxial Fibers - Number of Groups			Abaxial Fibers - Number/Fibers per Group		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>A. oleifera</i>	184- 262	226.6	39.51	9-12	10.3	1.52	21-68	39.0	25.35	3-4	3.2	0.57
x <i>A. minarum</i>	255	255	-	8	8	-	42	42	-	3	3	-
<i>O. oleifera</i>	345- 390	365.0	22.91	7-9	8.3	1.15	110- 187	137.3	43.08	3-4	3.6	0.57

Table 68. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum - Chlorenchyma.

Taxa	Palisade Differentiation	Palisade Number of layers	Palisade - Tannins	Spongy Differentiation
<i>A. oleifera</i>	poorly differentiated	2	frequent	poorly differentiated
x <i>A. minarum</i>	poorly differentiated	2	frequent	poorly differentiated
<i>O. oleifera</i>	poorly differentiated	2	frequent	poorly differentiated

Table 69. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum. Quantitative characters - Chlorenchyma.

Taxa	Palisade - Thickness (μ)			Spongy Mesophyll - #layers			Spongy Mesophyll - Thickness (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>A. oleifera</i>	60-80	73.4	11.54	7-10	8.2	1.52	120-140	130.0	10.00
x <i>A. minarum</i>	100	100	-	9	9	-	180	180	-
<i>O. oleifera</i>	92-120	104.0	14.42	6-8	7.0	1.00	150-190	165.3	21.57

Table 70. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum - Venation.

Taxa	Prim. Veins Position	Prim. Veins Type of Fibers	Prim. Veins Shape	Sec/Tert Veins Buttresses	Sec/Tert Veins Position	Sec/Tert Inner Sheath	Transverse Vein - Pattern
<i>A. oleifera</i>	Centered	Small - thick walls	pear-shaped	present	through hypodermis	incomplete	short
x <i>A. minarum</i>	Centered	Small - thick walls	pear-shaped round	absent	above hypodermis	incomplete	short
<i>O. oleifera</i>	Centered	Small - thick walls	round	absent	above hypodermis	incomplete	short

Table 71. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum. Quantitative characters - Primary veins.

Taxa	Primary Veins- Number			Primary Veins Height (μ)			Primary Veins - Width (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>A. oleifera</i>	10-12	11.0	1.00	171.0-215.3	197.2	23.26	161.0-178.5	169.4	8.76
x <i>A. minarum</i>	12	12	-	188.8	188.8	-	152.7	152.7	-
<i>O. oleifera</i>	8-13	11.0	2.64	184.4-211.7	199.8	13.98	152.8-182.8	171.4	16.24

Table 72. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum. Quantitative characters - Secondary and tertiary veins.

Taxa	Sec./Tert. Veins - Number			Sec./Tert. Veins - Number/Between L. V.			Secondary Veins - Height (μ)			Tertiary Veins Height (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>A. oleifera</i>	83-126	102.6	21.73	10-14	12.3	2.08	69.6-90.8	83.1	11.77	51.7-72.0	64.2	10.95
x <i>A. minarum</i>	145	145	-	11	11	-	88	88	-	71.5	71.5	-
<i>O. oleifera</i>	116-138	127.3	11.01	13-16	14.6	1.52	80.7-112.0	91.9	17.44	48.2-63.1	54.0	7.94

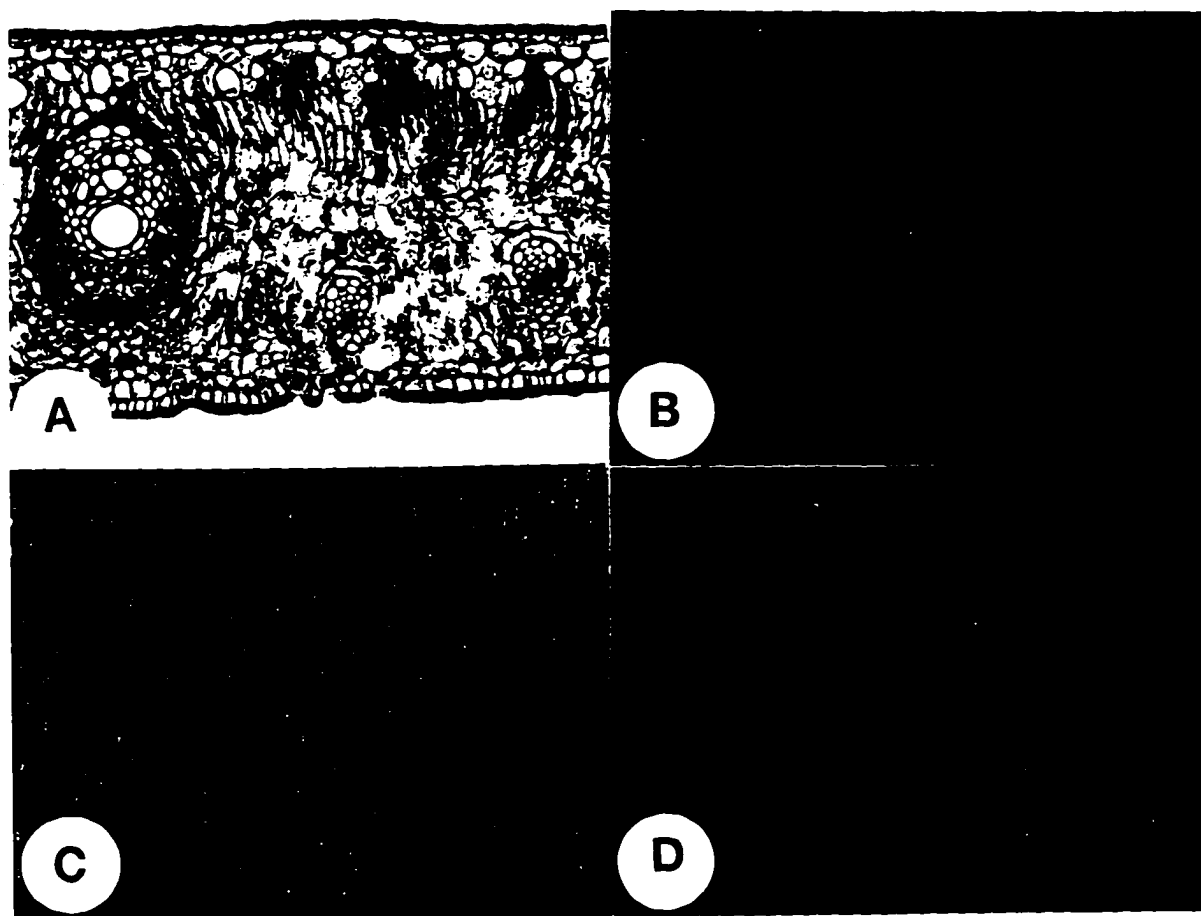
Table 73. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum - Midrib.

Taxa	Midrib Cuticle (mm)	Midrib Shape	Midrib Number of VBs	Midrib Expansion Cells # layers	Midrib Expansion Cells - Confluence	Fibers Bundles on Midrib
<i>A. oleifera</i>	0.012	rectangular	10-16	4-5	confluent	upper portion only
x <i>A. minarum</i>	0.014	rectangular	14	3	confluent	upper portion only
<i>O. oleifera</i>	0.010 - 0.020	rectangular	18-20	3-5	confluent	upper portion only

Table 74. Comparison of anatomical characters in Attalea oleifera, Orbignya oleifera and x Attabignya minarum. Quantitative characters - Midrib.

Taxa	Midrib - Size			Midrib - Number of VBs		
	range	mean	SD	range	mean	SD
<i>A. oleifera</i>	1.5-2.0	1.8	0.24	10-16	12.6	3.05
x <i>A. minarum</i>	1.96	1.96	-	14	14	-
<i>O. oleifera</i>	2.7-3.1	2.9	0.20	20	20.0	-

Fig. 60. Cross section, adaxial and abaxial epidermis, and clearing: A, B, C, D -
x Attabignya minarum (AXM-75).



Case 4. Attalea x piassabossu Bondar

This taxon is known from the northeastern Brazilian state of Bahia (Figure 62); its hybrid status was speculated on by Bondar (1964). Attalea oleifera Burret is an arborescent species, up to 20m tall, which has a more widespread distribution, leaving the limits of Bahia State, possibly reaching ca. 10 other states throughout most of the Brazilian Atlantic coast. Attalea funifera Mart. ex Spreng. is also an arborescent palm, up to 15 m tall, with a shorter range of distribution along the Brazilian Atlantic coast, where it is known to occur in only 3 states (Alagoas, Bahia, and Sergipe), especially in Bahia (Henderson et. al., 1995). These two Attalea species supposedly hybridize, producing Attalea x piassabossu. Its hybrid status was formally established by Glassman and Noblick (19?), but no studies were carried out to substantiate this action.

Attalea oleifera possesses in general, the characteristic anatomical structure of Attalea (Figure 46A-D). Attalea funifera (Figure 47A-D), on the other hand, although maintaining most of the Attalea patterns, showed a few other features that make it, anatomically, very distinctive within the group:

1. a very thick adaxial cuticle (0.022 mm).
2. both adaxial and abaxial hypodermal cells are filled with tannins.

3. some hypodermal cells are eventually replaced by large, thick fibers (hypodermal fibers).
4. there is an accumulation of thick hypodermal fibers on the upper and lower portions of primary veins, which increases the size of the upper and lower buttresses, and connects the veins to both surfaces.
5. the midrib is completely surrounded by a layer of hypodermal fibers, which entirely replaces the normal hypodermis.
6. stomates with superficial guard-cells (the only species in this group to show this character state).

From those characters listed above, only the tannin-filled hypodermal cells are not present in the putative hybrid (Figure 61A-D) . Its hypodermis is mostly clean of tannins on both surfaces. Another possible, but weak indication of the crossings between the two Attalea species, in A. x piassabossu, is the size of the buttresses formed by secondary and tertiary veins: they are smaller, approximately the size of those formed in A. oleifera, compared to the large ones formed in A. funifera. In the case of two species in the same group, and with one of them expressing dominance in relation to the other, the identification of mixed patterns becomes really difficult. Although some quantitative characters (Tables 76 - 87) appeared to be intermediate in the purported hybrid (e.g., number of fiber bundles, number of individual fibers per bundle, midrib size, number of vascular bundles in the midrib), no conclusive sign of

this hybridization could, unquestionably, be found. The putative hybrid, in general, is very similar, anatomically, to A. funifera; this similarity certainly contributed to the results obtained from the analyses performed: in the all-taxa PCA and cluster analyses, A. x piassabossu could either cluster with A. funifera, or form a cluster of its own; in the cladistic analysis, no changes are produced in the cladogram by its inclusion, and it resolves with A. funifera.

Table 75. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu - Adaxial epidermis.

Taxa	Adaxial Cuticle (mm)	Epidermis - Size Cross Section View	Adaxial Epidermis Thickness	Adax.Epid. Cell Extension	Adaxial Epidermis -Cell Shape	Adaxial Epidermis - Cell Walls
<i>A. funifera</i>	0.022	approximately same size	thick	oblique	rhombohedral	linear
<i>A. xpiassabossu</i>	0.020	adaxial smaller than abaxial	thick	oblique	rhombohedral	linear
<i>A. oleifera</i>	0.010	adaxial smaller than abaxial	thick	oblique	rhombohedral	linear

Table 76. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu - Abaxial epidermis.

Taxa	Abaxial Cuticle (mm)	Abaxial Epidermis Costal Cells Orientation	Abaxial Epidermis Costal Cells Shape	Abaxial Epidermis Costal Cells - Walls	Abaxial Epidermis Intercostal Cells Walls	Stomates Guard-Cells	Stomates Arrangement
<i>A. funifera</i>	0.010	longitudinal	spindle-shaped	linear	linear	superficial	not in def. files
<i>A. xpiassabossu</i>	0.010	longitudinal	spindle-shaped	linear	linear	superficial	not in def. files
<i>A. oleifera</i>	0.012	longitudinal	spindle-shaped	linear	linear	slightly sunken	not in def. files

Table 77. Comparison of anatomical characters in Attalea funifera,
Attalea oleifera and A. x piassabossu - Hypodermis.

Taxa	Adaxial Hypodermis # layers	Adaxial Hypodermis Shape - Cells	Fibers Replacing Hyp. Cells	Tannins in hypodermal Cells
<i>A. funifera</i>	1	rectangular	present	strong
<i>A. xpiassabossu</i>	1	rectangular	present	absent
<i>A. oleifera</i>	1	rectangular	absent	absent

Table 78. Comparison of anatomical characters in Attalea funifera,
Attalea oleifera and A. x piassabossu - Non-vascular fibers.

Taxa	Adaxial Fibers Lignification	Adaxial Fibers Position	Abaxial Fibers - Distribution	Abaxial Fibers Position
<i>A. funifera</i>	lignified	below hypodermis	irregular	above hypodermis
<i>A. xpiassabossu</i>	lignified	below hypodermis	irregular	above hypodermis
<i>A. oleifera</i>	lignified	above, in between and below hypodermal cells	irregular	above hypodermis

Table 79. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu. Quantitative characters - Non-vascular fibers.

Taxa	Adaxial Fibers - Number of Groups			Adaxial Fibers - Number/Fibers per Group			Abaxial Fibers - Number of Groups			Abaxial Fibers - Number/Fibers per Group		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>A. funifera</i>	254-265	260.0	5.56	4-8	6.3	2.08	31-53	40.6	11.23	4-5	4.3	0.57
<i>A. xpiassabossu</i>	153	153	-	16	16	-	21	21	-	3	3	-
<i>A. oleifera</i>	184-262	226.6	39.51	9-12	10.3	1.52	21-68	39.0	-	3-4	3.2	0.57

Table 80. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu - Chlorenchyma.

Taxa	Palisade Differentiation	Palisade Number of layers	Palisade - Tannins	Spongy Differentiation	Spongy - Number of layers
<i>A. funifera</i>	poorly differentiated	1-3	very frequent	poorly differentiated	5-7
<i>A. xpiassabossu</i>	poorly differentiated	2-3	frequent	poorly differentiated	8
<i>A. oleifera</i>	poorly differentiated	2	infrequent	poorly differentiated	6-10

Table 81. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu. Quantitative characters - Chlorenchyma.

Taxa	Palisade - Thickness (μ)			Spongy Mesophyll - #layers			Spongy Mesophyll - Thickness (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>A. funifera</i>	80-120	100.0	20.00	6-7	6.3	0.57	100-120	106.6	11.54
<i>A. xpiassabossu</i>	120	120.0	-	8	8.0	-	160	160.0	-
<i>A. oleifera</i>	60-80	73.4	11.54	7-10	8.2	1.52	120-140	130.0	10.00

Table 82. Comparison of anatomical characters in Attalea funifera, Attalea oleifera, A. x piassabossu - Venation.

Taxa	Prim. Veins Position	Primary Veins Type of Fibers	Prim. Veins Shape	Sec.&Tert. Veins Buttresses	Sec.&Tert. Veins Position	Sec.&Tert. Veins Inner Sheath	Transverse Veins
<i>A. funifera</i>	Centered	Small - thick walls	pear-shaped	present	through hypodermis	incomplete	short
<i>A. xpiassabossu</i>	Centered	Small - thick walls	pear-shaped	present	through hypodermis	incomplete	short
<i>A. oleifera</i>	Centered	Small - thick walls	pear-shaped	present	through hypodermis	incomplete	short

Table 83. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu. Quantitative characters - Primary veins.

Taxa	Primary Veins - Number			Primary Veins - Height (μ)			Primary Veins - Width (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD
<i>A. funifera</i>	10-13	11.6	1.52	188.0-240.0	212.6	26.10	141.5-166.2	156.2	13.04
<i>A. xpiassabossu</i>	7	7.0	-	242.8	242.8	-	150	150.0	-
<i>A. oleifera</i>	10-12	11.0	1.00	171.0-215.3	197.2	23.26	161.0-178.5	169.4	8.76

Table 84. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu. Quantitative characters - Secondary and tertiary veins.

Taxa	Sec.&Tert. Veins - Number			Sec.&Tert. Veins - Number/Between L. V.			Secondary Veins - Height (μ)			Tertiary Veins - Height (μ)		
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD
<i>A. funifera</i>	77-108	89.0	16.64	8	8.0	-	92.8-106.1	97.7	7.26	73.3-77.0	74.8	1.92
<i>A. piassabossu</i>	94	94.0	-	14	14.0	-	110.8	110.8	-	79.0	79.0	-
<i>A. oleifera</i>	83-126	102.6	21.73	10-14	12.3	2.08	69.6-90.8	83.1	11.77	51.7-72.0	64.2	10.95

Table 85. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu - Midrib.

Taxa	Midrib Cuticle (mm)	Midrib Shape	Midrib Expansion Cells # layers	Midrib Expansion Cells - Confluence	Fibers Bundles on Midrib
<i>A. funifera</i>	0.022	Round	3-4	confluent	around midrib
<i>A. xpiassabossu</i>	0.024	Round	3	not confluent	around midrib
<i>A. oleifera</i>	0.012	Rectangular	4-5	confluent	upper portion only

Table 86. Comparison of anatomical characters in Attalea funifera, Attalea oleifera and A. x piassabossu - Quantitative characters: Midrib.

Taxa	Midrib - Size			Midrib - Number of VBs		
	range	mean	SD	range	mean	SD
<i>A. funifera</i>	1.1-1.2	1.1	0.03	8-10	9.3	1.15
<i>A. xpiassabossu</i>	1.1	1.1	-	9	9.0	-
<i>A. oleifera</i>	1.5-2.0	1.8	0.24	10-16	12.6	3.05

Fig. 61. Cross section, adaxial and abaxial epidermis, and clearing: A, B, C, D -
Attalea x piassabossu (AXP-74).

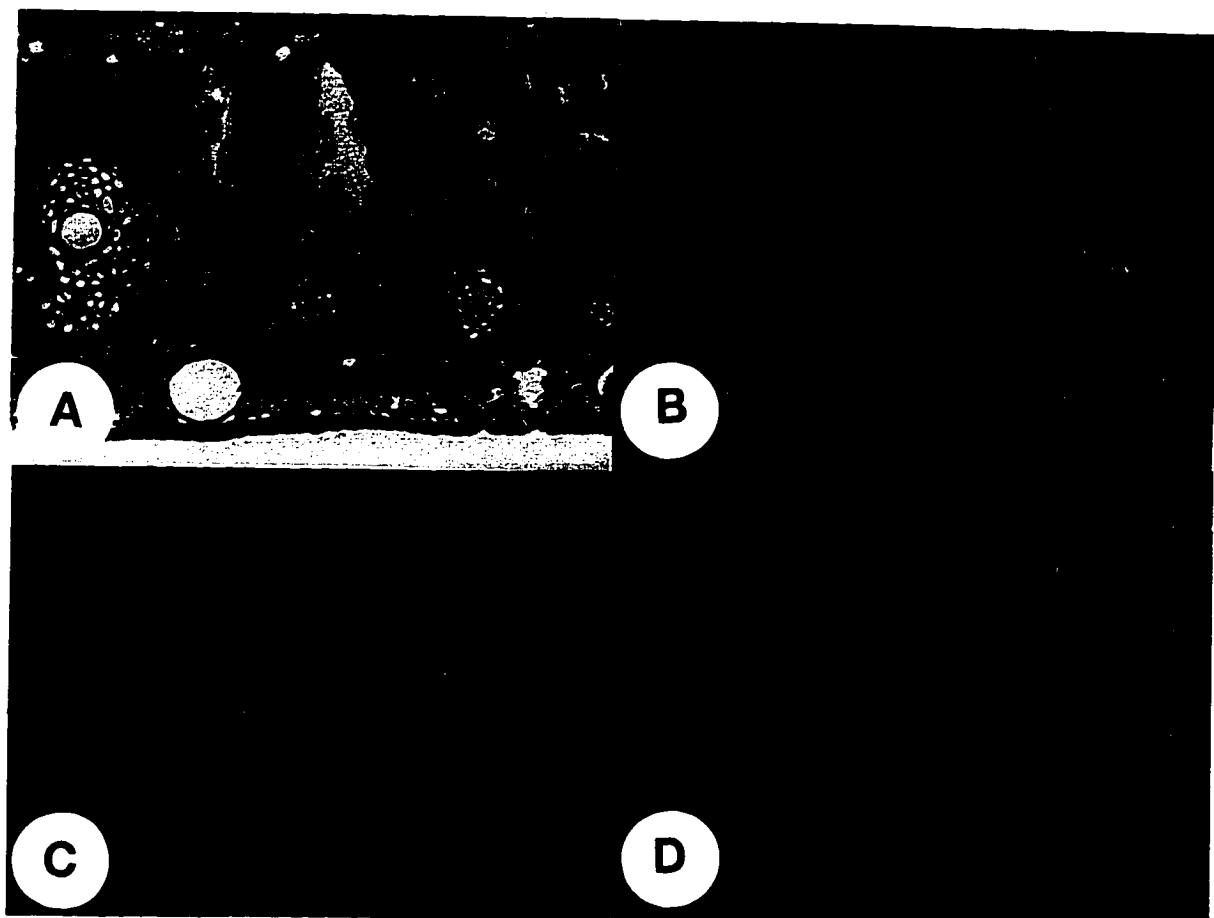
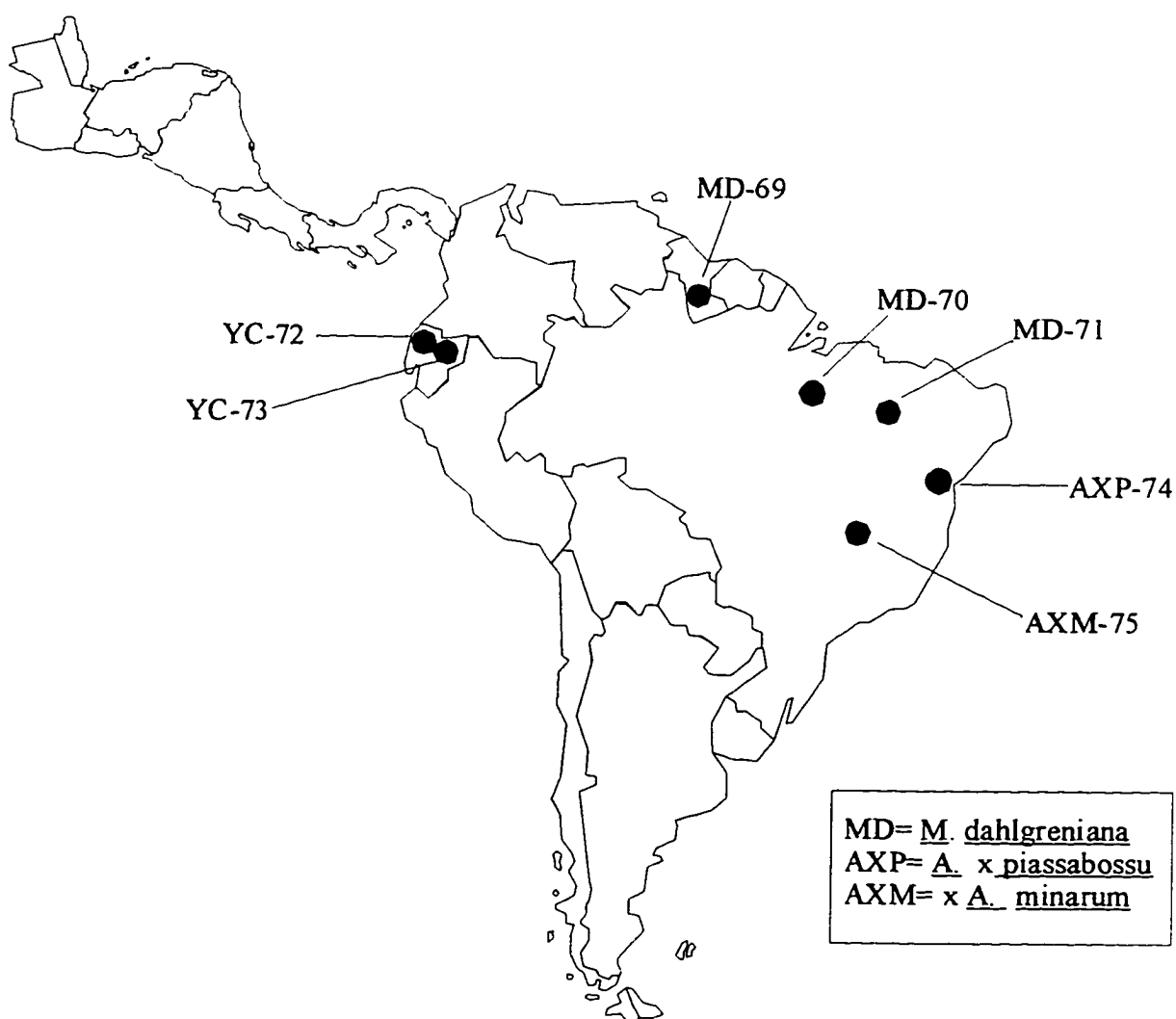


Fig. 62. Distribution of specimens of the purported hybrids Markleya dahlgreniana, Attalea colenda, Attabignya minarum, and Attalea x piassabossu studied.



Hybrids and Hybridization

In many plant groups, hybridization and polyploidy are common features. Stebbins (1974) believed that up to 80 % of the flowering plants originated from polyploidy, not including the cases of hybridization at the diploid level (Funk, 1981). Hybridization in plants is fairly common; many authors have described natural hybrids in many groups, with most of the attention paid to trees and shrubs, where hybrid individuals can be more easily detected (Grant, 1981). A list of natural hybrids among plant groups would be extremely long, given the high number of cases reported. Kerner (1891), cited by Grant (1981), listed over one thousand interspecific combinations in many groups, including mosses, ferns, horsetails, conifers, and herbaceous angiosperms.

In the palm family, hybrids have more often been suggested than studied, more speculated on than confirmed as such. Including those five in the Attaleinae, a total of 15 hybrids have been reported among palm genera, as follows: Bactris (1), Butia (1), Chamadorea (1), Copernicia (6), and Oenocarpus (1); only one is supposedly interspecific: x Butiarcasium nabonnandii Robertson-Prochowsky. Bondar (1954, 1957, 1964) had a good eye for such cases; he spotted and described several putative palm hybrids (e.g., O. x teixeirana, M. dahlgreniana, , A. X piassabossu), all

in the subtribe Attaleinae. He speculated much on this matter, but his hybrid suspicions were never substantiated with study results, and he never formally established the hybrid status of any of those species, always describing them as new species.

The subtribe Attaleinae has probably been cited the most, as the group where hybrid individuals are likely to be found. This fact, as seen by many palm taxonomists, would explain so much variation among species in this group, and the existence of intermediates, which have been seen sometimes as races, or subgenera (Glassman, unpublished; Henderson, 1995). The fact is that these cases have never been sufficiently studied, and most of what has been said and suggested on the subject has been speculative. The role of these intermediates on the establishment and evolution of the group is still to be determined, but the problems with the generic delimitation of the subtribe have been partially blamed on the presence of these intermediates. They are supposedly responsible for a great deal of the morphological variation observed among species in the group. The anatomical results confirm this variation, as they support the existence of many intermediates, or "mixed" types in the subtribe. Considering the high number of mixed patterns found, these intermediates or hybrids may be playing an important role in the evolutionary mode of the group.

Hybridization can occur at either the diploid or polyploid level. A first generation of hybrids can be fertile, semisterile, highly sterile, or completely sterile. Only in the last case, it is impossible for some later-generation progeny to be produced (Grant, 1981). A semifertile F1 hybrid may reproduce sexually by selfing, sib crossing with sister hybrid plants, or backcrossing to one or both parental species. Hybrid swarms are known in many plant groups, and they result from the crossing between two second-generation progenies, and with the original plants, producing over time, an extremely variable mixture of species, hybrids, backcrosses, and later-generation recombination types (Grant, 1981). The establishment of a hybrid swarm indicates the availability of a range of ecological niches that satisfy the requirements of a wide variety of hybrid individuals. Conditions for the establishment of hybrid swarms are apparently created in disturbed areas, with the artificial establishment of new many micro-niches (Stace, 1989); the process was called hybridization of the habitat by Anderson (1948). Hybridization of the habitat, however, is not the only condition which will permit the establishment of segregating hybrid progenies (Grant, 1981). When these conditions are not created, introgressive hybridization may occur: the repeated backcrossing of a hybrid to one or the other parent, with the hybrid becoming quite similar to that parent, but differing from it by having some features of the other parent species (Stace, 1989).

In the palm family, particularly in the Attaleinae, the remarkable variation in a hybrid swarm has been studied in a population of *O. x teixeirana*, located in the

basin of the Parnaíba and Itapecuru rivers of Maranhão and Piauí States, in northeastern Brazil. Medeiros-Costa, Campos Mendes, and Castro Brito (1985), studying this hybrid swarm, could identify at least three distinctive morphotypes between O. phalerata and O. eichleri, morphologically intermediate between them, or closer to one of them. Recognition of these morphotypes was based on morphological observations (e.g., measurements of the rachis, number of pinnae, number of and percentage of grouped and regular pinnae, percentage of rachis with regular pinnae and number of stamens in the flower), and phenology. This exhaustive study of a single population provided further evidence that Orbignya x teixeirana comprises a highly variable hybrid swarm, and substantiated the possibility of other such cases in the group.

Introgression is more likely to occur than hybrid swarms in a situation where the habitats are suitable for the parents but not for the intermediates. This seems to be because the ecological requirements of a hybrid resembling one of the parents are more likely to resemble the requirements of that parent (Grant, 1981). It usually goes only in the direction of one parent, but a few examples exist where introgression occurred in one direction in some areas, and in the opposite direction in others. Environmental factors seem to play a major role in the decision of whether hybrid swarm or introgressive hybridization will take place (Stace, 1989).

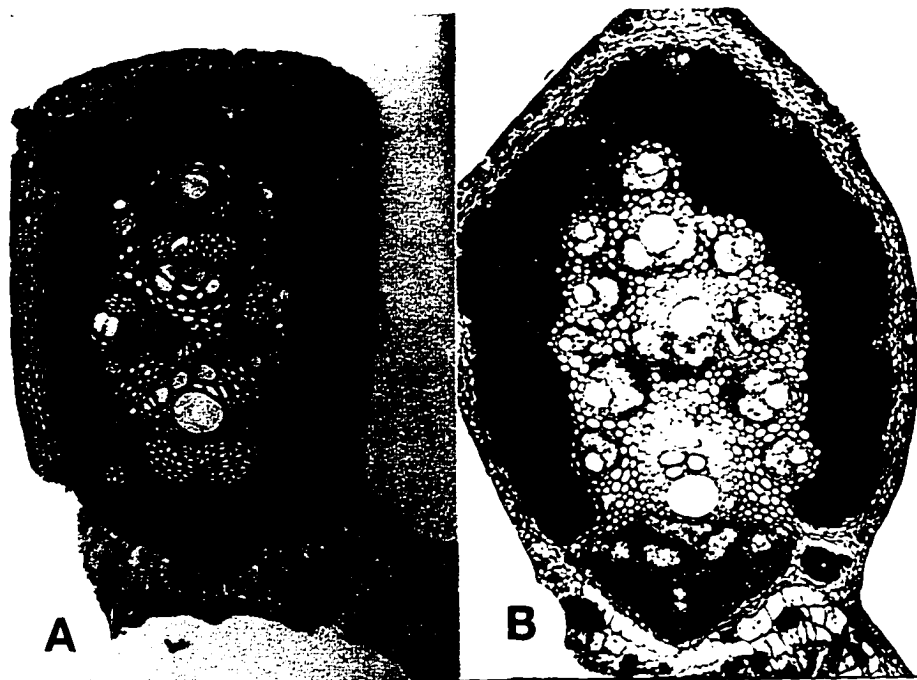
Hybrids are usually expected to be phenetically intermediate between the putative parents, and quantitative and qualitative characters can be used for their identification. However, intermediacy does not necessarily correlate with hybridization. There are some reasons, pointed out by Wagner (1983), why some or all of the characters in a hybrid may not be intermediate, with both meristic and metric characters providing exceptions to the rule of intermediacy. Hybrid vigor may be responsible for the production of hybrids considerably larger than the parents; or, on the other hand, they can develop into weak, or even dwarf plants, compared to the parents. If two species differ only by qualitative characters, their hybrid product may have some characters of one parent, some of the other, and some intermediate. In hybrid swarms with massive backcrossing, the characters tend to be one-sided for all or most, especially if introgression is progressively taking place (Anderson, 1949). In its most exaggerated expression, some or all the backcross hybrids may be so close to one or to the other of the parents that their hybrid origin may be undetected (Wagner, 1983).

Hybrids may vary in their intermediacy in one individual, producing a range of asymmetries and irregularities (Wagner, 1983). Various plant organs may show these irregularities, especially leaves, which may show asymmetrical leaf lobes, among other irregularities (Wagner, 1962). My results confirm this tendency to asymmetry in some leaf characters. The midrib appears to be especially affected by a mixture of anatomical patterns: it is mostly asymmetrical in these cases, irregularly

shaped, even if both supposed parents had it regularly shaped. Another interesting fact observed from the cases of mixed anatomical patterns, was that some characters were more subject to changes in shape, size or thickness, than others. In most of such cases, non-vascular fibers were usually bigger in the “mixed” specimen than in both possible parents. When a “mixing” between a species in the Scheelea group (which has large fibers, of thin walls) and another in the Orbignya or Attalea groups (with small fibers of thick walls) occurred, the product was always an individual with large fibers, of thick walls.

Simple dominance is considered to be rare in cases of hybridization although there is not much evidence to confirm this assertion. Wagner (1962), considers that to be partially true in ferns, showing that some patterns of venation may be dominant or partially dominant over others. Some of the characters observed in this study were apparently dominant over others, making them sort of predictable in appearance when species of different groups crossed. One of these characters is certainly venation: the long transverse vein pattern of the Scheelea group was always dominant over the short transverse pattern, in the cases of crossings between Scheelea and other groups. Another apparent case of dominance is that of the location of small fiber bundles in the midrib: if the Scheelea group was involved, these fibers were located all the way around the midrib (Figure 63B), as opposed to only on its upper portion when the mixing occurred between the other groups (Figure 63A).

Fig. 63. Midribs: A - Orbignya-Attalea group (usually rectangular, with small fiber bundles located on the upper portion); B - Scheelea group (usually asymmetrical, with small fiber bundles surrounding sclerotic sheath).



The Detection of Hybrids

Stace (1989) considers the anatomical, chemical and cytogenetic (chromosomal counts) characters very useful in the identification of hybrids. Technically, an intermediate number of chromosomes is expected in hybrids between species with different chromosome numbers. However, some species will occasionally form unreduced gametes that may participate in fertilization, and in this case, the hybrids formed will not have an intermediate number of chromosomes (Stace, 1989). Uhl and Dransfield (1987), based on the work of many authors, list the number of chromosomes for a few Attaleinae species: Attalea allenii; Scheelea sp., Orbignya cohune, O. lydiae (= O. phalerata); and Maximiliana; all of them with 16 chromosomes. The authors, however, advise these reports to be cautiously interpreted, due to possible problems of misidentification of the specimens used, and mistakes made in the chromosome counts, as the result of improper preparation of the material. Unfortunately, none of the putative hybrids had their chromosome numbers in that list, for comparison with the anatomical results.

Very few chemical analyses have been made in palms, and particularly, in this group. Glassman et al. (1981), tested species of Scheelea, and showed weak chemotaxonomic differences between them, in flavonoids and lipids. He found S. rostrata differed from S. preussii and S. zonensis by three and four flavonoid

compounds, respectively; and it differed from S. lundellii and S. liebmännii by only one and two compounds, respectively. All these species have been placed in synonymy with S. butyracea (Henderson et al. 1995), and these weak differences only confirm that they are conspecific. Williams et al. (1983), surveyed a number of species of the Attaleinae, and found flavonoid sulphates, and flavonoid C-glycosides and tricin in two of the four collections of Maximiliana (regarded as different species), and it was concluded that these characteristics separate Maximiliana from the other genera in the Attaleinae. Uhl and Dransfield (1987), considered these results mostly equivocal in taxonomic decisions.

The geographical distribution of the species involved in a suspected case of hybridization added to the results obtained by other means, constitutes the circumstantial evidence for the identification of hybrids and its parents. The morphological, anatomical, and distributional evidence and the results obtained from the analyses performed are used in this study, to test the possibility of hybridization cases. Almost all cases of mixed patterns and of known purported hybrids were supported by the morphological, anatomical and distributional evidence combined, although in most cases, the parent species could only be hypothesized, given that more than one possibility exists.

Hybrid Complexes

A hybrid complex, as defined by Grant (1953), "is a species group, consisting of three or more original ancestral species and their hybrids or hybrid derivatives, in which natural hybridization has obscured the morphological discontinuities between the ancestral forms." The members of a hybrid complex are characterized by being taxonomically extremely difficult to identify by conventional methods (Stace, 1989). The components of a hybrid complex exhibit a similar pattern of variation, including several forms. They are poorly defined as species, but have in common similar morphological and ecological preferences. The reproduction of the natural hybrids or the hybrid progeny can stabilize by several ways, both asexually or sexually. Sexually, recombinational speciation or hybrid speciation with external barriers may occur. A hybrid complex may be established with the independent repetition of the process of hybrid speciation in different lineages (Grant, 1981).

On the basis of distributional patterns, observed and reported ecological preferences, and anatomical as well as morphological patterns, four major hybrid complexes can be tentatively circumscribed:

1) the possible hybridization cases of Attalea crassipatha(?), Attalea colenda (?), and Scheelea butyracea, which probably had Orbignya cohune as the most likely

parent; the other parent in each case, is an unknown species of Attalea in the first two cases, and Scheelea, in the latter. Geographically, it encompasses southern Mexico, the entire Central America, and northwestern South America (Figure 64).

2) the cases of S. phalerata, A. tessmannii, A. racemosa. In the first, one parent (an Attalea species) could not be hypothesized, as it can be done for a putative second parent: S. insignis. In the other two cases, one of the unknown parents of A. tessmannii would have to be an arborescent species: S. butyracea as the tall parent Scheelea, and A. racemosa; or, an acaulescent Scheelea, which could be S. insignis plus an arborescent Attalea (unknown). The area is located mostly in the Amazon region, its northwestern portion the in Brazil, Peru, Colombia and Venezuela (Figure 64).

3) the most variable cases, in which more than two parents may be involved: O. polysticha, O. sagotii, O. spectabilis, and O. luetzelburgii (?). The results showed anatomical signs of Orbignya, Attalea, and Scheelea in the different specimens examined. The hypothesis that these species are part of the same hybrid complex, is supported by their overlapping distribution, and a very similar anatomical structure (except O. luetzelburgii, which shows a very peculiar anatomical structure, although following the same overall pattern). Putative parents are difficult to guess, given the wide area where these intermediates occur, the anatomical signs of three groups, and several possibilities for putative parents. Apparently these intermediates

followed different directions in the hybridization process, at different points of their distributional range. They have in common the fact that they are all acaulescent species, and somehow share the same environmental preferences, being distributed over a continuous range in the Amazon region, northwards from west, in the Guyanas, Brazil, Venezuela, Colombia, and Peru (Figure 64).

4) those cases involving the Brazilian Orbignya as one of the parents: Markleya dahlgreniana, O. x teixeirana, x A. minarum, and A. dubia (?); apparently clear in relation to both parents in the first two cases, involving O. phalerata, M. maripa, and O. eichleri; and in the third case of O. oleifera and A. oleifera; and unclear for one parent in the case of A. dubia, since more than one possibility exists: A. humilis, or A. oleifera, which share most of their distribution range. A. funifera occurs in the same area, but it has very distinctive anatomical features that were not observed in A. dubia. This complex encompasses a wide area, from northern to eastern Brazil (Figure 64).

In the case of A. nucifera, it can either be the result of misidentification of the two specimens, since they both came from the exact same area, and they are both sterile, or that this is indeed a species of Scheelea, mistakenly described as an Attalea. Still on speculative grounds, it is possible to hypothesize that A. nucifera represents another kind of taxonomic problem associated with hybridization: a semi-cryptic species. In such species, the differences are mostly observed in anatomical,

cytological, genetic, or chemical characters rather than morphological (Stace, 1989).

They may represent incipient species or old taxa that did not diverge morphologically; these cases have been well documented in the Orchidaceae (Stace, 1989). Attalea x piassabossu could not have its hybrid status confirmed anatomically, given the dominance of A. funifera over the other parent, if this in fact a case of hybridization; therefore it is left out of the proposed hybrid complexes. If confirmed, it would certainly be part of the Brazilian complex.

Fig. 64. Hypothetical hybrid complexes.



The Usefulness of Leaf Anatomy as a Taxonomic Tool

The phenetic school states: "the species level is that at which distinct phenetic clusters can be observed" (Sneath, 1976; cited by Stuessy, 1990). The phenetic clusters could result from cytology, chemistry, anatomy, etc., although in practice they would tend to be based on morphology (Stuessy, 1990). Morphology and anatomy have traditionally been used for the recognition of genera, and the usefulness of exomorphic features obviously, does not need to be emphasized (Stuessy, 1990). Anatomical data has been the second most important tool in delimitation of genera. It is, however, a tool not readily available, since it requires a minimum of equipment and material, and a considerable amount of time with the preparation of material and extraction of anatomical data. These difficulties have contributed to the use of anatomy, mainly to resolve particular problems, and not as routine in taxonomy (Stuessy, 1990). Anatomical data, both from reproductive and vegetative plant organs, has been very useful in generic boundary (Stuessy, 1990).

Anatomical research has focused mostly on leaf characters; first, because this plant part is more easily available; second, leaves are apparently more taxonomically useful, due to their greater variability, in comparison with other plant organs (Tomlinson, 1961). Leaf anatomy, however, has not been extensively used in palm taxonomy. Lack of tradition, and the technical difficulties mentioned above

as well, may have contributed to the under-utilization of this important technique. In the case of palms, the difficulties common to this type of work are considerably increased. Problems, such as the size of the palm leaves, the hardness derived both from their cellular nature (often containing silica bodies, sclereids, crystals of calcium oxalate, raphides) and frequent occurrence of fibers, can make sectioning, sometimes, a very frustrating experience. The methods described by Martens and Uhl (1980), provide the means to overcome most of these difficulties, although additional experimentation and adjustments to the methodology are still necessary for a successful preparation of the palm leaf material.

Tomlinson (1961) described the leaf anatomy of 250 species of palms, a landmark in the use of anatomical data in this group of plants. A few other researchers have made use of the anatomical tool in palm taxonomy, including Glassman (1972) in the genus Syagrus, Uhl (1972) in the Chelyocarpus alliance; Read (1975) in Thrinax; Uhl (1978) in Hyophorbe; Balick et al. (1987) in Orbignya; Barfod (1988) in Ammandra, Palandra and Phytelephas; Borchsenius and Bernal (1996) in Aiphanes, and Henderson and Galeano (1996) in Euterpe, Prestoea, and Neonicholsonia. Tomlinson (1961) stated that leaf anatomy is often more helpful in taxonomy in the delimitation of taxa at or above the genus level; this is certainly true in the case of closely related specie, as pointed out by that author, and could be confirmed by my own results as well. Successful results, however, were obtained at the specific level by the authors cited above.

The results obtained by Tomlinson (1961) did not match the results from the present study. According to his results, Attalea, Scheelea, and Maximiliana could just barely be distinguished from each other; as opposed to Orbignya, which showed a more distinctive anatomical structure in comparison to the others. Attalea and Scheelea were found to be very similar anatomically, and as such, they were described together. An examination of the species studied in each genus provided the explanation for such “similarity”. The species of Attalea examined by Tomlinson was A. spectabilis Mart., a synonym for O. spectabilis (Mart.) examined in this study, one of the most confusing species examined, along with O. sagotii, and O. polysticha: all three showed mixed patterns with Scheelea, involving more than one group (Orbignya and Attalea).

Tomlinson’s two species of Scheelea were: S. amylacea Barb. Rodr., synonymies to S. phalerata, named in this study the “false Scheelea” for its clear intermediacy between Scheelea and Attalea; and S. urbaniana Burret (which is S. butyracea used in this study), another mixed Scheelea species (in this case with Orbignya). It is then completely understandable the similarity found between Scheelea and Attalea in Tomlinson’s study, since most of the specimens examined have been found to be intermediate or have mixed patterns between these two groups.

The species of Orbignya used was unknown, cultivated at Fairchild Tropical Garden; it was probably misidentified as an Orbignya, since most of the anatomical

characters described do not match the patterns identified for Orbignya in this study.

The presence of buttresses observed by Tomlinson supports only three possibilities of his specimen being an Orbignya: it could be O. eichleri, or O. cuatrecasana, or one of the hybrids; from the description provided, however, it is not possible to tell. Two specimens of Maximiliana were examined, obviously the of same species (M. maripa), credited as two different species, since it was not known, at that time, that Maximiliana was a monotypic genus.

It is, in general, difficult to compare his results with the results in this study (which could certainly be used to support (or not) each set of independent results), since most of the characters were just vaguely described, and most of the anatomical features considered here to be very important in distinguishing the groups, were not even mentioned. Additionally, the number of specimens used was very small, all of them unvouchered, and there is no assurance, whatsoever, whether they were in fact, what they were labeled.

Glassman (in unpublished manuscript of the taxonomic revision of subtribe Attaleinae) surveyed the leaf anatomy of Attalea and related genera by cross sections of middle series pinnae, with no conclusive results. A key to the genera and species in the subtribe could not be constructed, and only a few differences could be found to separate a large number of species. No details on the study are given, but it

seems that too much attention was paid to characters, such as frequency of non-vascular fibers, midrib, and expansion cell tissues, mostly superficially examined.

Martens and Uhl (1980) identified between 50 and 60 anatomical characters in palm leaves with a potential taxonomic, evolutionary, or biological importance. This study in the subtribe Attaleinae resulted in the use of 87 anatomical characters (both qualitative and quantitative) from the leaf material prepared with the use of the three microtechniques (cross sections, epidermal peels and clearings). It was found, in general, that anatomical data can be extremely reliable, and for taxonomic purposes, as valuable as molecular data (Uhl, 1995, pers. Comm.).

On the Generic Controversy

The morphological-geographic approach (or the traditional taxonomic species concept), by which "species are based on multiple, correlative morphological characters, as well as on cohesive geographic distributions" (Henderson, 1995), was used by Wessels Boer (1965), and followed by Henderson et al., (1995). The application of a broader concept of species, with due appreciation given to the existing morphological plasticity, constituted the major argument for the lumping of the genera in the Attaleinae. The problem, however, has not been the taxonomic separation of specific entities, although the abusive number of names has indeed created problems in the determination of the so-called "good" species within this

subtribe. The problem has been, in fact, the definition and delimitation of these specific entities, which are known to exist, and that have been traditionally recognized as genera. That has not been solved, or even explained, by simply shrinking the way these groups (genera, if you will) have been traditionally seen. On the other hand, the basis for this separation has been defined is weak, inconsistent and limited to a few morphological features of the male flower.

Robinson (1906) described a genus "as a group of species which in all likelihood appear to be more nearly related to each other than they are to other species." This view, however, although completely acceptable as a definition, may become vague and inapplicable for classificatory purposes given the extremely variable degrees of similarities and the diversity in human judgment (Stuessy, 1990). Du Rietz (1930), cited by Stuessy (1990), stated: "The taxonomic units superior to the species can hardly be called 'fundamental' to the same degree as the species and its subordinate units, since the delimitation of the higher units is to much greater an extent a matter of taste and convenience." Bisby and Ainsworth (1943) summarized the most pessimistic view of the naturalness of genera by stating that "nature may make species, but man has made the genera." These statements reflect the nature of the difficulty that the genus concept has encountered throughout its historical existence, which for some would even antedate the concept of species.

Generic delimitation has been traditionally done by morphological and anatomical data, coupled in many instances, with geography. More recently, the use of cytology (basically number, size, and shape of chromosomes) and cytogenetics have joined the relatively limited arsenal of taxonomic weapons. The latter is for many, regarded as the provider of the most absolute criterion for generic delimitation, on the basis that genera do not cross naturally (Stuessy, 1990). Although intersterility has been mostly abandoned as a species criterion, it is still sometimes used as a means for delimiting genera (Stace, 1989). However, a large number of intergeneric hybrids are known within the angiosperms, especially in the Gramineae, but also in the Orchidaceae, Brassicaceae, Scrophulariaceae, Asteraceae, Caryophyllaceae, Cyperaceae, Leguminosae, Saxifragaceae, Solanaceae, and Rosaceae, (Stace, 1989; Stuessy, 1990). This list can be expanded with the Arecaceae with one case (x Butiarcistrum nabonnandii), or many cases if the traditional delimitation of the genera in the subtribe Attaleinae is to be maintained.

The high number of “intergeneric” hybrids detected in the Attaleinae by this anatomical study, enforces the view against the validity of the genera, as traditionally seen, if the criterion of the crossability is to be applied, and the high number of exceptions listed above is not to be considered. Stuessy (1990) considers four possibilities if a hybrid between two species of two separate genera is obtained: 1) the two genera should be merged; 2) one or the other of the species is misplaced and should be moved into the other genus; 3) the crossability shows that the genera

are closely related, and in this case, no changes are necessary; 4) the two species could be placed together in their own genus.

In the Attaleinae, four genera as traditionally seen, are involved. Before this study, four hybrids had been reported: two, presumably intergeneric; two, interspecific. The anatomical data supported the two cases proposed as “intergeneric” hybridization (M. dahlgreniana; x A. minarum), and one case of interspecific hybridization had been previously confirmed, O. x teixeirana (Balick et al., 1987). The confirmation of the two “intergeneric” hybrids would be a good enough reason to start considering one of the possibilities listed by Stuessy (1990). The problem is made worse with the detection, by this study, of at least seven new possibilities of hybridization involving all four “genera”. These seven cases were supported by the evidence obtained and results of analyses (A. racemosa, A. tessmannii, S. phalerata, S. butyracea, O. polysticha, O. sagotii, and O. spectabilis). Such a number of possible hybrids (if only the new ones supported by the results were taken) would represent almost ca. 25% of the total number of valid species, according to Henderson et al. (1995).

All groups had mixed anatomical patterns, suggesting crossings and hybridization among them. However, besides M. dahlgreniana (with Orbignya), no new case involving Maximiliana was detected, despite the wide distribution of this species which overlaps with the distribution of many species in all other groups. It is also interesting to note that although Maximiliana is anatomically more closely related to

Scheelea than to any other group, no signs of hybridization between these two groups were found. Two possibilities can be considered: 1) Maximiliana does hybridize with Scheelea, but the anatomical proximity of the two groups makes it difficult to detect; 2) or else some type of incompatibility exists between these two groups: either morphological and/or physiological (e.g. type of inflorescence, pollination system), or an internal breeding barrier, i.e. where different races are genetically unable to interbreed, usually for a chromosome-related reason. Cases of structural hybridity are known in other plant groups; the species are phenetically very similar, but they are intersterile, because of chromosomal differences, in number or structure (Stace, 1989).

The following situations result from the consideration of each of the alternatives proposed by Stuessy (1990): 1) on merging the genera: the genera have been merged (Wessels Boer, 1965; Henderson, 1995); the question remains whether they should be kept merged; 2) on misplacement of species: the high number of cases discards this alternative, and too many species would have to be misplaced; or maybe they are, and the reason why they are misplaced is because they are hybrids; 3) on closely related species: there is no doubt they are closely related; the question is whether or not they are genera; 4) on breaking up the genera: I do not see how to break up the four genera into a smaller number, given the high crossability observed in all four groups, except maybe in Maximiliana, with only one case.

Henderson's solution (1995), after Wessels Boer (1965), consisted of the merging of the four genera (M. dahgreniana should have its hybrid status formally established). Attalea is considered the only genus; a large genus, whose species have been poorly collected and misunderstood. The existence of groupings inside this large "natural" genus is, however, recognized, but downgraded to the level of subgenera. Six subgeneric groups are defined, all of them overlapping the circumscription of the old controversial genera: "Scheelea", "Orbignya", "Attalea", "Maximiliana", "Markleya", and "Parascheelea".

Glassman (unpublished), also felt there were subgeneric categories in the subtribe, but maintained the traditional generic division. In this view, the subgenera were still established on the basis of growth habit, pinnae arrangement, and the traditional characters of the staminate flowers. As a result, a number of subgeneric groupings were defined, inside each genus. In Attalea, the use of characters from the male flower, pinnae arrangement, and growth habit, led to the establishment of two subgeneric groups, but due to the large number of species recognized, they are excessively subdivided into sections. Scheelea also ended up with two subgeneric groups, and the great number of species recognized had to be accommodated in many different sections and subsections. The features utilized were the same as for Attalea (male flower, pinnae arrangement, and growth habit). In Orbignya, four subgenera, with sectional division, were circumscribed on the basis of growth habit

and staminate flower morphology. What is interesting in Glassman's subgeneric and sectional groupings is that all possible hybrids in all four genera identified in the anatomical study had to be placed in their own subgenus, section, or subsection, for having some awkward feature that would not allow their placement together with the other "good" species. The subgeneric groupings of Orbignya completely coincide with the groups defined anatomically: the Brazilian Orbignya (O. eichleri, for being acaulescent, is placed in a different section) form their own subgenus; the non-Brazilian Orbignya are grouped together, although in different sections and subsections, separated by growth habit (acaulescent: O. cuatrecasana, O. polysticha, and O. sagotii; arborescent: O. cohune, and O. quacuyule); O. crassipatha and O. luetzelburgii are each placed into different subgenera.

Henderson's and Glassman's views of the Attaleinae differ basically in their broadness of concepts, both generic and specific. Henderson drastically reduced the number of species in the subtribe, as well as the number of genera; Glassman has adding to the size of the subtribe, with the addition of new species and combinations. I have to recognize that the way Henderson sees the subtribe, with only 29 species, facilitates its understanding as a group, as much of the confusing and excessive names have disappeared. However, such a drastic reduction (ca. 60 % of the old species were eliminated) requires more carefully explained and documented arguments, other than just the use of a crude broad species concept. At

the generic level, the discussion may be more extensive and still inconclusive, as the understanding of a genus may be more subjective than that of a species.

Practicability as an argument for the lumping was enforced by Wessels Boer (1965), who defended the practical importance of classifying the doubtful species as a single genus instead of many questionable genera. The recognition of only one genus would avoid new equivocal and useless combinations. This argument loses much of its power if we consider that most of the doubtful species were eliminated by the drastic lumping. If the genera were maintained, they would now each be formed by a small number of species, easy to recognize and understand as separate small genera. In this scenario, Orbignya would include only 7 species; Attalea 15-16; Scheelea 3-4; and, Maximiliana 1. Practicability, therefore, as an argument for the generic lumping becomes weak, and may be put aside as an issue of importance in this discussion.

Henderson (1995), while merging the genera, recognized the existence of these groupings, the former genera, but treated them as subgeneric categories (six in number, including Parascheelea and Markleya). Glassman (unpublished) organized the groups into categories that coincide with Henderson-Wessels Boer's view in another level (as genera). My anatomical results fully support the existence of distinct groups that coincide mostly with the traditional genera, and based on that, it could be proposed that the traditional generic delimitation be maintained. However,

the problem of the crossability among the groups, has to be addressed and understood. Of course these groups can be crossing with each other and still be good genera, as the existence of a wide number of intergeneric hybrids is a known fact, as discussed earlier. The problem is that crossability seems to be far too easy and frequent in the Attaleinae to be considered at the same level as the other cases in other groups. Additionally, not many other hybrids have been reported in other palm groups (only 10 other cases, in 5 genera; only one case of putative intergeneric hybridization), and not as frequently and not as obviously as in the Attaleinae. No reproductive barriers seem to exist between these groups in the Attaleinae; the crossings have apparently been so widespread and frequent that a high number of the drastically reduced, most recently considered valid species (Henderson et al., 1995) still have problems concerning their correct identification and taxonomic placement. The suggestion of the hybrid complexes formed in many points of the distribution range of these palms is acceptable given the evidence of the frequent crossings among many of them.

The distribution range of the species in all groups does not show any considerable gaps between each one. However, apparently Maximiliana and Scheelea do not overlap with the Brazilian Attalea; but they do overlap with A. racemosa, A. nucifera, and A. tessmannii, in the northern and western portions of their distribution. From the four species of Scheelea, only S. phalerata reaches the Brazilian *planalto*; the other three are distributed throughout Central America (S. butyracea reaches

western South America), and in the western (S. insignis) and northern (S. attaleoides) portions of the Amazon. Scheelea's range coincides mostly with Maximiliana's, and these two groups barely come in contact with the Brazilian Orbignya and Attalea. The geographical patterns of distribution of the groups correlates with the anatomical results: the Brazilian groups of Orbignya and Attalea are more closely related to each other than to any other group, and their species show "pure" anatomical patterns, except in the areas where they come in contact (e.g. A. dubia; x A. minarum); Scheelea and Maximiliana are anatomically closer to each than to any of the other groups; the confusing group of species in the northern Amazon region (O. polysticha, O. sagotii, O. spectabilis, and O. lutzburgii) occur in areas which overlap with Scheelea and Attalea species (at least A. racemosa). It is not clear, however, whether the crossings involving Orbignya happened with the Brazilian species (which is the same in Surinam?) or O. cohune, which clearly has reached the western and possibly the northwestern portions of South America. This latter possibility seems more likely.

5. Conclusions

My results show a significant discontinuity in pattern variation within the subtribe *Attaleinae*. Three major groups, three major evolutionary lineages were determined by the analyses of the anatomical data. These groups could preliminarily be separated by their overall resemblance and differences found on a number of anatomical characters (during the anatomical description of the taxa), and a high number of intermediates were found. The multivariate analyses confirmed the discontinuity of the patterns of variation among characters, between characters and taxa, and supported the separation of groups. The extreme complexity of character variation within the subtribe was shown by the multivariate analyses, particularly when the intermediates were included. Finally, the subtribe was characterized as a monophyletic group, which diversified in three, maybe four, evolutionary directions. Overall, the results indicated that hybridization has been the most probable mechanism of speciation within the subtribe.

The resulting phylogeny (when the putative hybrids are excluded) is almost completely resolved, and it appears congruent with other sources of evidence to a great extent. The cladograms obtained are mostly a reproduction of the scatterplots and dendrograms resulting from the multivariate analyses (PCA and cluster). A complete lack of resolution in both PCA and cluster analyses matched the cladistic

results with collapsed cladograms, when the putative hybrids and some of the intermediates were included. Well delineated groups resulted from the analyses of character correlation and similarities of these characters among taxa, as well as resolved cladograms were generated without the presence of the hybrids/intermediates. The re-inclusion of some of the species classified as previously intermediates and tested as so, did not cause any significant changes in the topology of the cladogram. The differences between cladograms, scatterplots based on principal components, and clusters were minimal, and should be attributed to differences in type of data used and the method of coding for the different analyses. One of these few differences between the results of the analyses performed refers to the position of O. cuatrecasana, O. guacuyule, and O. cohune in the dendrogram that resulted from the cluster analysis without the hybrids/intermediates. These three species clustered in the Scheelea group with Maximiliana, as opposed to appearing in a separate position on the cladogram as sister species to the Orbignya-Attalea clade. This difference is minimal and irrelevant as the position of O. cuatrecasana in the strict consensus tree was not well supported. Moreover, in some of the trees generated, the clustering pattern was repeated in the cladogram. The presence of O. eichleri in the Attalea clade is also understandable, as at a higher level both Orbignya and Attalea form a single cluster; moreover, on the cladogram these two groups ended up forming a large evolutionary unit.

From both phenetic and cladistic approaches the delineation of groups within the subtribe was clear. The groups preliminarily identified in the descriptive work coincided with the groups formed by the use of principal components derived from the analysis of character correlation, and with the clusters formed on the basis of the analysis of the similarities of characters among the taxa. These groups mostly coincided with the circumscription of the genera as traditionally delimited in the subtribe. The evolutionary lineages derived from the cladistic analysis (Figure 65) are basically the same as the groups delimited by the other approaches. These groups were as follows:

. Maximiliana maripa – It seems to represent a separate lineage that is anatomically, more closely related to Scheelea than to any other group in the subtribe. The initial hypothesis, that it could belong in the subtribe Butiinae was not confirmed, and its placement in the Attaleinae is well supported on the anatomical grounds. However, M. maripa continues to be the member of the Attaleinae which is the closest to Syagrus, as indicated by the possession of many character states shared with that genus. Morphologically, the production of inflorescences with both staminate and pistillate flowers, in addition to the usual Attaleinae type (all-staminate or all-pistillate), approximates even more closely Maximiliana to Syagrus.

. Scheelea – It represents the second evolutionary group in the subtribe, and it is represented by two “good” anatomical species: S. insignis and S. attaleoides. The

other two species included in this study ended up in the group of putative hybrids.

Possibilities of hybridization involving Scheelea occurs mostly in three different areas: 1) Central America reaching up North and Northwest of South America in the case of S. butyracea; 2) the northern and northwestern portion of the Amazon region, in Colombia, Venezuela, the Guyanas, Peru, and Brazil (in the case of the “messy” group of Orbignya; 3) the southern and western periphery of the Amazon region, in Brazil (reaching up to the central plateau), Peru, Bolivia, and Paraguay (in the case of S. phalerata). No signs of Scheelea could be found in the range of distribution of the Brazilian Attalea, which does not seem to overlap with neither Maximiliana or Scheelea.

. O. cohune (including O. guacuyule) and O. cuatrecasana. As a result of the descriptive work, these three species had to be grouped together, along with O. eichleri, since they lacked some of the most characteristic features of the other three Orbignya. In the results of the multivariate analysis, where both qualitative and quantitative data were used, O. eichleri joined the Attalea cluster, close to Orbignya; O. cuatrecasana, O. guacuyule, and O. cohune formed a cluster of their own, next to Scheelea. The cladistic results indicated that these three species comprise separate evolutionary lineage related to the Orbignya-Attalea group. In conclusion, O. cuatrecasana and O. cohune are defined here as belonging to the Orbignya-Attalea group; O. cuatrecasana comprising a lineage that could not be fully understood for the reasons already discussed. Orbignya cohune is anatomically closely related to

O. guacuyule, or conspecific, and they can be both safely placed into the Orbignya-Attalea group, representing the Central American lineage of evolution of the group. O. luetzelburgii could not be confirmed as a possibility of hybridization and joined this group, although its position was weakly supported.

. Orbignya-Attalea – This group comprised the most closely related species in the subtribe. In the descriptive analysis they could be separated into two different groups, on the basis of a number of characters. In the multivariate analyses, plotting of components and clusters could still separate the Brazilian Orbignya from the Attalea group, with O. eichleri always joining the latter. At a higher level, the two groups formed a larger cluster. Cladistic results were similar: the two groups could still be distinguished in two smaller clades. The Attalea clade was not well supported, and the two groups can be suggested as comprising the same evolutionary line. O. eichleri ended up as a sister species to the other Brazilian species of Orbignya, which formed a trichotomy that could not be resolved by the anatomical data. Attalea oleifera resolved with A. pindobassu, and A. geraensis as the sister species to the clade formed by A. funifera and A. humilis. With the re-inclusion of some of the intermediates a few changes occurred inside the Attalea clade: Attalea oleifera was placed unresolved as sister species to the rest of the clade; A. dubia resolved with A. pindobassu; A. geraensis with A. colenda; O. crassispatha and A. humilis resulted unresolved as sister species to A. funifera and its putative hybrid A. x piassabossu. Orbignya crassispatha defined its position as

more appropriate in the Attalea group than in Orbignya, and this is fully supported by the anatomical data. On the basis of the results from the analyses, Orbignya and Attalea (the Brazilian species) comprise the same evolutionary line, and their separation at the generic or subgeneric levels is just a matter of taste. The results showed that outside Brazil, the Attalea group is more complicated in terms of anatomical patterns: A. racemosa, A. tessmannii, and A. nucifera ended up in the intermediate group. Attalea colenda and O. crassipatha were also tested as belonging in this group, and their status of possible hybrids could not be characterized on anatomical grounds. These two taxa seem to be examples of species of hybrid origin. They carry anatomical signs of the Orbignya parent (probably O. cohune), but most of their leaf anatomy is characteristic of the Attalea group. The isolation of A. colenda and O. crassipatha, respectively in Ecuador and Haiti, and consistent anatomical patterns in the specimens examined, indicating no segregation, support the suggestion that they are fully speciated taxa of hybrid origin.

Fig. 65. Evolutionary lineages in the subtribe Attaleinae.



. Hybrids and Intermediates - Four putative hybrids were included in the study for the purpose of testing leaf anatomical data, as a tool for identification of such cases in palms. From these five, two could be confirmed as showing anatomical evidence of crossings between the putative parents: M. dahlgreniana, x A. minarum. Attalea colenda and A. x piassabossu could not be confirmed as such a case. Ten other species revealed crossed and/or conflicting anatomical patterns. From these, seven can be suggested as hybrids, given the evidence for this: A. racemosa, A. tessmannii, S. phalerata, S. butyracea, O. polysticha, O. sagotii, and O. spectabilis. Orbignya polysticha and O. sagotii have recently been placed in synonymy under O. microcarpa Martius by Henderson et al. (1995). The results from this study agreed with that, and further suggested that O. spectabilis is probably also conspecific with the other two species. If the conspecificity of O. polysticha, O. sagotii, and O. spectabilis is followed, five possibilities of new cases of hybridization are suggested, and should be the subject of further study. Attalea nucifera ended up inconclusive, either a case of mistaken identification, or wrong description. The results indicated that this species has been placed in the wrong group.

The delimitation of genera could be relatively easy to do, on the basis of the results from the analyses without hybrids/intermediates. The three approaches clearly showed that distinct "natural" groups exist within the subtribe, and that they

mostly coincide with the circumscription of the former controversial genera. On the basis of the anatomical results, it could alternatively be concluded:

a. Maximiliana, Scheelea, Orbignya and Attalea are “good” genera. The number of “good” species in each genus is, however, much smaller given the high number of hybrid individuals. Intergeneric hybridization does not invalidate them as “good” genera.

b. Maximiliana, Scheelea and Orbignya-Attalea comprise three different genera. As pointed out before, the separation or grouping of Orbignya and Attalea is just a matter of taste given the evidence found. This three-genera alternative, however, may be partially invalidated by the fact that two other species of non-Brazilian Attalea could not be included in this study, including the type species. This alternative would have also to consider the high level of intergeneric crossability as a normal event.

c. Crossability among species of different groups within the subtribe is considered abnormal at the generic level, and the lumping of the genera is accepted. Since it has already been done, it would not involve much work. However, Maximiliana does not cross with the same frequency as the other groups. It has shown evidence of a different evolutionary trend (e.g. bisexual inflorescences), and it is relatively close to the Butiinae. It appears that the lumping of Maximiliana into the same genus with

Scheelea, Orbignya and Attalea could not be fully justified. Its separation, on the other hand, as a single genus, while the others are lumped, does not seem to be the right solution either.

d. The lumping is accepted, and subgeneric groups are formed by Maximiliana, Scheelea, the Brazilian Orbignya-Attalea, and O. cohune and O. cuatrecasana, and O. luetzelburgii. The three latter can alternatively be placed into the Orbignya-Attalea group.

The anatomical evidence was, overall, very strong, but it still represents a source used alone. However, an attempted combination of morphological and anatomical information attempted did not change the results from leaf anatomy alone. The results were very clear and congruent with other lines of evidence. The variation in the subtribe is discontinuous and groups can be discerned. The groups mostly coincide with the traditional delimitation of genera in the subtribe; the classification of these groups and their positioning at a taxonomic rank, however, fall out of the scope of this study.

What is, then, the truth on the taxonomic position for the groups in the Attaleinae? Maybe this truth does not exist as a general truth. Maybe, it exists, as fragmentary truths, which fit each case; or as subjective truths constructed on the basis of knowledge (which is also fragmentary, as it comes mostly from incomplete,

fragmentary botanical specimens), biological concepts (frequently more than one exists), and/or convenience (practicability, or just a matter of personal taste). This study was conceived to be a contribution to palm taxonomy, resulting from an application of methods to a data set constructed by using reliable techniques. The results obtained may not put an end to the controversy as desired, but given the extreme complexity of the evolutionary history of this group of plants, I doubt any results will come out with a final truth. However, they can surely contribute to a better understanding of this important group of palms, and in this regard, I believe the goal was achieved.

6. Appendices

Appendix I

Toluene Series for Paraffin Embedding

1. 70% ETOH
2. 95% ETOH
3. 100% ETOH
4. 90% ETOH / 10% Toluene
5. 70% ETOH / 30% Toluene
6. 50% ETOH / 50% Toluene
7. 10% ETOH / 90% Toluene
8. 100% Toluene
9. 100% Toluene
10. Add paraffin chips until saturated at room temperature. Wait at least 12 hours.
11. Put on slide warming plate, and add paraffin until saturated. Wait at least 12 hours.
12. Put in 60°C oven. Replace 1/2 of the liquid in the vial with melted paraffin and leave the lids off. Wait at least 24 hours.
13. Take the vials out the oven, keep on a warming plate, and move the material in the melted paraffin to a tray. Arrange the samples in the tray and float them on icewater. When the surface of the paraffin is hard, sink the tray on the ice water.
14. Put the embedded samples in the refrigerator.

Appendix II

Staining of Cross Sections - Aqueous Safranin 0.5% and Fast Green

1. 100% Xylene
2. 100% Xylene
3. 50% Xylene / 50% ETOH
4. 100% ETOH
5. 95% ETOH
6. 70% ETOH
7. 50% ETOH
8. Safranin 0.5%
9. 50% ETOH
10. 70% ETOH
11. 95% ETOH
12. Fast Green
13. 100% ETOH
14. 100% ETOH
15. 50% ETOH / 50% HEMO-DE
16. 100% HEMO-DE

2-3 hours in Safranin; 15-20 seconds in Fast Green; 5 minutes in each of the other steps.

Appendix III

Dehydration Series for Epidermal Peels

Peels stained in Safranin 0.5% overnight.

1. Water - quick bath to wash the excess Safranin.
2. 50% ETOH
3. 70% ETOH
4. 95% ETOH
5. 100% ETOH
6. 100% ETOH
7. 50% ETOH - 50% HEMO-DE
8. 100% HEMO-DE

5 minutes in 100% ETOH; 2-3 minutes in each of the other steps.

Peels mounted in Kleermount.

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Systematic and Agro-ecological Studies in the Attaleinae (Palmae)

by

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II. Agro-ecological Studies

A. Soil and Nutrient Requirements of the Babassu (Orbignya phalerata Martius) Seedling

1. Introduction

The babassu palm (Orbignya phalerata Martius; Anderson & Balick, 1988) is a plant species of great ecological success for its ability to colonize large areas of secondary vegetation. The domination of babassu is much more significant in the tropical dry forest of Maranhão, in the Cocais region (Figure 66), where the predominant Red-Yellow Podzolics and Plintosols are relatively fertile in relation to soils over most of Maranhão's territory and the Amazon basin as well (Anderson & Anderson, 1983).

Under the program for domestication of the babassu palm, collection of germplasm and several related projects have been carried out since 1980. The project of germplasm collection led to a series of other studies that included the development of methods and techniques for seed germination and large scale production of seedlings used in the establishment of an *ex situ* germplasm bank, in 1981 in Bacabaí, Maranhão, in a 50-hectare area located at the EMAPA (Empresa Maranhense de Pesquisa Agropecuária) Research Station. This experiment, included as a section of this dissertation, is part of the major study initiated in 1980. It is intended to fill a gap in the knowledge of nursery production of babassu, yielding information on growth of babassu seedlings in different types of soil under different fertilization regimes.

A study of the correlation between the presence of the babassu palm and the occurrence of major groups of soils has not been done. However, the mapping of the native stands of the babassu palm in the State of Maranhão carried by MIC/STI (1982) determined that the most extensive populations of this palm occur in areas of Podzolics and Plintosols, and less intensively, in Latosols and Sands. The most important characteristics of these major groups of soil in relation to the State of Maranhão, and to the babassu palm as well are briefly described below.

Latosols (USDA system=Oxisols) are the most common type in Maranhão, occupying 115,260 Km^2 , which corresponds to approximately 35% of state's total area (EMBRAPA, 1975). The low nutrient status and low content of organic matter give these soils a very low fertility but they often support high forest. They are, in general, soils of lowlands, occurring on sites that vary from flat to steeply sloping but they tend to be more common on moderate slopes. When the forest is removed and agriculture is practiced, fertility is quickly exhausted, requiring applications of correctives and fertilizers. The upper parts of these soils have free drainage but may become saturated with water during the rainy season. These soils have a clayey texture and clay contents can range from 15% to 35%. Acidity is remarkably uniform with pH values about 5.5 in the surface, decreasing to about 4.5 in the middle horizon then increasing to 5.0 in the mottled clay. The

productivity of natural stands of babassu, which are widespread throughout the areas of Latosols, is reported as low (MIC/STI, 1982).

Podzolics (USDA system=Red-Yellow Podzolics, Ultisols) constitute the second most important group of soils in Maranhão in terms of area, occupying 91,390 Km^2 , ca. 28% of the total surface of the state (EMBRAPA, 1975). These soils were the main areas of babassu stands where high productivity (2,148.9 Kg/ha), in areas of the Cacaís region) has been recorded in the past (MIC/STI, 1982). Today, an extensive portion of the area occupied by Podzolics is now covered by pastures alternating with disturbed babassu stands. These are, in general, well developed soils, mostly of clay texture, that range from low to medium natural fertility. They have thick, acidic and strongly leached upper horizons that create many problems for agricultural utilization, following removal of natural vegetation. As a consequence, large amounts of fertilizers are required, particularly nitrogen and phosphorus. Podzolics usually occupy areas of flat to undulating topography.

Plintosols (Laterita Hidromórfica; USDA system=Laterite) occupy ca. 14% of the state's territory (47,443 Km^2), and constitute the third most important group of soils (EMBRAPA, 1975). They are highly acid, with low natural fertility, and require chemical correction of pH and fertilization. They usually occupy flat to moderately sloping, agriculturally productive areas. This group comprises soils

formed by material that is hard or will harden on exposure and is composed mainly of iron oxides and /or aluminium. They are usually under restriction to percolation of water, subject to the temporary effect of excessive moisture; in general, they are soils of moderate to imperfect drainage, conditioned by the nature of the parental material. This class of soil is characterized by concretions, which under especial drying conditions are termed plinthite. Eutrophic Plintosol is the type that occurs in areas where babassu stands are highly productive (e.g. in parts of the Cocais region), with ca. 2,000 Kg/ha (MIC/STI, 1982). Plintosols comprise the main areas of occurrence of babassu in Maranhão.

Sands (USDA system=Cambic Arenosols) occupy 27,750 Km^2 in Maranhão, ca. 8% of the state's area (EMBRAPA, 1975). They are basically soils with a poorly developed profile, usually deep, sandy (clay contents not more than 15%), with a light texture, well drained, and extremely poor in terms of fertility. In spite of the high quartz content sandy soils are often only weakly acid, with pH values ranging from 6.0 - 7.0, coupled with a high base saturation; cation-exchange is very low due to the low clay content. These soils are continuously aerobic and have very rapid through drainage. Their water-holding capacity is very low and plants usually suffer moisture stress. Their reserve of nutrients is low due to their poor capacity to adsorb and hold nutrients, therefore a supply of fertilizers is required for good crop yields. They normally occur in areas of flat to moderately sloping topography, covered by vegetation such as cerrado,

caatinga and forest. Native stands of the babassu palm are reported to have low productivity in such soils, with less than 1,000 Kg per ha (MIC/STI, 1982).

Apparently soil type has a considerable effect on the adult plant's productivity. However, the type of soil where these palms occur does not seem to be a limiting effect on the early growth of the palm, as indicated by the high number of seedlings and juvenile individuals observed in different types of soil. Different soil conditions produce palms differing in their vegetative growth. Experiments carried out with the African oil palm showed that palms grown under soil conditions that led to a rapid and extended vegetative development, when planted at high or normal density, often failed to respond to fertilizers (Hartley, 1988). The babassu palm represents the opposite situation, forming very dense stands in the wild, with over 10,000 seedlings and juvenile individuals per hectare. As result of this study several questions were expected to be answered: 1) Would the palm respond positively to improved growth conditions? 2) What would these responses be in terms of growth and development? 3) Would the differences in growth and biomass production resulting from fertilization be significant enough to justify higher production costs? 4) Is the soil chemical composition more important than its physical structure for growth of babassu seedlings? The experiment described in the following paragraphs was implemented to answer these questions, and to test the effects of the type of substrate and the application of different doses of fertilizers on the growth of babassu seedlings in their phases of post-germination and establishment. The major

hypothesis tested was that neither soil substrate or fertility significantly affect the early growth of the babassu seedling.

Results from this experiment were expected to provide useful information on the growth of babassu seedlings in their post-germination phase until their establishment. Additionally, they would provide a basis for a regimen of fertilization for babassu seedlings, if the responses were satisfactory. It was also intended to complete the goals of the study on establishment of babassu in degraded soils (described in the next section) by generating information and developing techniques for large-scale production of seedlings for reforestation and site restoration.

2. Material and Methods

This experiment was set up at the EMAPA Research Station in Bacabal, *Cocais* region of Maranhão State (Figure 66), and carried out during a four-year period (1991-1994). The first step in this trial was seedling production. To accomplish this, a small greenhouse (10 x 5 m) was built, in order to provide the necessary protection for the germinating seeds (Figure 67). For germination, plastic boxes (60 x 30 x 20 cm) were utilized with a substrate of medium sized granules of vermiculite (Figure 68). Individual kernels were removed from the fruits, using a technique previously developed for babassu seedling production (Frazão and Pinheiro, 1985; Pinheiro and A. Neto, 1987).

Fig. 66. Physiographic regions of Maranhão State, Northeastern Brazil.

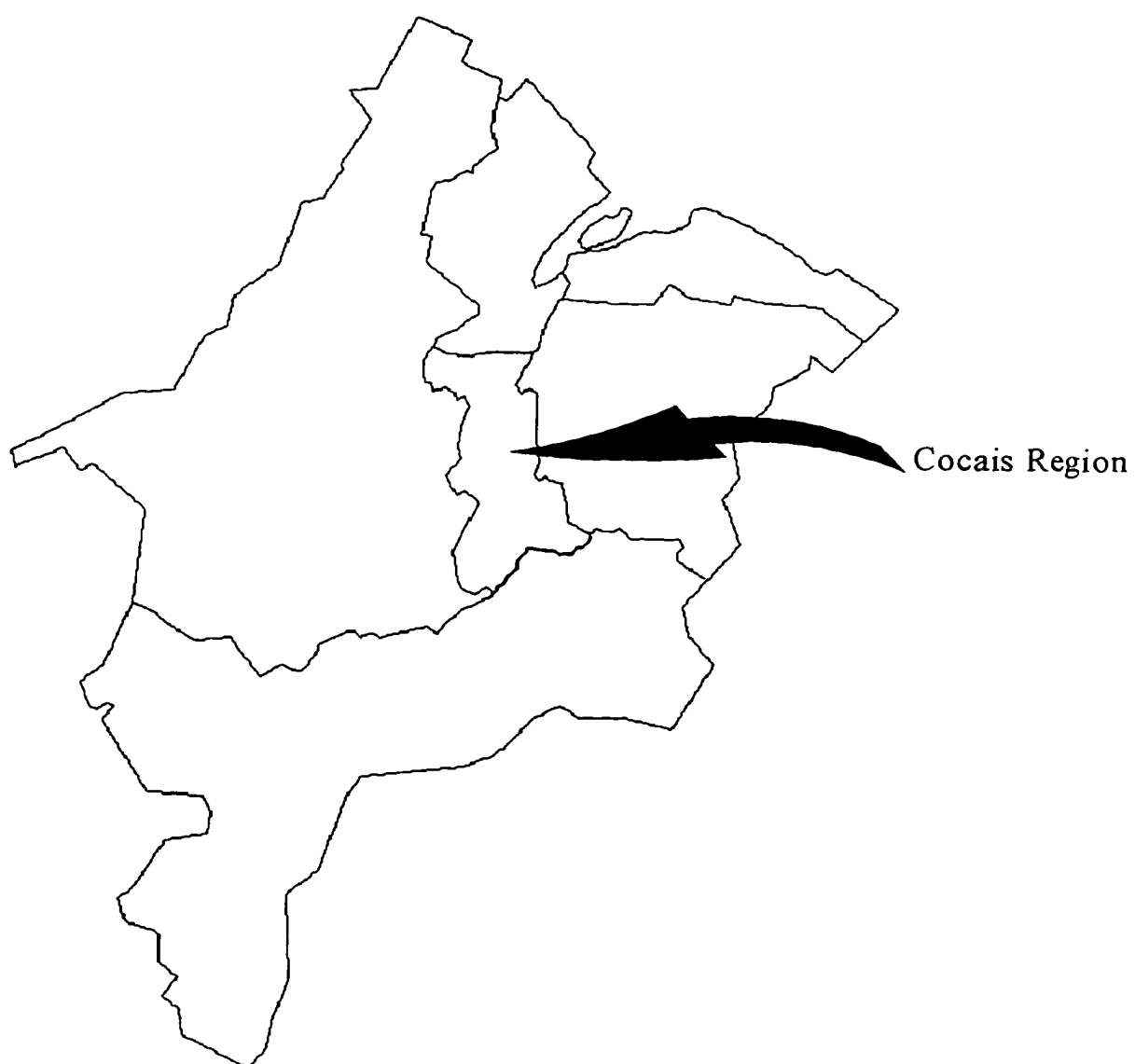


Fig. 67. Small greenhouse for seed germination and early growth of seedlings.

Bacabal, Maranhão - September, 1990.



Fig. 68. Boxes with vermiculite for seed germination - September, 1990.



The seedlings produced in the small green house were kept in the germinators until they had 2-3 leaves, and then moved to 20 liter plastic bags with four types of soils. The root system of the seedlings measured on average 10 to 40 cm in length by the time the seedlings were transplanted to the plastic bags (Figure 69).

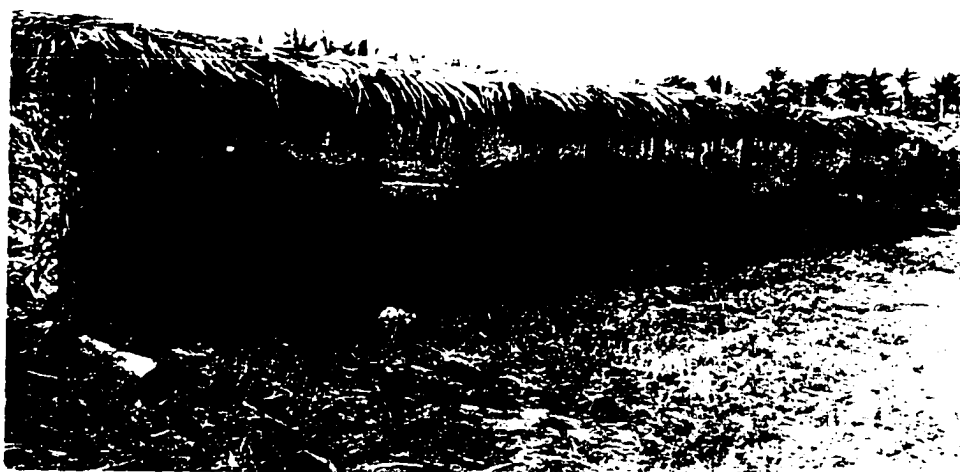
Fig. 69. A. Transplanting of seedling from the germinator to plastic bags;
B - View of plastic bags with seedlings in the nursery by the time
of transplanting. January, 1991.



Four types of soils were used: Sand, Podzolic, Latosol and Plintosol, which were selected as they are the most important types found in Maranhão, in terms of area of occurrence and habitat for babassu stands. The nomenclature follows the soil classes recognized in Brazil (after Bennema and Camargo, 1964); however, the approximate equivalent in the USDA system is provided.

The type of Latosol used in the experiment was Yellow Latosol, medium texture. The class of Podzolics taken for this experiment was the Red-Yellow Podzolic, sandy-clay texture (12-15% clay), phosphorus deficient. The Plintosol used was the Eutrophic type. The sandy soil tested was the type with high quartz content. The experimental design was a factorial arranged as follows. Four fertilizer levels (ranging from 0 to the complete recommended NPK regimen for Elaeis guineensis) were applied to seedlings growing in four types of soil. Each treatment combination (soil-level of fertilization) comprised 20 seedlings. Fertilizer was applied quarterly, using a 12-17-10 formula, as used for the Oil Palm. Observations were made on general aspects of seedling development, number of leaves, and length of seedlings. To protect the seedlings against an excess of sunlight, rain and wind, a close-sided shed was built, using babassu leaves as the main construction material. This shaded nursery (Figure 70) measured 20 m long by 6 m wide, and the babassu leaves used for thatching were gradually removed in order to permit increasing amounts of sunlight on the seedlings.

Fig. 70. Close-sided shed built with babassu leaves for seedlings protection -
January, 1991.



The bags with seedlings were put on the nursery at ground area leaving 1m space between lines of bags and 20 cm between bags in the lines. The experiment was installed with 20 seedlings for each level of fertilization-soil type combination, comprising 80 seedlings per soil type and per level of fertilizers, and totaling 320 seedlings in the whole experiment.

The first application was made beginning with the 2nd month, as I considered that a two-month period would be enough time for seedlings to recover from the stress of transplanting, and the initiation of subsequent development. The measured doses of fertilizers were directly applied in the bags, followed of irrigation. During the transplanting operation the general characteristics of seedlings were observed as well as general data on leaf and root development. The treatments are shown in Table 86.

Table 86. Treatment Combinations \ Levels of Fertilization and Types of Soil.

Soils	Levels of Fertilization			
	I	II	III	IV
Sand	0	1	2	3
Podzolic	0	1	2	3
Latosol	0	1	2	3
Plintosol	0	1	2	3

Levels of Fertilization (NPK):

0 - Control (No Fertilization)	1 - 4 g : 1st application - 2nd month 8 g : 2nd application - 4th month 12 g : up to 48th month
2 - 8 g : 1st application - 2nd month 16 g : 2nd application - 4th month 24 g : up to 48 month	3 - 12 g : 1st application - 2nd month 24 g : 2nd application - 4th month 36 g : up to 48th month

Five censuses were carried out at two, ten, fifteen, twenty-one, and forty months after the seedlings were transplanted from the germinators to plastic bags. In each of regular censuses number of leaves and length of seedlings were recorded. The final collection of data (at 40 months) was made with destructive measurements, and the final evaluation included the following parameters: number of leaves, length of seedlings, number of pinnae, number of roots, and fresh and dried weight of leaves, roots and rhizome. The results were statistically analyzed by census, using analysis of variance, contingency table analysis (tests of independence), and linear regression. The data were analyzed using JMP version 3.1.5. (SAS Institute, Inc., Cary, North Carolina).

3. Results and Discussion

First Census - Two Months After Transplanting

No significant effect was expected to happen at this point given the short space of time elapsed after transplanting. This first data collection was carried out as a way to record and characterize the state of the seedlings in relation to growth and number of leaves in the beginning of this experimental phase, and their recovery following transplanting. Length of seedlings in the experiment at that point averaged 55.43 cm, ranging from 30-73.5 cm (Table 87). Leaf production per seedling averaged 1.98, ranging from 1-3 (Table 89). Figures 71 and 72 show the mean length of seedlings and number of leaves at the beginning of the experiment (2 months after the seedlings were transplanted).

Analysis of variance of the treatments for the data collected two months after transplanting showed an overall significance among types of soil (Table 88). No fertilizer had been applied at this point; therefore, any possible differences in the recovery of seedlings after transplanting was probably related to the substrate (soil type). In order to detect possible differences in the growth of seedlings after transplanting that could be produced by the substrate, an exploratory analysis of this first collection of data was carried out. This initial data analysis showed

that seedlings grown in sandy soil had the lowest growth rate compared to other soil types. This probably means that seedlings used the natural fertility of the different types of soils and the physical structure of the substrate to recover from the stress associated with transplanting. It is known that among the types of soil utilized in this experiment, Sand was the poorest in terms of natural fertility. Comparison between Sand and the other three soil types showed significant difference at the 5% level ($p=0.0001$). The Plintosol type showed the highest mean seedling length for the period, and the difference between this soil type and the other three was statistically significant at the 5% level ($p=0.0001$). No statistically significant differences among soil types were detected in the number of leaves produced by the seedlings at this phase of the experiment (Tables 89 and 90).

Any conclusion about the seedlings' growth performance related to soil type was premature at that point since many other factors could be accounting for the differences observed. The overall better recovery of seedlings after transplanting in the Plintosol type was, however, quite noticeable. Good results were also recorded in the Podzolic type of soil, the natural soil of the Cocalis region of Maranhão, where the native stands of babassu used to be more expressive and more productive (SUDENE, 1981).

Fig.71. Mean length of seedlings (cm) two months after transplanting.

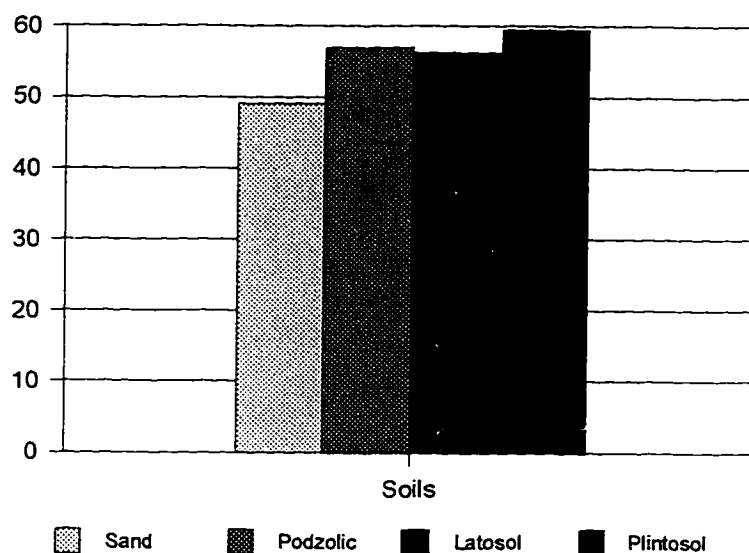


Table 88. Descriptive statistics for length of seedlings recorded two months after transplanting from the germinators to plastic bags with four types of soil.

Soil	Mean	SD	Range
Sand	49.039	7.257	30 - 68
Podzolic	56.888	8.988	36 - 73.5
Latosol	56.281	8.021	38 - 70
Plintosol	59.513	7.654	39 - 73
Totals	55.430	8.867	30-73.5

Table 89. Anova table for a one-factor analysis of variance on length of seedlings two months after transplanting.

Source	df	Sum Squares	Mean Square	F-test	Prob>F
Between Soils	3	4829.105	1609.702	25.115	0.0001
Error	316	20253.647	64.094		
Total	319	25082.752			

Fig. 72. Mean number of leaves two months after transplanting.

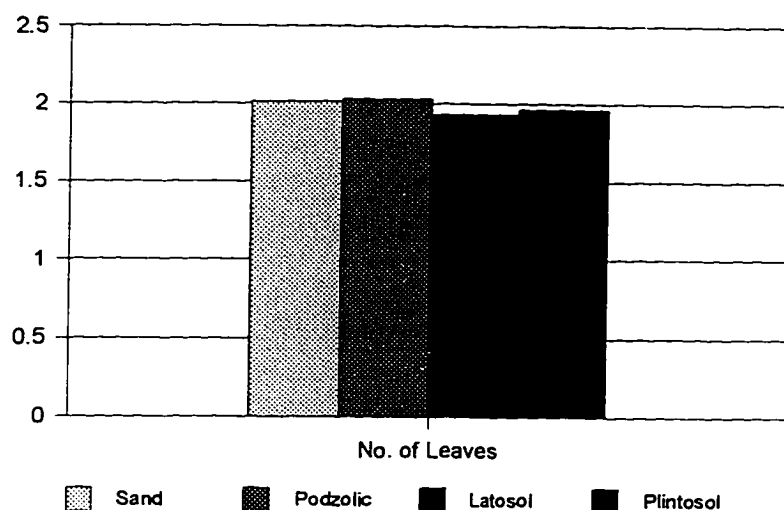


Table 90. Descriptive statistics for number of leaves recorded two months after transplanting from the germinators to plastic bags with four types of soil.

Soil	Mean	SD	Range
Sand	2.013	0.112	2 - 3
Podzolic	2.037	0.460	1 - 3
Latosol	1.938	0.460	1 - 3
Plintosol	1.962	0.404	1 - 3
Totals	1.987	0.388	1 - 3

Table 91. Anova table for a one-factor analysis of variance on number of leaves two months after transplanting.

Source	df	Sum Squares	Mean Square	F-test	Prob>F
Between Soils	3	0.5	0.167	1.11	0.3452
Error	316	47.45	0.15		
Total	319	47.95			

Second Census - Ten Months After Transplanting

Three applications of fertilizers were carried out during the 10-month period elapsed after the seedlings were transferred to plastic bags in the nursery. Analysis of the data attained, revealed that there were continued significant differences in the growth of seedlings in relation to soil type. Fertilization, however, did not produce any significant effect on seedling growth, at this point. The overall mean length of seedlings after ten months after transplanting was 48.848 cm (Table 91), lower than the mean recorded in the beginning of the experiment (55.430 cm). A high percentage of seedlings (54.9%), however, showed an average length ranging from 44.8 to 57.4 cm. Three main factors may be responsible for reducing the overall mean length of growth: 1) the stress caused to the seedlings by the transplanting operation caused many of the older leaves to wither, and new leaves were produced during the recovery period; 2) the number of seedlings that died (18); and, 3) the irregular development of a number of seedlings, caused by insects, fungi, excess of moisture, etc., following the transplanting operation. Root fracture is the main cause of blackening off of African oil palm seedlings transferred to bags (Hartley, 1988), and some damage to the root system is inevitable in transplanting bare-root seedlings. The damage to the roots is obviously reflected on growth of the seedlings even though seedlings are still being nourished by the seed endosperm. Following

transplanting, several abnormalities in leaf development were observed such as crinkles, rolls and collantes, although the number of leaves produced increased in that period. Figure 73 graphically represents the situation in terms of growth of seedlings recorded ten months after transplanting.

The effect of soils on growth of seedlings was still significant (Table 92), although the p-value ($p = 0.0240$) was lower than in the previous analysis. Interaction between soils and levels of fertilization was not significant (Table 92). A continued lower growth rate in Sand and a higher rate in Plintosol were recorded (Table 91) keeping the pattern observed in the beginning of the experiment. Comparison between Sand (the lowest rate) and the other three soil types showed that the difference between them was statistically significant ($p = 0.0301$). Comparison between Plintosol (the highest rate) and the other three types of soil also showed statistically significant differences between the means ($p = 0.0061$). This means that the worst (Sand) and the best (Plintosol) performances among soil types were in fact accounting for the differences observed in growth of seedlings.

Levels of fertilization were responsible for a weak statistical significant effect on the growth of seedlings (Table 92), with a p-value on the borderline of significance (0.0452). Contrasts among the levels showed significance when control (the highest mean) was compared to the other three levels ($p = 0.0098$),

and no significance was obtained in the analysis when level 3 (the lowest mean) was compared to the other three ($p=0.1576$). Neither was significant the comparison between the two lowest overall means among levels (level 1 and level 3). These results mean that only the control was statistically different from the other three levels, which in turn were not individually different from each other. In other words, the differences in growth among levels of fertilization did not statistically exist at that point of the experiment, and seedlings apparently were doing better in the absence of fertilization. This makes sense, if we keep in mind that the seedlings were still attached to the seed for at least 2-4 months following transplanting, and therefore, still using the endosperm reserves during part of the time between the first and this data collection, though they already had a young, but functional root system.

For number of leaves, the situation was quite different. The overall mean was 5.04 leaves/seedling, much higher than that formerly recorded (1.98). The range was 1-7 leaves (Table 93), but the majority of seedlings showed an average number of leaves between 4.5 - 5.2. Figure 74 shows graphically the mean number of leaves computed for soils and levels of fertilizers ten months after transplanting. Analysis of variance on number of leaves did not reveal statistical significance for the means computed for the different soil types ($p=0.1263$). On the other hand, levels of fertilization produced a highly significant effect on leaf production ($p=0.0001$). Interaction between soils and levels of fertilization was

not significant (Table 94). The highest means were recorded in the control (level 0) and in level 1 of fertilization (Table 93). However, there was no significance between the highest mean (control) and the second higher (level 1) ($p=0.3653$). Contrast between control and the three levels of fertilizers indicated a significant difference between them ($p=0.0043$). It was clear that major source of variation accounting for the overall significance in leaf production among levels resided in the difference between the lowest mean (recorded for level 3, the highest dose of fertilizers applied). Comparison between level 3 and the other three levels was highly significance at the 5% level ($p<0.001$). It therefore seems, that the highest dose of fertilizers could be having a deleterious effect on leafing rather than stimulative, a conclusion supported by contrasting the lowest two means (level 3 x level 2) which showed statistical significance for the difference between them ($p<0.0001$). It is important to point out that the data analyzed for this 10-month period after transplanting certainly reflected the effect of the dry season prior to the collection. Although some irrigation was provided after transplanting, it was quite irregular for most of the period, and this fact must be considered.

Fig. 73. Mean length of seedlings (cm) ten months after transplanting.

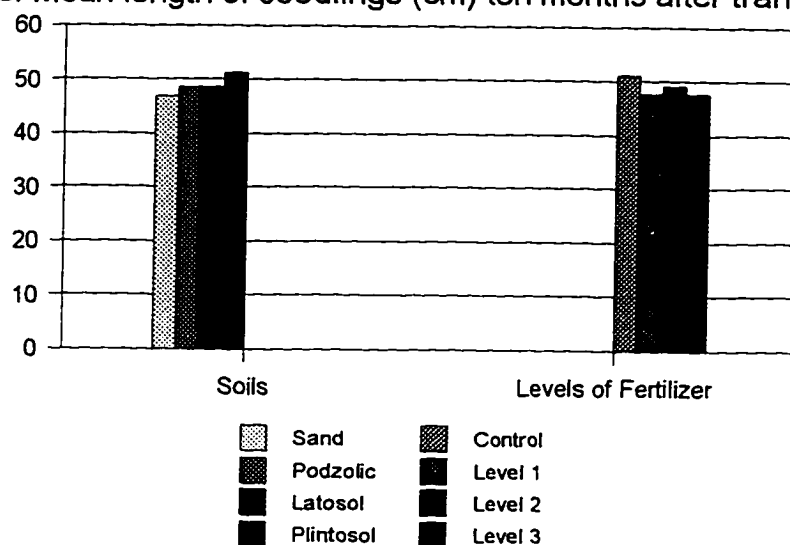


Table 92. Descriptive statistics for length of seedlings recorded ten months after transplanting from the germinators to plastic bags with four types of soil.

Soil	Mean	SD	Range	Died	Levels	Mean	SD	Range	Died
Sand	46.949	7.277	18 - 61	02	0	51.118	9.306	13 - 69	04
Podzolic	48.556	10.043	13 - 65	08	1	47.644	7.478	27 - 63	07
Latosol	48.649	9.055	29 - 69	03	2	49.039	9.428	7 - 67	04
Plintosol	51.307	9.092	7 - 68	05	3	47.558	9.259	18 - 68	03
Totals	48.665	8.866	7 - 69	18	Totals	48.839	8.868	7 - 69	18

Table 93. Anova table for a two-factor analysis of variance on length of seedlings ten months after transplanting.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soils	3	745.444	248.481	3.193	0.0240
Levels	3	622.159	207.386	2.665	0.0482
SoilsXLevels	9	685.386	76.154	0.979	0.4579
Error	286	22258.365	77.826		
Total	301	24311.354			

Fig. 74. Mean number of leaves ten months after transplanting.

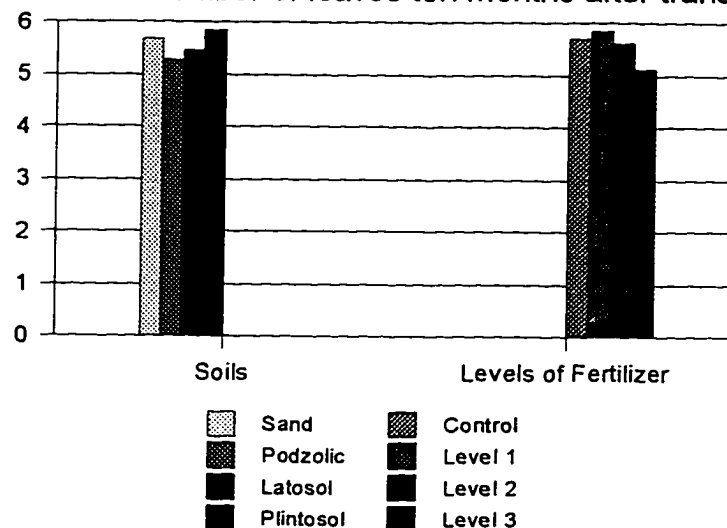


Table 94. Descriptive statistics for number of leaves recorded ten months after transplanting of seedlings from germinators to plastic bags.

Soil	Mean	SD	Range	Levels	Mean	SD	Range
Sand	4.987	1.110	1-7	0	5.329	0.943	1-7
Podzolic	4.903	1.063	1-7	1	5.192	1.049	2-7
Latosol	5.000	1.123	2-7	2	5.105	1.001	2-7
Plintosol	5.267	0.890	2-7	3	4.545	1.070	1-7
Totals	5.039	4.186	1-7	Totals	5.043	1.016	1-7

Table 95. Anova table for a two-factor analysis of variance on number of leaves ten months after transplanting.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soils	3	5.632	1.877	1.921	0.1263
Levels	3	26.047	8.682	8.884	0.0001
SoilsXLevels	9	23.322	2.591	2.652	0.0058
Error	286	279.514	0.977		
Total	301	334.515			

Analysis of the data collected up to this point did not quite reflect the true effect of the treatments on growth and biomass production. During part of the experiment time (up to ca. 12 months), seedlings were still partially fed by their endosperm reserves, despite the fact that they already had functional adventitious roots. Therefore, I concluded that only from the time the seedling became independent from the seed, the analysis could reflect the true effect of fertilizer on seedling development. The seedlings that died after 4 weeks the transplanting was carried out were not replaced. I chose to delete these from the experiment as the development of replacement seedlings would always be lower than the rest of the group's average.

Third Census - Fifteen Months After Transplanting

Seedling growth did not show any significant change since the first observation was carried out 5 months before. The overall mean for the length of seedlings was 54.578 cm (Table 95). This may be considered the same as in the beginning of the observations after the seedlings were transplanted to the nursery. Figure 75 shows the means for length of seedlings computed after the fifteen-month period after transplanting. Figure 76 provides a view of seedlings in the nursery at that point of the experiment. Range of length was 27-84 cm, but 27.2% of the

seedlings had length in the interval between 55 and 62.5 cm. The overall monthly rate of growth for the last six months was 1.146 cm/seedling/month. The same rate calculated separately for soils was 1.134 cm/seedling/month; for levels of fertilization this rate was 1.115 cm/seedling/month.

Analysis of variance showed that the differences among the means of the soils and levels were statistically significant at the 5% level, but there was no significant interaction between soils and levels (Table 96). Although not highly significant ($p=0.0472$, still on the borderline of significance), levels of fertilization continued to show a consistent, but weak effect on the model. The highest mean was recorded for level 0 (control), decreasing as the levels increased (Figure 75). However, comparison between control and the other three levels did not show statistical significance for the difference among the means. Statistical significance only resulted from the comparison between the lowest mean (level 3) and the other three levels (either together or individually). This means that, at this point, it does not make a difference in growth whether fertilizers are applied in different doses or not for level 0 through level 2, but it starts to affect growth negatively as the dose of fertilizers reaches level 3. Babassu seedlings, therefore, are not responding positively to the lower doses of fertilizers, but they are negatively affected by the highest dose.

Soils continued to produce consistent overall major effect on growth of seedlings (Table 96). Consistent also was the value of the means among the soil types: Sand still showed the lowest (52.520 cm) and Plintosol, the highest (57.573 cm) (Table 95). There was no significant difference between Plintosol and Latosol ($p=0.18033$), but it existed when Plintosol+Latosol was contrasted to Sand+Podzolic ($p=0.0026$). Comparison between the highest mean (Plintosol) and the other three soil types showed that the difference was statistically significant ($p=0.0047$). Comparison between the lowest mean (Sand) and the other three showed that the difference between them was just barely significant ($p=0.0571$).

Soil type produced a (barely) statistically significant overall effect ($p=0.0053$) on number of leaves (Table 98), in contrast to the result obtained six months before when there was no statistical differences among the means of growth shown by the seedlings in the four different types of soil. The overall mean for the period was 5.56 leaves per seedling, and the range 2-7 (Table 97). Figure 77 represents the mean number of leaves recorded in the census for both soil types and levels of fertilizers. Plintosol was still the soil type responsible for the highest mean number of leaves produced. Comparison between the highest mean number of leaves produced per seedling (Plintosol) and the other three showed statistical significance for the difference obtained ($p=0.0076$). On the other hand, the lowest mean (recorded for Podzolic), when compared to the

other three was not significant ($p=0.2452$) . Except again for Plintosol, where both length and number of leaves seemed to be stimulated by that particular type of soil, the other three types did not show statistically significant differences among their means, compared in pairs or individually, as done also for the analysis of growth.

Levels of fertilization, statistically significant ($p=0.0003$) at the 5% level (Table 98), showed some interesting results for separate consideration. At this point, the highest mean number of leaves was recorded for level 1 of fertilization (Figure 77, Table 97), in contrast to the 10-month period analysis when the control showed the highest mean. However, comparison between the control and level 1 showed that the difference between these two means were not statistically significant; neither was the difference between level 1 and level 2, meaning again that there is no difference in leaf production whether fertilizers are applied in doses 1 or 2, or are not applied at all. At level 3, negative results were obtained, apparently decreasing or slowing down the number of leaves produced. This, in fact, seemed to have produced a negative statistically significant difference, which can be confirmed by comparison of the highest dose's mean with the other individual means or pairs of means.

Fig. 75. Mean length of seedlings (cm) fifteen months after transplanting.

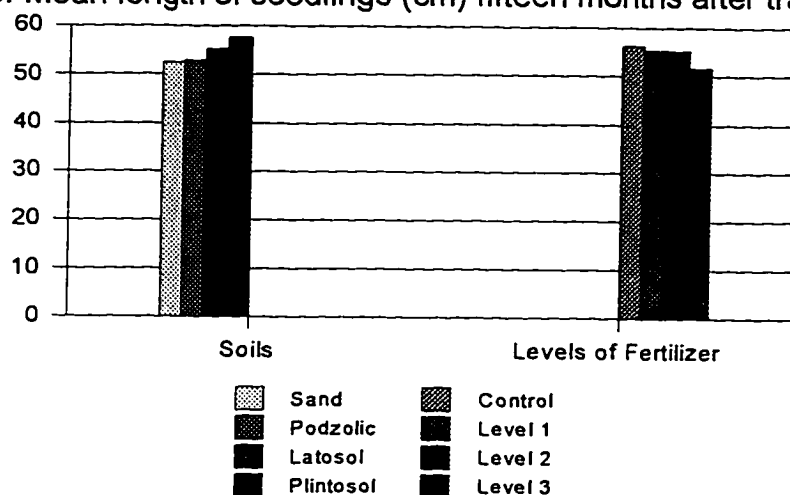


Table 96. Descriptive statistics for length of seedlings recorded fifteen months after transplanting from the germinators to plastic bags with four types of soil.

Soil	Mean	SD	Range	Died	Levels	Mean	SD	Range	Died
Sand	52.520	9.598	27-71	05	0	56.243	10.180	32-84	06
Podzolic	52.797	10.385	27-75	11	1	55.333	10.155	27-80	08
Latosol	55.260	12.113	32-83	03	2	55.133	11.555	27-78	05
Plintosol	57.573	10.425	34-50	05	3	51.653	10.972	28-83	05
Totals	54.590	10.630	27-83	24	Totals	54.590	10.715	27-84	

Table 97. Anova table for a two-factor analysis of variance on length of seedlings fifteen months after transplanting.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soils	3	1243.909	414.636	3.669	0.1280
Levels	3	909.051	303.017	2.681	0.4720
SoilsXLevels	9	790.826	87.870	0.777	0.6374
Error	280	31646.463	113.023		
Total	295	34590.249			

Fig. 76. Seedlings in the nursery under ca. 70% sun light and increased spaced between plants, 15 months after transplanting - January, 1993.

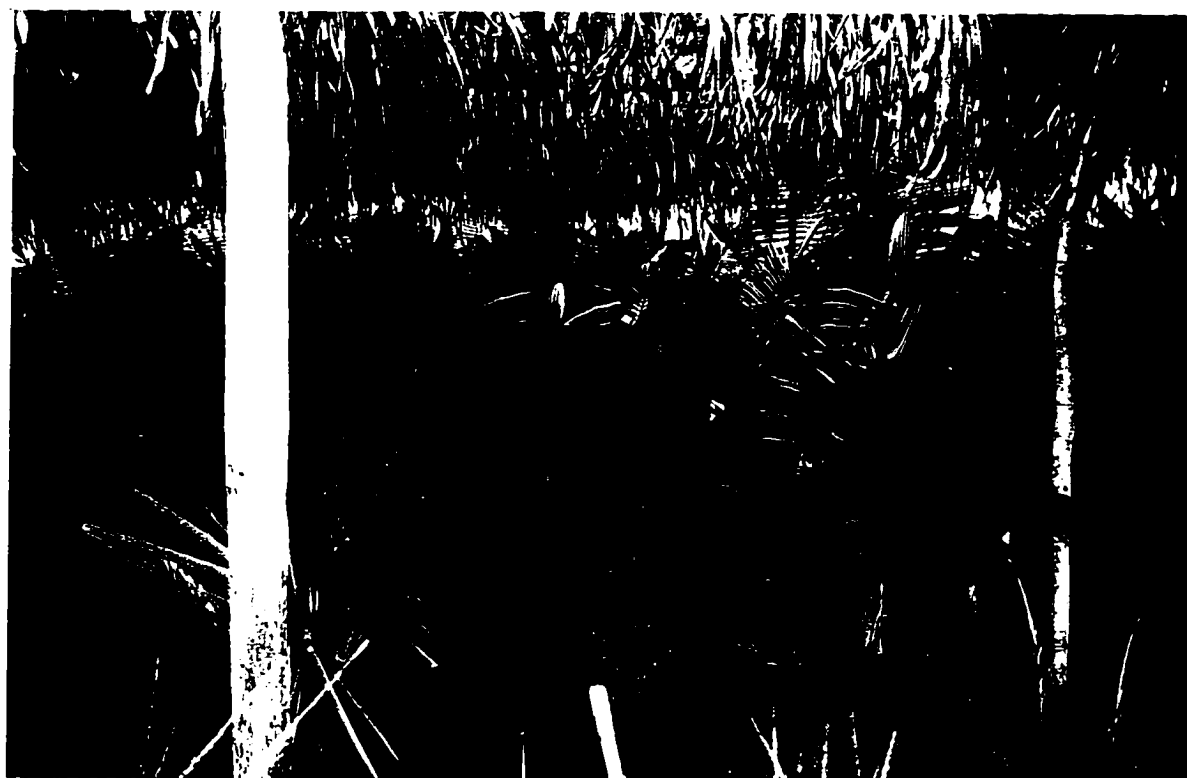


Fig. 77. Mean number of leaves fifteen months after transplanting.

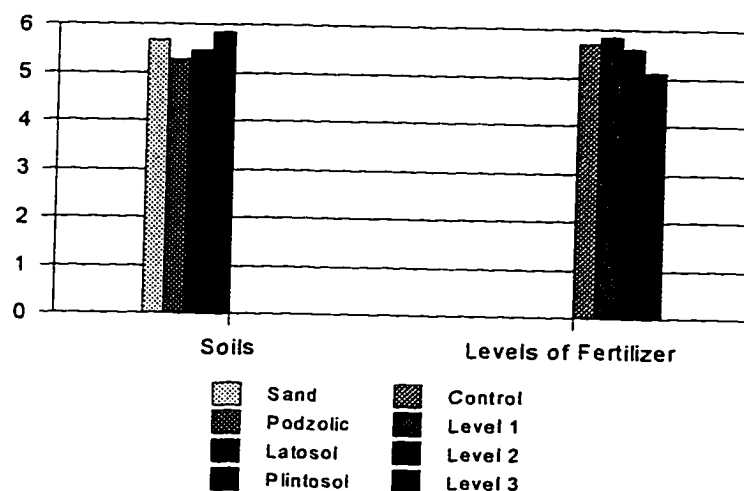


Table 98. Descriptive statistics for number of leaves recorded fifteen months after transplanting of seedlings from germinators to plastic bags.

Soil	Mean	SD	Range	Levels	Mean	SD	Range
Sand	5.680	1.164	2-8	0	5.703	0.961	4-8
Podzolic	5.261	0.980	3-8	1	5.847	1.122	3-9
Latosol	5.468	1.154	2-8	2	5.613	1.150	2-8
Plintosol	5.840	1.053	3-9	3	5.120	1.078	2-8
Totals	5.562	1.088	2-8	4	5.570	1.078	2-8

Table 99. Anova table for a one-factor analysis of variance on number of leaves fifteen months after transplanting.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soils	3	13.870	4.623	4.332	0.0053
Levels	3	20.771	6.924	6.487	0.0003
SoilsXLevels	9	28.198	3.133	2.935	0.0024
Error	280	298.860	1.067		
Total	295	461.699			

Fourth Census - Twenty-one Months After Transplanting

Twenty-one months following seedling transplant, 5 applications of fertilizers had been made. Shading in the nursery had been reduced 6 months before, leaving the seedlings under ca. 70 % direct sun light. At this point, the results of soil and fertilizer variations were expected to reflect a greater difference upon the seedlings.

The overall area of the nursery was doubled in January, 1993 to increase spacing between plants, initially set up with 1.0 m between lines and 0.20 m between plants in the line. It was increased to leave 1.0 m between plants in the line (Figure 78). During the relocating of bags in the nursery, it then could be noticed that the majority of seedlings had their root system coming out of the plastic bags, growing into the ground in the nursery.

Length of Seedlings - The overall mean recorded for the experiment (94.553 cm) represented a considerable average increase in the length of seedlings (39.975 cm), e.g., 6.662 cm a month, since the last observation six months before (54.578 cm). The growth rate by seedling per month computed for all four soil types was 6.628 cm; the same rate for levels of fertilization was 6.641 cm. It ranged from 28 to 178 cm (Table 99), although the majority of seedlings

(25.43%) had a mean length between 92 and 108 cm. The extremes of the range consisted of a few outliers formed by atrophied seedlings (in the lower extreme) and abnormally developed individuals (in the upper extreme). Figure 79 depicts the means computed for length of seedlings in this census for types of soil and levels of fertilizers.

Analysis of variance clearly reflected the effect of treatments on length of seedlings. For both soils and fertilizer levels a highly significant p-value was obtained from the analysis (0.0003 and 0.0002, respectively), although interaction between treatments was (barely) not statistically significant ($p=.0505$). The results (Table 100) showed that as the seedlings were primarily on their own, – nourishing themselves totally from the substrate they were growing rather than from the seed –, soils and levels separately made a difference in the growth rate.

For soils, the highest growth rate mean continued to be obtained in Plintosol (103.908 cm); the lowest, however, was not recorded in Sand as in the previous analyses (Table 99). Podzolic showed the lowest mean among soils (85.710 cm), although the difference between this and the second lowest (Sand=92.443 cm) was not significant ($p=0.2046$). Neither was there statistical significance when the means for Podzolic and Latosol (95.171 cm) were compared. However, the difference between the highest mean (Plintosol) and the other three others

was highly significant ($p=0.0001$), as was the difference between the lowest mean (Podzolic) and the other three soil types ($p=0.0020$). These results showed that although there was a change in the soil type with the lowest mean growth rate, the differences between Sand, Podzolic, and Latosol were not significant. Therefore, the overall pattern is maintained with the continued significant differences recorded for Plintosol as compared to the other three types of soil.

In relation to levels of fertilization, the pattern so far observed continued: a decrease in the growth rates as the levels of fertilizer increases (Figure 79). Control (Level 0) again showed the highest mean growth (101.877 cm); the differences, however, between control and the second (Level 1=96.658 cm) and third (Level 2=95.427 cm) means, individually, were not statistically significant. High statistical significance was found (Table 100), on the other hand, for the differences between the highest mean (Control) and the other three levels of fertilization ($p=0.0036$), as well as between the lowest mean (level 3) and the other three ($p=0.00003$).

Leaves - The average number of leaves produced since the last observation increased from 5.56 to 5.84 leaves per seedling (Table 101). This represents an average increase of ca. 0.28 leaf produced by seedling in a six-month period. The number of leaves produced by seedling ranged from a minimum of 1

(atrophied plant, outlier) to 9. The mean values for number of leaves in this census are shown in Figure 80.

Examining leaf production for this period, in the different types of soil tested, an interesting situation in terms of average number of leaves produced was observed. First, analysis of variance showed that the overall differences among the means computed for soil types of soil were not statistically significant (Table 102); second, among the different types of soil, an alteration of the pattern so far observed was recorded: Plintosol no longer showed the highest mean number of leaves produced, and Sand, was no longer, the lowest (in fact, it was the highest). Comparison between individual and groups of means, however, revealed no statistical significance for the differences among them, except for the difference between the highest mean (Sand) and the other three soil types when taken as a group for comparison.

The explanation for this situation may involve climatic factors. The data used in this analysis were collected right after the dry season in the region. Since the seedlings at that point were not receiving any supplementary irrigation, all the water they got had to come from rainfall, which is absent in the region from June to November. The data were collected in the beginning of January, after the seedlings had gone through the dry season. In the absence of water, the results

showed that type of soil does not make a big difference, since biomass production is slowed down.

Examination of the results for levels of fertilization also revealed variation in relation to the results so far recorded for number of leaves. Fertilizers did have a significant effect on leaf production, even in water stress conditions. Overall differences among means were found highly significant ($p=0.0001$). No significant interaction between soil type and levels of fertilization was detected. In relation to the situation observed in the last observation, the pattern is basically the same: the higher the dose of fertilizer applied the lower the average number of leaves produced by seedling. However, the differences among the means (previously not significant, except when the level 3 was compared) start to get into the significance level. This is true for the comparison between the control and the other three levels ($p<0.0001$); between the lowest mean (level 3=5.143 cm) and the other three ($p<0.0001$); and between the control (the highest mean) and the other individual levels, except level 1 (mean=6.02) where no statistical significance was detected for the difference ($p=0.0698$). It suggests that no application of fertilizers and application of the lowest dose basically have the same effect on leaf production (probably not stimulant, but not restrictive, either); from level 2 to level 3, however, the effect is restrictive, or negative.

Fig. 78. View of seedlings in Plintosol with level 3 of fertilizer applied, ca. 21 months after transplanting.



Fig. 79. Mean length of seedlings (cm) twenty-one months after transplanting.

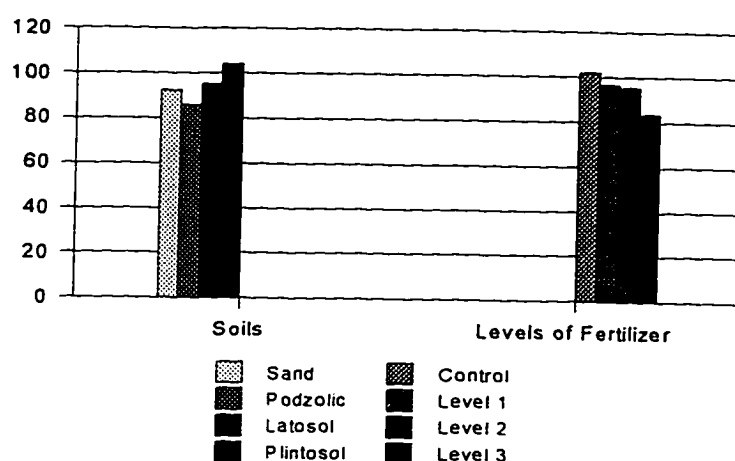


Table 100. Descriptive statistics for length of seedlings recorded twenty-one months after transplanting from the germinators to plastic bags with four types of soil.

Soil	Mean	SD	Range	Died	Levels	Mean	SD	Range	Died
Sand	92.443	27.657	28-176	10	0	101.87	25.784	50-176	07
Podzolic	85.710	21.244	38-142	11	1	96.658	23.861	50-150	07
Latosol	95.171	30.083	47-178	04	2	95.427	28.703	41-159	05
Plintisol	103.90	25.865	51-156	04	3	83.786	27.365	28-178	10
Totals	94.308	26.212	28-178	29	Totals	94.437	26.428	28-178	29

Table 101. Anova table for a two-factor analysis of variance on length of seedlings twenty-one months after transplanting.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soils	3	12578.770	4192.923	6.480	0.0003
Levels	3	13130.506	4376.835	6.764	0.0002
Soils X Levels	9	11124.225	1236.025	1.910	0.0505
Error	275	177946.030	647.076		
Total	290	214779.531			

Fig. 80. Mean number of leaves twenty-one months after transplanting.

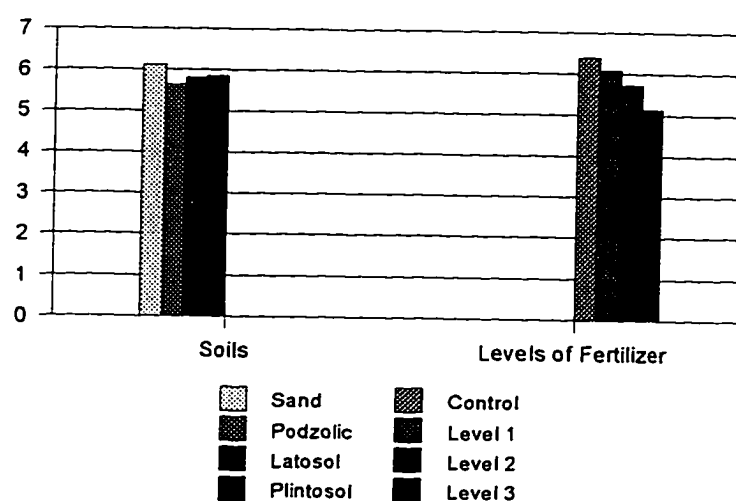


Table 102. Descriptive statistics for number of leaves recorded twenty-one months after transplanting of seedlings from germinators to plastic bags.

Soil	Mean	SD	Range	Levels	Mean	SD	Range
Sand	6.100	1.276	3-9	0	6.397	0.939	4-9
Podzolic	5.638	1.124	3-8	1	6.082	1.037	4-8
Latosol	5.803	1.296	1-9	2	5.733	1.298	1-9
Plintosol	5.842	0.939	4-8	3	5.143	1.011	3-7
Totals	5.846	1.159	1-9	Totals	5.839	1.071	1-9

Table 103. Anova table for a two-factor analysis of variance on number of leaves twenty-one months after transplanting.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soils	3	5.796	1.932	1.685	0.1705
Levels	3	61.105	20.368	17.765	0.0001
Soils X Levels	9	14.719	1.635	1.426	0.1764
Error	275	315.292	1.147		
Total	290	396.912			

Fifth Census - Forty Months After Transplanting

This final collection of data was carried out 19 months after the previous collection, and 40 months after the experiment was installed in the nursery area. At this phase of the experiment the plants had been left under direct sun light for ca. 12 months since shading was completely removed. It was decided that the experiment should be terminated following this collection of data, because it would be difficult to keep control on the seedlings and monitor the effects of soils and levels of fertilization since other factors also started to interfere with the results. These factors included the significant growth of the root system outside the bags, and the remarkable development of the aerial parts requiring a new increase of spacing that would damage the well developed root system of the seedlings.

Destructive measurements were used in this final collection of data. The seedlings, now over 1.5 m tall on average (Figure 81), were removed from the bags and the roots freed from eventual attachment to the nursery soil (Figure 82). After the seedlings were taken to a working area, the following measurements and counts were taken: length of seedlings, number of leaves, length of rhizome, diameter of rhizome, number of roots, fresh and dry weight of roots, fresh and dry weight of the aerial part, and number of pinnae. Plant parts

were measured and separated for counting, measuring and fresh weighting (Figure 83). They were then placed in paper bags and dried in a dryer built for this particular purpose for 48-72 hours depending on the material (rhizomes usually took longer), at temperature of ca. 70 °C (Figure 84).

Analysis of the data obtained for length of seedlings after the total period of time the experiment lasted (40 months) showed a mean length of 155.12 cm (Table 103), a considerable increase since the previous collection of data (94.55 cm). This represents an average increase of 60.564 cm for a period of 19 months, which in turn represents a monthly average increase of 3.187 cm, the second highest obtained during the entire experiment. Growth rate obtained separately for soils showed an average increase of 3.184 cm per month per seedling, just slightly higher than that obtained for levels of fertilization (3.184 cm). This seems to confirm a pattern observed in nature; babassu seedlings are slow growing in their early phases of development. Length of seedlings ranged from 39 to 240 cm, although the extremes of this range are formed by a few outliers. The highest percentage of seedlings (25.9%) showed length between 144.5 and 165.6 cm. Figure 85 graphically shows the means computed for length of seedlings at 40 months.

Analysis of variance (5% level) revealed an overall significant effect of soil types of soil ($p=0.009$), levels of fertilization ($p=0.0017$), and surprisingly for the

interaction between soils and levels ($p=0.0052$). The overall significant effect of soil treatments confirmed the previous results. Plintosol kept the overall highest mean among soil types (Figure 85), a difference that continued statistically significant when compared to each other type of soil or to the other three as a group. Therefore, Plintosol (the highest mean) compared to Sand, Podzolic and Latosol as a group is statistically different from them, the same way Podzolic (the lowest mean) shows a difference in comparison to the other three soils that is also significant.

Levels of fertilization also produced an overall significant effect (Table 104). The results obtained in this final collection of data showed what had been preliminarily concluded throughout the other phases of this experiment. Again the control showed the better performance in terms of mean length, followed by the next two levels (1,2), and finally, confirming the negative effect of the highest dose of fertilizers (level 3) on growth rate of the seedlings (Figure 85). No statistical significance was detected for the difference between each of the first three levels (0,1,2), while the differences between these three levels (either as a group or individually) and level 3 (the lowest mean) were always highly significant.

The results suggest that while growth rate is clearly affected by climatic factors, leaf production follows a stable rate throughout the year, with little or no

variation. It is important to point out that the previous collection of data, as mentioned before, was carried out after the dry season, and this collection was carried out in August, just after the rainy season ended. This fact apparently did not make a difference in the leafing rate recorded from the data collected after these two different seasons. Number of leaves ranged from 1 (outlier) to 10 (Table 105); the majority of seedlings (24.4%), however, bore 6-7 leaves by the time this last data collection was made. Figure 86 shows the mean values for number of leaves at 40 months for soils and fertilizers.

For the first time during the experiment interaction between soils and levels of fertilization had an overall significant on the model ($p=0.0383$) (Table 106). Although only barely significant it showed that the effect of type of soil may somehow have something to do with effect of fertilizer. Providing that water, the vehicle of absorption and translocation of nutrients is not lacking, the physical structure of soil may be an additive, interactive factor for a combined overall effect. What is not clear, however, is why this effect was produced in leafing, and not in growth. Separate effects of soils ($p=0.0001$) and levels of fertilizers ($p=0.0001$) were highly significant.

Anova of types of soils confirmed Plintosol as the type in which the most significant differences were produced in terms of number of leaves (Table 106). The differences between Plintosol (mean=7.395) and the other three types when

contrasted as a group or individually (i.e. Plintosol x Sand+Latosol+Podzolic; Plintosol x Latosol; Plintosol x Podzolic; Plintosol x Sand) showed statistical significance, that confirmed the results of the previous analyses. Contrast between the two lowest means (Podzolic x Sand) detected no significant difference between them, showing these two types of soil as the worst substrates for leafing, confirming the results obtained for growth. Contrast between the lowest mean (Sand) and the other three showed that they are significantly different.

Levels of fertilization also had a significant effect on leafing of seedlings. A slight variation from the previous results, however, could be observed. Control (mean=6.534) did not show the highest mean any more; that was held by level 1 (mean=7.056), followed by level 2 (mean=6.534) (Table 105). The differences among them, in contrast with previous analyses, were this time, statistically significant, although not highly so. Individual comparison between the highest mean obtained (level 1=7.056) and the second highest (level 2=6.609) showed a barely statistically significant difference ($p=0.050$). When the same level 1 is compared to the control, now the third highest mean (6.534), significance is statistically higher than in the former comparison, although still not highly significant. Highly significant differences were found only when the lowest mean (level 3) is compared to the other three, confirming the negative effect of the

highest dose of fertilizers on leaf production. Control (level 0) compared to level 3 was not significant.

These results showed a slightly positive effect of the lowest dose of fertilizers applied to the seedlings in terms of leaf production. The weakness of this positive effect may be extended to the second highest dose of fertilizers; also, the difference from this to the control was barely significant. In conclusion, dose 1 of fertilizers produces a positive effect (increase) on the number of leaves produced by the seedlings, although it seems that this effect is not significant enough to justify application of fertilizers with its resulting costs. This point may be reinforced by the fact that growth did not increase from application of dose 1 of fertilizers, raising the question why one would add fertilization costs to seedling production in order to have as result a few more leaves per seedling? The initial positive effect becomes increasingly negative as the dose of fertilizer is increased.

Fig. 81. Seedlings under direct sunlight ca. 40 months after transplanting -
August, 1994.



Fig. 82. Seedling removed from the plastic bag for the final collection of data - August, 1994.



Fig. 83. Seedling part separated: after counted, and measured leaves were weighed - August, 1994.



Fig. 84. Drying of seedling parts in paper bags - August, 1994.



Fig. 85. Mean length of seedlings (cm) forty months after transplanting.

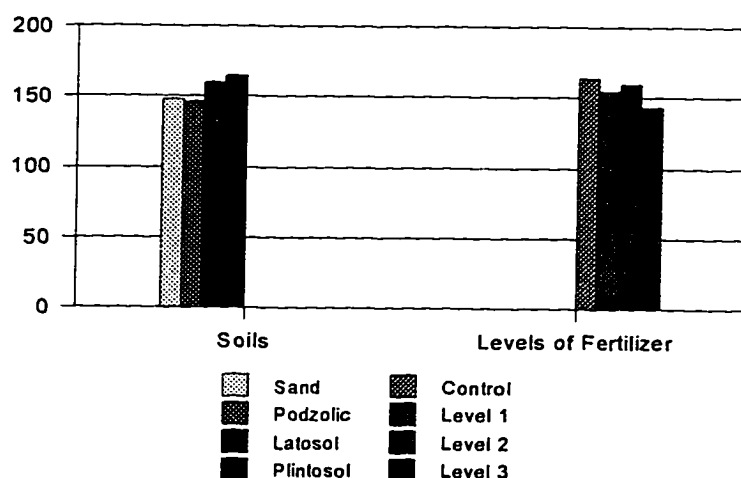


Table 104. Descriptive statistics for length of seedlings recorded forty months after transplanting from the germinators to plastic bags with four types of soil.

Soil	Mean	SD	Range	Died	Levels	Mean	SD	Range	Died
Sand	148.197	37.292	57-230	19	0	163.56	33.883	77-238	07
Podzolic	146.246	44.989	39-240	15	1	154.31	28.564	70-207	08
Latosol	160.097	35.162	74-213	08	2	159.07	41.470	57-218	11
Plintosol	164.750	32.801	85-238	04	3	142.78	46.090	39-240	20
Totals	154.822	37.561	39-240	46	Totals	154.93	37.502	39-240	46

Table 105. Anova table for a two-factor analysis of variance on length of seedlings forty months after transplanting.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soils	3	21860.479	7286.826	5.644	0.0009
Levels	3	20154.368	6718.123	5.204	0.0017
SoilsXLevels	9	31326.008	3480.668	2.696	0.0052
Error	258	333094.995	1291.066		
Total	273	406435.850			

Fig. 86. Mean number of leaves forty months after transplanting.

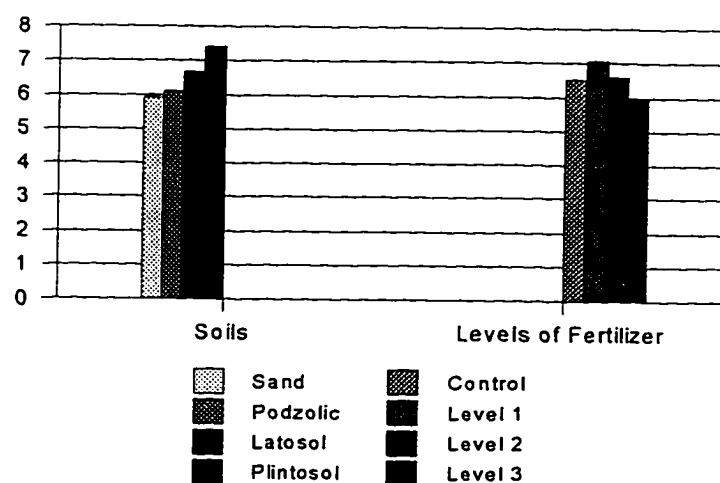


Table 106. Descriptive statistics for number of leaves recorded forty months after transplanting of seedlings from germinators to plastic bags.

Soil	Mean	SD	Range	Levels	Mean	SD	Range
Sand	5.934	1.263	3-9	0	6.534	1.385	2-10
Podzolic	6.108	1.977	1-10	1	7.056	1.393	4-10
Latosol	6.667	1.278	4-9	2	6.609	1.437	4-10
Plintisol	7.395	1.317	3-10	3	6.000	1.974	1-9
Totals	6.526	1.459	1-10	Totals	6.550	1.547	1-10

Table 107. Anova table for a two-factor analysis of variance on number of leaves forty months after transplanting.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soils	3	99.926	33.309	16.721	0.0001
Levels	3	45.846	15.282	7.671	0.0001
SoilsXLevels	9	36.090	4.010	2.013	0.0383
Error	258	513.950	1.992		
Total	273	695.812			

Also as a character for measuring biomass production during the period of the experiment, data on length and diameter of rhizome were taken in the final collection. The average length of the rhizome was 22.1 cm (SD=0.045), with a range of 9.0-32 cm (Table 107); however, 65.7% of the plants had a rhizome between 21.0 and 28.2 cm long. Figure 87 shows the mean length for rhizomes recorded for the different types of soils and levels of fertilizers at the 40-month census. The most important conclusion of the Anova was a significant interaction between soils and fertilizer levels ($p=0.0489$) (Table 108). Apparently, effect of soil on the length of rhizomes depended on the level of fertilizer applied. Therefore, conclusions about the differences due to the main effects alone would not mean much because of the interaction between them, but analysis of variance showed a significant p-value for soils ($p=0.0028$), and levels of fertilization was not significant ($p=0.0914$). The highest overall mean rhizome length for the soils was recorded for Sand (23.8 cm), followed by Plintosol (22.2 cm) (Table 107). Comparison between this pair of means showed no statistical significance for the difference between them ($p=0.15182$). However, Sand compared to the group of the other three soils was statistically different ($p=0.00418$), and so it was compared individually to Latosol and Podzolic (p-values: 0.04130, and 0.00024, respectively).

Although with no significant overall effect, levels of fertilization also showed the same constant pattern seen for other characters. Length of rhizome, in this case, decreases as the dose of fertilizers applied is increased, in a very regular gradient from the control (level 0) through level 3 (Figure 87). This only confirms that underground biomass production is negatively affected by the higher doses of fertilizers.

Number of pinnae produced per leaf and measured by counting the pinnae in one side of a fully formed leaf ranged from 14 (outlier) to 71, with a great percent of seedlings (44.93%) ranging from 37 to 49. The mean number per leaf was 39.2 (SD=10.20). Again, interaction between soils and levels was statistically significant ($p=0.0321$), as in the previously discussed case of the rhizome length. However, the opposite situation was recorded in relation to the main effects: soil type was not significant ($p=0.0543$), but levels of fertilization was ($p=0.0216$). As the source of variation in this model is not the separate effect of soils and fertilizer levels, but the combined effect of both, the significant individual effect of each will not be discussed.

Fig. 87. Mean length of rhizomes (m) forty months after transplanting.

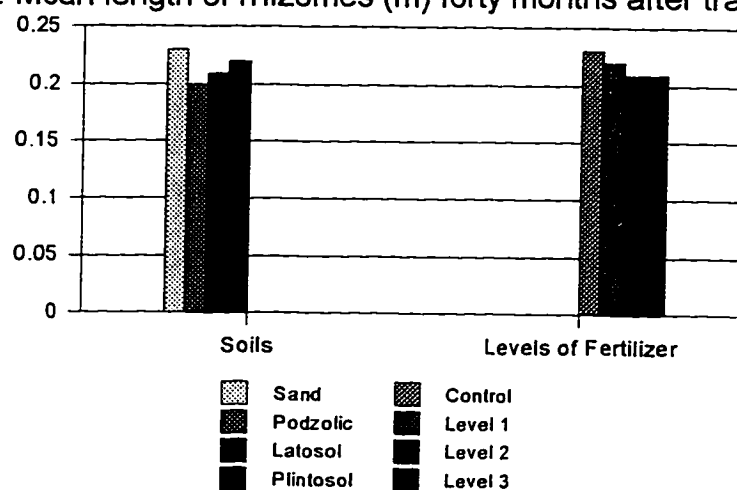


Table 108. Descriptive statistics for length of rhizome (m) forty months after transplanting of seedlings to plastic bags.

Soil	Mean	SD	Range	Levels	Mean	SD	Range
Sand	0.238	0.038	0.110-0.320	0	0.231	0.036	0.140-0.320
Podzolic	0.205	0.044	0.090-0.290	1	0.220	0.048	0.090-0.310
Latosol	0.218	0.045	0.120-0.300	2	0.216	0.047	0.100-0.300
Plintosol	0.222	0.048	0.100-0.300	3	0.214	0.047	0.110-0.300
Totals	0.220	0.043	0.090-0.320	Totals	0.220	0.044	0.090-0.320

Table 109. Analysis of variance for length of rhizome forty months after transplanting to plastic bags.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soil	3	0.027	0.009	4.819	0.0028
Levels	3	0.012	0.004	2.175	0.0914
SoilxLevels	9	0.033	0.004	1.925	0.0489
Error	258	0.485	0.002		
Total	273	0.557			

The number of primary roots were counted for each seedling. The average number per seedling was 30.45 (SD=10.297); the highest percentage of individuals (46.34) ranged in the interval of 25 - 37 roots/seedling. Anova showed no overall statistical significance for the difference among the means either in types of soil or levels of fertilization; interaction between them was not significant either. It seems, therefore, that number of primary roots produced by the seedlings in their earlier phases of growth is not affected by the types of soil and doses of fertilizers applied.

The bulky structure formed by the rhizome and roots was also studied as a indicator for biomass produced. It was weighed after separation from the aerial part, and average weight ranged from 84 g (in atrophied plants) to 2.68 Kg (Table 109); the interval with the highest percentage of seedlings (44.89%) weighed between 624-1.16 Kg. Figure 88 shows the means for this character in soils and levels of fertilizers. Anova showed significant p-values for soils, levels and for the interaction between them as well (p-values= 0.0002, 0.0124, and 0.0003, respectively) (Table 110). The highly significant interaction between the two factors tested, showed that at this point of growth, seedlings responded to both soils and fertilizers, and that the response produced in the fresh weight of roots is the combined result of both.

Since the rhizome was also taken with roots for weighing, it would be expected that those seedlings with longer rhizomes would also have the heavier root+rhizome combination, as only the length of the rhizome was significantly affected by the treatments, as previously shown. This is what was observed. For root production, Plintosol was not the best soil for the seedlings, as it was for growth and leaves. For roots, Sand showed the best results, both for rhizome length and weight of roots+rhizome. This makes sense, as the physical structure of sandy soils allow better development of the root system in contrast to Plintosols where the presence of concretions can be obstacles for a good root system development. What is interesting is that the good root development in Sand is not reflected also in good growth of the aerial parts in the same soil -- Sand was the worst substrate in terms of aerial growth. Therefore, when the analysis involved roots, the pattern observed for aerial parts along the experiment was not confirmed.

Regarding the levels of fertilization, results were as expected. The control still had the highest overall mean (Table 109), which decreased as doses of fertilizers increased. There were no statistical differences between the control and the next two levels (1,2), but the difference between the highest level (3) and the others was highly significant. In conclusion, fertilizers have no effect until the dose is increased to level 3, when a deleterious effect is produced.

Anderson & Anderson (1983) found no apparent effect on the performance of juvenile individuals of babassu in the field after application of substantial levels of N, P, and K at 2-month and 4-month intervals and measured at 10, 14 and 18 months after the initiation of the experiment.

Fig. 88. Mean fresh weight of rhizome+roots (gms) forty months after transplanting.

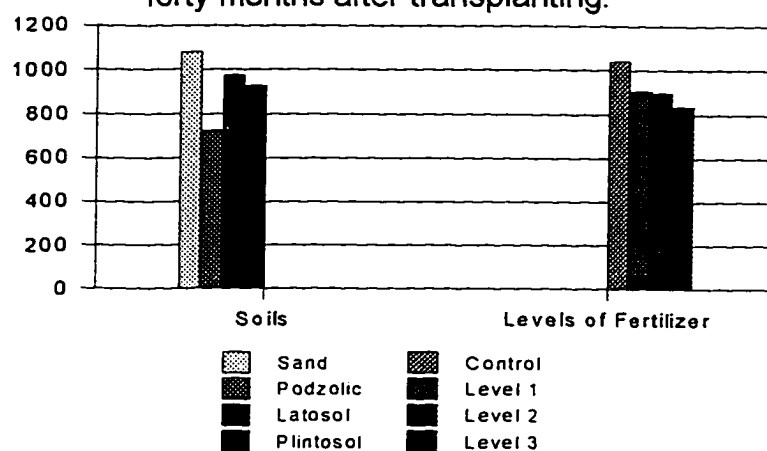


Table 110. Descriptive statistics for fresh weight of rhizome+roots (gms) forty months after transplanting of seedlings to plastic bags.

Soil	Mean	SD	Range	Levels	Mean	SD	Range
Sand	1079.08	520.136	92-2686	0	1042.88	452.585	260-2686
Podzolic	722.35	370.074	84-1514	1	909.71	421.393	104-1922
Latosol	974.50	436.187	146-2290	2	896.65	431.431	114-1700
Plintosol	929.88	409.351	114-1852	3	835.23	483.396	84-2290
Totals	926.45	433.937	84-2686	Totals	921.117	447.201	84-2686

Table 111. Analysis of variance for fresh weight of rhizome+roots forty months after transplanting to plastic bags.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soil	3	3494003.834	1164667.945	6.817	0.0002
Levels	3	1893327.775	631109.258	3.694	0.0124
SoilxLevels	9	5606380.713	622931.190	3.646	0.0003
Error	258	44077383.616	170842.572		
Total	273	55071095.930			

In relation to the fresh weight of leaves measured right after the seedlings were taken from the bags for the final collection of data, the results (Table 111; Figure 89) showed an overall mean of 841.229 g (SD=496.499). Although the range was 1.2 (atrophied, outlier) to 2.64 Kg, the majority of seedlings (42.32%) were found in the interval of 558 g - 1.10 Kg. As observed and confirmed in previous analyses, when the aerial part was the object of the analysis, the highest mean was always recorded in Plintosol, decreasing from Latosol to Sand to Podzolic (or sometimes, from Latosol to Podzolic to Sand). In this final analysis the former was true, although statistically, no difference existed between the means obtained for Sand and Podzolic. The same way, Plintosol and Latosol were statistically equal in terms of means for fresh weight of leaves. Since the overall effect of soil type was significant (Table 112), it is concluded that the best soils, among the four tested, in terms of early stage aerial biomass production, were Plintosol and Latosol.

Levels of fertilization confirmed the pattern detected in previous results, showing the same decrease in overall growth, and aerial and underground biomass production as a consequence of the increase of the dose of fertilizers applied to the seedlings (Figure 89). Although the overall differences among the four levels were not significant ($p=0.1414$), in terms of means for fresh weight of leaves (Table 112), the pattern so far observed for other characters analyzed

was again noticeable: control and the first two levels (1,2) are not significantly different, but as the dose applied goes beyond the second level, it produces a detectable decrease in the seedling performance, as seen throughout the experiment.

Since a significant interaction was detected by the analysis performed, conclusions should be cautiously drawn. However, some conclusions based on the separate analysis of the main effects could still be supported by patterns that have been confirmed with or without the presence of possible confounding effects produced by the significant interaction between soils and levels.

Dry weight of leaves also presented results similar to those obtained for fresh weight: types of soil producing a highly significant effect ($p=0.0001$) (Tables 113 and 114); no significant effect from levels of fertilization, and a significant interaction between these two factors. No major differences can be drawn from dry weight of leaves (Figure 90) in relation to fresh weight already discussed. Therefore, the conclusions are basically the same.

In terms of underground biomass production, both fresh and dry weight showed better overall results in Sand, showing that the more open soil structure of this soil is favorable to development of the root system. There is no corresponding similar effect on growth or aerial biomass production. Significant

p-value for soils (0.002), not significant for levels of fertilizer (0.0124), and a significant interaction (0.003) were obtained for both fresh and dry weight of roots (Table 110). Although not statistically different, levels of fertilization produced means that decreased from the lower to the highest level.

Since there was an overall significant interaction between the two main factors tested, I could not easily separate what was in fact the result of the presence of each factor. It seems clear, however, that soils played a positive role for most of the characters measured during this experiment, with the best performances being achieved in Plintosol. I have to assume that the factors acted in combination because of the significant interaction showed by the analysis. However, since that type of soils (at least for two types) was always a positive factor when the interaction was not significant, I conclude that soils accounted positively when lower doses of fertilizers applied (0, 1, 2) and levels of fertilization accounted negatively when the worst substrates (Sand, Podzolic) were combined with level 3 of fertilizers.

Figures 91 and 92 provide a general view of the means computed in each census, respectively for growth and number of leaves.

Fig. 89. Mean fresh weight of leaves (gms) forty months after transplanting.

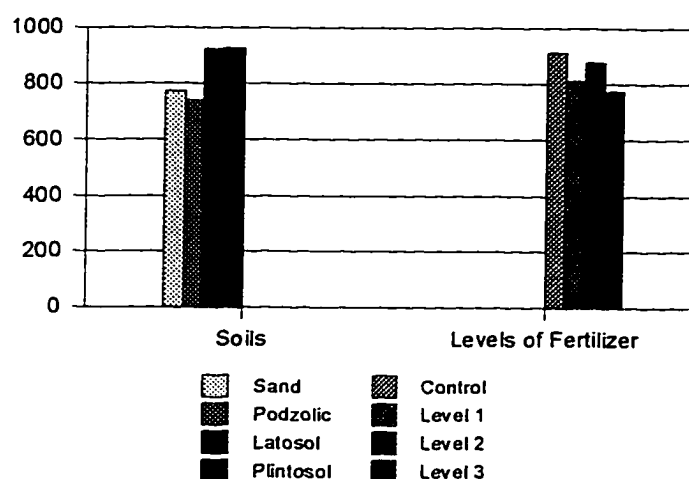


Table 112. Descriptive statistics for fresh weight of leaves (gms) forty months after the transplanting of seedlings to plastic bags.

Soil	Mean	SD	Range	Levels	Mean	SD	Range
Sand	773.082	475.725	60-2392	0	913.89	482.85	104-2392
Podzolic	740.369	501.004	12-1864	1	811.27	387.16	80-1620
Latosol	924.333	517.627	92-2642	2	878.87	537.66	62-2054
Plintosol	927.132	491.640	96-2258	3	775.46	595.23	12-2642
Totals	841.229	496.499	12-2642	Totals	844.87	500.72	12-2642

Table 113. Analysis of variance for fresh weight of leaves (gms) forty months after transplanting to plastic bags.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soil	3	2744974.276	914991.425	3.937	0.009
Levels	3	1278708.829	426236.276	1.834	0.1414
SoilsxLevels	9	5953977.650	661553.072	2.847	0.0033
Error	258	59960574.97	232405.329		
Total	273				

Fig. 90. Mean dry weight of leaves (gms) forty months after transplanting.

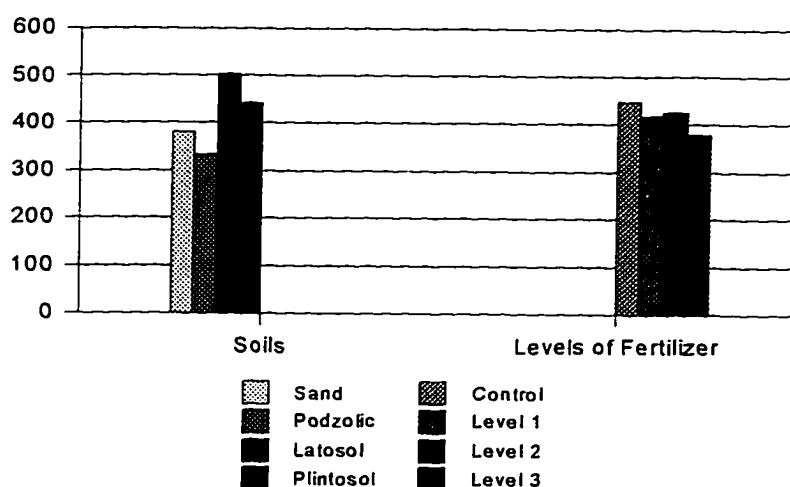


Table 114. Descriptive statistics for dry weight of leaves (gms) forty months after transplanting of seedlings to plastic bags.

Soil	Mean	SD	Range	Levels	Mean	SD	Range
Sand	381.197	231.653	26-1066	0	448.041	245.816	48-1140
Podzolic	333.016	247.164	6-1142	1	418.333	229.047	32-1142
Latosol	504.278	315.268	40-1812	2	426.147	282.795	28-1056
Plintosol	442.553	251.672	42-1130	3	378.383	329.463	6-1812
Totals	415.261	261.439	6-1812	Totals	417.726	271.780	6-1812

Table 115. Analysis of variance for fresh weight of leaves (gms) forty months after transplanting to plastic bags.

Source	df	Sum of Squares	Mean Square	F-test	Prob>F
Soil	3	1378219.993	459406.664	7.029	0.0001
Levels	3	298195.654	99398.551	1.521	0.2095
SoilsxLevels	9	1901816.111	211312.901	3.233	0.0010
Error	257	16796718.046	65356.880		
Total	272	20374949.79			

Fig. 91. Mean length of seedlings (cm) computed for each census.

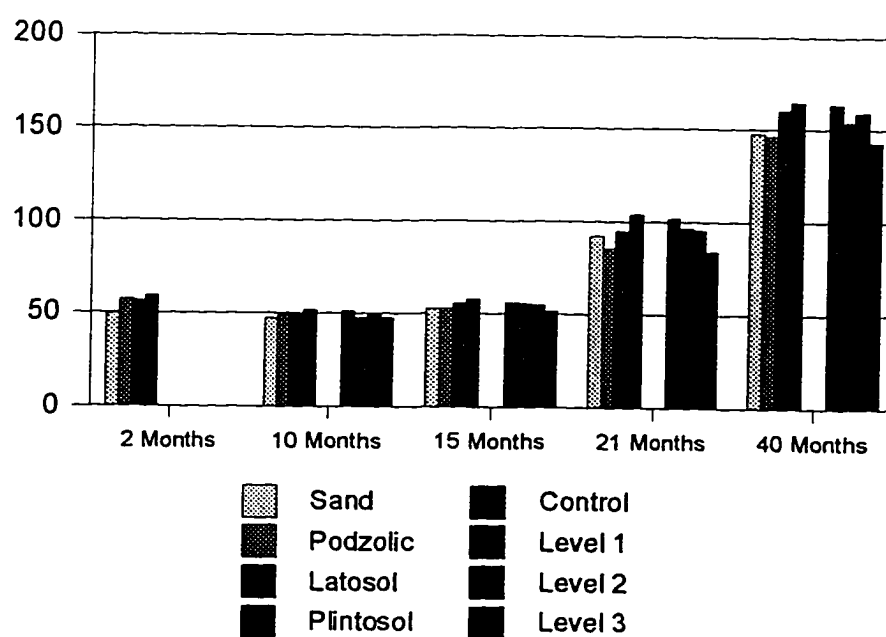
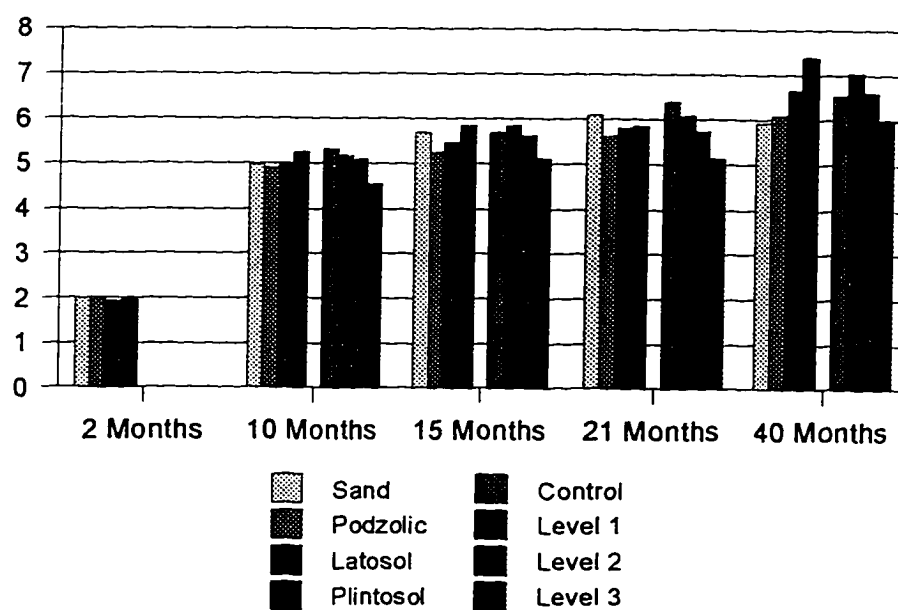


Fig. 92. Mean number of leaves computed for each census.



Death of Seedlings and Its Relation to Soils and/or Levels of Fertilization

A total of 46 seedlings died along the experiment. The highest number of deaths was recorded for Sand (19), followed by Podzolic (15), the two types of soils that have been showing the overall worst performances for several characters measured along the experiment. Plintosol showed the best performance also in this regard, with the lowest number of deaths (only 4). When only levels of fertilization is considered in this analysis of death of seedlings, level 3 appears with the highest number of dead seedlings (20) at the end of the experiment, and this number decreases as the level of fertilizers decreases (Table 115). The worst combined performance in terms of deaths was observed in treatments where Sand soil and Level 3 of fertilization were applied.

A test of independence (or a test of marginal homogeneity) was performed to address the question whether the deaths of seedlings were related to soils and levels of fertilizers combined (or whether the distribution of deaths of seedlings was the same across soil types and levels of fertilizers combined). For that a 4x4 contingency table was set up and Likelihood ratio (G2-test) and Pearson test were applied. The result (Table 116) was not significant (p-values 0.4268 and 0.4965, respectively for soils and fertilizers), showing that the death of seedlings were independent of the combined effects of soils and levels of fertilizers (or that

death of seedlings had the same distribution across the combined effect of soil types and levels of fertilizers).

Table 116. Number of dead seedlings for each soil type and level fertilization recorded at the last census (40 months after transplanting).

Soils Levels	Sand	Podzolic	Latosol	Plintisol	Totals
Level 0	2	3	0	2	7
Level 1	2	4	2	0	8
Level 2	5	3	2	1	11
Level 3	10	5	4	1	20
Totals	19	15	8	4	46

Table 117. Independence test - Statistical details of the Test of Marginal Homogeneity of the distribution of death of seedlings across the interactive effect of soil type and tevels of fertilizers.

Source	DF	-LogLikelihood	RSquare
Model	9	4.557034	0.0765
Error	34	55.012073	
C Total	43	59.569107	
Test	ChiSquare	Prob>ChiSquare	
Likelihood Ratio	9.114	0.4268	
Pearson	8.378	0.4965	

What if soils and levels of fertilizers were taken separately in order to test the hypothesis of no association between each factor and the observed deaths of seedlings? (or whether the distribution of the death of seedlings across the levels of each factor is the same?) For that, two 2x4 contingency tables were set up including in each one the observed frequencies of dead and living seedlings for each of the four types of soil and each level of fertilizers (Table 117).

The significance of the independence test for soils (G-test, $p=0.0020$; Pearson, $p=0.0030$) showed a higher probability of seedling mortality in Sand than in Plintosol. Figure 93 shows that the probability of mortality is ca. 0.25 in Sand and considerably below this level in Plintosol (ca. 0.05). On the other hand, Figure 94 shows that as the level of fertilizers increases from control to level 3, the probability for seedling death also increases. The tests performed for this 2x4 contingency table (testing the hypothesis of no association between deaths and levels), resulted significant for both G-test (G^2) and Pearson (Table 118), showing that the deaths recorded during the experimental time were associated to the levels of fertilization tested.

Nominal logistic regression of seedling survival (dead/living) on levels showed that the probability of predicting seedling death increases as levels of fertilizers increases from the control to the highest dose applied (level 3). In Figure 95 the

left Y axis represents probability, and the proportions shown on the right Y axis represent relative size of each dead/living group of seedlings. A logistic probability curve vertically partitions the total probability of 1 at each point of the levels of fertilizers axis (x). At any point on the fertilizer level axis, the probability associated with the response is the vertical response between the curve on the probability axis corresponding to the response. If levels of fertilizers had no effect on death/survival of seedlings the fitted line would be horizontal, and the probability would be constant for the response across the continuous factor range (JMP, 1995). Tests shows significant Chi-Square value for the logistic regression performed (Table 119).

Fig. 93. Contingency Table Mosaic Chart for the Distribution of Seed Mortality Across Types of Soil After 40 Months.

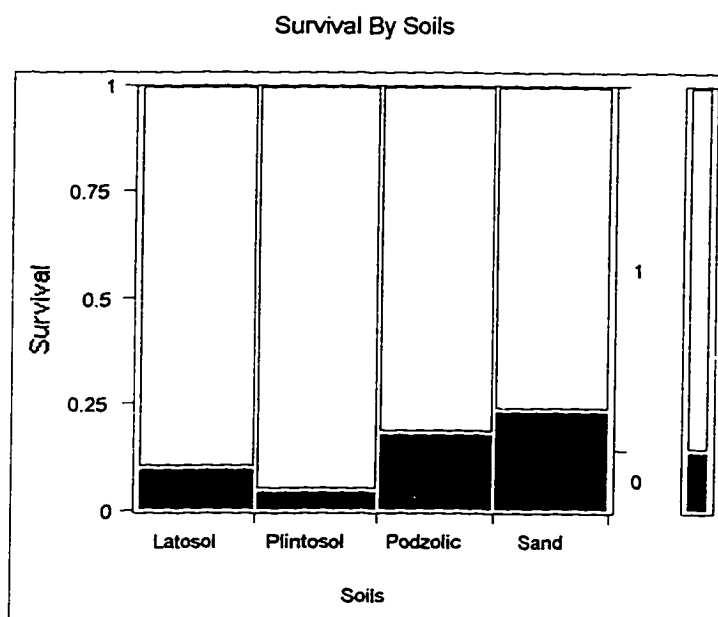


Table 118. Statistical Details for the Contingency Table Analysis for the Distribution of Seedling Mortality Across the Four Types of Soils.

Forty Months Following Transplanting

Crosstabs

Survival Count	Soils				
	Latosol	Plintosol	Podzolic	Sand	
0	8	4	15	19	46
1	72	76	65	61	274
	80	80	80	80	320

Tests

Source	DF	-LogLikelihood	RSquare (U)
Model	3	7.39957	0.0562
Error	316	124.34855	
C Total	319	131.74811	
Total Count	320		

Test	ChiSquare	Prob>ChiSq
Likelihood Ratio	14.799	0.0020
Pearson	13.913	0.0030

Fig. 94. Contingency Table Mosaic Chart for the Distribution of Seed Mortality Across Levels of Fertilizers After 40 Months.

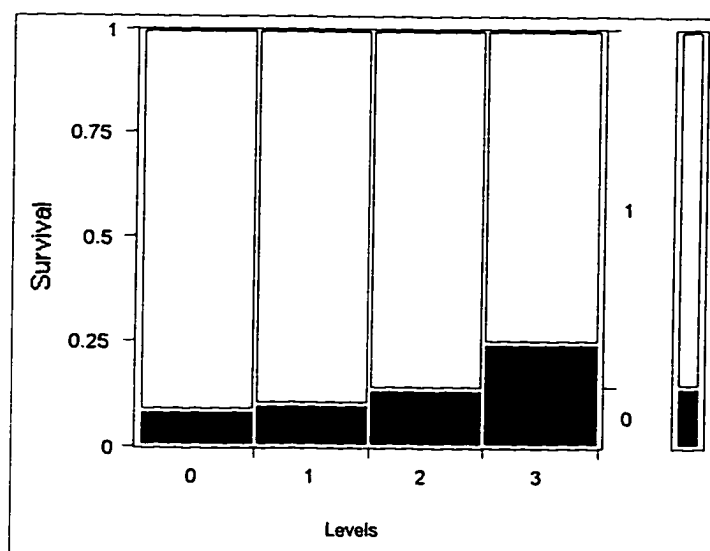


Table 119. Statistical Details for the Contingency Table Analysis for the Distribution of Seedling Mortality Across Levels of Fertilizers.

Forty Months Following Transplanting

Crosstabs

Survival Count	Levels				
	0	1	2	3	
0	7	8	11	20	46
1	73	72	69	60	274
	80	80	80	80	320

Tests

Source	DF	-LogLikelihood	RSquare (U)
Model	3	4.98551	0.0378
Error	316	126.76260	
C Total	319	131.74811	
Total Count	320		

Test	ChiSquare	Prob>ChiSq
Likelihood Ratio	9.971	0.0188
Pearson	10.663	0.01

Fig. 95. Graphical Representation of the Nominal Logistic Regression of Seedling Survival on Levels of Fertilizers after 40 Months.

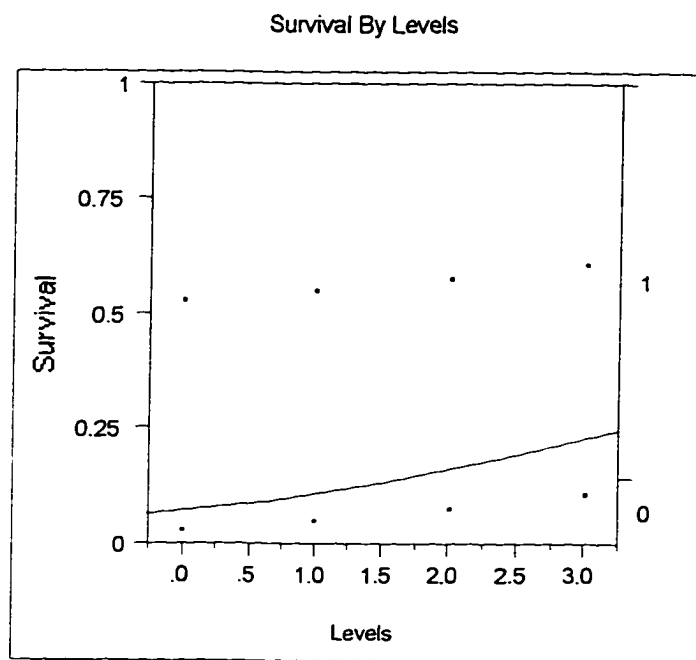


Table 120. Statistical Details for the Nominal Logistic Regression of Survival of Seedlings on Levels of Fertilizers After 40 Months.

Whole-Model Test				
Model	-LogLikelihood	DF	ChiSquare	Prob>ChiSq
Difference	4.57584	1	9.151688	0.002485
Full	127.17227			
Reduced	131.74811			
RSquare (U)			0.0347	
Observations (or Sum Wgts)			320	
Parameter Estimates				
Term	Estimate	Std Error	ChiSquare	Prob>ChiSq
Intercept	-2.5396169	0.3290776	59.56	0.0000
Levels	0.44548968	0.1521609	8.57	0.0034

Regression Analysis for Growth and Number of Leaves

Both mean growth and number of leaves per seedling decreased with increasing doses of fertilizers. Simple linear regression performed on data collected at forty months, showed that for each increase in the dose of fertilizers from one level to another, departing from control, the length of seedlings decreased by 5.594 cm (Tables 120 and 121; Figure 96) The same pattern is observed for leaves regressed on levels of fertilizers: a decrease of 0.190 leaf produced per seedling for each increase in the dose of fertilizer applied (Table 122, Figure 97). Analysis of variance showed significance for the amount of variation explained by the regression, both for length and number of leaves ($p=0.0073$ and 0.0276 , respectively), although the variation that may be accounted for levels effect on the model is not high ($R^2=0.026$ and 0.017 , respectively for length and number of leaves). (Tables 121 and 122).

Table 121. Simple Linear Regression of Length of Seedlings on Levels of Fertilizers.

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob>F
Model	1	10420.52	10420.5	7.3075	0.0073
Error	272	387873.36	1426.0		
C Total	273	398293			
Regression					
Term	Estimate	Std Error	t Ratio	Prob>t	
Intercept	163.41613	3.725984	43.86	0.0000	
Levels	-5.594922	2.069712	-2.70	0.0073	

Fig. 96. Linear Regression of Length of Seedlings on Levels of Fertilizers.

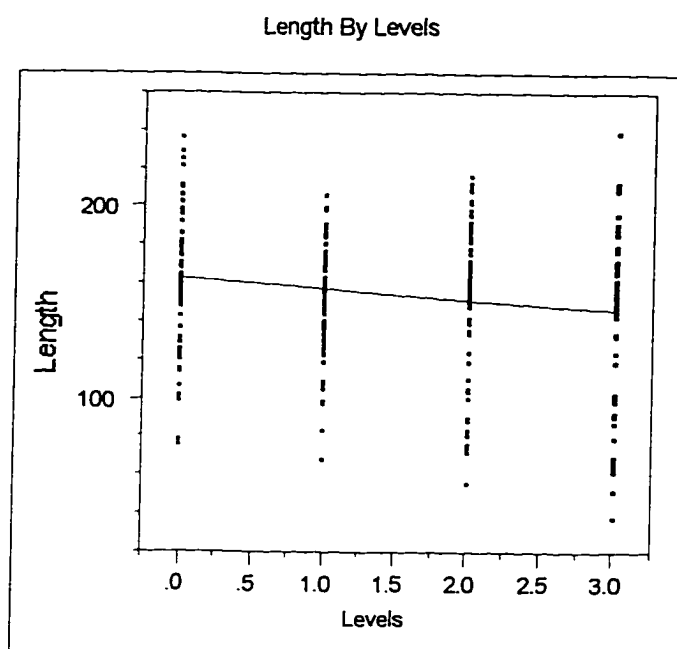


Table 122. Statistical Details for a Simple Linear Regression of Length of Seedlings (Recorded at 40 Months) on Levels of Fertilizers.

Linear Fit Summary of Fit				
RSquare				0.026163
RSquare Adj				0.022583
Root Mean Square Error				37.76248
Mean of Response				155.4526
Observations (or Sum Wgts)				274
Analysis of Variance				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	10420.52	10420.5	7.3075
Error	272	387873.36	1426.0	Prob>F
C Total	273	398293.88		0.0073
Parameter Estimates				
Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	163.41613	3.725984	43.86	0.0000
Levels	-5.594922	2.069712	-2.70	0.0073

Fig. 97. Linear Regression of Number of Leaves on Levels of Fertilizers.

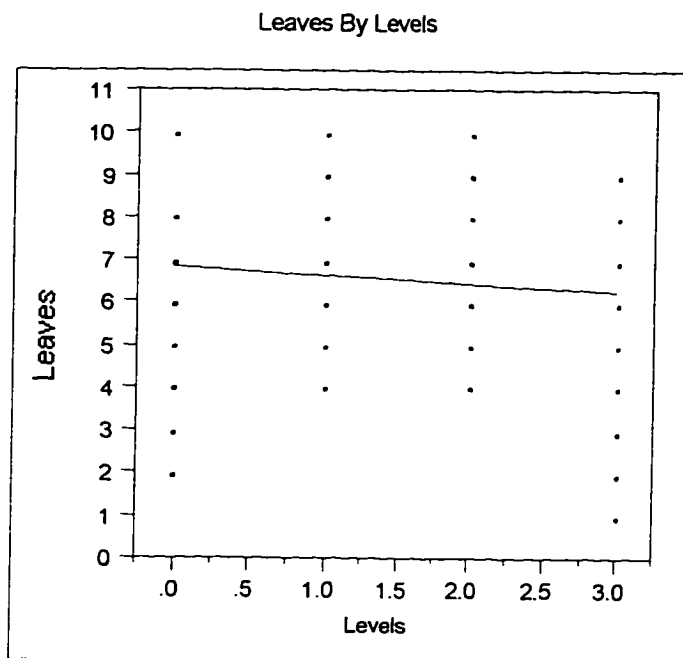


Table 123. Statistical Details for a Simple Linear Regression of Number of Leaves (Recorded at 40 Months) on Levels of Fertilizers.

Linear Fit Summary of Fit				
RSquare		0.017715		
RSquare Adj		0.014104		
Root Mean Square Error		1.57057		
Mean of Response		6.572993		
Observations (or Sum Wgts)		274		
Analysis of Variance				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	12.10031	12.1003	4.9055
Error	272	670.93983	2.4667	Prob>F
C Total	273	683.04015		0.0276
Parameter Estimates				
Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	6.8443626	0.154967	44.17	0.0000
Levels	-0.190655	0.086081	-2.21	0.0276

Data Transformation

The presence of extreme variates (outliers) was noted in the examination of the data sample for normality. These are due to several factors which included on one extreme, stunted seedlings with imperfect development (in some cases, atrophy) caused by insects, fungi, disease (more rarely), cultural deficiencies (bad planting or insufficient water), or even of genetic origin. On the other extreme, the exaggerated development of individuals caused in a few cases by flaws in the shading, leading to excessive growth, or as observed in seedlings that were growing on ant hills formed in the plastic bag. The presence of outliers creating nonnormality conditions in the data sample may not be serious, since according to the central limit theorem, the means tend to follow the normal distribution more closely than the distribution of the variates themselves (Pimentel, 1979; Sokal and Rohlf, 1995). Although this data sample did not show a very skewed distribution, data transformation was performed to observe how much the presence of outliers could be affecting the significance level of the F-test and the efficiency of the design.

The data for length of seedlings and number of leaves at 40 months were transformed to normality using the Box-Cox transformation (JMP, 1995). Analysis of variance and regression analysis were again performed using the

transformed data for the two variables. The p-values of transformed analyses (both Anova and Regression Analysis) became in general, lower than those in the non-transformed analyses. This is particularly true for length of seedlings, since number of leaves was not affected by the transformation, showing that extreme variates in the sample cause no effect on the model. In the case of length, the p-values were also lower for the analyses performed with the transformed data, but not lower enough to change the overall results and conclusions (Table 123). This shows that the data meet the overall assumptions required for the analyses performed.

Table 124. P-values Obtained for Transformed and Non-Transformed Data Using Box-Cox Transformation for Length of Seedlings and Number of Leaves at 40 Months.

	Anova P-values Nontransformed		Anova P-values Transformed		Regression Nontransformed		Regression Transformed	
	Length	Leaves	Length	Leaves	Length	Leaves	Length	Leaves
Soils	0.0009	0.0001	0.0019	0.0001				
Levels	0.0017	0.0001	0.0038	0.0001	0.0073	0.0276	0.0174	0.0460
Int.SL	0.0052	0.0383	0.0181	0.0383				

4. Conclusions

The results obtained in this experiment showed that although the type of soils on which babassu seedlings are growing can make a positive contribution in terms of growth rate and biomass production, fertilizers can account for a significant negative effect if higher doses are applied. Small amounts such as those applied for levels 1 and 2 do not differ significantly from seedlings growing without any artificial fertilization.

The differences produced by soil types began to appear as soon as the seedlings were transferred from the germinators to the plastic bags. Previous observations revealed that although the seedlings are still attached to seed up to ca. 12 months after initiation of germination, the developing root system suffers from transplanting and requires time for adaptation to the new medium. At the time of transplanting, the root system is functional and part of the nutrients used by the growing seedling come from the substrate. Taking that in consideration, the results obtained following two months after transplanting make a great deal of sense, since the type of soil and its natural fertility can become (as in fact happened) a factor of effect in the recovery of the seedling from the stress associated with transplanting, influencing growth rate and leaf production. Therefore, the first significant results suggested that the seedlings used

Plintosol's natural fertility, and the little they could get from Sand, making these two soil types, respectively, the best and the worst media for recovery and early growth of babassu seedlings after transplanting. It is obvious that other factors contributed to the differences observed in growth rates among soils (that can be detected by the low R-Square), including the inherent genetic vigor, and the ability of individuals to recover from or withstand stressful situations such as transplanting. However, this information on seedling recovery was used as the starting point for the subsequent analyses. Regarding to leaf production, there was no difference among soil types at that point, and this was expected, since the time elapsed from transplanting and the first data collection was only two months, not enough to produce differences in that character.

Fertilizers seemed to produce a more consistent detectable effect only during the period between 10 and 15 months after transplant (Figure 91). Only at 10 months after the seedlings were transferred to the nursery, and 8 months after the first dose of fertilizers was applied, there was a significant difference among levels of fertilization. However, these differences were still barely significant with a p-value on the borderline of the significance level. From this, it was clear that the control performed better in terms of growth rate in comparison with the fertilized treatments. In a more rigid interpretation of the results, it can be said that 8 months after the first fertilization was carried out no differences existed among the treatments. This finding has practical application, as it shows that

early use of fertilizers (up to 1 year) is a waste of money and time. Babassu seedlings will do well enough whether they receive fertilizer or not, by using the nutrients they still can absorb from reserves of the seed (still attached) and from the growing medium as well, since the root system is already functional. This is true, at least for seedling growth.

In soils, the situation was quite the same 10 months after transplanting, as expected, since the differences in terms of natural fertility in each type of soil, continued to have an effect on the growth rate of seedlings (Figure 91). What is still to be determined is why the differences produced by different soil types on the growth rate were not noticeable in leaf production. On the contrary, the difference among means for leaf production in the different soils was not significant. However, they were statistically different for levels of fertilizers, generating a situation opposite to that already discussed for growth rate. A physiological explanation has to be found for having the same factor producing a barely detectable effect on growth, but highly significant in leaf production.

More consistent results could be obtained for growth of seedlings only at the 15-month analysis (Figure 91). That was a period of time long enough for the effects of both major treatments to appear. The results indeed confirmed this expectation, showing an overall statistical significance for both soils and fertilizers in the analysis of variance performed with data collected in this period.

The results obtained marked the beginning of a pattern that remained consistent until the end of the experiment: the decrease in both the growth rate and number of leaves produced as the result of the increase in the dose of fertilizers applied to the seedlings (Figures 91 and 92). Although the overall p-value for fertilizers effect was not highly significant at that point, it statistically validated the detected pattern. At that phase of the experiment, there was no significant differences between the control and the fertilized treatments; this difference only existed when the highest dose (level 3) was compared to the other levels. It means that the level 3 accounted (negatively) for most of the variation among fertilizers detected in the Anova.

This consistent effect of fertilizer, although negative with level 3, may have also partially accounted for the differences observed among soil treatments.. When fertilizers may have started to produce an effect on growth, the differences among soils tended to decrease, as suggested by the reduced differences between sand and the other soils. This pattern was also observed in leaf production. The difference between Plintosol and the other types was highly significant, consistently confirming its status as the best substrate to grow babassu seedlings in nursery conditions.

Leafing, at the 15-month analysis, showed no difference in the results whether fertilizers were applied in doses 1 or 2, or were not applied at all (Figure 92).

The difference only appeared in the same consistently negative way, with an apparent decrease or slowing down in the number of leaves produced when fertilizer dose 3 was applied.

Both analyses performed on the data at 21 months and 40 months after the seedlings were transplanted mostly confirmed the patterns observed. At 21 months, both soils and fertilizers continued to produce an overall, highly significant effect on growth (Figure 91). No interaction between effects, however, was detected. In relation to soils, there was only a noticeable change: the lowest means produced up to this point had been those computed for Sand. At this time, however, Podzolic took this position. The fact that a statistically significant difference only existed between Plintosol and the other soil types, individually or as a group, confirmed this type as most beneficial for seedling growth.

In fertilization, a noticeable change was that the differences between control and the other levels were significant as were the differences between level 3 and the others. This shows both extremes (no fertilization and the highest dose) statistically different from the others, leading to the conclusion that fertilizers should not be applied since growth progressively decreases as fertilizer dose increases. In terms of results for number of leaves produced in 21 months, they showed another important change, with Sand having the highest mean among soil types. A possible explanation would only come after the 40-month analysis

was performed, when the results revealed that the sandy medium also gave the largest rhizome. A large rhizome perhaps retain higher amounts of water, and that may help the plant to minimize the effects of water shortage during the dry season.

In the final analysis, performed for the data collected 40 months following transplanting, the most important results confirmed most of the patterns obtained throughout the experiment as well as the conclusion stated in earlier analyses. Growth rates obtained for the period (3.187 cm per month in a 19 month-period) were consistent with the situation observed in nature: babassu seedlings are slow growing in their early phase of development (Figure 91). The hypothesis on which this experiment was based – soil type and/or fertilizer regimen would not significantly accelerate this growth rate was partially proven up to this point in the experiment. However, the considerable increase in seedling length showed after the last 19 months may in part reject the initial hypothesis, although other factors may have been influential, as discussed throughout this section.

The final results for soil types confirmed what has been postulated in the partial analyses: Plintosol had the overall highest mean growth among soils, and this was statistically significant from the others. Based on these results, it was concluded that Plintosol is the best soil type for babassu seedlings, and Podzolic

is the worst. However, there was no significant difference between Plintosol and Latosol, raising the latter to the category of good substrate for babassu seedling growth. On the other hand, there was no statistical difference between Podzolic and Sand; Podzolic falls therefore in the category of worst growing medium along with Sand. Comparison between Plintosol+Latosol and Podzolic+Sand shows highly statistical significance for the difference between these two groups, confirming the separation as the first two to the group of best substrates and the last two to the category as the worst soil substrates to grow babassu seedlings. The better growth performance of seedlings on Plintosol and Latosol may have been based on the imperfect drainage shown by these soil types, particularly the first. The retention of water for longer periods of time, especially during the dry season, can make a considerable difference on growth performance. The better results obtained in Plintosol, may just confirm what is observed in nature. It has been reported that higher productivity of babassu stands is usually recorded in soils of the hydromorphic class, such as that used in this experiment (MIC/ST1, 1982).

The failure of the Red-Yellow Podzolic type used in this experiment is surprising, since this particular type of soil has been the main support for stands of babassu, particularly in the ecological region of Cocais, where the native formations were more expressive in the past, both in terms of productivity and area of occurrence. The explanation may be related to the process of conversion

of the original forest to the pastures and agricultural fields during the last two decades. This type of soil is affected by the hydromorphism present in all soils of the region and by the thickness of an originally existing sand layer. As the forest is removed the soil becomes more exposed, producing a decrease of the clay layer on the upper portion of the soil, and an increase of the sand layer. This leads progressively to thicker, more acid and strongly leached upper horizons, with deficiencies in many macro and microelements that make fertilization increasingly important and costly in the agriculture based on these soils. All this, associated to the high rate of conversion of babassu formations and other vegetation to pastures in the region.

Decrease of the clay content, increase of sand content, and leaching of nutrients may be an acceptable explanation for the results obtained in this experiment for the Podzolic type of soil in relation to the expectation that this type would produce the best results. Data on productivity, production and coverage of babassu stands in the Cocaís region refers to 15 years ago. I believe, that today, the situation has changed considerably, and a new survey of the babassu stands in the area, would show a completely different situation, with lower rates of productivity, production, and reduced area effectively covered by babassu. What seemed to be the best soil environment for the establishment and growth of babassu in the past is no longer true, because of the significant

changes in the physical and chemical properties of the soil during the past two decades.

Fertilization was shown to be unnecessary for the early development of babassu seedlings. The final results support the early statement based on the preliminary analysis: addition of fertilizers did not have a statistically significant positive effect on growth of babassu seedlings when the lower doses were applied; however, the highest dose produces a deleterious effect on the growth performance of the seedlings. Throughout the experiment this pattern was observed, and confirmed as statistically significant. Combined effect with types of soil can only be shown after 21 months (in the 19-month period between these two observations) since interaction between these two treatments was never significant up to this point.

Leafing rate at the end of the experiment compared to those obtained before showed that babassu seedlings while having their growth rates clearly affected by climate, apparently keep a stable production of leaves both in the dry and rainy seasons. This pattern is confirmed in nature by adult individuals which keep a stable leafing rate throughout the year, and little or no effect of climate has been observed on this phenological event.

In summary, the following general conclusions can be drawn from the results and analyses performed on the data:

1. The early development of the babassu palm (up to 4 years) is very slow.
2. Different types of soils do make a difference in early growth.
3. Fertilizers do not produce a positive significant effect on growth of seedlings up to four year. The slight increase produced on growth and on number of leaves by the first two levels does not justify investment in fertilizers.
4. Higher doses of fertilizers have a negative effect both on growth and biomass production.
5. Leafing rate in babassu seedlings follow the same stable pattern shown by adult babassu palms, being little or not affected at all by soil type, fertility, or climate.
6. Growth rates of seedlings are clearly affected by cultural care in the nursery.

B. Establishment of Babassu (Orbignya phalerata Martius) in Degraded Soils

1. Introduction

Much of the Pre-Amazon region of the State of Maranhão (Figure 98) falls into the category of degraded area. This region constitutes a large portion of Maranhão's territory and is bounded by the mangrove areas of the northwestern coast and the *cerrado* vegetation to the south. In the central-western part of this area, much of the originally moist evergreen forest has been devastated by logging and ranching settlements during the past decade. In some areas, the deforestation has been so severe that the soil has been degraded into infertile sand, and the vegetation is now composed mostly of grasses and weeds.

For recuperation of areas that suffer deforestation, the utilization of species that regenerate easily and have high economic value is advisable. Many palm species fit this description. As a group they are often adapted to withstand the environmental extremes found in cleared areas. They are also the most important group of plants used by man throughout the tropics and subtropics (Balick, 1984; Pick et al., 1985; Balick and Beck, 1990). The babassu palm (Orbignya phalerata Martius) is considered to be one of the best examples of use of palms by people (Markley,

1971; May, 1985; May et al., 1985). Distributed over 10 million hectares in Maranhão, this palm is more than a source of income for people (Anderson et al., 1991). It is also of great ecological importance, because of its persistence as the main soil cover where other less resilient species have failed. The use of this resilient palm for reforestation of degraded areas in Maranhão, shows great promise for converting unproductive into productive land.

This experimental study was intended to test the ability of the babassu palm to overcome adverse ecological conditions. If this hypothesis is confirmed, this palm can be included in the list of species recommended for reforestation of degraded areas in Maranhão, and in other parts of Northeastern and Northern Brazil where soil degradation has become an increasingly serious ecological problem.

2. Material and Methods

This on-site study was designed to test the feasibility of introducing the babassu palm into degraded sites for reforestation and site restoration. It tested the hypothesis that the babassu palm is capable of tolerating the stress associated with cleared areas, degraded soils, and competition. It measured the germination of seeds and seedling growth in control plots (with no treatments) versus plots subjected to shading and weeding. This experiment was installed at the EMAPA Research Station in the municipality of Santa Luzia do Paruá, in the pre-Amazon region of the state of Maranhão (Figure 98). The experimental design used in this experiment was that of randomized complete blocks. The experiment was initially designed with four replications per treatment and eight treatments, totaling 32 plots. The initial treatment combinations planned to be tested were as shown in Table 124.

Fig. 98. Physiographic regions of Maranhão State - Area of the experiment on the establishment of babassu in degraded soils.

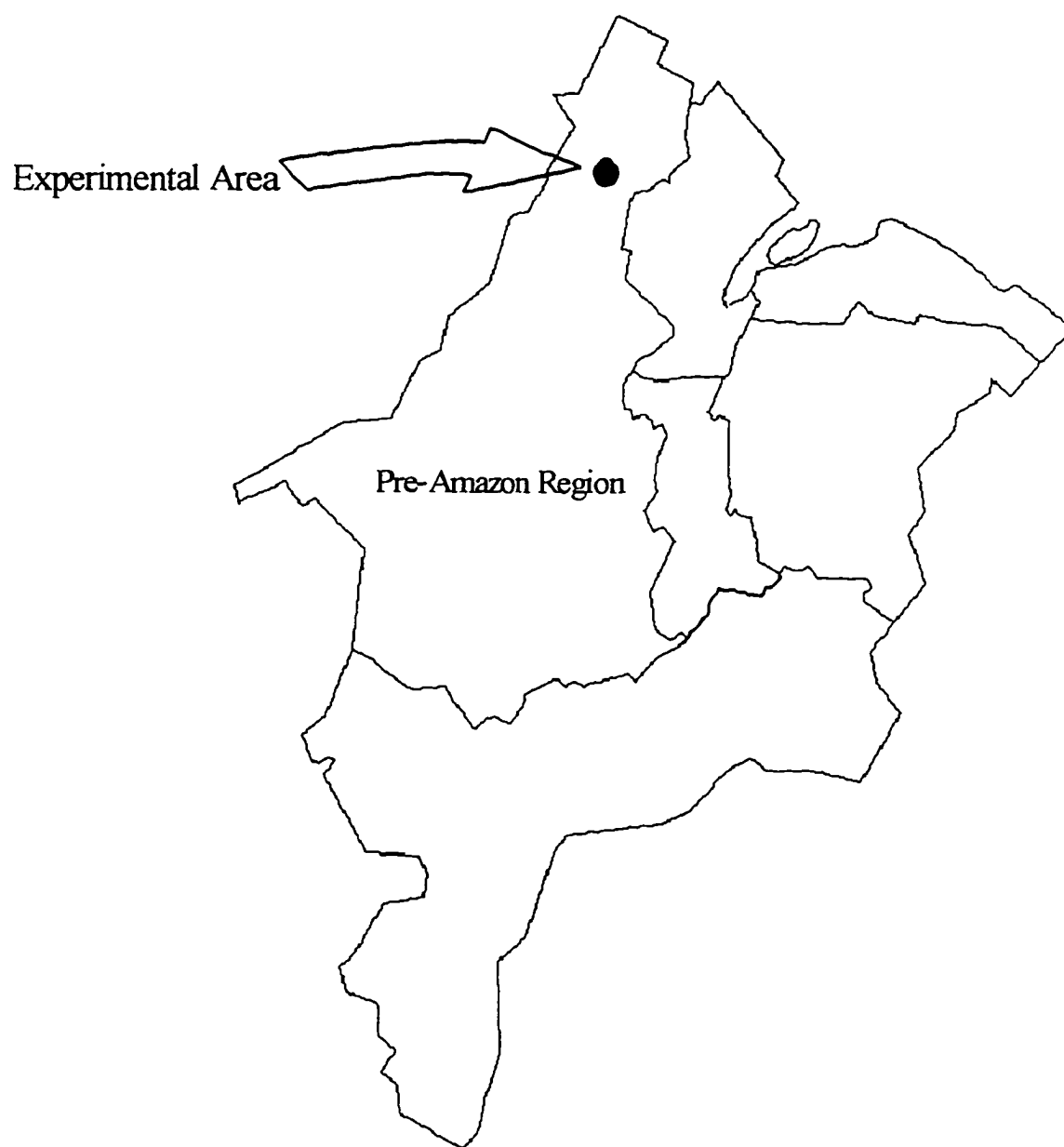


Table 125. Initial Treatments for Testing the Establishment of Babassu in Degraded Soils.

Treatment #	Initial Combination
1	Irrigation - Shading - Weeding
2	Irrigation - Shading - No Weeding
3	Irrigation - No Shading - No Weeding
4	No Irrigation - No Shading - No Weeding
5	No Irrigation - Shading - Weeding
6	No Irrigation - No Shading - Weeding
7	No Irrigation - Shading - No Weeding
8	No Irrigation - No Shading - Weeding

Since irrigation of plots could not be maintained on a regular basis, it was decided to eliminate this factor from the combinations tested. As the result, each treatment gained a replication within each block. The experimental design then ended up with four blocks, four treatments, 8 replications per treatment, in a total of 32 plots. The final treatment combinations tested are shown in Table 125 and Figure 99.

Table 126. Final Combinations of Treatments Used in the Experiment.

Treatment	Final Combination
1	Shading - Weeding
2	Shading - No Weeding
3	No Shading - No Weeding
4	No Shading - Weeding

The blocks were set up in dimensions of 32 x 12 m and divided into eight plots of 2 x 10 m (Figure 99). This experiment was initiated in March, 1989. The seeds were placed horizontally about 5 cm deep in the soil, with 1 x 1 m spacing left between seeds. A total of 33 seeds were used for each treatment, placed in 3 rows of 11 seeds each. Data collection was carried out as follows:

a) Germination - because of the long time required for germination of whole fruits and the lack of uniformity in germination, it was decided that a period of time sufficient to reflect the actual state of germination would be 12 months, which became then the starting point of data analysis.

b) General data collection - measurements and counts were made at 1, 2.4, 2.9, 3.3, 4.8 and 5.4 years after the experiment was initiated, and the following information was recorded: 1) germination rates; 2) number of established seedlings; 3) number of leaves per seedling; 4) total number of leaves in each plot; 5) length of seedlings. Data recording on germination, number of established seedlings, leaf production, and growth of seedlings followed the procedures described next.

Germination - Whole fruits were used as seeds in this experiment, instead of individual kernels. Since babassu fruits usually have more than one kernel per fruit (2-5, on average), more than one seedling may have arisen from the fruits.

However, each fruit was counted as an individual seed and only one germination was considered per fruit, no matter how many kernels germinated. In this way, it was possible to simplify the experiment and data recording. Moreover, the babassu palm is not a clustering species; although many kernels may germinate and produce more than one seedling per fruit, only one plant will survive. Therefore, for the purpose of this study, individual fruits are considered individual seeds.

Number of established seedlings - Although only one germination per fruit was considered in the analysis of germination rates, the total number of seedlings per plot was counted. The objective of this procedure was to follow the post-germination evolution of seedlings, the progressive disappearance of the least fit, and determination of the final number of seedlings established in each plot-treatment at the end of the experiment.

Leafing - Since the main purpose was to measure biomass (leaf) production per treatment, the total number of leaves per plot was counted and averaged. The number of leaves per individual in the plot is here taken as the total number of leaves of all individuals in the plot by the number of individual seedlings. This was expected to provide a general idea of aerial biomass production per treatment, per season, per year, and for the entire period of the experiment.

Growth of seedlings was measured by the longest leaf of one of the seedlings if more than one seedling existed per seed. This measure, for a certain period of time, reflected the growth of the tallest seedling per seed until the establishment of the final seedling. The individual measures of seedlings were then averaged per treatment and analyzed.

The final data collection was carried out using destructive measurements since information on dry weight of roots and leaves had to be recorded. Statistical analyses were carried out on the data collected over the five years of this study, looking for responses of the treatments on individual parameters, and on the seedlings as a whole in each treatment. The analysis was also oriented to search for among-season and among-censuses differences in growth and development of seedlings. The data were analyzed using JMP version 3.1.5 (SAS Institute, Inc., North Carolina).

Fig. 99. Arrangement of blocks and treatments for experiment on establishment of babassu in degraded soils.

Shading + Weeding	No Shading + No Weeding		
No Shading + Weeding	No Shading + Weeding		
No Shading + No Weeding	Shading + No Weeding		
Shading + No Weeding	Shading + Weeding		
Shading + No Weeding	No Shading + No Weeding		
Shading + Weeding	Shading + Weeding		
No Shading + Weeding	Shading + No Weeding		
No Shading + No Weeding (I)	No Shading + Weeding (II)		

Shading + Weeding	No Shading + Weeding
Shading + Weeding	No Shading + No Weeding
No Shading + Weeding	No Shading + No Weeding
Shading + No Weeding	Shading + No Weeding
No Shading + No Weeding	Shading + Weeding
No Shading + No Weeding	Shading + No Weeding
Shading + No Weeding	Shading + Weeding
No Shading + Weeding (III)	No Shading + Weeding (IV)

3. Results and Discussion

First Census (April, 1990): One Year after Planting

Seed Germination

Figure 100 provides a view of the area one year after the experiment was installed. For this period, the highest germination rate was recorded in treatment 4 (No Shading, Weeding; mean=25.00/plot), with 75.7% of germination, in relation to the total number of seeds in the plots. Treatment 3 (No Shading, No Weeding) showed the second best performance among treatments with 68.9% of germination recorded in the plots (mean=22.75/plot). Treatment 2 (Shading, No Weeding) had 63.2% of germination computed at that time. The lowest rate of germination (53.0%) was recorded in treatment 1 (Shading, Weeding) with a mean of only 17.5 seeds germinated per plot (Table 126). The mean percentages of germination by treatment are graphically compared in Figure 101.

Fig. 100. View of the experimental area one year after the experiment was installed. Santa Luzia do Paruá - April, 1990.



Analysis of variance for the data (Table 127) showed an overall significant effect of treatments on germination, although not highly significant ($p=0.0492$). High R-Square shows that ca. 28.2% of the variation in the model was due to treatments effect. The Least Significant Number (LSN) calculated in the power analysis performed was 31.87, less than the actual sample size n (32). It means that the sample size used in this experiment was enough to achieve a significant result with the given values of the significance level (α), the standard deviation of the error (σ), and the effect size (δ). The power of the analysis for treatment effect (the probability of getting a significant result) was 0.6, a little below the level considered by some as the desirable minimum (0.8). These values are shown in Table 27.

Finally, as expected, no significant effect of blocks was obtained in the Anova performed ($p=0.9129$), and there was no interaction between treatments and blocks ($p=0.5096$) (Table 127). No statistically significant difference was found between treatments 3 and 4 ($p=0.3788$), with the highest rates of germination; neither were there differences between 2 and 3 (the lowest rates). Comparison between the lowest mean (treatment 1) and the other three, however, showed significance for the difference between the means ($p=0.0175$), suggesting that treatment 1 accounted for most of the variation in the model, having the lowest means among the treatments. Since the comparison between treatments 1 and

2 showed no difference ($p=0.1934$), I assumed that shading in the treatment combinations may have been the factor responsible for the lowest rates of germination. This is reinforced by comparing the treatments with shading (treatments 1 and 2) with those without it (treatments 3 and 4), which shows that the difference between the means of the two groups is statistically significant ($p=0.0168$). The treatments under sunlight (both with and without weeding) yielded the best germination results for the period (Figure 102).

Table 127. Descriptive statistics for number of seeds germinated per treatment and block one year after the experiment was installed.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	17.50	6.256	8-26	Block I	20.625	7.836	8-33
Treat.2	20.87	3.136	17-26	Block II	22.375	5.012	12-29
Treat.3	22.75	4.367	16-29	Block III	21.375	4.340	16-19
Treat.4	25.00	4.535	19-33	Block IV	21.750	3.991	17-27
Totals	21.53	4.573	8-33	Totals	21.531	5.294	8-33

Table 128. Analysis of variance for number of seeds germinated one year after the experiment was installed.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	241.594	80.531	3.258	0.0492	0.2802
Blocks	3	12.844	4.281	0.173	0.9129	0.0149
Treat./Blocks	9	212.031	23.559	0.953	0.5096	0.2459
Error	16	395.500	24.719			0.4588
Total	31	861.969				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	4.971795	2.747691	32	31.87091	0.6332
Blocks	0.0500	4.971795	0.633535	32	484.7945	0.0754
Treat.*Block	0.0500	4.971795	2.574097	32	69.20931	0.3091

Fig. 101. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.

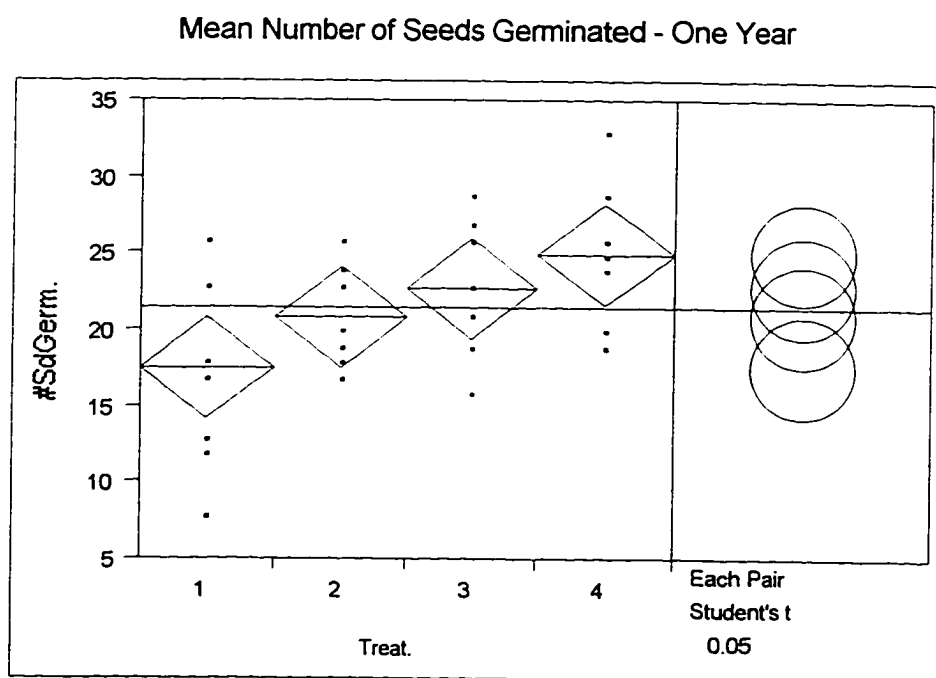


Fig.102. Germinated seed in a non-weeded plot one year after planting -
April, 1990.



Number of established seedlings

One year was enough time to measure only the initial establishment of seedlings, since germination did not cease until later than one year, as will be discussed. However, it constituted a good measure of the effect of treatments on the early development of seedlings in nature, under stressful conditions. The overall analysis of variance showed a significant p-value (0.0406) for treatments as an effect on number of seedlings (Table 129). These results showed the importance of light for both germination and for initial establishment of the babassu seedling. Shading conditions seem to have had an initial delaying effect on germination which is in turn, reflected on the number of seedlings established in each plot. The power of the analysis for the treatment effect on the model was 0.6, and the least significant number 30.47 for an $\alpha=0.05$. Blocks had no significant effect on seedling establishment ($p=0.7355$), and interaction between the two factors was not significant ($p=0.3613$). Table 129 shows the values for power details of the analysis. The greatest mean number of established seedlings (46) was recorded in treatment 3 (No Shading, No Weeding), followed by treatment 4 (No Shading, Weeding). The two shaded treatments, 1 (Shading, Weeding) and 2 (Shading, No Weeding), showed the lowest mean number of seedlings established after one year (30 and 38.375, respectively) (Table 128; Figure 103). Comparison between the two highest

means (treatments 3 and 4) showed that the difference was not statistically significant ($p=0.8425$), and neither was the difference between the two lowest means (1 and 2; $p=0.1524$). The difference, however, between these two groups of treatments (shaded x non-shaded) was significant ($p=0.0114$), showing that the results obtained for number of seedlings was mostly a reflection of the results already shown for germination, also confirming the importance of light in early stages of development of this palm species. On the other hand, there was no statistical difference between the treatments weeded and not weeded ($p=0.2456$), indicating that babassu seedlings are more successful in germinating in a sunny spot.

Table 129. Descriptive statistics for number of seedlings established per treatment and block one year after planting.

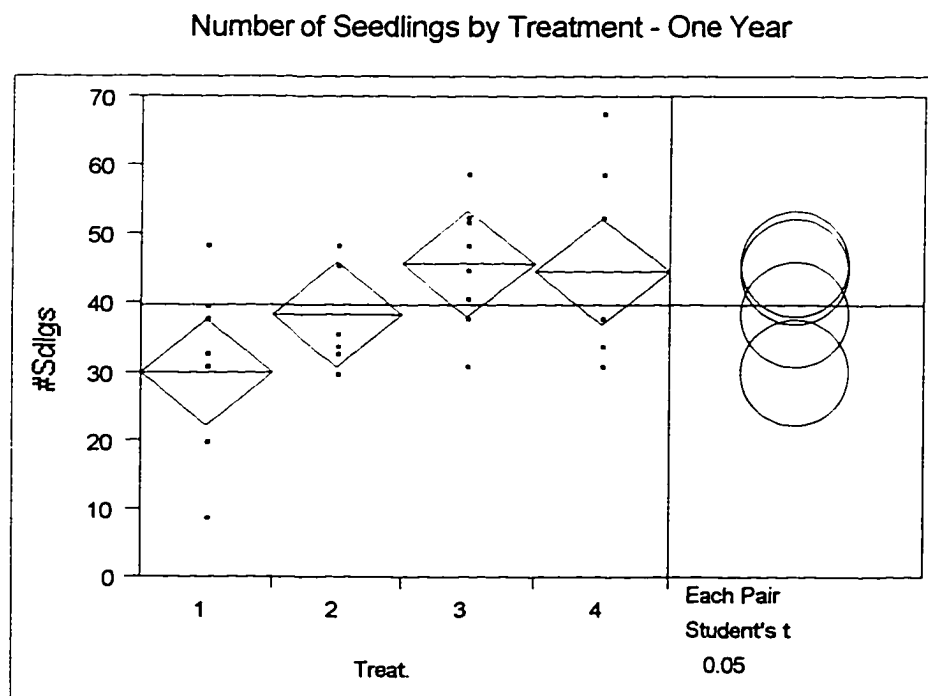
Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	30.000	12.961	9-49	Block I	37.125	18.098	9-68
Treat.2	38.375	8.262	30-49	Block II	43.250	11.756	20-59
Treat.3	46.000	9.086	31-59	Block III	38.875	10.736	31-59
Treat.4	44.875	13.378	31-68	Block IV	40.000	8.912	30-53
Totals	39.812	10.921	9-68	Totals	39.812	12.275	9-59

Table 130. Analysis of variance for number of seedlings one year after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	1298.125	432.708	3.483	0.0406*	0.2714
Blocks	3	159.625	53.208	0.428	0.7355	0.0333
Treat./Blocks	9	1337.125	148.569	1.196	0.3613	0.2795
Error	16	1988.000	124.250			0.4156
Total	31	4782.875				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	11.14675	6.369176	32	30.47146	0.6654
Blocks	0.0500	11.14675	2.233446	32	198.3317	0.1170
Treat.*Block	0.0500	11.14675	6.464144	32	56.72323	0.3887

Fig. 103. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.



Leafing

Leaf production was considerably higher in treatment 4 (No Shading, Weeding) with a mean of 102.12 leaves recorded in those plots (Table 130; Figure 104). Germination, number of seedlings and number of leaves are directly related to each other and therefore, the results are practically the same obtained for the other two variables already shown. Treatment 3 (No Shading, No Weeding) followed treatment 4 with the second best mean number of leaves in the period (95.375), and again the shaded plots (treatments 1 and 2) showed the lowest means in the experiment.

Analysis of variance showed again an overall significant p-value for treatments, but not significant for blocks ($p=0.2291$) and for the possible crossing effects between both ($p=0.7215$). Table 131 shows the values for power and the least significant numbers for the effects tested on the model. The interpretation here is basically the same: shading inhibits germination, and consequently seedling production, which in turn results in a lower number of leaves produced per plot. Orthogonal comparisons revealed an expected situation, which can be summarized as follows: 1) no difference between treatments 3 and 4 with the highest means ($p=0.6029$); 2) statistical significance for the difference between 1 and 4 ($p=0.0108$); 3) no difference between the lowest means shown by 1 and 2 ($p=0.2956$); 4) the difference between the treatments with shading and with no

shading is statistically highly significant ($p=0.0097$); and 5) treatments with weeding are not statistically different from those without weeding ($p=0.7022$).

Table 131. Descriptive statistics for number of leaves produced per treatment and block one year after the planting of seeds.

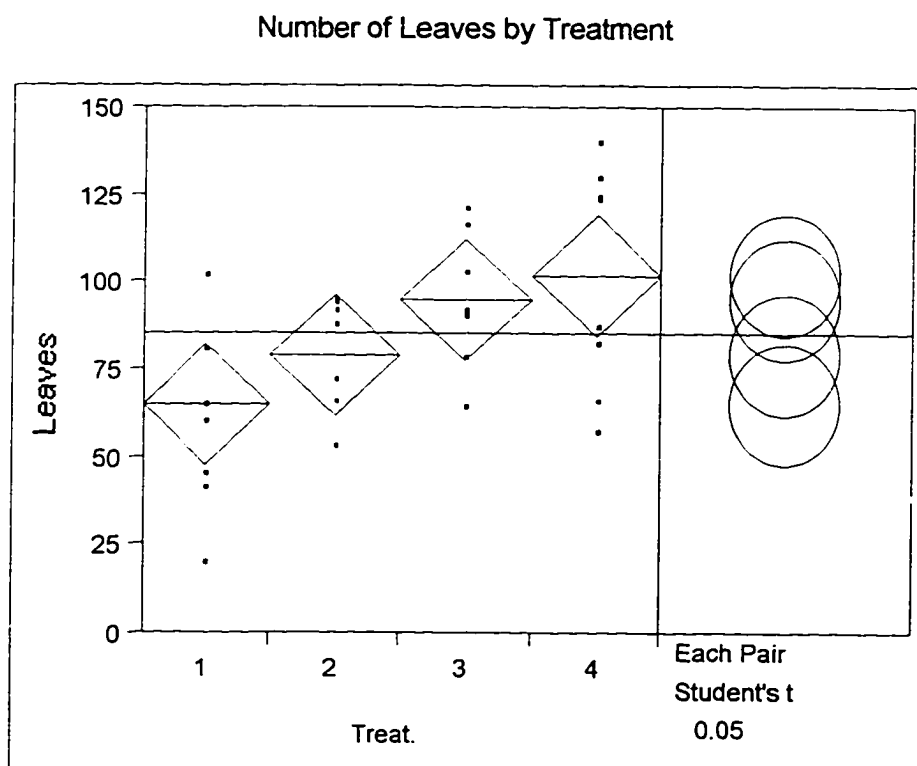
Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	65.500	29.320	21-103	Block I	74.250	36.421	21-141
Treat.2	79.250	15.988	54-96	Block II	101.125	27.068	42-125
Treat.3	95.375	18.814	65-122	Block III	81.375	23.706	58-131
Treat.4	102.125	31.831	58-141	Block IV	85.500	18.639	66-117
Totals	85.562	23.988	21-141	Totals	85.562	26.458	21-141

Table 132. Analysis of variance for number of leaves produced one year after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	6503.625	2167.875	3.350	0.0455	0.2723
Blocks	3	3101.625	1033.875	1.598	0.2291	0.1298
Treat./Blocks	9	3923.625	435.958	0.674	0.7215	0.1642
Error	16	10353.000	647.062			0.4335
Total	31	23881.875				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	25.43742	14.25617	32	31.26807	0.6467
Blocks	0.0500	25.43742	9.845089	32	56.761194	0.3400
Treat.*Block	0.0500	25.43742	11.07309	32	95.02227	0.2200

Fig. 104. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.



Growth

Results - The overall effect of the non-shaded treatments that produced better responses in terms of germination, number of seedlings and leaf production, did not result in a concomitant increase in length (Table 132). Treatments and blocks had no significant effect on growth of seedlings (Table 133) at this point (p -values=0.1370 and 0.9448, respectively). Table 133 shows the values for power and least significant number for the effects tested on the model. For treatments it can be noticed that power was low (0.4), although the least significant number was not very far from the actual sample size. It shows that with a number of 44.29 observations for those given Alpha, Sigma and Delta a significant p -value for this analysis could have been gotten. The same is not true for blocks effect since the LSN was much higher (677.69). Although the means for treatments were not statistically different, they show slightly higher values for the treatments where weeding was not performed (treatments 2 and 3) (Table 132). Visual comparison of treatments is provided in Figure 105.

For this first year, the analysis of the recorded data reflected mostly the performance on germination, that in turn reflected on the other variables measured. As mentioned before, during up to ca. 12 months after germination, babassu seedlings still remain attached to the seed through the cotyledonary

axis, and are partially fed by endosperm reserves. Therefore, a more accurate evaluation of the real behavior of babassu seedlings (especially that regarding growth) in degraded soils is more likely to be achieved after the detachment of seedlings from the seed, when they begin to grow and develop by exclusively using their young root system for absorbing soil nutrients. These overall results on growth of seedlings, however, showing no differences up to this point, confirm previous non-experimental observations on the extended attachment of the seedling to the seed, and the continued use of the endosperm reserves up to one year after the germination of the babassu seed. Figure 106 shows the percentage of seeds germinated, and the means for number of seedlings, number of leaves, and length of seedlings recorded one year after the experiment was installed.

Table 133. Descriptive statistics for length of seedlings (cm) per treatment and block one year after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	40.500	4.375	34-46	Block I	41.250	4.131	37-48
Treat.2	43.875	3.044	39-48	Block II	40.500	4.566	34-45
Treat.3	40.625	4.470	34-48	Block III	41.500	3.664	36-46
Treat.4	38.750	2.866	36-45	Block IV	40.500	4.472	36-48
Totals	40.938	3.688	34-48	Totals	163.75	4.208	34-48

Table 134. Analysis of variance for length of seedlings (cm) one year after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	109.625	36.542	2.126	0.137	0.2167
Blocks	3	6.375	2.125	0.124	0.9448	0.0126
Treat./Blocks	9	114.875	12.764	0.743	0.667	0.2270
Error	16	275.000	17.188			0.5436
Total	31	505.875				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	4.145781	1.850887	32	44.29458	0.4420
Blocks	0.0500	4.145781	0.446339	32	677.6946	0.0679
Treat.*Block	0.0500	4.145781	1.894688	32	86.82717	0.2414

Fig. 105. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.

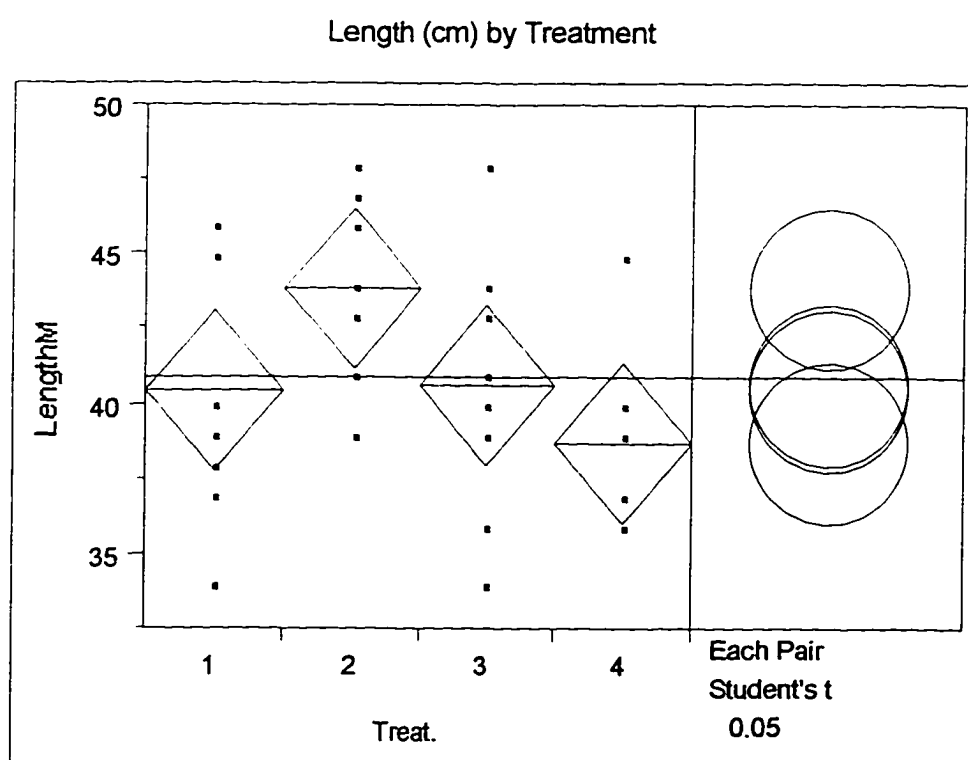
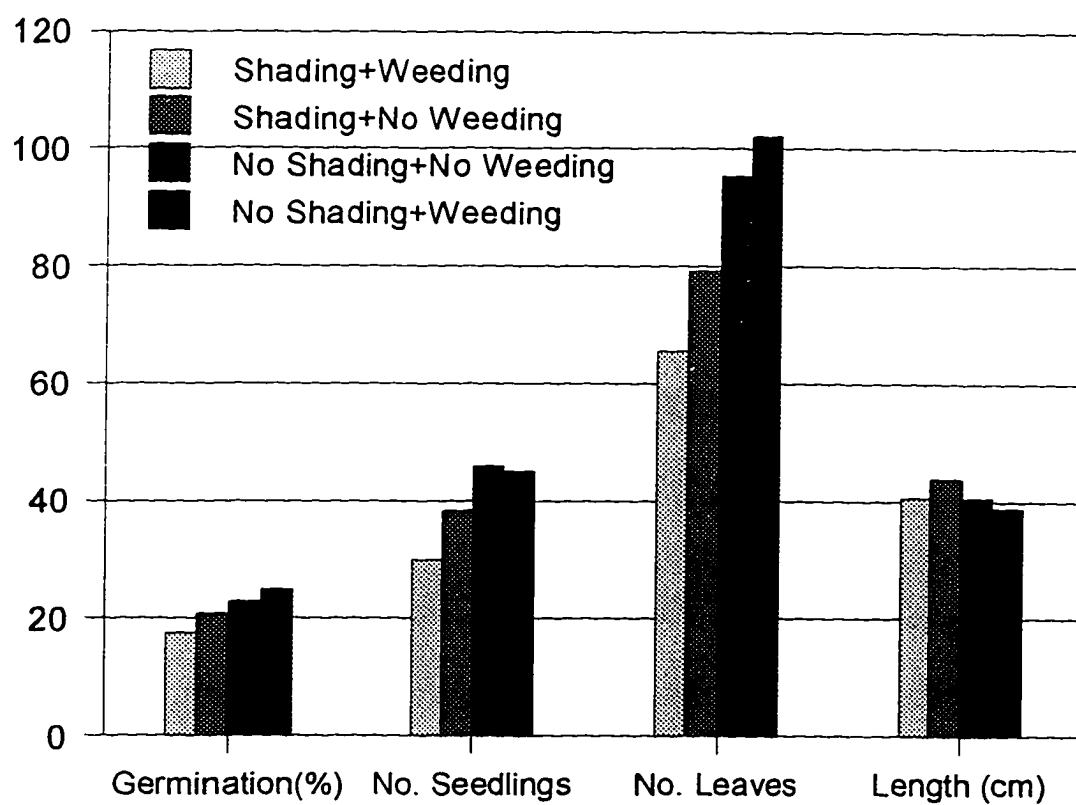


Fig. 106. Mean values for germination of seeds, number of seedlings established, number of leaves, and length of seedlings one year after planting.



Second Census (August, 1991): 2.4 Years after Planting

Germination

After the second year, data were collected including germination rates, the number of established seedlings, the total number of leaves, and the length of seedlings (Table 134; Figure 107). These data indicated that the seeds continued to germinate during part of the second year, producing a slight alteration in the previous data recorded (a mean increase of 5.2 additional seed germination/plot). With the additional germination, the overall percentage of germination reached the total of 80.9%, somewhat higher than the previous overall rate of 65.2%. This does not represent a considerable increase (16 seeds more than the number recorded in the one-year data), but it leads to conclude that babassu seeds may retain their viability for more than one year in field conditions.

The overall mean germination rate per plot was 26.71, but analysis of variance showed that there was no statistical difference among the means for each treatment ($p=0.9643$) (Table 1350; Figure 107). Since this census was carried out 1.4 years after the previous one, it would be expected that no effect would be detected in the analysis since germination ceased ca. one year before and the

differences among treatments were very small. It is possible that light had a more significant effect on the germination of the last seeds as compared to the treatments themselves. Blocks produced a slightly significant effect on germination($p=0.0429$), which is difficult to explain. It may be related to the position of blocks in the area and the resulting different angles of light received. Interaction between treatments and blocks effects was not significant ($p=0.6905$).

Table 135. Descriptive statistics for number of seeds germinated per treatment and block 2.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	26.00	7.453	12-28	Block I	30.000	7.423	16-32
Treat.2	27.00	3.856	19-30	Block II	28.375	5.113	21-31
Treat.3	27.00	4.587	18-31	Block III	23.625	4.465	17-26
Treat.4	26.87	4.671	17-30	Block IV	24.875	3.876	16-25
Totals	26.71	5.141	12-31	Totals	26.718	5.264	16-32

Table 136. Analysis of variance for number of seeds germinated 2.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	5.594	1.865	0.090	0.9643	0.0082
Blocks	3	211.844	70.615	3.419	0.0429	0.3113
Treat./Blocks	9	132.531	14.726	0.713	0.6905	0.1947
Error	16	330.500	20.656			0.4856
Total	31	680.469				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	4.544915	0.418097	32	926.9572	0.0629
Blocks	0.0500	4.544915	2.572959	32	30.84784	0.6564
Treat.*Blocks	0.0500	4.544915	2.035093	32	90.1685	0.2321

A similar situation was found for number of established seedlings and number of leaves produced, as would be expected since these numbers are partially a result of the number of seeds that germinated. There was a noticeable increase in the number of seedlings (mean increase of 7.125 seedlings) and total number of leaves (mean increase=66.781 leaves in all treatments) during the past period of 1.4 years. The mean number of leaves per seedling also jumped from 2.14 in the previous census to 3.24. Tables 136 and 138 and Figure 107 show the means recorded for number of seedlings and leaves in this census.

Despite these mean increases, there was no statistical difference among the treatment means (p-values= 0.9609 and 0.5295, respectively for number of seedlings and leaves) (Tables 137 and 139). These increased numbers are a good indication of the ability of babassu seedlings to overcome unfavorable conditions in their early phases of growth. Although treatments did not produce significant differences among their means, a noticeably higher increase in mean was obtained for both number of seedlings and leaves were obtained in those treatments with weeding, indicating that seedlings can benefit from this intervention (Figure 107). Blocks produced a significant effect on number of seedlings ($p=0.0026$), but not on number of leaves ($p=0.0722$). Interaction was not significant in both cases (p-values= 0.9033 and 0.7122, respectively for number of seedlings and leaves).

Table 137. Descriptive statistics for number of seedlings established per treatment and block 2.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	45.125	16.392	19-61	Block I	58.750	7.440	48-72
Treat.2	47.250	13.166	29-63	Block II	53.625	3.889	49-60
Treat.3	48.250	13.317	24-64	Block III	33.375	6.759	24-44
Treat.4	47.125	15.216	30-72	Block IV	42.000	17.088	19-64
Totals	46.938	14.522	19-72	Totals	46.938	8.794	19-72

Table 138. Analysis of variance for number of seedlings 2.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	41.125	13.708	0.096	0.9609	0.0068
Blocks	3	3140.625	1046.875	7.366	0.0026	0.5236
Treat./Blocks	9	542.125	60.236	0.424	0.9033	0.0903
Error	16	2274.000	142.125			0.3791
Total	31	5997.875				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	11.92162	1.133647	32	867.7409	0.0638
Blocks	0.0500	11.92162	9.906792	32	21.60885	0.9500
Treat.*Blocks	0.0500	11.92162	4.115994	32	147.3718	0.1470

Table 139. Descriptive statistics for number of leaves produced per treatment and block 2.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	153.87	45.599	93-220	Block I	173.875	45.028	139-275
Treat.2	137.75	35.419	90-198	Block II	175.500	42.848	111-229
Treat.3	147.37	38.913	78-203	Block III	123.625	32.802	78-181
Treat.4	170.37	61.307	94-275	Block IV	136.375	43.996	90-220
Totals	152.34	45.309	78-275	Totals	152.344	41.168	78-275

Table 140. Analysis of variance for number of leaves produced 2.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	4521.094	1507.031	0.766	0.5295	0.0698
Blocks	3	16636.594	5545.531	2.819	0.0722	0.2568
Treat./Blocks	9	12134.031	1348.226	0.685	0.7122	0.1873
Error	16	31471.500	1966.969			0.4859
Total	31	64763.219				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	44.35052	11.8863	32	112.7141	0.1778
Blocks	0.0500	44.35052	22.80117	32	35.37012	0.5646
Treat.*Blocks	0.0500	44.35052	19.47276	32	93.51487	0.2236

Mean length of seedlings increased considerably in the period of 1.4 years since the last census: it jumped from 40.938 cm to 52.231 cm (Table 140), an overall mean increase of 11.293 cm in the period, which represents a monthly growth rate per seedling of 0.7 cm. The major increases in the height of seedlings were recorded in treatments 2 (mean=56.9 cm) and 3 (mean=56.0 cm), those with no weeding provided (Table; Figure 107). Analysis of variance (Table 141) showed that treatment effect was highly significant ($p=0.002$), but no effect of blocks ($p=0.8301$) or interaction ($p=0.8205$) was detected in the analysis. Treatments 2 and 3 (non-weeded plots), with the highest means were statistically different ($p=0.0003$) from treatments 1 and 4 (weeded plots) which had the lowest means (50.275 cm and 45.75 cm, respectively). Visual comparison of treatments using Student's *t* tests is provided in Figure 108. Figure 109 shows a non-shaded weeded plot in between two non-weeded plots. Figure 110 shows seedlings in shaded and non-shaded plots, both weeded.

The main effect seemed to have been the presence of other vegetation, what is the opposite of what one would expect. This may mean that in the early stage of development competition does not affect growth of the babassu seedling; on the contrary, the presence of other vegetation in the area may even favor it by maintaining higher moisture levels in contrast to weeded plots, even those shaded ones, where moisture can still evaporate more easily. This shows that

with the competitive vegetation at the same level of development, babassu seedlings are able to keep up with relatively high growth rates by taking advantage of the higher moisture content in these areas. This is confirmed by observing that the third highest mean obtained in this census was recorded for treatment 1 (50.275 cm), a weeded plot, where the babassu seedling could take advantage of shading as a factor for maintenance of a fair moisture level in the soil. Growth performance dropped dramatically in treatment 4 (No Shading, Weeding), where seedlings were growing under direct sunlight. The difference between this treatment and the other three was highly significant ($p=0.0010$). The analyses to be presented, show how long babassu seedlings are able to cope with competition in higher moisture levels of the non-weeded plots, and still maintain growth rates at reasonable levels.

Seedling development up to the second year does not appear to be directly related to the growth in length. It seems that the production of green mass (leaf) for photosynthetic activity is the priority for the babassu seedling, at least during its early development. Percentages of germination, and means for number of seedlings, number of leaves, and length of seedlings for the period are graphically shown in Figure 107.

Table 141. Descriptive statistics for length of seedlings (cm) per treatment and block 2.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	50.275	6.879	38.9-60.4	Block I	52.287	6.086	43.6-62
Treat.2	56.900	2.767	53.6-60.8	Block II	52.700	7.886	38.9-60.8
Treat.3	56.000	3.340	50.1-62	Block III	53.137	6.779	38.6-60.4
Treat.4	45.750	4.647	38.6-50.5	Block IV	50.800	5.703	39.7-56.4
Totals	52.231	4.408	38.6-62	Totals	52.231	6.613	38.6-62

Table 142. Analysis of variance for length of seedlings (cm) 2.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	654.674	218.225	7.743	0.002	0.5159
Blocks	3	24.741	8.247	0.293	0.8301	0.0194
Treat./Blocks	9	138.474	15.386	0.546	0.8205	0.1091
Error	16	450.960	28.185			0.3554
Total	31	1268.849				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	5.308955	4.523113	32	21.32447	0.9594
Blocks	0.0500	5.308955	0.879287	32	288.4688	0.0943
Treat.*Block	0.0500	5.308955	2.080217	32	115.7784	0.1815

Fig. 107. Mean values for germination of seeds, number of seedlings established, number of leaves, and length of seedlings 2.4 years after planting.

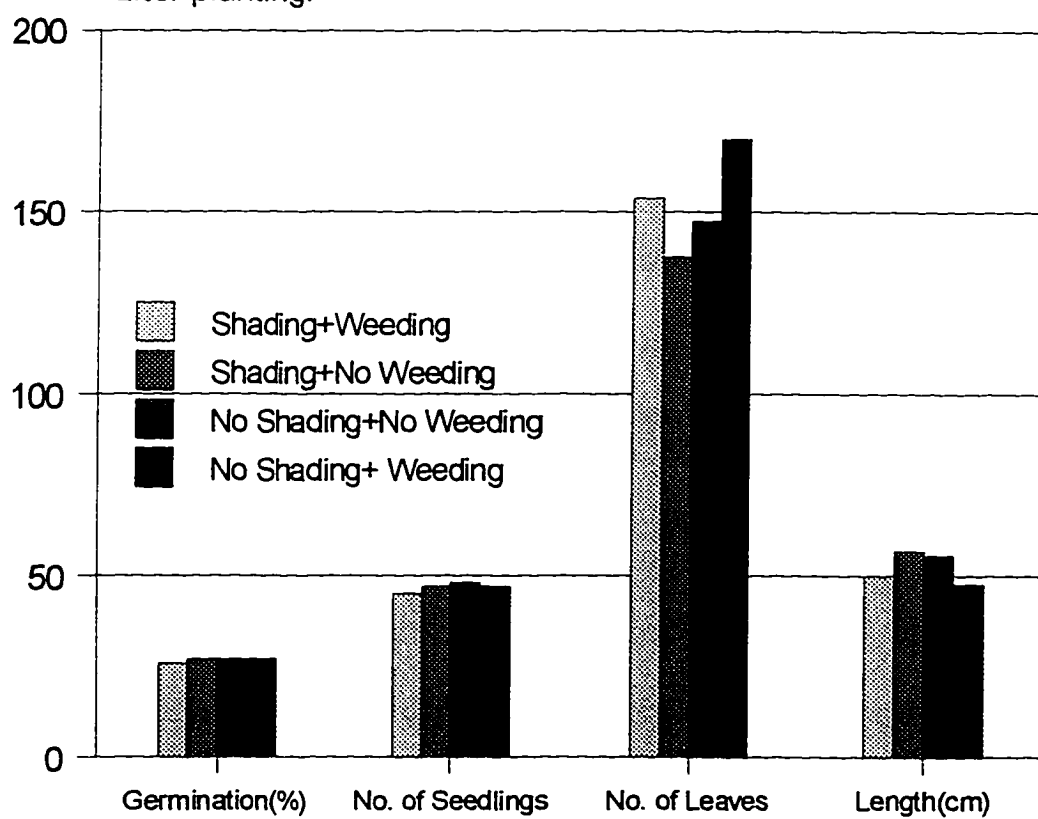


Fig. 108. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.

Length (cm) by Treatment - 2.4 Years

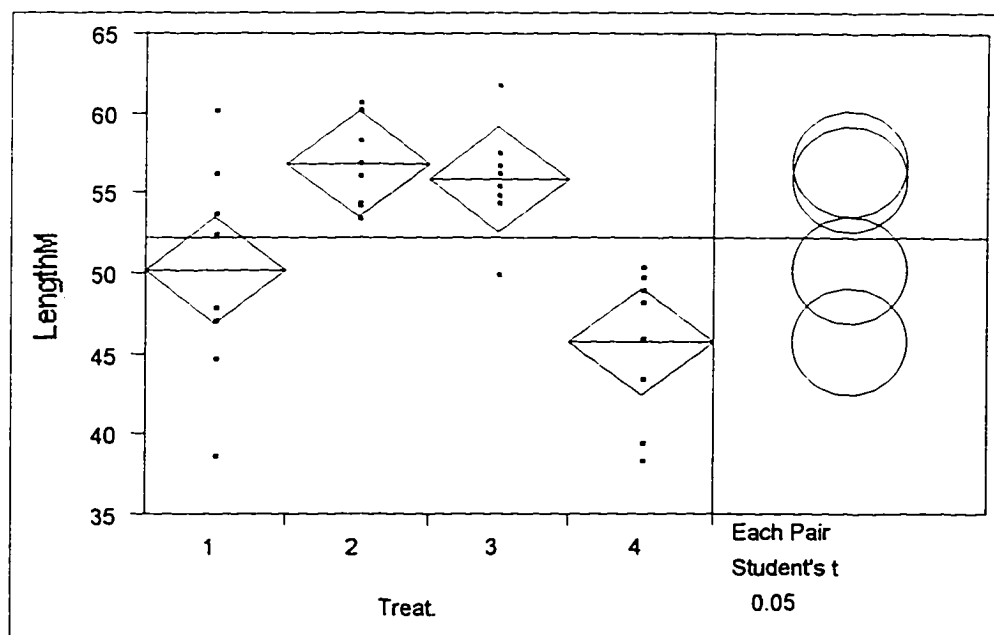


Fig. 109. View of weeded plot with no shading in between two non-weeded plots, 2.4 years after planting - August, 1992.



Fig.110. View of seedlings in shaded and non-shaded plots
(both weeded), 2.4 years after planting - August, 1992.



Third Census (January, 1992): 2.9 Years after Planting

The results obtained in this third general collection of data are shown in Table and Figure 111. Data was taken in January, 1992, 5 months after the previous census. The data recorded in this collection have a particular importance as they may reflect the behavior of seedlings immediately after a dry period (July - December). The dry season clearly affected the experiment, which showed death of many seedlings, an overall decrease of the number of leaves and the maintenance of the length of plants at almost the same levels as recorded five months before. Germination of seeds was no longer recorded and the number of dead plants was very variable throughout all treatments in all blocks. I believe that from this point on, the plants demonstrated their ability for establishment in degraded soils, competing more aggressively, in different conditions, for the nutrients and light they need for growth and biomass production.

The overall mean number of seedlings decreased from 46.938 to 37.531 (Table 142). This indicates that excess number of seedlings have gradually been eliminated; the more resilient seedlings survived, and the dry season seemed to have selected for the strongest ones. The highest number of seedlings was eliminated in treatment 4 (no shading + weeding), with a mean decrease of 11.250 seedlings. This suggests that the primary competition was not for nutrients, but for water. Treatment 2 (shading + no weeding) had the second

highest decrease in number of seedlings (10.0), showing that after the competition for moisture, nutrients play the next crucial role in the elimination of the excess of seedlings. The mean number of seedlings (37.531) came very close to the expected mean number per plot (33). From some point in the past period, the babassu seedlings in the plots began to compete only with other plant species rather than primarily their own .

The total mean number of leaves produced in the period (128.218) decreased in comparison to the last census (152.344) as the result of the decrease in the number of seedlings (Table 144). However, the mean number of leaves per seedling increased from 3.24 to 3.41, showing that the seedlings produced few new leaves. Analysis of variance showed no significant effect of treatments on both number of seedlings and leaves produced ($p=0.8301$ and 0.9536 , respectively). The analysis detected a significant effect of blocks on number of seedlings ($p=0.0225$), but not on number of leaves ($p=0.1011$); no interaction of effects was detected ($p=0.8148$ and 0.3547 , respectively for number of seedlings and leaves). Although the differences were not statistically significant, the highest number of seedlings and leaves continued to be recorded in the treatments where shading was directly or indirectly provided (Tables 142 and 144). The treatment under direct sunlight had the lowest number of seedlings and leaves after the dry period. The results of the analyses of variance for number of seedlings and leaves are shown in Tables 143 and 145.

Table 143. Descriptive statistics for number of seedlings established per treatment and block 2.9 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	37.125	9.862	19-52	Block I	39.000	4.567	32-45
Treat.2	37.250	9.223	26-53	Block II	45.500	5.682	38-53
Treat.3	39.875	11.012	21-54	Block III	30.375	5.630	21-39
Treat.4	35.875	8.219	25-48	Block IV	35.250	12.510	19-54
Totals	37.531	9.579	19-54	Totals	37.531	7.097	19-54

Table 144. Analysis of variance for number of seedlings 2.9 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	67.844	22.615	0.293	0.8301	0.0254
Blocks	3	976.594	325.531	4.212	0.0225	0.3663
Treat./Blocks	9	385.031	42.781	0.554	0.8148	0.1444
Error	16	1236.500	77.281			0.4638
Total	31	2665.969				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	8.790975	1.456062	32	288.4478	0.0943
Blocks	0.0500	8.790975	5.52436	32	27.14013	0.7557
Treat.*Blocks	0.0500	8.790975	3.46875	32	114.2575	0.1838

Table 145. Descriptive statistics for number of leaves produced per treatment and block 2.9 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	127.250	33.669	78-173	Block I	143.250	25.532	107-184
Treat.2	129.250	59.329	70-248	Block II	150.000	47.171	93-248
Treat.3	133.875	47.103	56-211	Block III	102.000	31.245	56-150
Treat.4	122.500	33.316	77-184	Block IV	117.219	49.908	70-211
Totals	128.219	43.354	56-248	Totals	128.219	38.464	56-248

Table 146. Analysis of variance for number of leaves produced 2.9 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	533.594	177.865	0.109	0.9536	0.0094
Blocks	3	12000.094	4000.031	2.450	0.1011	0.2127
Treat./Blocks	9	17754.281	1972.698	1.208	0.3547	0.3147
Error	16	26121.500	1632.594			0.4630
Total	31	56409.469				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	40.40537	4.083479	32	768.5967	0.0657
Blocks	0.0500	40.40537	19.36499	32	39.43582	0.5013
Treat.*Blocks	0.0500	40.40537	23.55464	32	56.21599	0.3928

After this 6-month dry period, seedlings showed a few slight changes in terms of growth (Table 146; Figure 111). The increase in the overall mean length of seedlings was only 1.393 cm which corresponds to a monthly growth rate of 0.28 cm per seedling, much lower than for the previous period. Treatments continued to produce an overall significant effect on growth ($p=0.0130$), as shown by the results of the analysis of variance (Table 147). No significant effect of blocks ($p=0.7727$) and interaction (0.7249) was detected. Again, the best growth rates were recorded in treatments 2 (Shading, No Weeding; mean=57.75 cm) and 3 (No Shading, No Weeding; mean=57.125 cm). However, it is important to point out that the better performance of those two treatments is still a result of the better growth performance before the past dry season. This can be seen by observing the mean increases for each treatment; the highest increase was that obtained for treatment 1 (Shading, Weeding; mean increase= 2.975 cm). The other treatments had their means very close to those recorded previously. It means that in times of water scarcity, shading (by retaining moisture) and weeding (by reducing competition for water) combined, produce a very beneficial effect on the growth of babassu seedlings. Figure 112 provides a visualization of treatments using Student's *t* tests.

Contrast between the two highest means (treatments 2 and 3) showed no difference between them ($p=0.8534$). Neither there was significant difference between treatments 1 and 2, and 1 and 3. However, there was a significant difference between the lowest mean (treatment 4) and the other three ($p=0.0026$), showing that most of the variance and overall significance for treatment effect was produced in a negative way by the absence of shading and weeding combined. In dry times shading made a difference: first, in the non-weeded plots (2 and 3) where the presence of other vegetation provided the shading for keeping moisture in the plot; second, in the plot where shading was directly provided as a treatment (1), and where the highest increase was recorded for this dry period. Up to this point of development, the babassu seedlings have been able to overcome the presence of competition by taking advantage of the higher levels of moisture in these plots. Weeding had a beneficial effect on growth only when shading was provided. Figure 111 shows mean number of seedlings, number of leaves, and length of seedlings for each treatment at 2.9 years after the experiment was initiated.

Table 147. Descriptive statistics for length of seedlings (cm) per treatment and block 2.9 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	53.250	8.647	40-66	Block I	52.125	4.642	44-59
Treat.2	57.750	4.166	52-64	Block II	55.250	10.194	40-64
Treat.3	57.125	4.189	52-64	Block III	54.375	8.158	38-66
Treat.4	46.375	6.069	38-55	Block IV	52.750	6.408	41-60
Totals	53.625	5.767	38-64	Totals	53.625	7.350	38-66

Table 148. Analysis of variance for length of seedlings (cm) 2.9 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	655.750	218.583	4.933	0.013	0.3899
Blocks	3	49.750	16.583	0.374	0.7727	0.0295
Treat./Blocks	9	267.000	29.667	0.669	0.7249	0.1587
Error	16	709.000	44.312			0.4216
Total	31	1681.500				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	6.656763	4.52683	32	25.02684	0.8248
Blocks	0.0500	6.656763	1.246871	32	226.3828	0.1078
Treat.*Block	0.0500	6.656763	2.888555	32	95.58545	0.2187

Fig. 111. Mean values for number of seedlings established, number of leaves, and length of seedlings 2.9 years after planting.

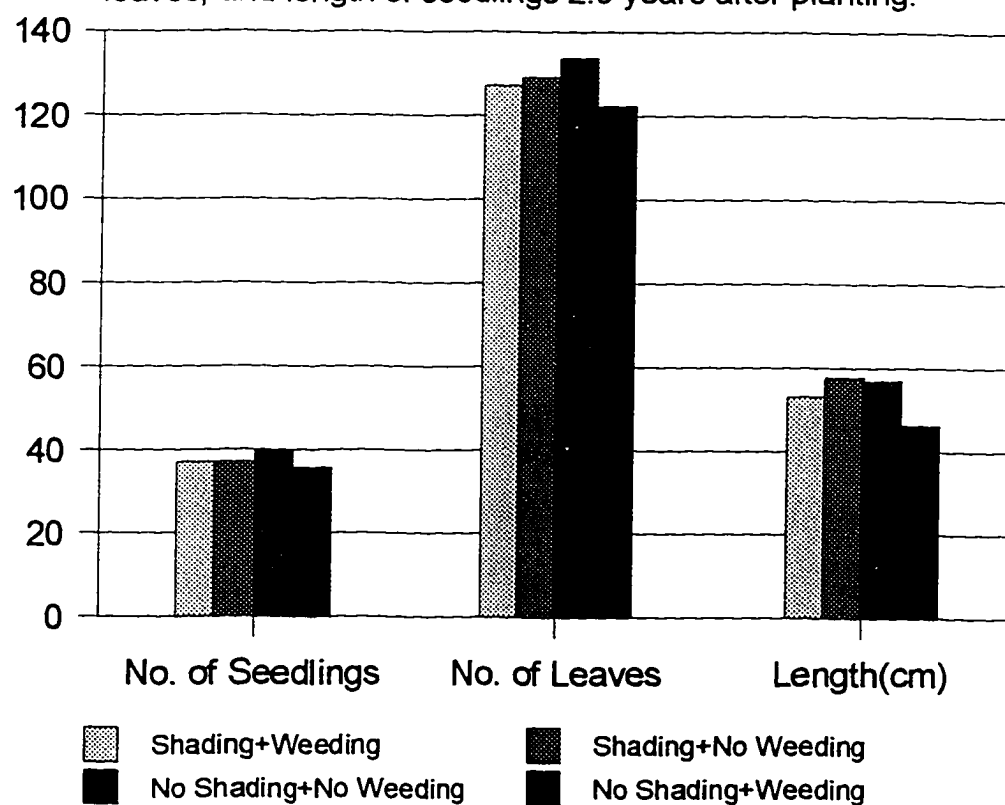
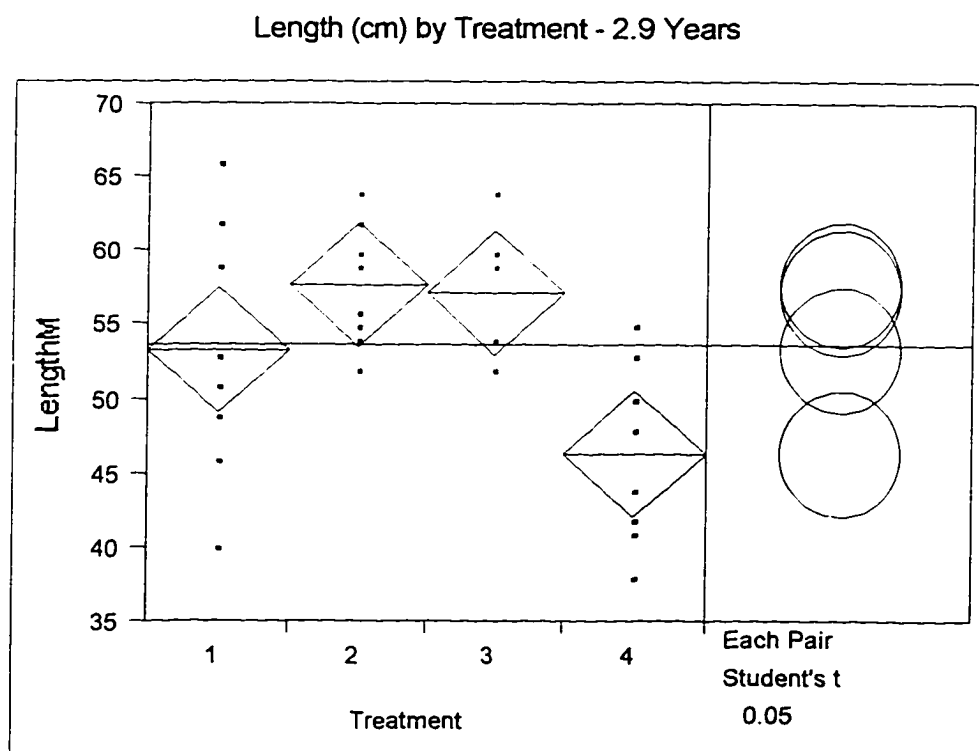


Fig. 112. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.



Fourth Census (July, 1992): 3.3 Years after Planting

The fourth general collection of data was carried out in July 1992, 3.3 years after the experiment was installed and 6 months following the previous collection. These data were collected at the end of the rainy season and were expected to reflect the effects of the availability of moisture in the period, in contrast with the previous period.

A small decrease in the number of established seedlings made the actual mean number (35.219) approach the expected number per plot (33) (Table 148). All treatments got very close to the ratio of 1 seedling per seed planted, as expected. The plots with shading were those where the highest numbers of excess seedlings (above 33) were recorded in the previous census, and therefore, these were the treatments with the highest number of seedlings that died in this period (Table 148; treatments 1 and 2). When moisture was not the limiting factor, the overall vigor and ability to absorb and use the scarce nutrients in the soil may then become the most important factor of effect on seedling survival. Effect of treatments was not statistically significant ($p=0.6853$), and blocks once again maintained a significant p -value (0.008), showing that the continued difference among the blocks persisted up to this point (Table 149). It cannot be taken as an effect, since no additional differences in the number of

seedlings per plot were produced. Interaction between blocks and treatments did not significantly exist ($p=0.5837$).

Table 149. Descriptive statistics for number of seedlings established per treatment and block 3.3 years after planting.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	32.250	8.940	19-49	Block I	44.500	8.960	30-55
Treat.2	35.500	10.583	23-53	Block II	36.000	4.869	29-44
Treat.3	36.750	10.740	19-54	Block III	29.000	5.014	19-34
Treat.4	36.375	8.830	28-55	Block IV	31.375	10.500	19-49
Totals	35.219	9.773	19-55	Totals	35.219	7.335	19-55

Table 150. Analysis of variance for number of seedlings 3.3 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	100.594	33.531	0.504	0.6853	0.0359
Blocks	3	1121.594	373.865	5.614	0.008	0.4009
Treat./Blocks	9	509.781	56.642	0.851	0.5837	0.1822
Error	16	1065.500	66.594			0.3808
Total	31	2797.469				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	8.160499	1.773007	32	169.2795	0.1300
Blocks	0.0500	8.160499	5.920288	32	23.66035	0.8744
Treat.*Blocks	0.0500	8.160499	3.991324	32	76.6843	0.2758

Biomass (leaves) produced during this period showed a considerable overall increase (Table 150; Figure 113) in contrast with the previous period when leaf biomass decreased due to seedling mortality. The mean number of leaves increased by 23.469, representing a mean increase of 3.911 per month per plot. The number of leaves per seedling increased from 3.41 recorded six months before to 4.30 in this post-rainy season period. Analysis of variance showed no difference among treatments and blocks or a combined effect of both (p -values=0.8563, 0.1748, and 0.655, respectively) (Table 151). Leafing seems to be follow a very stable phenological pattern with very little or no variation at all throughout the year, or even between seasons. Although the differences among treatments were not statistically significant, it was noted that the highest increases in number of leaves produced during the last six months happened in shaded plots (treatments 1 and 2), whether weeded or not (Figure 113). My interpretation of this was that the photosynthetic leaf area of the seedlings (including number of leaves) must increase in shaded conditions, in order to better absorb the less incident sunlight on the seedling leaves, due to the surrounding taller vegetation.

Table 151. Descriptive statistics for number of leaves produced per treatment and block 3.3 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	158.875	48.096	84-246	Block I	171.125	31.988	137-232
Treat.2	155.875	62.279	64-246	Block II	170.125	37.429	129-246
Treat.3	152.500	40.977	71-204	Block III	123.625	43.762	64-184
Treat.4	139.500	37.298	86-202	Block IV	141.875	57.811	84-246
Totals	151.688	47.162	64-246	Totals	151.688	42.747	64-246

Table 152. Analysis of variance for number of leaves produced 3.3 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	1747.125	582.375	0.255	0.8563	0.0262
Blocks	3	12812.375	4270.792	1.873	0.1748	0.1924
Treat./Blocks	9	15548.375	1727.597	0.758	0.655	0.2335
Error	16	36475.000	2279.688			0.5478
Total	31	66582.875				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	47.74607	7.389023	32	329.8646	0.0883
Blocks	0.0500	47.74607	20.00967	32	49.33908	0.3938
Treat.*Blocks	0.0500	47.74607	22.04284	32	85.22198	0.2462

The mean increase in length (6.816 cm) for this six-month period was significantly higher than for the previous one (1.393 cm). A higher increase in monthly growth rate was consequently recorded (1.136 cm). This is a reflection of the availability of water to the seedlings during this period. The growth rate per seedling for the period was 0.193 cm in contrast with that recorded for the dry period of 0.037 cm. The monthly growth rate per seedling, per month was 0.033 cm. Table 152 provides the descriptive statistics for length of seedlings for this period.

Table 153 shows the results of the analysis of variance of the data pertaining to this period. Treatments had significantly different means ($p=0.0239$); blocks had no effect on the model ($p=0.9232$), and no interaction of effects was detected ($p=0.4484$). The best growth performances were maintained by those treatments where shading was provided, either directly (as for treatments 1 and 2), or indirectly (as for treatment 3), where non-weeding was producing a confounding effect with shading. In those non-weeded plots the successional vegetation had grown to a height that produces shading over the shorter babassu seedlings, and therefore, this is confounded now with the effect of shading directly applied as a treatment in all non-weeded plots. From this point on, the differences in these plots reflected primarily competition for soil resources, rather than the absence of shading in the non-weeded plots. There

was no significant difference among these three treatments. Statistical difference only existed when treatment 4 was compared to each of the other three, both individually or as a group. This shows that direct sunlight has a negative (or delaying) effect on growth of babassu seedlings up to this stage. The highest mean increase was recorded in treatment 1, showing a very beneficial effect of shading in combination with weeding. This result is the satisfactory development of seedlings with significant biomass (leaf) production. This experimental observation is consistent with the observation of this species' behavior in nature. Table 153 shows the power details for this analysis. Figure 114 provides a visual comparison of treatments. Figure 113 provides a graphical representation of the means for number of seedlings, number of leaves, and length of seedlings for treatments at 3.3. years.

Table 153. Descriptive statistics for length of seedlings (cm) per treatment and block, 3.3 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	63.262	14.035	46.1-84.9	Block I	58.550	6.403	47.2-66.8
Treat.2	63.162	2.424	59-66.8	Block II	61.463	12.732	46.4-86.1
Treat.3	64.912	9.391	55.7-86.1	Block III	61.175	11.230	41.5-76.8
Treat.4	50.425	5.703	41.5-58.1	Block IV	60.575	11.979	46.1-84.9
Totals	60.441	7.888	41.5-86.1	Totals	60.441	10.586	41.5-86.1

Table 154. Analysis of variance for length of seedlings (cm), 3.3 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	1085.456	361.819	4.134	0.0239	0.3239
Blocks	3	41.408	13.803	0.158	0.9232	0.0123
Treat./Blocks	9	823.488	91.499	1.045	0.4484	0.2457
Error	16	1400.365	87.523			0.4179
Total	31	3350.717				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	9.355363	5.824131	32	27.42817	0.7470
Blocks	0.0500	9.355363	1.137547	32	532.0664	0.0730
Treat.*Block	0.0500	9.355363	5.072868	32	63.75538	0.3394

Fig.113. Mean values for number of seedlings established, number of leaves, and length of seedlings 3.3 years after planting.

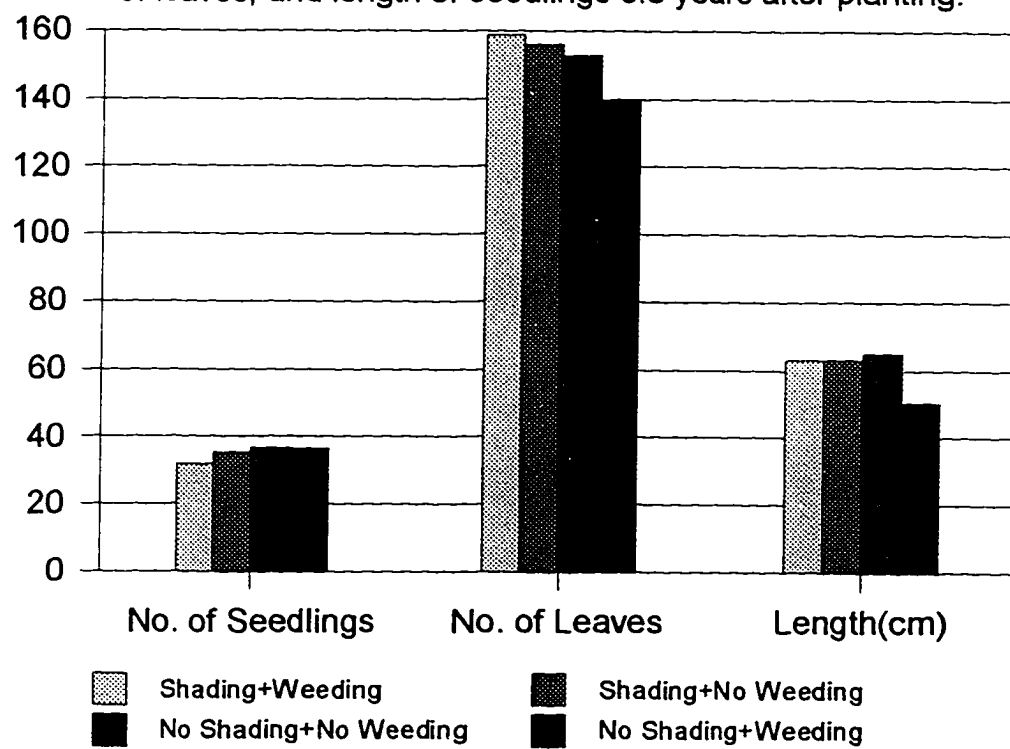
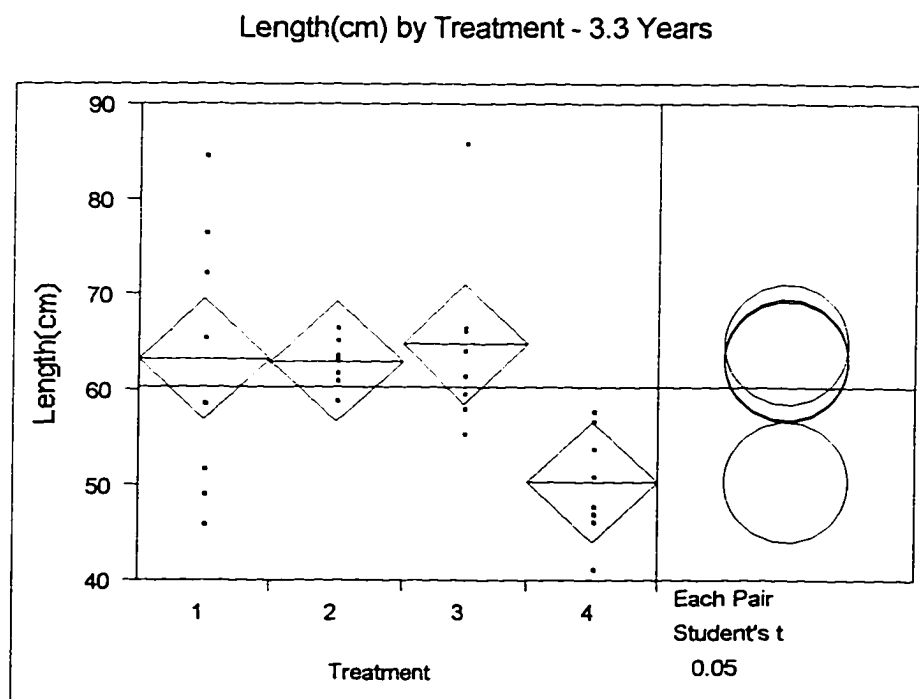


Fig. 114. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.



Fifth Census (December, 1993): 4.8 Years after Planting

These data were collected 1.5 years after the previous census, and following a dry season which ended in December; again, the data appear to reflect that situation. During the 18 month period since the previous census, the mean number of established seedlings remained stable, with no seedling death recorded (Table 154). This is an important observation, as it shows that the established seedlings were able to come through two dry seasons and one rainy season without dying. More important, yet, is that treatments did not produce significant differences on the number of seedlings, confirming the expected resilience of this palm species.

Analysis of variance did not show a significant p-value (0.3172) for treatments on the number of seedlings; blocks again were statistically significant (p-value=0.0024); and, no interaction between effects was detected by the analysis (p=0.4096) (Table 155). Although the differences among treatments were not significant, it is noteworthy to mention that once more the highest means were recorded in those treatments where no weeding was applied, followed by treatment 1, where weeding was applied but so was shading (Table 154; Figure 115). This repeats what was seen in the previous analyses: the major effect seems to be produced by shading (Figure 116), which at this point of the experiment comes both from the shading applied to plots directly and from those non-weeded treatments, indirectly.

Table 155. Descriptive statistics for number of seedlings established per treatment and block 4.8 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	34.375	4.926	26-43	Block I	43.500	5.345	36-54
Treat.2	37.625	14.070	21-57	Block II	40.875	7.827	32-57
Treat.3	39.750	5.946	29-48	Block III	29.750	6.734	20-38
Treat.4	33.750	9.361	19-42	Block IV	31.375	8.798	19-45
Totals	36.375	8.575	19-57	Totals	36.375	7.176	19-57

Table 156. Analysis of variance for number of seedlings 4.8 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	190.750	63.583	1.273	0.3172	0.0730
Blocks	3	1119.250	373.083	7.471	0.0024	0.4292
Treat./Blocks	9	498.500	55.389	1.109	0.4096	0.1911
Error	16	799.000	49.938			0.3064
Total	31	2607.500				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	7.06647	2.441503	32	69.78048	0.2759
Blocks	0.0500	7.06647	5.914099	32	21.52576	0.9528
Treat.*Blocks	0.0500	7.06647	3.946913	32	60.53341	0.3603

Analysis of variance showed exactly the same situation for number of leaves produced (Table 157). No significance for treatment effect ($p=0.3261$), a significant effect of blocks ($p=0.0068$), and no interaction between effects (0.9824). However, although the number of seedlings remained the same throughout 18 months, number of leaves decreased (Table 156) in comparison with the last census, from 4.30 leaves per seedling to 3.85. This represents a mean decrease of 0.45 leaves per seedling. The overall mean number of leaves produced in the plots decreased from 151.688 in the last census to 140.156 in this census; the highest losses of leaves occurred in the non-weeded treatments (2 and 3), with a much smaller number of leaves lost in the weeded treatments (1 and 4). This shows that during stressful times, as in the dry season, competition has a strong effect on the seedlings, which is in turn reflected on the number of leaves produced, significantly reduced. At this point, the beneficial effect of shading and maintenance of a higher moisture level by the surrounding vegetation no longer existed. Seedlings began to react to the effect of the competition, shown by the decrease in the number of leaves. This number would be expected to increase in order to be able to absorb more efficiently the scarce sunlight in the understory of the successional stands. Climatic factors (especially rainfall and light) may have had a strong effect on these results.

Table 157. Descriptive statistics for number of leaves produced per treatment 4.8 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	156.000	28.086	125-198	Block I	172.500	20.227	138-198
Treat.2	128.375	29.760	78-174	Block II	147.625	25.286	110-178
Treat.3	136.250	32.631	86-181	Block III	118.500	30.561	57-150
Treat.4	140.000	41.015	57-187	Block IV	122.000	27.018	78-152
Totals	140.156	32.873	57-198	Totals	140.156	25.773	57-198

Table 158. Analysis of variance for number of leaves produced 4.8 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	3240.844	1080.281	1.246	0.3261	0.0947
Blocks	3	15204.344	5068.115	5.844	0.0068	0.4446
Treat./Blocks	9	1870.531	207.837	0.240	0.9824	0.0547
Error	16	13876.500	867.281			0.4058
Total	31	34192.219				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	29.44964	10.06362	32	71.21157	0.2704
Blocks	0.0500	29.44964	21.79761	32	23.29432	0.8881
Treat.*Blocks	0.0500	29.44964	7.645528	32	256.2504	0.0999

Growth increased during this period; but no significant effect of treatments ($p=0.0602$) existed, indicating that treatments did not affect growth performance of the seedlings. Neither did blocks ($p=0.8449$), and no interaction existed between the effects tested ($p=0.8177$). There were no differences among the means for growth (Table 159). It seems that at this point, the seedlings reached a stable growth rate that was not affected by the treatments, or even by the shortage of rainfall in the dry season. Reduction of the number of leaves produced during the dry period may have been a biological strategy used by the seedlings. A higher investment was made in growth rather than in leafing, since the competing vegetation was taller, which could result in difficulties of development for the seedlings. Table 158 shows the means for treatments. Figure 117 compares graphically the means for pairs of treatments. It can be noticed that treatment 1 was higher than the others, but that difference was not significant enough to be detected by the analysis. Although the power value was not high (0.5977), the least significant number (33.58538) was not far from the actual number used in the experiment (32). This means that the not significant result for treatment effect could have changed with a somewhat higher sample size. Probably there would be a significant difference between treatment 1 and the other three. Still, the results showed the resilience of the babassu seedlings under the different treatments applied, although it appears that they can benefit from shading and weeding. Figure 115 shows graphically the results in each treatment for number of seedlings, number of leaves, and length of seedlings after 4.8 years.

Table 159. Descriptive statistics for length of seedlings (cm) per treatment and block 4.8 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	98.819	21.791	65.01-125.1	Block I	73.094	14.096	60-15-97.8
Treat.2	72.071	10.519	59.12-87.6	Block II	77.253	15.449	65.28-110.44
Treat.3	69.704	10.253	59.8-89.5	Block III	82.749	27.632	43.4-125.1
Treat.4	72.518	29.389	42.3-135.8	Block IV	80.016	30.715	42.3-135.8
Totals	78.278	17.988	42.3-135.8	Totals	78.278	21.973	42.3-135.8

Table 160. Analysis of variance for length of seedlings (cm) 4.8 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	4537.178	1512.393	3.025	0.0602	0.2942
Blocks	3	407.498	135.833	0.272	0.8449	0.0264
Treat./Blocks	9	2473.383	274.820	0.550	0.8177	0.1604
Error	16	8000.054	500.003			0.5188
Total	31	15418.113				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	22.36075	11.90743	32	33.58538	0.5977
Blocks	0.0500	22.36075	3.568516	32	310.4161	0.0909
Treat.*Block	0.0500	22.36075	8.791656	32	115.0321	0.1826

Fig. 115. Mean values for number of seedlings established, number of leaves, and length of seedlings 4.8 years after planting.

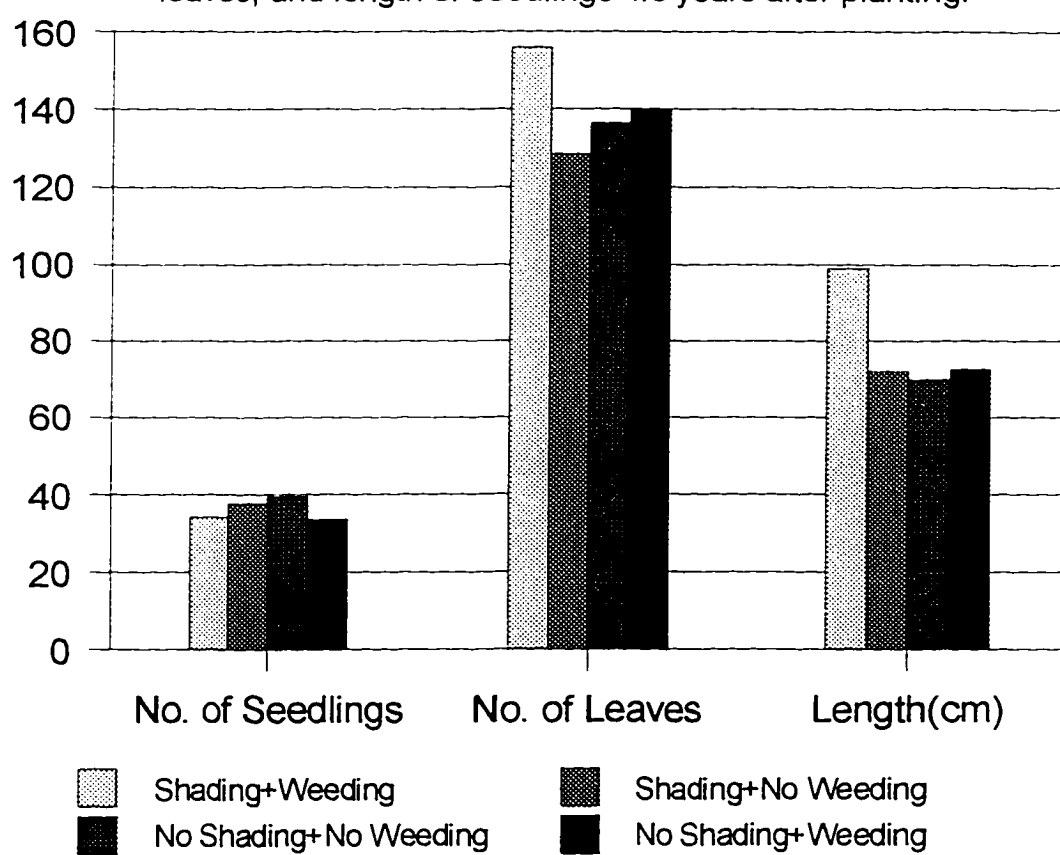
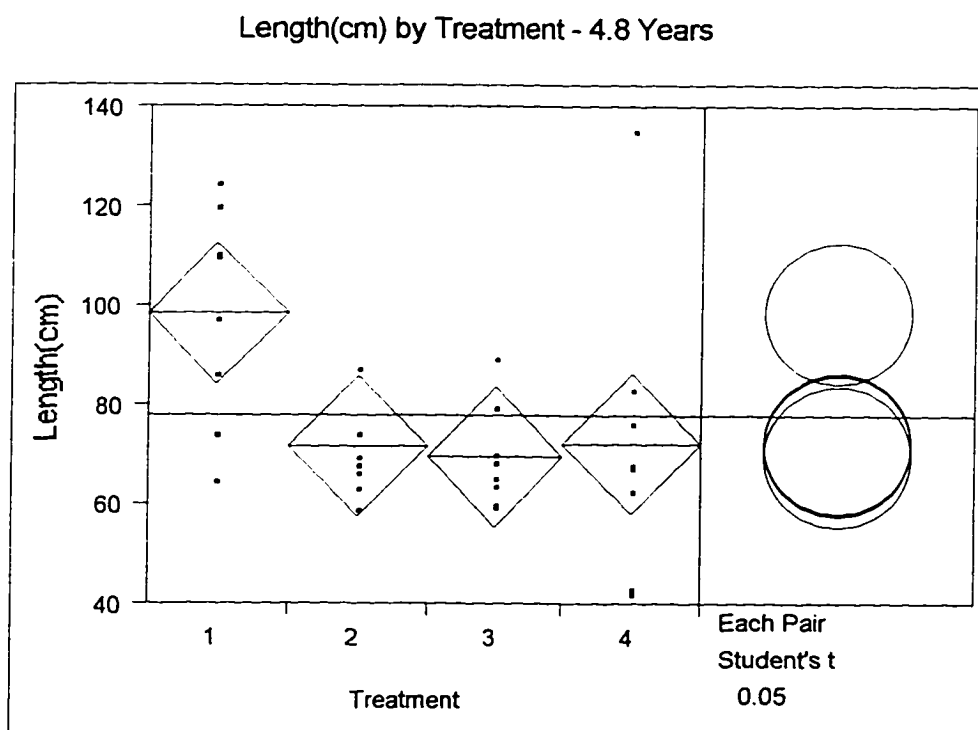


Fig. 116. Seedlings in shaded plot 4.8 years after planting - December, 1993.



Fig. 117. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.



Sixth Census (August, 1994): 5.4 Years after Planting

After a period of 5.4 years since its installation in 1989, the experiment was concluded. Up to this point, only non-destructive measurements had been made for collection of information on germination, number of seedlings, number of leaves produced, and growth rate. For this final census, however, destructive measurements were made in order to obtain information on additional characters such as fresh and dry weight of leaves and roots. Seedlings were counted and dug out of the soil (Figure 118), the leaves counted, plant parts cut and weighed in the field to obtain fresh weight data. The plant material was then placed in separate paper bags and dried for 48 hours (leaves) to 72 hours (rhizome-roots) at temperature of ca. 70°C. After drying, the material was re-weighed.

Number of Seedlings

This last collection of data yielded a surprise regarding the number of seedlings in the experimental plots. In the last census it was found that the number of established seedlings had achieved a stability, and no variation on that number was recorded. It seemed at that time, that selection brought the number of seedlings to ratio of 1 seedling per seed, expected since the babassu palm is not a clustering species. Given the environmental difficulties of the area plus the treatments applied, one

could expect that competition between seedlings sharing the same spot would cause the death of the less-fit seedlings. This was especially noticeable following the dry season, when the number of seedlings was reduced to the point where stability was thought to have been achieved. However, this last data collection proved that notion to be wrong: some of the “dead” seedlings in fact did not die. What seems to have happened is that a number of seedlings that disappeared and consequently, were not counted during two census, only lost their aerial part, but kept the apical meristem alive, underground. Those seedlings were again able to retake growth at some point and produce new leaves (Figure 119). This may explain in part the aggressiveness of this palm species as a colonizer, succeeding where other plant species fail. The difference in the number of seedlings was not big, however; only 9 seedlings “reappeared”. Another explanation for this increase in the number of seedlings may be a miscounting of during the censuses, but this would require the mistake to be made more than once, which is unlikely.

This new situation increased the overall mean for number of seedlings (44.594; Figure 120) in contrast to the mean obtained 8 months before (36.375) (Table 160; Figure). The highest number of seedlings “reappeared” in those treatments where shading was provided, directly (1) or indirectly (2 and 3). In contrast, in treatment 4, with no shading and weeding, the number of seedlings was reduced slightly in comparison with the previous number recorded. This seems to support the “reappearance” hypothesis of viable underground apical meristems in seedlings

without leaves. Analysis of variance, however, did not detect difference among the means for treatment effect ($p=0.2674$), although blocks had a significant effect ($p=0.0049$); no interaction between the effects tested was detected by the analysis ($p=0.2582$) (Table 161).

Fig. 118. Seedling dug out of soil for the final collection of data - August, 1994.



Fig. 119. One of the the seedlings that "reappeared" after counted as dead in the previous census - August, 1994.

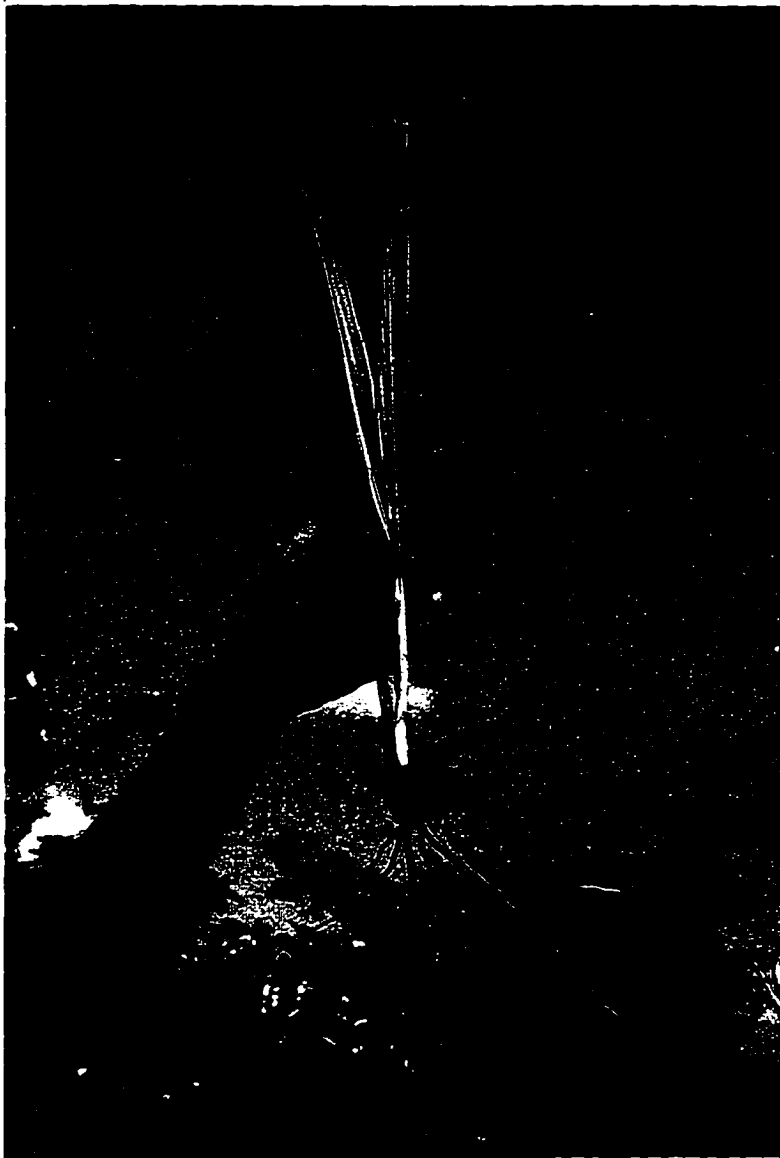


Fig. 120. Mean values for number of seedlings established, number of leaves, and length of seedlings 5.4 years after planting.

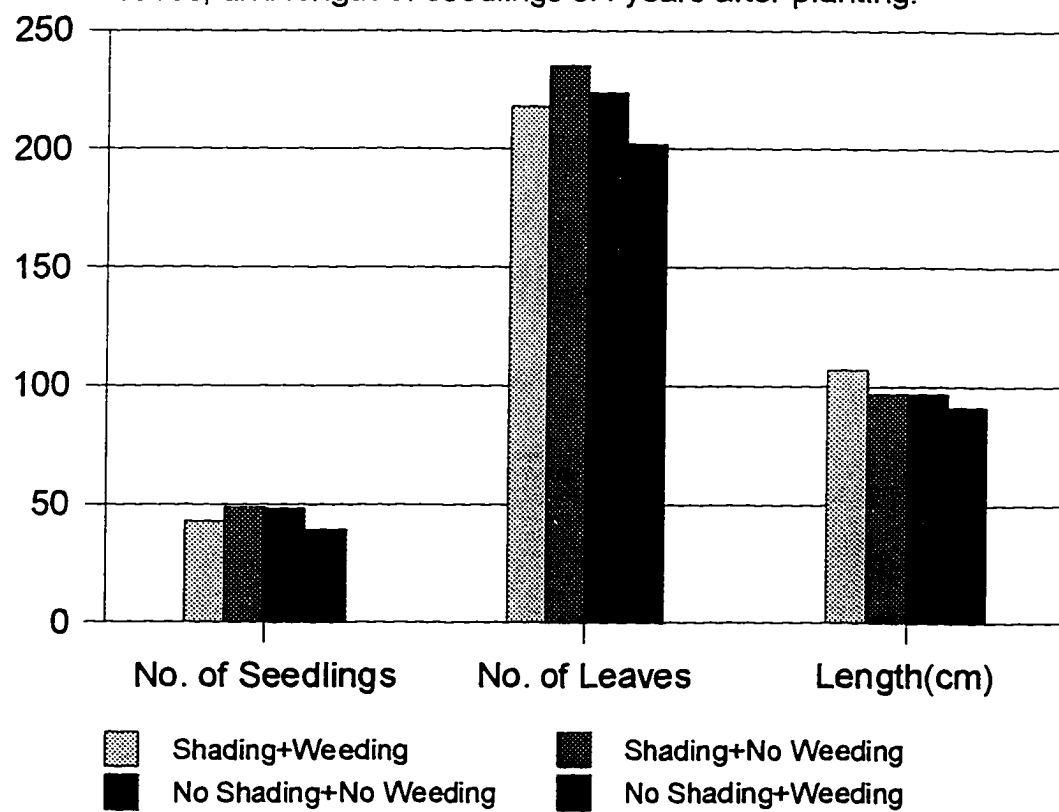


Table 161. Descriptive statistics for number of seedlings established per treatment 5.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	42.625	9.349	29-57	Block I	52.625	11.083	42-75
Treat.2	48.750	19.241	24-75	Block II	52.750	9.676	43-68
Treat.3	47.750	12.691	24-64	Block III	36.625	9.241	24-52
Treat.4	39.250	11.597	18-52	Block IV	36.750	14.831	18-59
Totals	44.594	13.219	18-75	Totals	44.594	11.207	18-75

Table 162. Analysis of variance for number of seedlings 5.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	477.344	159.115	1.443	0.2674	0.0830
Blocks	3	2096.594	698.865	6.337	0.0049	0.3646
Treat./Blocks	9	1411.281	156.809	1.422	0.2582	0.2454
Error	16	1764.500	110.281			0.3068
Total	31	5749.719				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	10.50149	3.862252	32	62.23046	0.3094
Blocks	0.0500	10.50149	8.094353	32	22.62663	0.9132
Treat.*Blocks	0.0500	10.50149	6.640974	32	49.03039	0.4618

Number of Leaves

This increased considerably in the last eight months: from an overall mean of 140.156 to 219.812 (a mean increase of 79.656 for the period) (Table 162). The mean number of leaves per seedling also increased from 3.85 to 4.92, which represents a mean increase of 1.07 leaves/seedling. The major increases in leaf production were obtained in the non-weeded treatments (2 and 3; Figure 120), showing how the presence of the surrounding vegetation may force the number of leaves to increase during the rainy season, as opposed to dry periods. The lowest increases were computed for the weeded treatments (1 and 4), particularly for treatment 4, where shading was not applied. However, again analysis of variance showed no difference among the treatment means ($p=0.7379$), and once again a significant effect of blocks on leaf production was recorded ($p=0.0068$); interaction between effects was not significant ($p=0.4611$) (Table 163).

Table 163. Descriptive statistics for number of leaves produced per treatment and block 5.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	218.250	45.455	136-292	Block I	256.875	51.954	193-354
Treat.2	234.875	98.313	85-354	Block II	270.000	48.544	228-339
Treat.3	224.000	70.648	109-336	Block III	177.375	52.314	94-249
Treat.4	202.125	68.865	94-286	Block IV	175.000	74.233	85-292
Totals	219.812	70.820	85-354	Totals	219.812	56.761	85-354

Table 164. Analysis of variance for number of leaves produced 5.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	4477.625	1492.542	0.425	0.7379	0.0289
Blocks	3	61612.125	20537.375	5.845	0.0068	0.3981
Treat./Blocks	9	32430.125	3603.347	1.026	0.4611	0.2095
Error	16	56215.000	3513.438			0.3632
Total	31	154734.875				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	59.27426	11.82902	32	199.8995	0.1164
Blocks	0.0500	59.27426	43.87914	32	23.29176	0.8882
Treat.*Blocks	0.0500	59.27426	31.83459	32	64.84211	0.3329

Growth of Seedlings

The mean increase for this eight-month period since the last census was 19.722 cm, which represents a mean growth rate of 0.442 cm per seedling . The best performances were recorded in treatments 2 and 3 (non-weeded) (Table 164), and surprisingly, the lowest mean increase in growth were computed for treatments 1 (although still the highest mean computed for this census) and 4, the two weeded treatments, a result completely different from the previous one. The means for treatments (Table 164; Figure 120), however, were not significantly different from each other ($p=0.2608$), as shown by the analysis of variance (Table 165), which also shows no significance for blocks, and, more surprisingly, a slightly significant interaction between treatments and blocks ($p=0.0044$). No significant effect of treatments existed, showing that in the last two years growth of seedlings was not significantly affected by the treatments applied. The values computed for treatments, although not statistically significant, may suggest a pattern, however. In the dry season, weeding seems to favor growth of babassu seedlings because of the lack of competition for the scarce moisture in the soil, but when water is not a limiting factor during the rainy season, the competition with other vegetation does not seem to be a problem for the seedlings. Figure 121 shows a non-weeded plot after 5.4 years the experiment began (Figure 119). Figure 122 shows seedlings in a shaded weeded plot.

Table 165. Descriptive statistics for length of seedlings (cm) per treatment and block 5.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	107.212	29.343	78.9-147.0	Block I	90.462	11.642	70.8-108.1
Treat.2	96.850	11.366	79-114.9	Block II	96.350	19.154	76.2-129.4
Treat.3	96.875	11.548	87.1-118.7	Block III	102.000	31.220	53-147.0
Treat.4	91.075	31.240	53-149.3	Block IV	103.200	25.690	78.9-149.3
Totals	98.003	20.874	53-149.3	Totals	98.003	21.926	53-149.3

Table 166. Analysis of variance for length of seedlings (cm) 5.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	1083.311	361.104	1.468	0.2608	0.0686
Blocks	3	820.611	273.537	1.112	0.3733	0.0520
Treat./Blocks	9	9940.813	1104.535	4.491	0.0044	0.6299
Error	16	3935.515	245.970			0.2493
Total	31	15780.250				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	15.68342	5.818373	32	61.25764	0.3144
Blocks	0.0500	15.68342	5.064000	32	79.13807	0.2442
Treat.*Block	0.0500	15.68342	17.62528	32	24.05313	0.9610

Fig. 121. View of a non-weeded plot 5.4 years after the experiment was installed
- August, 1994.



Fig. 122. Seedlings in a shaded-weeded plot - August, 1994.



Fresh and Dry Weight of Leaves

While treatments did not have a significant effect on the number of leaves produced, it did had a highly significant effect on the weight of leaves (p -values=0.0009 and 0.0001, respectively for fresh and dry weight); blocks had no significant effect in both cases (p -values=0.6601 and 0.1889), while interaction of effects could only be detected for the dry weight (p =0.0079). Tables 166 - 169 show the descriptive statistics and the results of the analysis of variance performed for both fresh and dry weight. Figure 120 graphically depicts the mean values for these characters. In both cases, the highest means were obtained in the weeded treatments 1 and 4, which shows that the overall better performance in growth was a result of the better absorption, use and accumulation of nutrients. Comparisons between these two treatments showed no statistical difference (p =0.0966) for fresh weight, but there was a slightly significant difference between them when dry weight was analyzed (p =0.0209). In both cases, the weeded treatments were significantly superior in terms of weight of biomass produced in relation to the other two treatments. These treatments compared to non-weeded treatments showed a highly significant difference (p -values= 0.0001 and <0.0001, respectively for fresh and dry weight), confirming that weeding has a positive effect on leaf biomass. For both fresh and dry weight of leaves, contrast between treatments 2 and 3 showed that the difference was not significant (p -value for fresh weight=0.9374; p -value for dry

weight=0.8219). On the other hand, comparison between treatments 2 and 4 showed a significant difference between them (p-values=0.020 and 0.004, respectively for fresh and dry weight of leaves). Visual comparisons of the means for fresh and dry weight of leaves by treatments are shown in Figures 123 and 124.

These results show that while the treatments did not produce differences in the of number of leaves, they did account for a significant difference among the means for their weight. The weeded treatments, where the seedlings did not have the competition of the successional vegetation, did much better in terms of the weight of the biomass produced probably from the better absorption and use of nutrients allowed by the absence of competition.

Table 167. Descriptive statistics for fresh weight of leaves (Kg) per treatment and block 5.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	7.445	4.694	2.3-15.6	Block I	4.691	3.668	1.91-12.5
Treat.2	2.084	0.825	0.42-3.05	Block II	3.519	1.995	2-8.1
Treat.3	1.985	0.793	0.96-3.2	Block III	4.796	5.160	0.75-15.6
Treat.4	5.259	2.757	0.75-9.2	Block IV	3.766	3.081	0.42-9.2
Totals	4.193	2.267	0.42-15.6	Totals	4.193	3.476	0.42-15.6

Table 168. Analysis of variance for fresh weight of leaves (Kg) 5.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	168.284	56.095	9.139	0.0009	0.4371
Blocks	3	9.991	3.330	0.543	0.6601	0.0259
Treat./Blocks	9	108.493	12.055	1.964	0.1145	0.2818
Error	16	98.209	6.138			0.2551
Total	31	384.977				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	2.477506	2.293225	32	20.53322	0.9818
Blocks	0.0500	2.477506	0.558769	32	157.3884	0.1369
Treat.*Block	0.0500	2.477506	1.841303	32	38.11695	0.6215

Fig. 123. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.

Fresh Weight of Leaves by Treatment - 5.4 Years

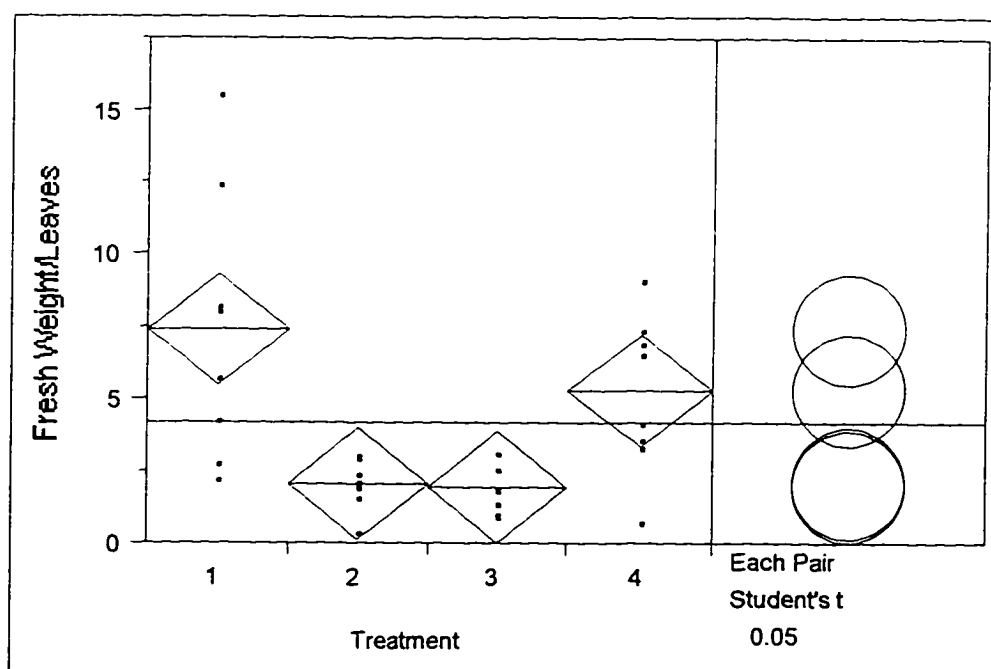


Table 169. Descriptive statistics for dry weight of leaves (Kg) per treatment and block 5.4 years after planting of seeds.

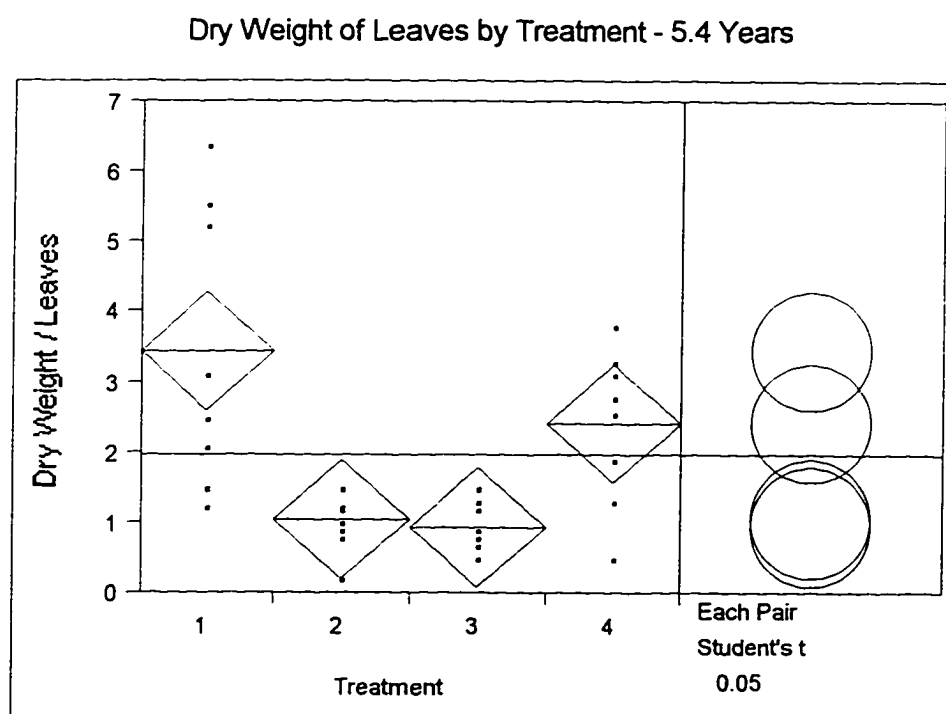
Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	3.456	1.994	1.25-6.4	Block I	2.212	1.537	0.8-5.25
Treat.2	1.044	0.427	0.2-1.5	Block II	1.556	0.678	1.0-3.1
Treat.3	0.950	0.346	0.5-1.5	Block III	2.369	2.355	0.5-6.4
Treat.4	2.406	1.102	0.5-3.8	Block IV	1.719	1.231	0.2-3.8
Totals	1.964	0.967	0.2-6.4	Totals	1.964	1.450	0.2-6.4

Table 170. Analysis of variance for dry weight of leaves 5.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	34.380	11.460	17.055	0.0001	0.4719
Blocks	3	3.616	1.205	1.794	0.1889	0.0496
Treat./Blocks	9	24.104	2.678	3.986	0.0079	0.3308
Error	16	10.751	0.672			0.1475
Total	31	72.851				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	0.819727	1.036515	32	18.83995	0.9999
Blocks	0.0500	0.819727	0.336148	32	51.24187	0.3784
Treat.*Block	0.0500	0.819727	0.867908	32	25.21688	0.9345

Fig. 124. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.



Fresh and Dry Weight of Rhizomes/Roots

To measure this, the rhizome and attached roots were separated from the aerial part of the seedlings. It was decided to weigh the rhizome together with roots, since this structure constitutes the main part of the underground bulk of the seedlings to which most of the roots are attached. Results for fresh and dry weight of rhizome/roots are shown in Tables 170 and 172. Treatments also accounted for significant differences in terms of fresh and dry weight of rhizomes/roots (Tables 171 and 173). These differences were reflected on a very significant p-value (0.0001) in the analysis of variance performed; blocks accounted for no significant differences ($p=0.2056$), and a significant interaction of effects was this time detected ($p=0.0171$). The situation here was very similar to that of leaves: the highest means were obtained in the weeded treatments (treatments 1 and 4), with that where shading was provided superior to that under direct sunlight. The superiority of treatment 1 (Shading + Weeding) over treatment 4 (No Shading + Weeding) is confirmed by comparing these two treatments separately. In both cases (fresh and dry weight), the differences between them was significant (although only barely significant in the case of fresh weight ($p=0.0522$; for dry weight= 0.02085)). Comparison between weeded and non-weeded treatments revealed a highly significant difference between them ($p\text{-values} < 0.0001$, for both fresh and dry weight). There was no difference between the two lowest means recorded in the

non-weeded treatments (p-values= 0.8992 and 0.8090, respectively for fresh and dry weight). In both cases, the beneficial effect of weeding on the weight of the biomass produced is clear. Figures 125 and 126 provide the comparison of the means for fresh and dry weight of rhizome/roots by treatment.

From a certain point of the experiment shading as an effect became experimentally confounded with that produced by the shade resulting from the developing vegetation in the plots. However, shading did not seem to have played any significant beneficial effect on rhizome and roots development. Weeding, on the other hand, was clearly beneficial for the underground biomass probably because of the elimination of competing vegetation, which provided more room for growth of rhizomes and roots. In the non-weeded plots, the use of the underground space by the babassu seedlings was certainly more restricted, since many other species competed for room for root development.

Table 171. Descriptive statistics for fresh weight of rhizomes+roots (Kg) per treatment and block 5.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	6.867	3.935	1.92-12	Block I	3.756	3.374	1.0-10.45
Treat.2	1.265	0.583	0.3-2.14	Block II	2.628	1.697	0.95-5.75
Treat.3	1.156	0.505	0.5-2.2	Block III	4.444	4.883	0.86-12.0
Treat.4	4.700	2.202	0.95-7.75	Block IV	3.161	2.705	0.3-7.75
Totals	3.497	1.806	0.3-7.75	Totals	3.497	3.164	0.3-7.75

Table 172. Analysis of variance for fresh weight of rhizomes/roots (Kg) 5.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	186.147	62.049	21.686	0.0001	0.5595
Blocks	3	14.658	4.886	1.708	0.2056	0.0440
Treat./Blocks	9	86.106	9.567	3.344	0.0171	0.2588
Error	16	45.780	2.861			0.1376
Total	31	332.691				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	1.691528	2.411867	32	18.4770	1.0000
Blocks	0.0500	1.691528	0.676813	32	53.5037	0.3616
Treat.*Block	0.0500	1.691528	1.640372	32	27.3552	0.8784

Fig. 125. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.

Fresh Weight of Rhizome/Roots by Treatment - 5.4 Years

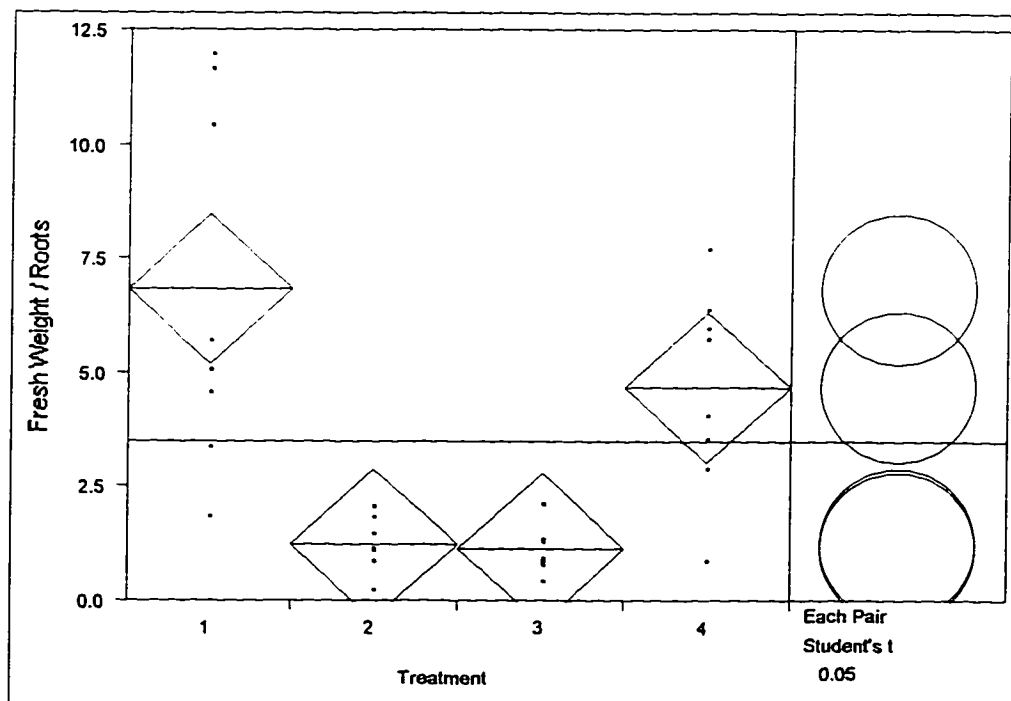


Table 173. Descriptive statistics for dry weight of rhizomes+roots (Kg) per treatment and block 5.4 years after planting of seeds.

Treatment	Mean	SD	Range	Blocks	Mean	SD	Range
Treat.1	2.869	1.632	0.9-5.2	Block I	1.694	1.553	0.4-4.8
Treat.2	0.600	0.249	0.2-1.0	Block II	1.119	0.616	0.4-2.2
Treat.3	0.506	0.212	0.25-0.9	Block III	1.825	1.942	0.25-5.2
Treat.4	2.069	1.012	0.5-3.6	Block IV	1.406	1.205	0.2-3.6
Totals	1.511	0.776	0.2-5.2	Totals	1.511	1.329	0.2-5.2

Table 174. Analysis of variance for dry weight of rhizomes/roots 5.4 years after planting of seeds.

Source	df	Sum of Squares	Mean Square	F-test	P-value	R-Square
Treatments	3	31.952	10.651	18.292	0.0001	0.5458
Blocks	3	2.375	0.792	1.359	0.2908	0.0405
Treat./Blocks	9	14.891	1.655	2.842	0.0329	0.2543
Error	16	9.316	0.582			0.1591
Total	31	58.534				

Source	Alpha	Sigma	Delta	Number	LSN	Power
Treatments	0.0500	0.763063	0.999251	32	18.72356	1.0000
Blocks	0.0500	0.763063	0.272409	32	65.70374	0.2929
Treat.*Block	0.0500	0.763063	0.682154	32	29.88138	0.8098

Fig. 126. Visual Comparison of Group Means for Treatments with Graph of Student's t tests for Each Pair of Means.

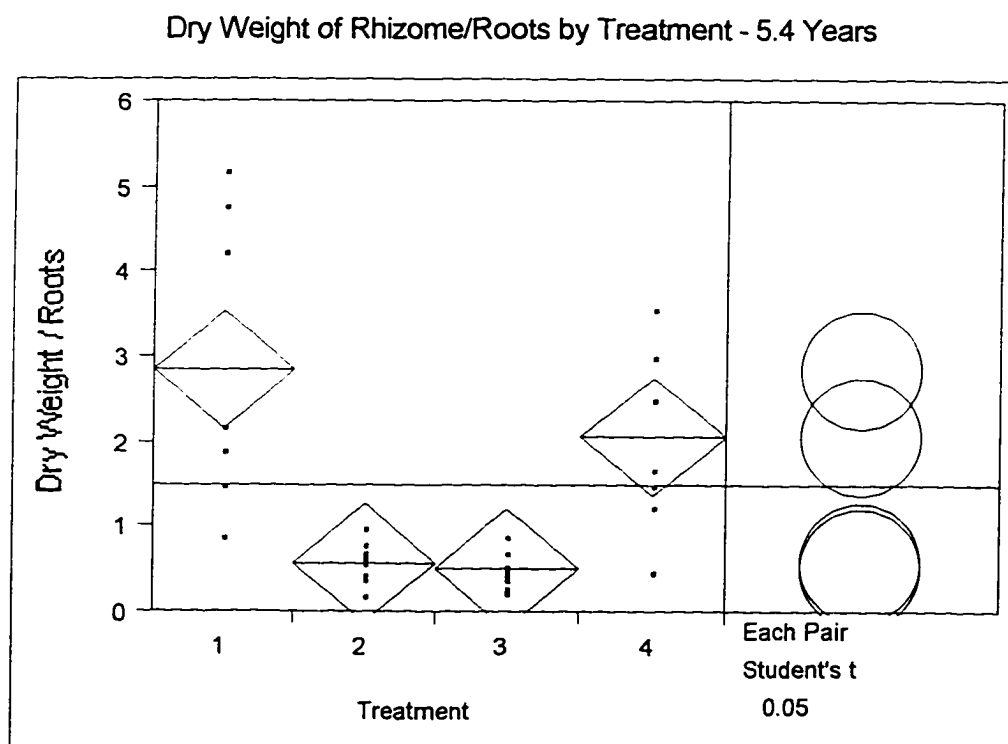


Fig. 127. Percentage of germination for each treatment recorded at 1 and 2.4 years.

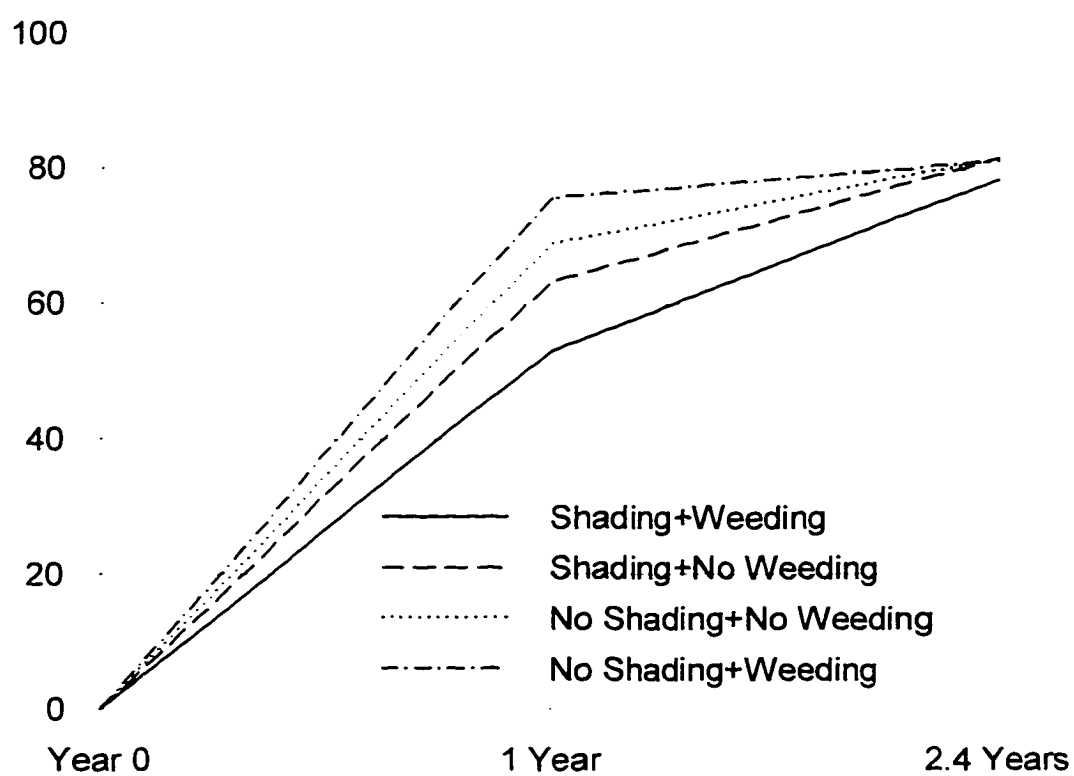


Fig. 128. Mean number of established seedlings by treatments for each census.

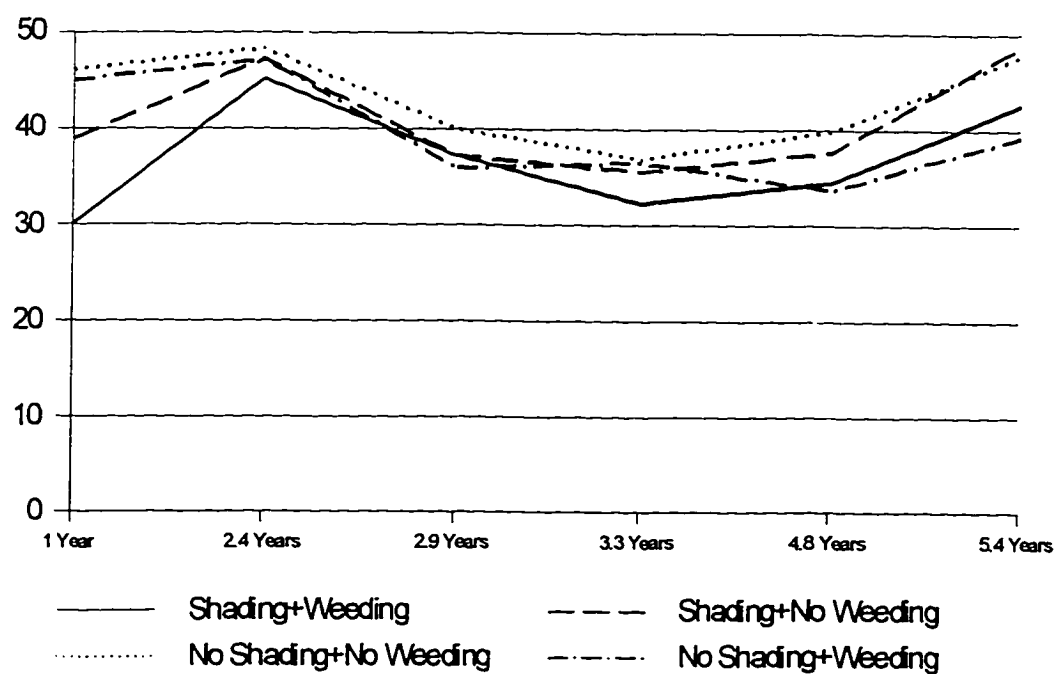


Fig. 129. Mean number of leaves by treatment for each census.

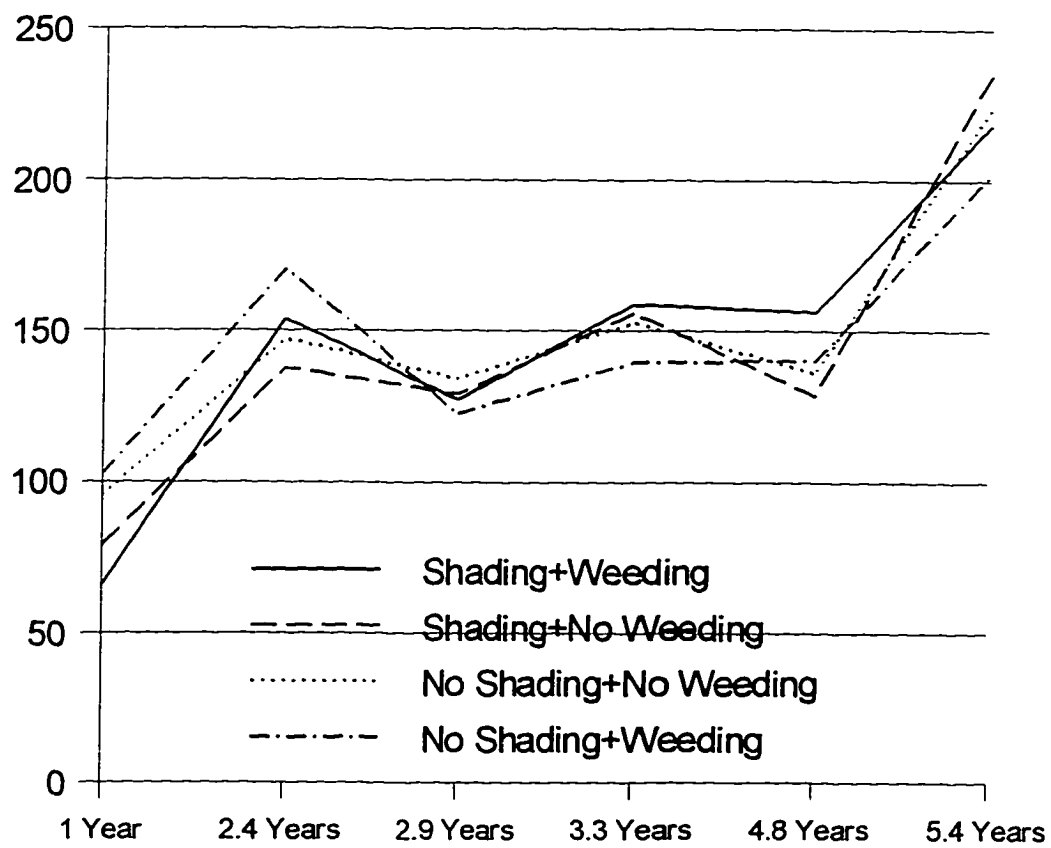
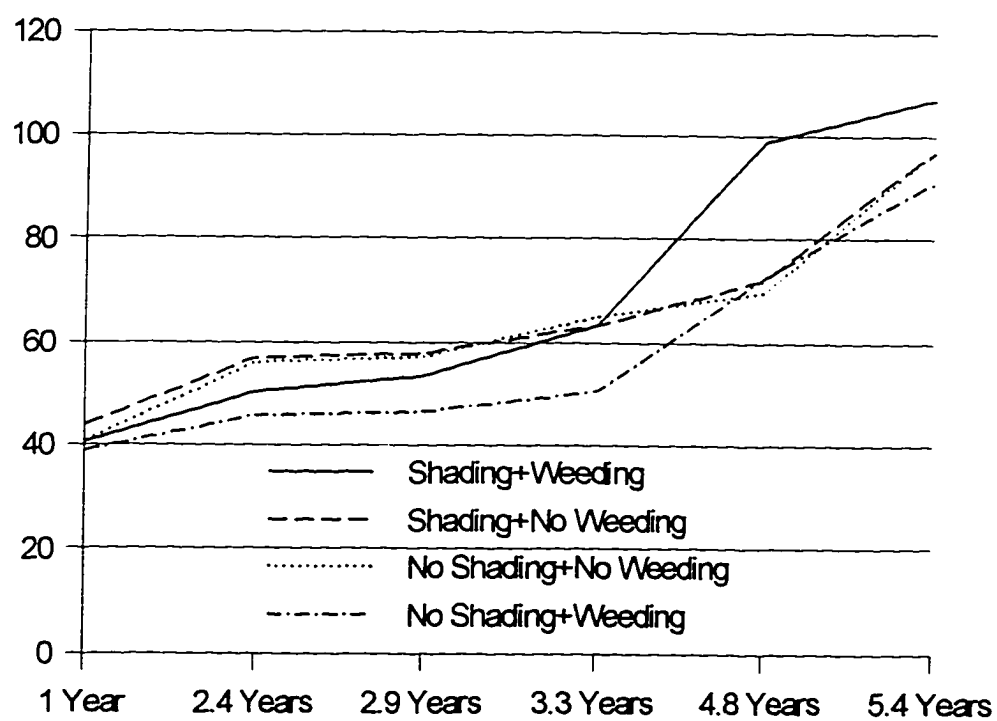


Fig. 130. Mean length of seedlings (cm) by treatment for each census.



4. Conclusions

Despite of the overall satisfactory response of babassu seedlings to the stress conditions, some separate conclusions can be drawn for each of the parameters measured for the experiment.

1. Germination - Germination of whole fruits in field conditions is very nonuniform, but the seeds protected by the hard pericarp may keep their viability for over one year. I estimated 18 months as the maximum period of time for seed germination (whole fruits). Treatments had a significant effect on germination, and this effect was clearly beneficial when no shading and weeding were applied in combination (Figure 127), suggesting that whole fruits germinate better under direct sunlight. In experiments where kernels were excised from fruits (Pinheiro & Araujo Neto, 1987) there was no difference in germination rate under shading or direct sunlight. However, whole fruits have a thick pericarp that may require the effect of light in order to give the seeds inside the signal for germination. This would facilitate the use of whole fruits as seeds in degraded areas, since light usually gets to the soil surface given the nature of the existing vegetation.

2. Number of seedlings - If the mean number of seedlings recorded in the first census (39.8) and in the last one (44.5) are considered, it tells us that in a period of

time of 5.4 years this number remained very stable and the losses of seedlings that occurred did not bring the number of seedlings below the 1 fruit/seed : 1 seedling ratio (33 seedlings per plot) . This is very important data for the purpose of this experiment, which confirms the resilience and aggressiveness of the babassu palm as a successional species, even in unfavorable conditions as those to which they were submitted. Obviously, this resilience cannot be measured only by the ability to remain alive, but this fact itself can be considered as a positive trait. The treatments had no effect on the number of seedlings throughout the experiment (Figure 128), although it could be observed that most of the seedlings' "disappearance" happened during the dry season in non-shaded plots. However, the ratio of 1 seedling to 1 seed never dropped below that in any period while the experiment lasted. The significant effect of blocks on the number of seedlings detected in the analyses of variance for all censuses (except for the one year census), is difficult to explain. Block 1 and 2 always showed the best mean number of seedlings and they were two blocks in the same position, one in front of the other (Figure 99). The position of the blocks in relation to the incidence of light on the plants could have some effect on this result; or, a slightly different soil condition; or any factor that could cause the difference from between these two and the others. However, since the number of seedlings remained unchanged throughout the experiment, this cannot be considered a matter for further investigation. An important point was the "reappearance" of 9 seedlings in the last census, confirming the ability of this palm

to keep the underground apical meristem alive for long periods of time, until more favorable conditions are achieved for the production and launching of new leaves.

3. Leafing - Treatments had no effect on seedling leaf production. A significant result for treatment effect was recorded only in the initial analysis (one year), but it can be interpreted mostly as a consequence of the germination results in that first year. From that point on, no significant effect of treatments could be detected in any census. The number of leaves, however, experienced increases and decreases (Figure 129) related to the dry and rainy seasons. A decrease in the number of leaves borne by the seedlings usually happened during the dry seasons. In general, during these seasons, the plots where shading was provided had seedlings with a smaller decrease in the number of leaves. In plots under direct sunlight, the seedlings tended to shed more leaves in order to reduce photosynthetic area, and ultimately, the overall physiological activity. During the rainy season, on the other hand, the tendency of seedlings seemed to be to increase the number of leaves, and to retake full physiological activity in order to compete for very scarce soil nutrients, rather than moisture. In this season, day length is shorter and the seedlings in non-weeded plots had surrounding vegetation as an obstacle for light absorption, – this was probably the reason why those plots had higher increases in number of leaves. This stable leafing pattern observed throughout the experiment matches the pattern observed in nature. This may suggest a genetically established continuous leafing rhythm which is not easily altered by external factors.

4. Growth - This was affected by treatments up to 3.3 years after the seeds were planted; after that, no significant effect could be detected by the analyses of variance performed. Up to this point, overall growth was much slower; higher growth rates were recorded after this point (Figure 130). Separate effects on different physiological processes could be observed: growth rate seems more likely to be affected by external effects than leafing rate, at least in the first three years of the seedling's life. This may be because, from physiological and ecological standpoints, the development of a strong root system and the maintenance of a balanced number of leaves according to the season and availability of resources (e.g., water, nutrients), can be more advantageous than spending physiological effort on growth in height, at least in the earlier phases of growth. From a certain developmental stage on, when the establishment phase is overcome, growth is fully retaken and babassu seedlings are ready to take over of the landscape. During the first three years, when treatments produced differences in growth, an alternating situation could be observed that was directly related to the season of the year. In the dry season, the best growth performances were achieved by the seedlings in non-weeded plots; probably not because the competition stimulated that, but because higher levels of moisture were maintained in those plots. In the rainy season, the situation was the opposite: weeded plots did better than the non-weeded plots, although the best results were obtained when the combination shading and weeding was provided. This suggests that the seedlings grow better in more shaded

conditions, in their early stages of growth. After the establishment point, shading does not significantly affect growth of seedlings. It is noteworthy, however, that even after 3.3 years, when treatment effects could not be detected any more, the higher means were recorded for treatments that combined shading and weeding.

5. Fresh and Dry Weight of Leaves and Roots - These were the characters measured for which the Anovas performed revealed the highest p-values for the treatments applied. This highly significant effect of treatments on both fresh and dry weight of leaves and roots shows that the features most affected were weight of the biomass produced, both aerial and underground. It appears that while unfavorable overall conditions (that including treatments, poor soil, and periodic water shortage in a soil type that does not hold much moisture for long periods of time even in the rainy season, had no apparent effect on survival of seedlings, leafing and growth, they did produce strong differences in terms of biomass accumulation in the whole plant. It is very clear that the treatments that account for most of this highly significant overall effects were the weeded treatments (1 and 4), which were clearly superior to the others in terms of leaf and rhizome/root weight. It shows that babassu seedlings, while withstanding well competition with the surrounding vegetation in the non-weeded plots, do better in the absence of the competitive vegetation.

The overall conclusion of this experiment is that babassu seedlings can successfully establish themselves in degraded sites. Although for separate characters measured at different developmental stages and after periods of shortage or availability of water, the responses were varied, the overall response to treatments and stress conditions for which the seedlings were subjected leads to the conclusion that babassu will succeed in establishing itself in degraded soils. Whether this palm will keep a reasonable level of productivity can be only be determined in a much longer term study. However, if we consider that these are areas where currently only grass and weeds can grow, the introduction of a valuable plant species which is likely to succeed, may be worth trying. This may be the beginning of the recuperation process of the plant coverage of the soil with a palm of recognized social and economic value. Moreover, the use of other Orbignya species which grows in areas often subject to water deficit and poor soil conditions can be an additional alternative. An example of such "babassu" species is Orbignya teixeirana (Bondar) Balick, Pinheiro & Anderson, an interspecific hybrid between the "true babassu" Orbignya phalerata Martius and the *piçava* palm Orbignya eichleri Burret (Medeiros-Costa et al., 1985; Balick et al., 1987). The establishment of babassu stands in those degraded areas would be a starting point for implementing many other alternative land uses, that are currently very restricted, including agro-forestry systems that are likely to be successful in association with the babassu palm.

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