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MORPHOLOGICAL, ANATOMICAL AND PHYLOGENETIC STUDY OF PALM GERMINATION AND SEEDLINGS

by

FLOR M. CHÁVEZ

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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1/14/03
Date

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Dr. Scott A. Mori, New York Botanical Garden

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Supervising Committee

The City University of New York

Abstract

MORPHOLOGICAL, ANATOMICAL AND PHYLOGENETIC STUDY OF PALM GERMINATION AND SEEDLINGS

by

Flor M. Chávez

Adviser: Professor Dennis W. Stevenson

A morphological and anatomical survey was carried out on seedlings of 62 taxa of palms representing all major groups. Results showed that the three previously recognized germination types in palms were not supported. A new seedling classification based on the orientation of the primary root is proposed. Plication types previously recorded as either reduplicate or induplicate are not supported for eophylls. There appears to be a third plication pattern that combines the two previous patterns. Cladistic analyses of anatomical and morphological seedling

data were carried out. A combined analysis was performed using data from adult morphology. Outgroup selection was done within the family and using the monocot family Dasypogonaceae. The calamoids and *Nypa fruticans* as outgroups resolved some of the major groups. The combined analysis using Dasypogonaceae as the outgroup provided better resolution. Most of the clades were monophyletic as shown in previous studies, the coryphoids and arecoids were paraphyletic.

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To Andrew, Lidia and Alfred

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I INTRODUCTION

The palm family (Arecaceae or Palmae) is one of the largest families of monocotyledons. The most recent estimate is that it contains 189 genera (Uhl & Dransfield, 1999) and approximately 2000 species. These are widespread in tropical areas throughout the world, with the greatest concentration of species in tropical America and Southeast Asia. Few palms are found outside the tropics. Individuals are usually abundant in tropical ecosystems, especially in lowland and montane moist forests.

The Palmae are also one of the most economically important families of plants to man, ranking after grasses and, in the tropics, equal with legumes. Apart from the well-known crops, coconut (*Cocos nucifera*), oil palm (*Elaeis oleifera*), and date palm (*Phoenix dactylifera*), other species of palm provide numerous useful products such as food stuffs, fibers, and medicines (detailed in Balick & Beck, 1990).

Because of this economic importance, and because of their abundance in tropical ecosystems, palms have received much attention from botanists. Numerous

aspects of the family have been extensively studied, such as systematics, reproductive biology, economic uses, and biogeography. Nevertheless, some important aspects of palm biology remain to be investigated, including seedling biology.

The present study takes as a starting point that there has been no recent survey of germination and seedlings in the palm family, and the subject remains poorly understood. In this study, the seedling morphology and eophyll anatomy of 62 genera in 14 major groups of palms are described. These data are used for a re-evaluation of germination types in palms, and for a cladistic analysis of the family. Although this study is carried out against an academic background, it is envisioned that it will have some practical consequences for understanding the germination of palms. Since almost all palms are propagated by seed, the subject of germination is clearly an important one.

Historical Survey

The scientific study of palm germination began in the early nineteenth century with the work of Martius

(1823-50). He recognized three distinct types of germination in palms: "germinatio admotiva", in which the seedling developed adjacent to the seed, and "germinatio remotiva", in which the seedling developed at some distance from the seed. This latter type was again divided into "germinatio remotiva tubulosa" in which the tubular part was open (e.g., *Arenga*, *Phoenix*) and "germinatio remotiva ocreata" in which an ocrea was present (e.g., *Brahea*, *Chamaerops*). These three types of germination described by Martius have served as the basis for all subsequent discussions of palm seedlings (see Fig. 1 and Table 1)

Mohl (in Martius, 1823-50) described and illustrated in great detail the anatomy of embryos and germinating palm seeds. Martius' work was reviewed by Micheels (1889), who studied 33 taxa. He proposed three germination types based on the attachment of the embracing (sheath) region. His results are basically similar to Martius', although he assigned new names, the "*Phoenix* type" with palms with the sheath at the base of the cotyledonary stalk (*germinatio remotiva-tubulosa* of Martius), "*Sabal* type" palms with a tubular sheath (*germination remotiva-ocreata* of

Martius) and "*Dictyosperma* type" for palms with a short sheath (*germinatio admotiva* of Martius). Micheels' anatomical studies included a detailed description of the primary root (radicle), hyperphyll, and first and second cataphylls.

Gatin (1906a) gave a comprehensive historical review of germination studies in palms, beginning with the works of Pliny and Theophrastus, including the first illustration of a palm seedling produced over 400 years ago (Camerarius, 1588). Gatin carried out detailed morphological and anatomical studies of embryos and germination of *Phoenix* and *Archontophoenix*. He then surveyed 33 other genera and 58 species of palms. His major conclusion was that there is a constant relation between the internal structure of the embryo and the germination pattern. The embryo could take one of three forms; the plumular-radicular axis could be curved or straight. The straight plumular-radicular axis could be parallel or oblique to the axis of the embryo. A curved plumular-radicular axis gave rise to ligulate (*ocreata* of Martius) germination. A straight axis gave rise to non-ligulate germination (*tubulosa* of Martius).

Gatin considered that Martius' remote germination types could be divided into three kinds. First, seedlings with the sheath opened laterally (e.g., *Phoenix*) (*germinatio remotiva-tubulosa* of Martius); second, seedlings with a ligule (*germinatio remotiva-ocreata* of Martius), so that the sheath opened apically (e.g., *Sabal*); and in the third, seedlings without a ligule but with the sheath opened apically with two tongues or an undeveloped ligule (e.g., *Trachycarpus, Livistona*) (palms with these characteristics were included in the *remotiva-tubulosa* type by Martius').

Gatin produced various other shorter works on palm germination: examples of germination (Gatin, 1904a), primary roots of palm seedlings (Gatin, 1904b), polyembryony (Gatin, 1905), chemistry of *Borassus* germination (Gatin, 1906b), anatomy of the hyperphyll (Gatin 1907a), roots of seedling palms (Gatin, 1907b), and morphology of germination (Gatin, 1908). He summarized all his work in a comprehensive book on palms (Gatin, 1912).

Several other studies followed Martius and Gatin's germination types without discussion.

Significant contributions to the field were provided by several researchers including Zurawska (1912), who gave extensive morphological descriptions of germination and seedlings of twenty-four species of palms. Unfortunately, she seemed unaware of Gatin's (1906a) work and her study does not include details of embryo structure. Yampolsky (1922), in a study of the oil palm *Elaeis guineensis*, gave a detailed historical review of studies on the leaf and haustorium in palms. Boyd (1932) carried out a survey of seedlings of all monocotyledons and included a few species of palms not treated by Gatin (1906a). She provided information on morphology and vasculature of the cotyledon, plumule, roots and few references to the lamina of *Cocos capitata* (= *Butia capitata*). In 1950, the French botanist Ginieis began an important series of studies of palm germination and seedlings. These are referred to below under the relevant genera. Saakov (1954) studied germination of economically important palms. He concluded that palms with remote tubular non-ligular germination (*remotiva tubulosa* of Martius) are primitive; remote ligular palms (*remotiva ocreata* of Martius) are intermediate between old remote tubular

and early admotive ligular types; and admotive ligular palms (*admotiva* of Martius) are phylogenetically younger groups. He also suggested that morphological features of germination blurred or disappear after the emergence of the second or third leaves.

Tomlinson (1960a, 1990), in important works on palm seedlings, gave a review of germination and seedling morphology, including illustrations and examples. He followed Martius' three germination types: remote non-ligular germination (*remotiva tubulosa* of Martius), remote ligular germination (*remotiva ocreata* of Martius) and adjacent ligular (*admotiva* of Martius), but suggested that both *Nypa* and *Phytelephas* may have different germination patterns. He considered *Elaeis* a fourth type because it does not correspond to any of the proposed types, being adjacent with a vigorous persistent primary root. He reviewed seedling anatomy and histochemical changes in the seed.

Moore & Uhl (1973) attempted to use germination characters to understand phylogeny. They considered remote-tubular (*remotiva-tubulosa* of Martius)and remote-ligular germination (*remotiva-ocreata* of

Martius) type to be less specialized groups, with the genus *Livistona* as the most advanced Coryphoid, with remote-ligular germination. The adjacent-ligular type (*admotiva* of Martius) corresponded to advanced groups, among them the Arecoids.

Low (1976), in an overlooked work on palm phylogeny, reviewed seedling morphology of 84 species in 82 genera of palms. He provided several original observations on morphological characteristics of germination. He listed several seedling characters and emphasized the number of scale leaves as a diagnostic character.

Recently, DeMason (1988) undertook a revision of Gatin's (1906a) three embryo categories (plumular-radicular axis straight or curved; if straight: parallel or oblique to the axis of the embryo). She considered that the root pole of *Washingtonia* was difficult to see, and therefore difficult to know if the embryo was straight or curved. Afterwards she suggested two embryo types based on the orientation of the epicotyls - embryos with epicotyls parallel to the cotyledon, and embryos obliquely angled with respect to the cotyledon.

Uhl and Dransfield (1987) provided information on germination type and eophyll shape for most genera of palms. They followed Martius' basic germination types with a variation in the terminology, remote tubular (*remotiva tubulosa*), remote ligular (*remotive ocreata*) and adjacent ligular (*germination admotiva*), and used anatomical information of adult leaves from Tomlinson (1961).

Tillich (1995) reviewed seedling morphology in all monocotyledons and demonstrated the usefulness of seedling characters in monocot systematics. In Tillich's review, the palm family formed an isolated group with basal characters. He also standardized germination terminology throughout the monocotyledons and this is used here (Appendix 1). Tillich (2000) stressed the importance of the cotyledon morphology and the nature of the first cataphyll versus the eophyll to define seedling types and evolutionary levels. He concluded that the ancestral seedling type in monocots is characterized by a compact cotyledon, one to several cataphylls, a short hypocotyl with inconspicuous collar, and a vigorously growing, branched primary root. He considered the seedling

structure as a key character to detect phylogenetic relationships.

Anatomical studies have been oriented mainly to understanding the germination process and the structure of the seedling, but little is known about the anatomy of seedling leaves. Tomlinson (1960b, 1990) studied the nature of young leaves, introducing the term "eophyll" (Greek eos-early; phyllon-leaf) to describe the first expanded, photosynthetic leaf of the seedling. His aim was to differentiate the first laminar leaf from succeeding leaves. He discussed the ontogeny of seedling leaves, suggesting that palm leaves go through a gradual transition from small, simple leaves to large compound leaves.

Tomlinson (1961) studied the leaf anatomy of 250 species of adult palms. He showed that palms could be recognized by distinctive anatomical features at the generic level. His results separated the bactroid palm from the cocoid with which it was associated, based on the absence of anatomical evidence that supported their relationship. The caryotoids appeared to be a very distinct group that showed morphological features of induplicate palms and anatomical features of

reduplicate palms. Tomlinson's work is a major contribution to palm anatomy, and it is the main source of reference for the present study.

Germination of various individual genera has been described and/or illustrated: Depoux (1968, 1969) for *Trachycarpus;* Clancy and Sullivan (1988) and Carpenter et al. (1993) for *Rhapidophyllum;* Ginieis (1950, 1952) for *Chamaerops;* Mahabale and Kulkarni (1972) and Lothian (1959) for *Livistona;* Fisher and Tomlinson (1973) and Hilmon (1969) for *Serenoa;* Ginieis (1952b) and De Mason (1988) for *Washingtonia;* Holm (1891) for *Sabal;* Camerarius (1588), Sachs (1862), and Ginieis (1951, 1957) for *Phoenix;* Dassanayake and Sivakadachchan (1973) and Padmanabhan et al. (1978) for *Borassus;* Thiselton-Dyer (1910) for *Lodoicea;* Miller (1977) for *Salacca;* Ginieis (1965) and Ilangovan and Padmanabhan (1993) for *Calamus;* Davis and Kuswara (1987) for *Pigafetta;* Tomlinson (1971), Fong (1986) and Bacon (2001) for *Nypa;* Sento (1971), Mahabale and Shirke (1967) for *Caryota;* Read (1968) for *Pseudophoenix;* Karsten (1857) for *Ceroxylon;* Belin-Depoux & de Queiroz (1971b) for *Euterpe;* Ginieis (1953a, 1953b) for *Archontophoenix;* Robertson (1980)

for *Jubaeopsis;* Yampolsky (1922) and Rees (1960) for *Elaeis;* and Sento (1971) for *Roystonea.*

Current classification

Palms form a distinct group among the monocotyledons. Their monophyly is strongly supported by means of morphological and molecular data analysis. Palms are resolved as an isolated group, sister to the Poales within the Commelinidae (Stevenson and Laconte 1995). Chase et al. (2000) placed the palms within the commelinoids as sister group to Dasypogonaceae, Zingiberales, Commelinales and Poales. In Stevenson et al. (2000) the palms resolved as a monophyletic branch with *Dioscorea* (Dioscoreaceae) as the sister group.

The most comprehensive statement of the relationships of palm genera is that of Uhl and Dransfield (1987). This traditional approach used morphological descriptions of adult individuals, flower and leaf anatomy, fossil record, and phytogeography to establish relationships among the taxa. Their classification divided the family into six subfamilies, 13 tribes, and 38 subtribes. This work

was written before cladistic methodology became widespread, and is therefore pre-cladistic in outlook. However, this outstanding study was the starting point for all subsequent phylogenetic studies.

Uhl et al. (1995) used morphological and chloroplast DNA restriction site variation to analyze the relationships among the members of the family, using cladistic methodology. Fifty-nine genera and 67 species representing all subfamilies and tribes were analyzed, using the genus *Dioscorea* as an outgroup. The results showed three major evolutionary trends. *Nypa* was resolved as sister to all remaining palms, and the Calamoideae were sister to all remaining palms except *Nypa*. The Coryphoideae and Phytelephantoideae were resolved as monophyletic, the Ceroxyloideae as polyphyletic, and Arecoideae as paraphyletic. The combined analysis of morphological and molecular data showed more resolution than the analysis of the independent data sets. Most of the clades supported the formal classification; but in the molecular analysis *Wallichia* (Caryoteae) appears within the Coryphoideae along with several Borasseae, *Phoenix* and *Corypha*. In the morphological analysis and the

combined analysis *Wallichia* appears as sister group to *Iriartea*.

Baker et al. (1999) used DNA sequences from the *trn*L-*trn*F region, which appear to be highly conserved in palms. Their results supported Uhl et al. (1995) for the most part, and completely agreed with the use of *Nypa* as an out group, even though this particular region was highly conserved, few sites were informative, and the level of ambiguity was high.

Asmussen et al.(2000) used rps16 Intron and *trn*L-*trn*F plastid DNA sequences. Sixty-five taxa were tested determine the monophyly of the currently accepted subfamilies, tribes, and subtribes of the family. Their results support the monophyly of the Calamoideae. The remaining subfamilies were not resolved as monophyletic but a major clade comprising all the Coryphoideae, Ceroxyloideae, Arecoideae and Phytelephantoideae was highly supported. The situation of the tribe Caryoteae supported Uhl and Dransfield's (1995) results, including the tribe with Coryphinae and Borasseae of the Coryphoideae. The authors suggested that the addition of sequences from other genes may help to resolve remaining problem

relationships within the family. Some of these questions focused on the monophyly of the Coryphoideae, the position of tribe Cyclospatheae and tribe Ceroxyleae from subfamily Ceroxyloideae, and finding more resolution for the clades of the subfamily Arecoideae.

Subsequently coding and noncoding plastid DNA were used by Assmusen & Chase (2001). They concentrated on finding the root of the family, and used, in addition to 94 palm taxa, 24 monocot outgroups. The results showed that the family was monophyletic and highly divergent in comparison to other monocot clades. The subfamily Calamoideae was resolved as sister to the rest of the palms, except to *Nypa*, but this result was poorly supported (jackknife support value 50%).

Lewis & Doyle (2001) using 428 bp of malate synthase exon regions, corroborated Asmussen and Chase's (2001) results. However, the subfamilies Arecoideae, Ceroxyloideae, Coryphoideae and Phytelephantoideae remained unresolved in the large clades that included 45 palm taxa and five outgroups. A second analysis was run including a sample size of

16 taxa and two outgroups. The use of 1002 bp increased bootstrap values, and placed *Nypa* as sister to the rest of the palms.

Hahn (2002) using atpB, rbcL, and 18S nr DNA sequences, reported incongruence among data sets, and between molecular and morphological data. He identified four main groups of palms: the Calamoideae, sister to the remainding palms, the Nypoideae, the Coryphoideae (including Caryotoideae) and the Arecoideae (except Caryoteae, Ceroxyloideae and Phytelephantoideae).

Objectives

The present study has three major objectives. First, to study the germination patterns of palms and see if the results support Martius' (1823-1850) germination types. If not, is there a better way to classify germination in palms? Secondly, to analyze morphological and anatomical characters using cladistic methodology and see if the data support previous phylogenies based on morphological and molecular data. Thirdly, to perform a combined

previous phylogenies based on morphological and molecular data. Thirdly, to perform a combined analysis of the seedling data with morphological data from adults, using a previously published data set (Uhl et al. 1995).

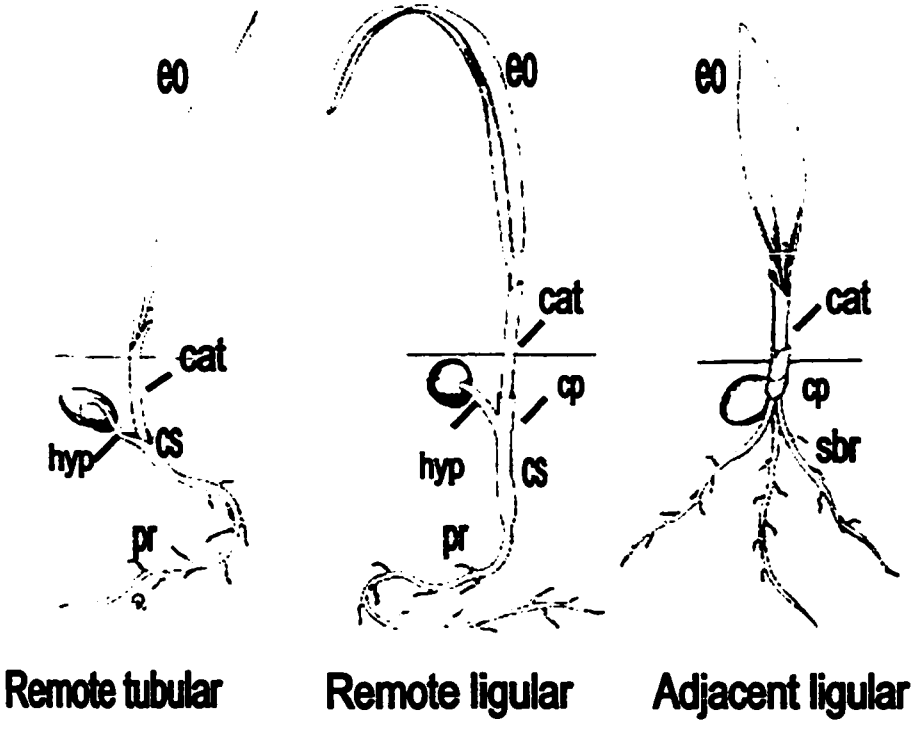


Figure 1. Germination types and seedling morphology. **cat**: cataphyll, **cp**: coleoptile, **cs**: cotyledonary sheath, **eo**: eophyll, **hyp**: hyperphyll, **pr**: primary root, **sbr**: shoot born roots. (*with permision from: Uhl and Dransfield 1987, drawings by Marion Ruff Sheehan*)

Table 1. Historical review of palm germination types

Moore	Micheels	Gatin		Saakov	Uhl and Moore	Tomlinson
1923-1850	1998	1906-1912		1954	1987	1990
Remotiva tubulosa	*Phoenix* type	straight embryo	sheath open laterally	Remote tubular non-ligular	Remote tubular	Remote non-ligular
Remotiva ocreata	*Sabal* type	curved embryo	sheath open apically undeveloped ligule/tonge	Remote ligular	Remote ligular	Remote ligular
Admotiva	*Dictyosperma* type	curved embryo	sheth open apically	Admotive ligular	Adjacent ligular	Adjacent ligular

II MATERIALS AND METHODS

Plant material

This study is at the generic level using the 15 major groups of palms as delimited by Moore (1973). Plant material (seeds and seedlings) representing all the major groups were gathered from various sources, such as botanical gardens, private gardens, personal contacts, and *fieldwork in Bolivia and Peru in 1996.* Two taxa, *Pododcocus barteri* and *Iriartella setigera,* were examined from herbarium specimens. The seeds were germinated and grown under uniform conditions in New York. In a few cases, adult leaf material was collected for comparison with seedling material of the same species. Seeds were collected under the mother plan and identification was made *in situ*. Each sample consisted of several seedlings at different stages of development.

Sixty-two taxa representing all the major groups were used in the study. Voucher specimens of seedlings were made and are deposited at NY (Table 2). The seedlings were fixed in FPA (formalin : proprionic

acid : alcohol - 5 : 5 : 90) and stored in 70% EtOH (ethanol).

Laboratory material and methodology

Seedling morphology was studied by direct observation using a hand lens and/or a Wild Heerbrugg MTr3 dissecting microscope. Anatomy of the lamina and petiole was studied by observation of transverse sections, epidermal peels, and leaf clearings using an Olympus Differential Interface Contrast Attachment model BH2-NIC microscope. Anatomical procedures followed Martens and Uhl (1980) and Ferreira (2001). Segments of 2 cm^2 from near the base and apex of the lamina and petiole were passed through a dehydration series using absolute ethanol and toluene (Appendix 2). Samples were embedded in paraffin, trimmed and attached to a stub, then each block was exposed to further softening using (glycerol : ethanol - 1 : 6), for a minimum period of 2 weeks. Blocks were sectioned on an AO Spencer 820 Rotary microtome at 12-17 µm (Appendix 3). Sections were stained in Safranin and Astra Blue series (Appendix 4).

Segments for epidermal peels were obtained from the hyperphyll of the lamina, the procedure followed Ferreira (2001), although the samples were exposed to the different solutions for shorter time (Appendix 5)

Complete eophylls were cleared and stained to observe venation patterns (Appendix 6). The diversity of size and shape of eophylls required each sample to be processed individually. The clearing period varied according to the size and/or thickness of the lamina, from 2-10 days. Permanently mounted clearings were allowed to dry for periods between four weeks to two years.

Imaging

Photographs of anatomical features were taken using a Nikon FX-35 camera attached to the microscope. For morphological features a Nikon Coolpix 990 Digital camera was used. Images were stored as JPEG files in Adobe PhotoShop.

Sampling and outgroup selection

Sixty three taxa (62 genera including two species of *Phytelephas*) were used. Seedling data for 18 morphological and 32 anatomical characters were scored for phylogenetic analysis. The resultant matrix is presented in (Table 3).

For the Combined Analysis, 37 adult characters were included. Data was provided by Dr. Natalie Uhl (Uhl and Dransfield 1995). Taxa for which seedling information was missing were excluded form the analysis. Twenty-seven taxa studied by me were not included in Ulh's matrix. The adult morphological information for these taxa was completed using Genera Palmarum (Uhl & Dransfield 1987). The added taxa were *Calamus* and *Pigafetta* (calamoid); *Archontophoenix, Dictyosperma, Dypsis, Hyospathe, Neonicholsonia, Nephosperma, Phoenicophorium, Roystonea* and *Veitchia* (arecoid); *Iriartella, Socratea* (iriarteoid); *Geonoma, Welfia* (geonomoid); *Astrocaryum, Bactris, Elaeis, Jubaea, Syagrus, Voaniola* (cocosoid); *Arenga* and *Caryota* (caryotoid); *Chamaerops, Trachycarpus* and *Trithrinax,* (coryphoid); *Borassus* (borassoid) (Table 4).

Choice of outgroup was guided by the studies of Uhl et al. (1995), Baker et al. (1999), Lewis et al. (2001), and Asmussen & Chase (2001). The genus *Nypa* and taxa in the Calamoids were used as outgroups in two separate analyses using the same data sets and the same search strategies. An additional outgroup was included in the combined analysis, the monocot family Dasypogonaceae. Character information for this taxon was obtained from Kubitzki (1998) and Tillich (2000).

Heuristic searches for the four matrices were run on 1000 random taxon entry sequences, 100 replication and holding 10 trees in each case, followed by tree bisection-reconnection branch swapping (max*). Characters were unordered and non-additive. Uninformative characters were excluded from all the analyses.

The data were edited in WinClada (Nixon 2000b) and examined using Dada (Nixon 1999, 2000a). Initial maximum parsimony analyses were run using NONA (Goloboff 1993), using the Mult* algorithm. Character distribution and calculation of the strict consensus tree were carried out using Clados (Nixon 2000a) and WinClada (Nixon 2000b).

Discussion of characters

0. PLUMULAR/RADICULAR AXIS: straight = 0; oblique = 1; angular = 2. These three states represent the axis formed by the plumule and the primary root. The plumule was similar in all three cases, vertically oriented (negative geotropism). In the first state the plumule arises in the same plane as the primary root, forming a vertically oriented straight axis (Figs. 2a, 2d, 3d and 4b). In the second state the primary root is diagonally oriented with reference to the plumule (Fig. 2b). In the third state the primary root is horizontally oriented and the plumule perpendicular to it (Fig. 2c).

1.PRIMARY ROOT: persistent = 0; ephemeral = 1. Primary roots are short living, and are soon replaced by shoot-borne roots. During the early stage of seedling development the primary root for all the taxa are present, this character was scored inapplicable for *Nypa*, because the radicle never develops. Stout primary roots were scored persistent (Figs. 2a, 2d, 3d, 4a and 5a), and primary roots of similar or less

thickness than shoot-borne roots were scored ephemeral (Figs. 2c, 3a, 4d, 5b and 5d).

2. SWOLLEN DISK COLLAR: absent = 0; present = 1. The disk collar develops as a distinct swollen structure with swollen contour. The primary root emerges in the center of the flat surface. (Fig. 3b).

3. LENTICELS: absent = 0; present = 1. Lenticels are portions of periderm with numerous intercellular spaces, allowing the flow of air through the periderm (Esau, 1977). Lenticels occur as cream-whitish circular spots on the hyperphyll, sheath and primary roots.

4. HYPERPHYLLS CONNECTION TO FRUIT: flat = 0; swollen = 1; constricted = 2. Morphologically the cotyledon is divided into three portions, the haustorium, the hyperphyll, and the sheath. Tillich (1995) refers to the hyperphyll as the proximal segment of the cotyledon that connects the haustorium with the sheath. This structure varies greatly in size. The portion in contact with the seed can be flat, swollen (Fig. 3c) or constricted (Fig. 3d).

5. COTYLEDONARY SHEATH: absent = 0; present = 1. The presence or absence of the cotyledonary sheath was

scored based on the attachment of the hyperphyll to the cotyledonary sheath. If the hyperphyll was attached to the collar it was scored as absent (Figs. 3b and 3d). There was not an obvious sheath. If the hyperphyll appeared attached at any point above the collar node, the sheath was scored as present (Figs. 2a, 2d, 4a, 4b, 4c, 5a and 5c).

6. COLEOPTILE: absent = 0; present = 1. Also known as the ligule or ocrea, this structure is formed by meristematic activity on the ring-shaped opening of the cotyledonary sheath of some taxa (Tillich, 1995). Coleoptile absent (Figs. 2a, 2d and 4b), coleoptile present (Figs. 3b, 3d, 4c and 5a).

7. COLEOPTILE SPLIT: non split = 0; split = 1. Coleoptiles are variable in length and they have distinctive opening features. Gatin (1906) divided the coleoptiles into three types, those with an apical opening, those with a lateral split and those with tongue-like projections. These differences were not sharp enough to discriminate all three stages. Therefore the coleoptiles were scored based on the non-splitting and splitting pattern (Fig. 4d).

8. CATAPHYLLS: one = 0; two = 1; three = 2; four = 3; more than four = 4. Cataphylls also know as scale leaves, are bladeless leaves (Fig. 5a and 5b)

9. EOPHYLL SHAPE: entire = 0; segmented = 1. Palm eophylls are often described as three distinct shapes: entire, pinnate or palmate. Here the shapes are scored based on their basic structure, either entire (Fig. 5c) or segmented (Fig. 5b and 5d).

10. THIRD LEAF: non-laminar = 0; laminar = 1. The term third leaf was used following a numerical series. The cotyledon is considered the first leaf, the cataphylls are considered as second, third leaves, etc. The first laminar leaf or eophyll continued the numerical series. The third leaf was chosen as a character state because it is at this number that variation mostly occurs. The third leaf falls in the category of cataphyll or laminar leaf.

11. SPLIT EOPHYLL: First = 0; second = 1; third = 2; fourth = 3; fifth = 4; sixth = 5; seventh = 6; eight = 7; nine = 8; ten = 9. The leaf succesional series from the first eophyll follows a distinct pattern in some groups (Tomlinson, 1960a). In some cases a plant will produce an entire eophyll and several eophyll-like

leaves before the first split leaf appears. The seedling leaves were numbered and the first that presented evidence of splitting was recorded. There was a large percentage of missing information for this character because most of the material was fixed once the first eophyll was fully expanded.

12. **EOPHYLL SPLITING SIDE**: adaxial = 0; abaxial = 1. In eophylls as in adult leaves splitting may occur along adaxial ribs or abaxial ribs (Uhl and Dransfield, 1987).

13. **AXIS AT BASAL END**: reduced = 0; distinct = 1. The proximal section of the eophyll was examined. A distinct axis was present in bifid and pinnate leaves. The axis of entire eophylls can have a major vascular bundle running along the whole length of the lamina (Figs. 5b and 5d), or it can be a short and restricted to the basal portion. In some cases the axis could not be observed and appeared like a cluster of individual strands, in this case the axis was considered reduced (Fig. 5c).

14. **VENATION PATTERN**: non-pinnate = 0; pinnate = 1. This characters appear directly associated with the previous one. The non-pinnate state includes those

eophylls with reduced axis, where the vascular strands run independently from a common starting point (Fig. 5c). Pinnate states were associated with eophyll with a short or long axis (Figs. 5b and 5d).

15. VASCULAR BUNDLES: convergent = 0; not convergent = 1. In most eophylls the vascular bundles converge at the apex, forming a distinct cluster of two or more vascular bundles (Figs. 5b and 5d). In others the vascular bundles diverge towards the lamina margins, forming praemorse margins (Fig. 5c)

16. EOPHYLL'S PROXIMAL PLICATION: V-shaped = 0; A-shaped = 1; A-margin-V-margin = 2. Plication refers to the folding of the lamina. Kaplan et al. 1982 and Dengler et al. 1982 showed that plication was originated by differential growth. Uhl and Dransfield (1987) classified palm leaves based on the splitting manner. Palms with A-shaped blade were called reduplicate, and those with V-shaped blades were called induplicate. For eophylls, in order to standardize information, only the marginal folds were examined. As expected, in most cases both margins were identical, some with V-shaped folds (Fig. 6b), others with A-shaped folds (Fig. 6a). However, for some taxa

a third type was detected. Those with one marginal fold was A-shaped and the other V-shaped. To corroborate the validity of the character, sections of unexpanded eophylls were obtained and examined.

17. EOPHYLL'S DISTAL PLICATION: V-shaped = 0; A-shape = 1; A-margin-V-margin = 2. The same principle for the previous character was applied to the distal part of the eophyll to observe. Entire eophylls maintain a uniform folding type along the whole length of the lamina, distal end resembles the plication of basal end. In divided eophylls the outer distal marginal folds remains the same as the basal marginal fold. The distal inner fold reflects directly the splitting pattern, if the splitting occur in the abaxial side the margin resulted on an A-shaped fold, if the splitting occur on the adaxial side it resulted on a V-shaped fold.

18. EPIDERMAL CELL SHAPE: rectangular = 0; fusiform = 1; rhombohedral = 2. Surface observations of epidermal peels were used to examined this character. The information is restricted and was obtained only from adaxial epidermis, information on abaxial cells was not always available (Figs. 7a and 7b).

19. ADAXIAL ANTICLINAL WALLS: linear = 0; sinuous = 1; dentate = 2. Tomlinson (1960s') noticed that cuticular deposit in the walls can give the walls a sinuous appearance. For eophylls a cuticle layer was not always present, and when present it was mostly restricted to the margin or above and below ribs. However the linear (Fig. 7a), sinuous and dentate states were distinct (Figs. 7b), although some intermediates were observed.

20. ABAXIAL ANTICLINAL WALLS: linear = 0; sinuous = 1; dentate = 2. Same as previous character.

21. EPIDERMAL HAIRS: absent = 0; present = 1. Hairs are usually present at costal (Fig. 8a) and intercostal (Fig. 8b) regions on both surfaces. The character was scored by examining the hair bases, which are usually persistent.

22. SINGLE CONICAL HAIR: absent = 0; present = 1. Hairs are variable in structure and form. The most distinct type of hair was a unicellular conical filament.

23. HAIR BASE: free = 0; associated to fibrous bundle = 1. Although evidence shows that hairs occur in costal and intercostal regions (Tomlinson, 1961), in

some taxa there was a distinct association with fibrous bundles. The epidermal cells surrounding the hair appear sunken in transverse view. (Fig. 8b)

24. STOMATA: superficial-epidermal = 0; sunken = 1. Stomata are restricted to intercostal areas and are more abundant on the abaxial surface. In transverse section, the position of the guard cells with relation to the epidermal layer shows two distinct patterns, stomata with guard cells restricted to the epidermal layer level and stomata with guard cells at the hypodermal layer level. However, in some taxa the guard cells are not completely sunken in the hypodermis, they occupy the epidermal layer and part of the hypodermal layers (Fig. 9a)

25. HYPODERMAL LAYER: absent = 0; present = 1. Usually leaves have a hypodermal layer of cells beneath the epidermis; the hypodermal cells are larger and colorless (Fig. 6a). Evidence shows that a hypodermis is usually present in plants exposed to xeric conditions (Esau, 1977, Tomlinson 1961, 1990), and a hypodermis is absent in plants growing in shade conditions. The apparent plasticity of the character was tested prior its inclusion in the matrix. For this

purpose samples of adult and seedlings of *Livistona chinensis* and *Pritchardia* sp. were collected from natural populations, these samples were examined and compared with seedlings grown under artificial conditions. The results showed that the hypodermis was present in all samples, and thus this character was retained.

26. HYPODERMAL FIBERS: absent = 0; present = 1. The colorless cells forming the hypodermis are in some cases replaced by fibers. The fibers occur alone, in bundles (Fig. 10a) or as a continuous layer (Fig. 9b). However, only their presence or absence was scored.

27. PALISADE LAYER: absent = 0, present = 1. Palisade parenchyma cells are elongate, and may be arranged in several layers. The palisade parenchyma in eophylls is not easy to differentiate, and it is usually present as a single layer.

28. SPONGY LAYERS: five or fewer = 0, six or more = 1. Although the thickness of the eophylls are relatively similar, the number of layers is variable. Eophylls with large cells tend to have fewer layers than eophylls with smaller cells. This character appear to be constant for certain groups.

29. MESOPHYLL NON-VASCULAR FIBERS: absent = 0; present = 1. Fibers are a common feature in leaves. These are aggregated into strands of few to several fibers (Fig. 10b).

30. FIBROUS BUNDLE DISTRIBUTION: equidistant bundle = 0. adaxial bundle = 1. abaxial bundle = 2. The distribution of the fibrous strands among the mesophyll layers are distinctive. Three different types were discriminated, however some taxa may present multiple states (Fig. 10b).

31. EXPANSION CELLS LAYERS: absent = 0, present = 1. Expansion cells are present in the lamina on most palms. Their main function is to unfold and expand the lamina at maturity (Tomlinson, 1961). Expansion cells are larger than the rest of the mesophyll cells. These cells differ from the bulliform cells of grasses because they are situated beneath the epidermal layer. Their arrangement is usually perpendicular to the surface layer, and they are located at the folding regions of the lamina (Fig. 6b and 10a)

32. FIBER LUMINA SIZE: small = 0, wide = 1. Tomlinson (1961) discussed the shape of the fiber lumen. He describes narrow, wide and septate lumen. In eophylls

it was not easy to observe the shape or any peculiar characteristic except a widely open luminar or an occluded one.

33. LONGITUDINAL MAJOR VASCULAR BUNDLE ASSOCIATION WITH RIDGE: not associated = 0; associated = 1. Three vascular bundle sizes were identified; major vascular bundles, median vascular bundles, and minor vascular bundles. Major vascular bundles are usually situated at the folding region, and are attached adaxially to the epidermis and abaxially to the expansion cells. In few taxa major vascular bundles are situated halfway between two folding regions.

34. LONGITUDINAL MEDIAN VASCULAR BUNDLE: free = 0; buttressed = 1. Longitudinal median vascular bundles are slightly smaller than major vascular bundles and are not situated at folding regions. These vascular bundles can be free or connected to epidermal layer by fibrous buttresses.

35. FREE LONGITUDINAL MEDIAN DISTRIBUTION: equidistant = 0; adaxial = 1; abaxial = 2. The free vascular bundles are distributed among the mesophyll and are not attached to the epidermal layers. Equidistant is the most common feature.

36. BUTTRESSED LONGITUDINAL MEDIAN VASCULAR BUNDLE DISTRIBUTION: adaxial = 0; abaxial = 1; adaxial and abaxial = 2. The vascular bundles are attached to either the adaxial or abaxial layers by fibrous buttresses (Fig.9a), in some cases the vascular bundles are attached to both layers.

37. LONGITUDINAL MINOR VASCULAR BUNDLE DISTRIBUTION: equidistant = 0; adaxial side = 1; abaxial side = 2. Minor vascular bundles are small and have a single phloem strand. In eophylls minor vascular bundles occur independently (Fig. 11a), or attached to the surfaces (Fig. 9a)

38. LONGITUDINAL MINOR VASCULAR BUNDLE ASSOCIATED TO GROOVE: not associated = 0; associated = 1. In general the grooved fold is occupied by expansion cells, but in some taxa the groove is occupied by a minor vascular bundles.

39. LONGITUDINAL MINOR VASCULAR BUNDLE OS: surrounding vascular bundle = 0; u-shaped = 1; lateral sides = 2; cap-shaped = 3. Vascular bundles are surrounded by two bundle sheaths. A parenchymatic colorless outer sheath (OS), and a sclerotic inner sheath (IS). The distribution of the OS can be complete and surround

the vascular bundle (Fig. 10a), or incomplete and cover the vascular bundle partially. In the second case the adaxial or abaxial sides of the vascular bundle are attached to the epidermal or sub-epidermal layers, and the OS shields only the free surfaces.

40. LONGITUDINAL MINOR VASCULAR BUNDLE RADIAL OS: absent = 0; present = 1. A second layer of ellipsoid parenchymatic cells were detected surrounding the first OS. These cells are arranged radially, with their narrow extremes towards the first OS.

41. LONGITUDINAL MINOR VASCULAR BUNDLE BUTTRESS: absent = 0; present = 1. Fibers form large buttresses continuous with the lignified or sclerotic IS. These are attached to the adaxial (Fig. 9a), or abaxial hypodermal or epidermal layers.

42. MIDRIB: not prominent = 0; prominent = 1. Midribs were examined from the proximal end of the eophyll. Midribs are usually prominent at either adaxial or abaxial sides, however some exceptions were found (Fig. 11b).

43. MIDRIB NUMBER OF BUNDLES: single bundle = 0; group of bundles = 1. Vasculated midribs were found for all taxa. Tomlinson (1961) recognized two vasculature

types. Leaves with one or more vascular bundles similar to the major vascular bundles, and leaves with vascular bundles enclosed by a fibrous cylinder. In eophylls the vascular bundles were either solitary (Fig. 11a, 12a, 12b and 13a) or scattered in the ground parenchyma(Fig. 11b).

44. MARGINAL RIBS: vascular bundle = 0; non-vascular bundle = 1. The margins can be occupied by vascular bundles (Fig. 6a, 6b and 9b) or fibrous bundles (Fig. 10b).

45. PHLOEM STRANDS: one = 0; two = 1; three = 2; four = 3. Although the single and double strands were the norm, three and four irregular strands were observed (Fig. 11a, 13a).

46. LARGE METAXYLEM: one = 0; two = 1. The metaxylem may have one (Fig. 13a) or two wide vessels (Fig. 11a).

47. SILICA BODY SHAPE: spherical/ellipsoid = 0; hat-shaped = 1; irregular = 2. Silica bodies or stegmata are found in longitudinal files adjacent to vascular or non-vascular fibers. Stegmata can be of different shapes, the most common being spherical or ellipsoid. Others look like a flying saucer or a hat (Fig. 13b),

and others do not have a specific shape or exhibit a range of shapes.

48. SILICA BODY MARGINS: spinulose = 0; smooth = 1. The margins of the silica body are generally smooth, but some present spine-like protuberances.

49. SILICA BODY DISTRIBUBION: around vascular bundle = 0; around non-vascular bundle = 1. silica bodies were found exclusively in association with vascular and non-vascular bundles (Fig. 6b)

Excluded characters

Several characters were excluded from the analysis because of homoplasy and autapomorphy; however, these characteristics were included in the taxa descriptions.

1. Haustorium: complete = 0, incomplete = 1. Haustorium is defined as the apical part of the cotyledon that develops in to an absorbing organ. The complete cotyledon may become the absorbing organ, or only the apical part will develop into an absorbing

organ while the remaining part will extend forming the hyperphyll.

2. Hyperphyll: absent = 0, present = 1. The elongation of the hyperphyll is not a discrete character. The length describes a continuous range of size.

3. Hyperphyll texture: smooth = 0, rugulose = 1. The cotyledonary stalk may appear either smooth or with distinct single or multiple longitudinal grooves lengthwise.

4. Shoot-born roots: absent=0; present=1. Roots that arise endogenously (Tillich, 1995), they may occur at nodal or internodal regions. Eventually all primary roots are replaced by shoot-borne roots.

5. Root hairs: absent = 0, present = 1. Root hairs in palms were formerly regarded as absent, but Seubert (1996a,b, 1997,1998a,b) demonstrated that root hair are a common feature in palm roots.

6. Transverse vascular bundles connections: connecting 2 vascular bundles = 0, connecting more than 2 vascular bundles = 1. Longitudinal vascular bundles although parallel, are not isolated from each other; a complex network of transversal vascular bundles connects them. Some transversal vascular bundles

connect several longitudinal vascular bundles bundles one after another. Other vascular bundles connect only a couple of vascular bundles and intercostal regions.

7. Shape of subsidiary cell: rectangular = 0; ellipsoid = 1, kidney-shape = 2. Stomata are similar in most taxa. Rectangular subsidiary cells resemble the adjacent epidermal cells, they occur in most Arecoids. Ellipsoid subsidiary cells are uncommon, they occur scattered among all major groups. The kidney-shaped subsidiary cells are characteristic of most Coryphoids, *Plectocomia* and *Pigafetta* of the Lepidocaryods, the Hyophorbeae and Phytelephantoideae.

8. Terminal subsidiary cells: overarching = 0; not overarching = 1. In surface view the arrangement of the terminal subsidiary cells shows two patterns. Some are wide enough and overreach the guard cells and the lateral subsidiary cells. The second state shows the terminal subsidiary cells restricted to the guard cell region.

9. Inner guard cells striations: absent = 0, present = 1. The inner walls of the guard cell in the caryotoids have distinct striations, this was observed earlier by Tomlinson (1961).

10. Single globose hair: absent = 0, present = 1. Single globose epidermal hair was recorded only from the geonomoid.

11. Mesophyll: indistinct palisade = 0, distinct palisade = 1. The mesophyll regions were difficult to discriminate. The cells may all look similar or be differentiated into slightly perpendicular cells forming a palisade layer.

12. Midrib: absent = 0, present = 1. Most taxa do have an distinct midrib.

13. Midrib shape: rounded = 0, angular = 1. There was a wide array of midrib shapes: rounded if the contour were curved (rounded, ellipsoid, pear-shape, etc.); or angular if the contours have any straight sides.

14. Petiole transverse section: terete = 0, crescent = 1, pentagonal = 2. Although most of the simple eophylls do not have a distinct petiole, when distinct, some petioles were terete, crescent shaped (the sheathing base of the leaf). Taxa with bifid eophyll (except *Caryota*) had a petiole with a rounded abaxial side and a slightly concave adaxial side. Taxa in the caryotoid have a distinct five-sided petiole (pentagonal).

Table 2. List of material examined

Genus, species and voucher specimen number*	
1. CORYPHOID PALMS	
Acoelorraphe wrightii (Griseb. & H. Wendl.) H. Wendl. ex Becc.	Chávez 909
Chamaerops humilis L.	Chávez 910
Chuniophoenix hainanensis Burret	Chávez 964
Colpothrinax cookii Read	Chávez 965
Copernicia baileyana León	Chávez 918
Corypha sp.	Chávez 911
Cryosophila grayumi R. Evans	Chávez 920
Itaya amicorum H. E. Moore	Chávez 955
Livistona chinensis R. Br.	Chávez 966
Nannorrhops ritchiana (Griff.) Aitchson	Chávez 915
Pritchardia remota (Kuntze) Becc.	Chávez 917
Rhapidophyllum hystrix (Pursh) H. Wendl. & Drude	Chávez 963
Sabal minor (Jacq.) Persoon	Chávez 912
Serenoa repens (Bartram) Small	Chávez 959
Thrinax excelsa Lodd. ex Griseb.	Chávez 903
Trithrinax brasiliensis (Mart.)	Chávez 967
Trachycarpus sp.	Chávez 902
Washingtonia filifera (Linden) H. Wendl.	Chávez 930

Table 2. continue

2. PHOENICOID PALMS	
Phoenix roebelinii O'Brien	Chávez 904
3. BORASSOID PALMS	
Borassus sp.	Chávez 968
Hyphaene coriacea Gaertn.	Chávez 969
Latania loddegesii Mart.	Chávez 957
4. CALAMOID PALMS	
Calamus flagellum Griff.	Chávez 945
Mauritia flexuosa L. f.	Chávez 948
Pigafetta filaris (Gis.) Becc.	Chávez 944
Plectocomia sp.	Chávez 946
5. NYPOID PALMS	
Nypa fruticans Wurmb	Chávez 949
6. CARYOTOID PALMS	
Arenga hookeriana (Becc.) Whitmore	Chávez 907
Caryota mitis Lour.	Chávez 916
Wallichia densiflora Mart.	Chávez 905
7. PSEUDOPHOENICOID PALMS	
Pseudophoenix sargentii H. Wendl.	Chávez 971
8. CEROXYLOID PALMS	
Ceroxylon sp.	Henderson 3019
Oraniopsis appendiculata (F. Bailey) Dransf., Uhl & Irvine	Henderson 3070

Table 2. continue

Ravenea rivularis Jum. & H. Perrier	Chávez 972
9. CHAMAEDOREOID PALMS	
Chamaedorea microspadix Burret	Chávez 937
Gaussia maya (O. F. Cook) Quero & Read	Chavez 978
Synecanthus fibrosus (H. Wendl.) H. Wendl.	Chávez 938
10. IRIARTEOID PALMS	
Iriartea deltoidea R. & P.	Henderson 3015
Iriatella setigera (Mart.) H. Wendl.	Henderson 647
Socratea exorrhiza (Mart.) H. Wendl.	Chávez 935
11. PODOCOCCOID PALMS	
Pododoccus barteri Mann & H. Wendl.	Reitsma 2840
12. ARECOID PALMS	
Archontophoenix alexandrae (F. Muell.) H. Wendl. & Drude	Chávez 932
Dictyosperma album (Bory) H. Wendl. & Drude	Chávez 934
Dypsis lutescens (H. Wendl.) Beentje & J. Dransf.	Chávez 931
Euterpe precatoria Mart.	Balslev 4813
Hyospathe elegans Mart.	Chávez 929
Neonicholsonia watsonii Dammer	Chávez 928
Nephosperma vanhoutteanum (H. Wendl.) Balfour	Chávez 939
Orania regalis Zipp.	Chávez 985

Table 2. continue

Phoenicophorium borsigianum (K. Koch) Stuntz	Henderson 2063
Roystonea borinquena O. F. Cook	Chávez 927
Veitchia montgomeryana H. E. Moore	Chávez 977
13. COCOSOID PALMS	
Allagoptera leucocalyx (Mart.) Kuntze	Chávez 941
Astrocaryum alatum Loomis	Stevenson 1200
Bactris killippii Burret	Henderson 2015
Elaeis guineensis Jacq.	Chávez 942
Jubaea chilensis (Molina) Baillon	Chávez 975
Syagrus coronata (Mart.) Becc.	Chávez 947
Voanioala gerardii J. Dransf.	Chávez 976
14. GEONOMOID PALMS	
Geonoma interrupta (R. & P.) Mart.	Henderson 30
Welfia regia H. Wendl.	Henderson 301
15. PHYTELENPHANTOID PALMS	
Phytelephas seemanii O. F. Cook	Chávez 950
Phytelephas tenuicaulis (Barfod) Henderson	Chávez 951

* All voucher specimens are deposited at NY.

TABLE 3. Matrix with anatomical and morphological data of seedlings

	0 |	5 |	10 |	15 |	20 |	25 |	30 |	35 |	40 |	45 |
Nypa fruticans	---0-	01141	00111	0?001	?1001	10111	*1100	2-*00	00101	0111*
Calamus flagellum	1010-	01111	00111	01202	21000	01001	2*010	2-201	0011-	1000*
Mauritia flexuosa	1010-	01111	00100	00102	21000	01101	2*010	2-20*	10111	1000*
Pigafetta filaris	1010-	01111	00111	01201	100-0	01000	-1110	2-201	10111	1000*
Plectocomia sp.	1010-	01100	1??11	00202	200-0	01000	-*?10	2-201	10111	1000*
Acoelorraphe wrightii	00000	11000	1??00	00000	000-0	11010	-0110	0-000	0010-	10000
Chamaerops humilis	00000	10-00	14000	00000	000-1	11010	-0110	0-000	00101	10000
Chuniophoenix hiananensis	00100	11000	1??00	00001	11011	10000	-1-11	-0000	0010-	20000
Colpotrinax cookii	00100	11100	1??00	000*0	010*1	10011	*1001	-0200	00111	1000*
Copernicia baileyana	00001	10-00	1??00	00000	01010	11010	-1010	0-000	0000-	1000*
Corypha sp.	00011	10-00	1??10	10001	01011	11010	-1000	1-101	01100	0000*
Cryosophila grayumi	00000	10-00	15000	00000	01001	01000	-0101	-0201	0010-	0000*
Itaya amicorum	00000	10-00	1??00	00001	11001	01000	-0000	2-200	0010-	11---
Livistona chinensis	00001	11000	13010	00001	11000	11001	*1010	0-000	0010-	1000*
Nannorrhops ritchiana	00000	01000	1??00	00000	01001	10110	-0-01	-0000	10010	20000
Pritchardia remota	00002	01020	0??10	00001	11010	11110	-1110	0-000	1010-	1000*
Rhapidophyllum hyxtrix	00102	11100	1??00	00000	01011	11010	-1110	0-000	0010-	10000
Sabal minor	00000	11000	19010	00000	01001	10010	-1101	-2101	0100*	2000*
Serenoa repens	00000	11100	17000	00000	01010	11110	-1110	2-000	00001	10000
Thrinax excelsa	00002	10-00	14000	00000	01000	11000	-100-	--000	0000-	00000
Trithrinax brasiliensis	00100	10-00	1??00	00000	000-1	00010	-0-01	-2201	0100-	01000
Trachycarpus sikkimensis	00000	10-00	1??10	00000	01001	11000	-1101	-2000	0010-	10000
Washingtonia sp.	00100	01000	18000	00000	000-1	10010	-1-10	2-000	00011	10000
Borassus sp.	00011	10-00	1??10	100*0	000-1	11111	*1101	-0111	0110*	20000
Hyphaene coriacea	00011	10-00	0??10	000*0	01001	10111	*1101	-2*11	0111*	20000
Latania loddegesii	00011	10-01	10000	000*0	01001	10111	*1101	-0111	01111	20000
Phoenix roebelinii	00000	10-00	16010	00000	000-1	11011	*1000	0-000	00001	00000
Arenga hookeriana	00001	10-00	1??00	10010	01000	10101	00100	0-001	10100	0011*
Caryota mitis	00001	10-01	10000	10011	11001	10000	---00	0-001	100--	00110
Wallichia densiflora	00001	10-00	1??00	10010	01001	10101	00100	0-001	00100	0011*

continue

Table 3. continue

Pseudophoenix sargentii	00000	10-10	0??11	01100	000-1	11110	-0111	-2000	00100	10000
Ceroxylon sp.	10100	01110	06111	002*1	11010	11000	-0011	-0201	1011-	0*200
Oraniopsis appendiculata	10100	01110	0??11	002*0	01010	11001	*0111	-0201	1011-	0*20*
Ravenea rivularis	10100	01111	00111	022*0	01000	11000	-0010	0-000	0011-	0*200
Chamaedorea microspadix	2010-	01111	00111	00220	000-0	00000	---10	0-001	1011-	01100
Gaussia maya	2010-	01111	00111	002*0	000-0	00000	-0-10	0-001	1011-	01100
Synecanthus fibrosus	2010-	01111	00111	00220	000-0	00000	-0-10	0-000	1011-	01100
Iriartea deltoidea	2110-	01110	0??11	10120	01100	10001	00000	0-000	00111	0*11*
Iriartella setigera	21?0-	01??0	-??11	111*0	01100	10001	00000	2-201	00101	0011*
Socratea exorrhiza	2110-	01131	00111	10120	01100	10001	00000	2-000	00111	0*11*
Podococcus barteri	?1??-	01??0	-??11	1?120	01100	00001	0--00	0-001	0010-	0000*
Archontophoenix alexandrae	2100-	01111	00111	10220	01000	10001	00010	0-200	10110	1000*
Dictyosperma album	2110-	01111	00111	00120	01000	01010	-0110	0-200	10111	10000
Dypsis lutescens	2110-	01111	00111	00120	01000	00011	01110	0-000	10110	10000
Euterpe precatoria	2110-	01111	00111	002*0	11000	01000	-0011	-2001	00110	10000
Hyospathe elegans	2110-	01111	00111	101*0	01001	00000	-0-10	0-200	10100	10000
Neonicholsonia watsonii	2110-	01111	00111	002**	*00-0	00001	*0110	0-000	00100	1000*
Nephosperma vanhoutteanum	2110-	01121	00111	00220	01000	01010	-1010	0-201	10111	10000
Orania regalis	20001	10-11	00111	101??	?1000	00111	01?10	2-210	00110	20000
Phoenicophorium borsigianum	2110-	01110	02111	001*1	11000	01010	-0010	2-200	1010-	1000*
Roystonea borinquena	2110-	01110	0??11	001*0	01000	10001	00100	0-000	00100	1010*
Veitchia montgomeryana	2110-	01121	00111	102**	*1001	10011	*1010	0-000	10110	1*00*
Allagoptera leucocalyx	00000	10-10	0??11	022*0	01001	11010	-0011	-2211	01110	30200
Astrocaryum alatum	1000-	01111	00111	00210	01001	10101	*1010	0-200	00110	30101
Bactris killippii	1000-	01111	00111	00210	01000	10001	00010	0-000	00111	30101
Elaeis guineensis	1010-	01010	05111	002*0	01001	10001	00100	0-000	1011-	3020*
Jubaea chilensis	10000	11010	0??11	02000	01001	11011	11101	-2211	01110	30000
Syagrus coronata	00100	10-10	0??11	02200	01001	11010	-1001	-2211	01100	30200
Voanioala gerardii	?0100	10-11	00111	022*0	01001	10101	11110	0-201	0011-	*0200
Geonoma interrupta	1010-	01011	00111	00220	01000	00001	00-10	0-000	0011-	10100
Welfia regia	1000-	01011	00111	00220	01000	00001	00-10	0-000	0011-	00200
Phytelephas seemanii	10001	11021	00111	0?200	01000	01010	-1000	0-000	00101	11000
Phytelephas tenuicaulis	10001	11021	00111	0?200	01000	01010	-0000	0-000	00101	11000

Inapplicable characters scored (-), unknown states scored (?), multistate characters scored (*)

TABLE 4. Matrix with seedling and adult morphological data

	0 |	5 |	10 |	15 |	20 |	25 |	30 |	35 |	40 |	45 |
Dasypogonaceae	00000	00000	*--*0	0--00	0**00	00001	??00*	**00?	?00-?	1?0?-
Nypa	---0-	01141	00111	0?001	?1001	10111	*1100	2-*00	00101	0111*
Calamus	1010-	01111	00111	01202	21000	01001	2*010	2-201	0011-	1000*
Mauritia	1010-	01111	00100	00102	21000	01101	2*010	2-20*	10111	1000*
Pigafetta	1010-	01111	00111	01201	100-0	01000	-1110	2-201	10111	1000*
Plectocomia	1010-	01100	1??11	00202	200-0	01000	-*?10	2-201	10111	1000*
Acoelorraphe	00000	11000	1??00	00000	000-0	11010	-0110	0-000	0010-	10000
Chamaerops	00000	10-00	14000	00000	000-1	11010	-0110	0-000	00101	10000
Chuniophoenix	00100	11000	1??00	00001	11011	10000	-1-11	-0000	0010-	20000
Colpotrinax	00100	11100	1??00	000*0	010*1	10011	*1001	-0200	00111	1000*
Copernicia	00001	10-00	1??00	00000	01010	11010	-1010	0-000	0000-	1000*
Corypha	00011	10-00	1??10	10001	01011	11010	-1000	1-101	01100	0000*
Cryosophila	00000	10-00	15000	00000	01001	01000	-0101	-0201	0010-	0000*
Itaya	00000	10-00	1??00	00001	11001	01000	-0000	2-200	0010-	11---
Livistona	00001	11000	13010	00001	11000	11001	*1010	0-000	0010-	1000*
Nannorrhops	00000	01000	1??00	00000	01001	10110	-0-01	-0000	10010	20000
Pritchiardia	00002	01020	0??10	00001	11010	11110	-1110	0-000	1010-	1000*
Rhapidophyllum	00102	11100	1??00	00000	01011	11010	-1110	0-000	0010-	10000
Sabal	00000	11000	19010	00000	01001	10010	-1101	-2101	0100*	2000*
Serenoa	00000	11100	17000	00000	01010	11110	-1110	2-000	00001	10000
Thrinax	00002	10-00	14000	00000	01000	11000	-100-	--000	0000-	00000
Thrithrinax	00100	10-00	1??00	00000	000-1	00010	-0-01	-2201	0100-	01000
Trachycarpus	00000	10-00	1??10	00000	01001	11000	-1101	-2000	0010-	10000
Washingtonia	00100	01000	18000	00000	000-1	10010	-1-10	2-000	00011	10000
Borassus	00011	10-00	1??10	100*0	000-1	11111	*1101	-0111	0110*	20000
Hyphaene	00011	10-00	0??10	000*0	01001	10111	*1101	-2*11	0111*	20000
Latania	00011	10-01	10000	000*0	01001	10111	*1101	-0111	01111	20000
Phoenix	00000	10-00	16010	00000	000-1	11011	*1000	0-000	00001	00000
Arenga	00001	10-00	1??00	10010	01000	10101	00100	0-001	10100	0011*
Caryota	00001	10-01	10000	10011	11001	10000	---00	0-001	100--	00110
Wallichia	00001	10-00	1??00	10010	01001	10101	00100	0-001	00100	0011*

TABLE 4 continue

	0 |	5 |	10 |	15 |	20 |	25 |	30 |	35 |	40 |	45 |
Pseudophoenix	00000	10-10	0??11	01100	000-1	11110	-0111	-2000	00100	10000
Ceroxylon	10100	01110	06111	002*1	11010	11000	-0011	-0201	1011-	0*200
Oraniopsis	10100	01110	0??11	002*0	01010	11001	*0111	-0201	1011-	0*20*
Ravenea	10100	01111	00111	022*0	01000	11000	-0010	0-000	0011-	0*200
Chamaedorea	2010-	01111	00111	00220	000-0	00000	---10	0-001	1011-	01100
Gaussia	2010-	01111	00111	002*0	000-0	00000	-0-10	0-001	1011-	01100
Synecanthus	2010-	01111	00111	00220	000-0	00000	-0-10	0-000	1011-	01100
Iriartea	2110-	01110	0??11	10120	01100	10001	00000	0-000	00111	0*11*
Iriartella	21?0-	01??0	-??11	111*0	01100	10001	00000	2-201	00101	0011*
Socratea	2110-	01131	00111	10120	01100	10001	00000	2-000	00111	0*11*
Podococcus	?1??-	01??0	-??11	1?120	01100	00001	0--00	0-001	0010-	0000*
Archontophoenix	2100-	01111	00111	10220	01000	10001	00010	0-200	10110	1000*
Dictyosperma	2110-	01111	00111	00120	01000	01010	-0110	0-200	10111	10000
Dypsis	2110-	01111	00111	00120	01000	00011	01110	0-000	10110	10000
Euterpe	2110-	01111	00111	002*0	11000	01000	-0011	-2001	00110	10000
Hyospathe	2110-	01111	00111	101*0	01001	00000	-0-10	0-200	10100	10000
Neonicholsonia	2110-	01111	00111	002**	*00-0	00001	*0110	0-000	00100	1000*
Nephosperma	2110-	01121	00111	00220	01000	01010	-1010	0-201	10111	10000
Orania	20001	10-11	00111	101??	?1000	00111	01?10	2-210	00110	20000
Phoenicophorium	2110-	01110	02111	001*1	11000	01010	-0010	2-200	1010-	1000*
Roystonea	2110-	01110	0??11	001*0	01000	10001	00100	0-000	00100	1010*
Veitchia	2110-	01121	00111	102**	*1001	10011	*1010	0-000	10110	1*00*
Allagoptera	00000	10-10	0??11	022*0	01001	11010	-0011	-2211	01110	30200
Astrocaryum	1000-	01111	00111	00210	01001	10101	*1010	0-200	00110	30101
Bactris	1000-	01111	00111	00210	01000	10001	00010	0-000	00111	30101
Elaeis	1010-	01010	05111	002*0	01001	10001	00100	0-000	1011-	3020*
Jubaea	10000	11010	0??11	02000	01001	11011	11101	-2211	01110	30000
Syagrus	00100	10-10	0??11	02200	01001	11010	-1001	-2211	01100	30200
Voanioala	?0100	10-11	00111	022*0	01001	10101	11110	0-201	0011-	*0200
Geonoma	1010-	01011	00111	00220	01000	00001	00-10	0-000	0011-	10100
Welfia	1000-	01011	00111	00220	01000	00001	00-10	0-000	0011-	00200
Phytelephas seemanii	10001	11021	00111	0?200	01000	01010	-1000	0-000	00101	11000
Phytelephas tenuicaulis	10001	11021	00111	0?200	01000	01010	-0000	0-000	00101	11000

TABLE 4. continue

	51	56	61	66	71	76	81	86
Dasypogonaceae	0-000	---00	00000	00-00	00110	00000	000?0	00
Nypa	10001	04100	00110	02010	-0100	-0000	00000	02
Calamus	00001	04101	00101	42100	01110	00110	00000	01
Mauritia	00000	04100	00101	42100	01110	00110	00000	10
Pigafetta	00001	04100	00101	42100	01110	00110	00001	00
Plectocomia	00001	04100	10101	42100	01110	00110	00000	01
Acoelorraphe	00100	00000	00100	10-00	0-110	10000	00011	00
Chamaerops	00100	00000	00100	10-00	0-110	10000	00011	00
Chuniophoenix	00000	00010	00101	10-00	1-110	00000	00000	00
Colpotrinax	00100	00000	00100	00-00	0-110	10000	00001	00
Copernicia	00100	00000	00111	10-00	0-110	10000	00000	00
Corypha	01100	00000	10100	10-00	0-110	01000	00102	00
Cryosophila	00100	00100	00100	00-00	0-100	-2000	00011	00
Itaya	01100	00100	00100	00-00	0-0--	-1000	00000	00
Livistona	00100	00000	00100	10-00	0-110	10000	00011	00
Nannorrhops	11000	00010	10101	10-00	1-110	00000	00100	00
Pritchiardia	00100	00000	00100	00-00	0-110	10000	00000	00
Rhapidophyllum	00110	03000	00100	11200	00100	-1000	00011	00
Sabal	01100	00110	00100	00-00	0-110	00000	00111	00
Serenoa	00100	00010	00?10	10-00	0-110	10000	00011	00
Thrinax	01100	00000	00100	00-00	0-0--	-3000	00011	00
Thrithrinax	00110	00110	00100	00-00	0-100	-1000	00011	00
Trachycarpus	00100	00000	00100	11200	00100	-1000	00011	00
Washingtonia	01100	00000	00100	10-00	0-110	10000	00011	00
Borassus	01100	00010	00100	12100	11110	03001	01002	00
Hyphaene	11100	00010	00100	12100	11110	03001	00102	00
Latania	01100	00010	00100	12100	11110	03001	01002	00
Phoenix	00000	01010	000-0	02100	00100	-0000	00011	00
Arenga	00001	12100	10100	32000	00110	01000	00001	10
Caryota	00001	12100	10100	32000	00110	01000	00001	10
Wallichia	00001	12000	10100	32000	00110	01000	00001	10

Table 4 continue

	51	56	61	66	71	76	81	86
Pseudophoenix	00001	04101	00100	00-00	0-110	02000	00101	00
Ceroxylon	00001	04100	01100	02110	00110	01000	00101	00
Oraniopsis	00001	04100	01100	02110	00110	01000	00101	00
Ravenea	00001	04100	01100	02110	00110	01000	00100	0-
Chamaedorea	00001	04101	00100	02100	00110	00000	00101	00
Gaussia	00001	04101	00100	22000	00110	02000	00101	00
Synecanthus	00001	04101	00100	22000	00110	00000	00101	00
Iriartea	00001	14101	00100	32000	00110	00000	00001	10
Iriartella	00001	14101	00100	32000	00110	0?000	00102	00
Socratea	00001	14101	00100	32010	00110	03000	00002	10
Podococcus	00001	14100	00100	32000	00110	00000	00100	00
Archontophoenix	00001	04101	00110	32000	00111	0?000	00011	00
Dictyosperma	00001	04101	00110	32000	00111	01000	00000	00
Dypsis	00001	04101	00110	32000	00111	0??00	00101	00
Euterpe	00001	04101	00110	32000	00111	00000	00000	00
Hyospathe	00001	04101	00110	32000	10111	0??00	00100	00
Neonicholsonia	00001	04100	00110	32000	00111	0??00	00010	00
Nephosperma	00001	04100	00110	32000	00111	0??00	00010	00
Orania	00001	14100	00110	32000	00110	00000	10101	00
Phoenicophorium	00001	04100	00110	32000	00111	02?00	00110	00
Roystonea	00001	04101	00110	32000	01111	0??00	00100	00
Veitchia	00001	04101	00110	32000	00111	0??00	00000	00
Allagoptera	10001	04100	00110	32000	01110	00002	00000	00
Astrocaryum	00011	04100	00110	32000	00110	03?02	00001	00
Bactris	00011	04100	00110	32000	00110	03?02	00000	00
Elaeis	00001	04100	00110	32000	01110	03?02	00002	00
Jubaea	00001	04100	00110	32000	11110	01?02	00000	00
Syagrus	00001	04100	00110	32000	01110	00?02	00010	00
Voanioala	00001	041?0	00110	32000	01110	0??02	00000	?0
Geonoma	00001	04100	00110	32000	01110	00?00	00100	00
Welfia	00001	04100	00110	32000	01110	01?00	00100	00
Phytelephas seemanii	00001	04100	00110	02111	00210	00000	11000	00
Phytelephas tenuicaulis	00001	04100	00110	02111	00210	00000	11000	00

Inapplicable characters scored (-), unknown states scored (?), multistate characters scored (*)

Figure 2. **A.** *Arenga hookeriana* showing well developed cotyledonary sheath, single cataphyll, persistent primary root and collar roots (scale bar = 1.25 cm). **B.***Calamus flagellum*, short coleoptile and persistent primary root (scale bar = 6 mm). **C.** *Socratea exorrhiza*, hyperphyll absent, four cataphylls, horizontally arranged and persistent primary root and shoot born roots (scale bar = 9 mm). **D.** *Chryosophyla grayumii*, hyperphyll elongate, single cataphyll, persistent and straight primary root (scale bar = 1 cm). cat: cataphyll, cp: coleoptile, cr: collar roots, cs: cotyledonary sheath, hyp: hyperphyll, pr: primary root, sbr: shoot born roots.

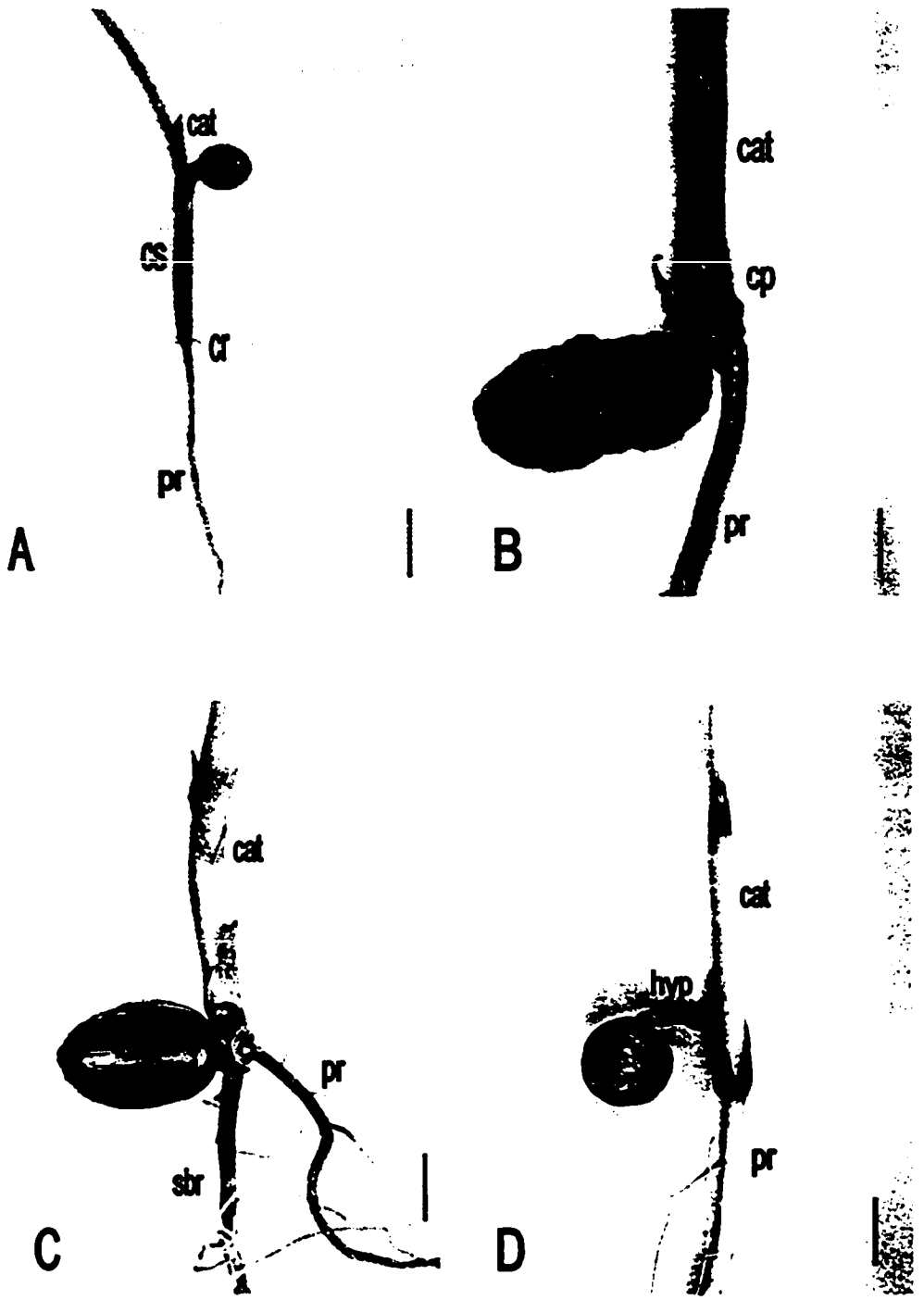


Figure 3. **A.** *Archontophoenix alexandreae*, deciduous primary root, shoot born roots present and two cataphylls (scale bar = 75 mm). **B.** *Calamus flagellum*, distinct swollen collar (scale bar = 25 mm). **C.** *Caryota mitis*, swollen hyperphyll (scale bar = 15 mm). **D.** *Nannorrhops ritchiana*, straight and persistent primary root, distinct coleoptile, hyperphyll attached to base of coleoptile (scale bar = 6 mm). cat: cataphyll, co: collar, cp: coleoptile, hyp: hyperphyll, pr: primary root, sbr: shoot born roots.

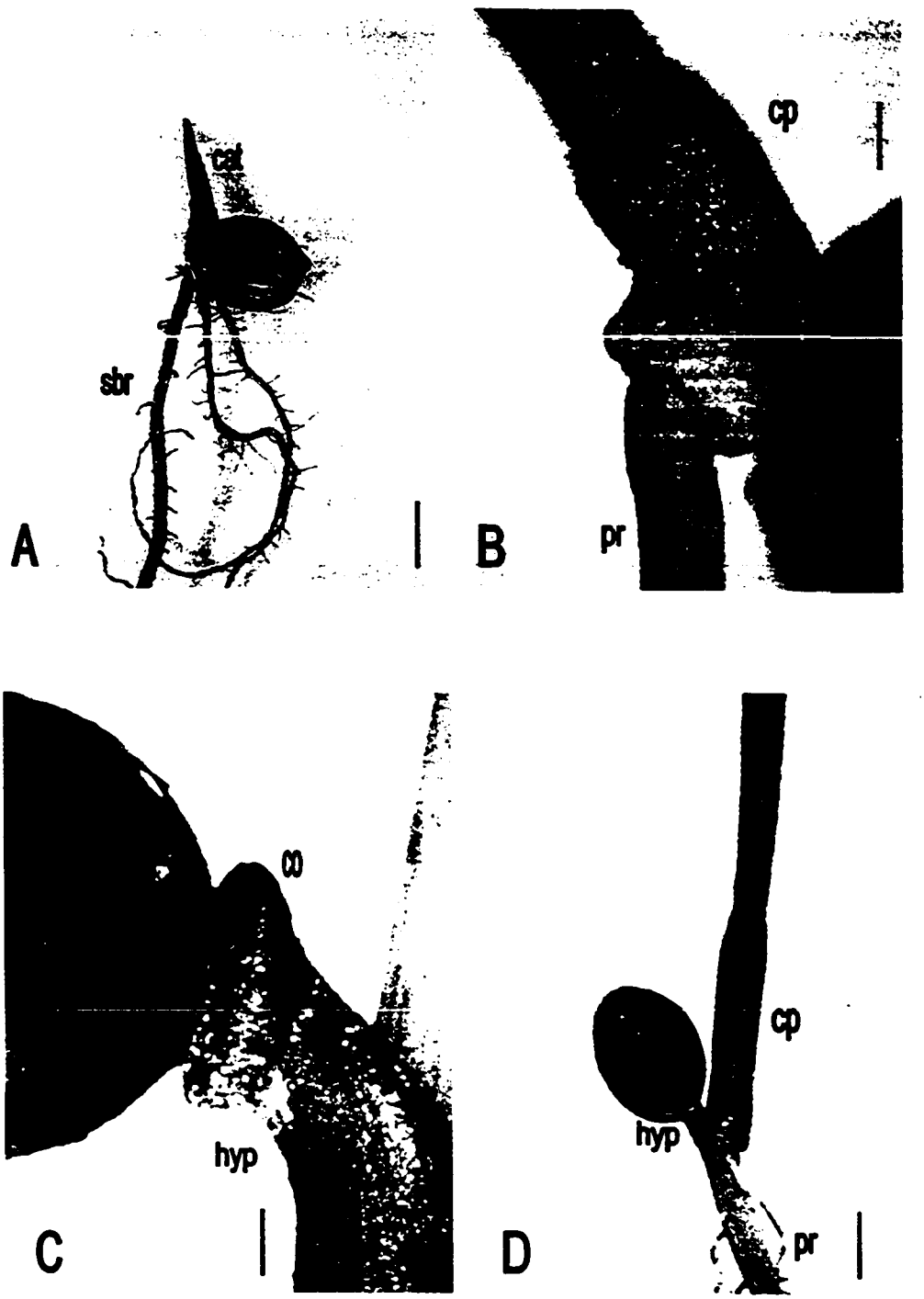


Figure 4. **A.** *Chamaerops humilis,* straight and persistent primary root, hyperphyll attached to distal end of cotyledonary sheath (scale bar = 70 mm) **B.** *Thrinax excelsa,* straight and persistent primary root, well developed cotyledonary sheath (scale bar = 5 mm). **C.** *Acoelorraphe wrightii,* vertically elongate hyperphyll, distinct coleoptile and short cotyledonary sheath (scale bar = 22 mm) **D.** *Ceroxylon* sp. Diagonally oriented primary root, short and split coleoptile (scale bar = 1 cm). cat: cataphyll, cp: coleoptile, cr: collar roots, cs: cotyledonary sheath, hyp: hyperphyll, pr: primary root, sbr: shoot born roots.

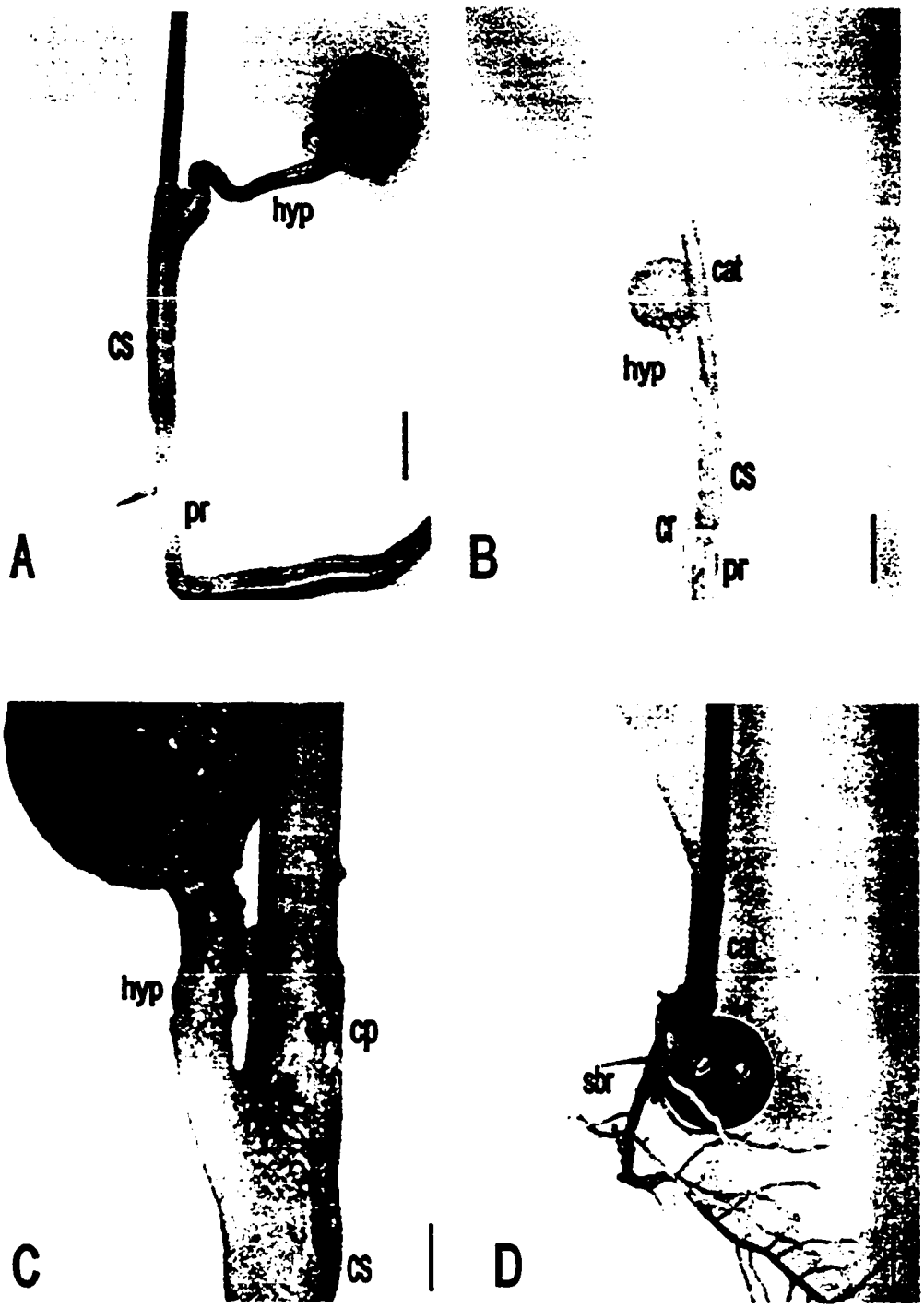
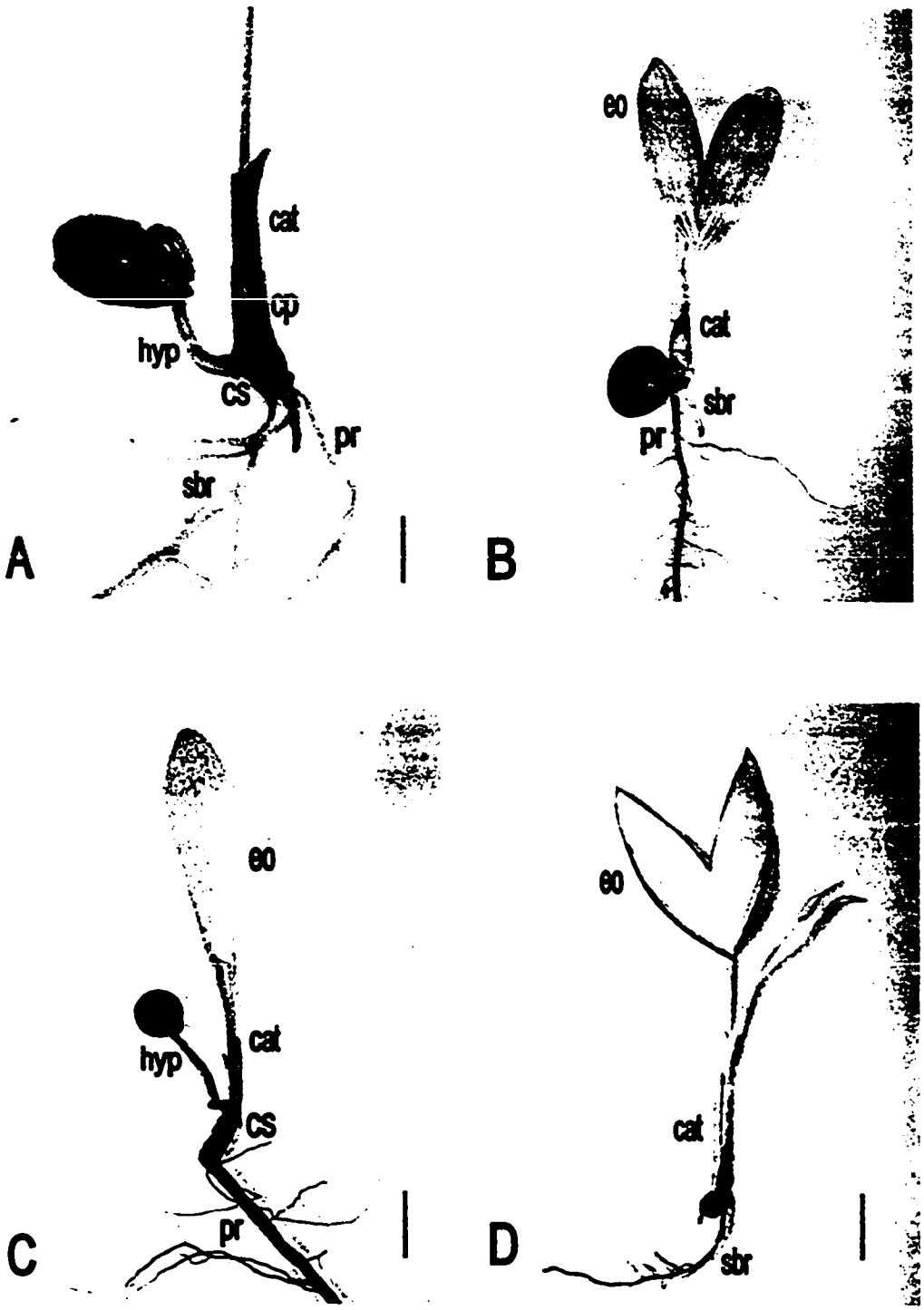
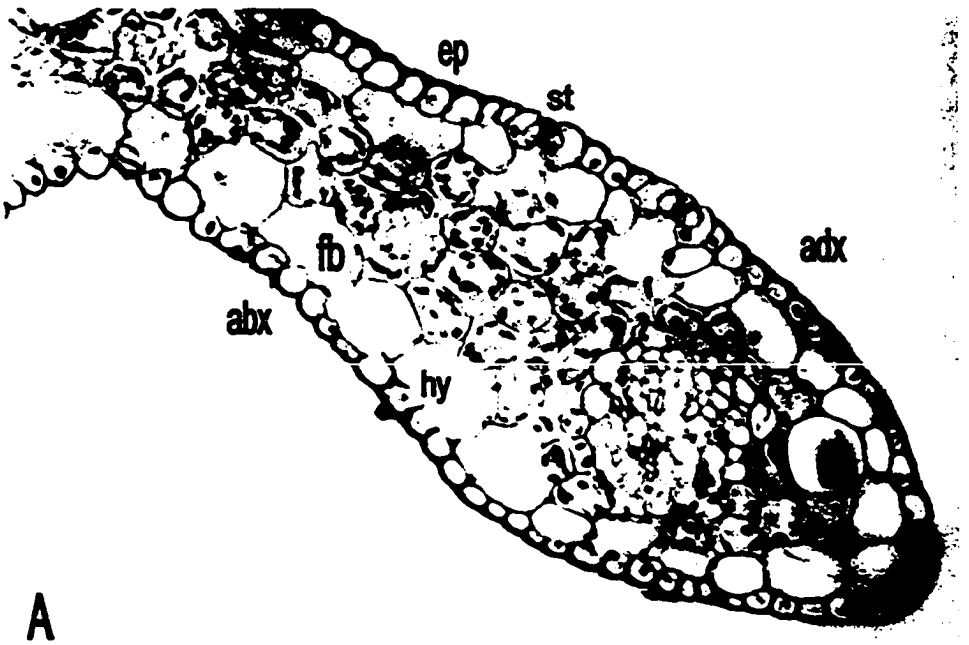


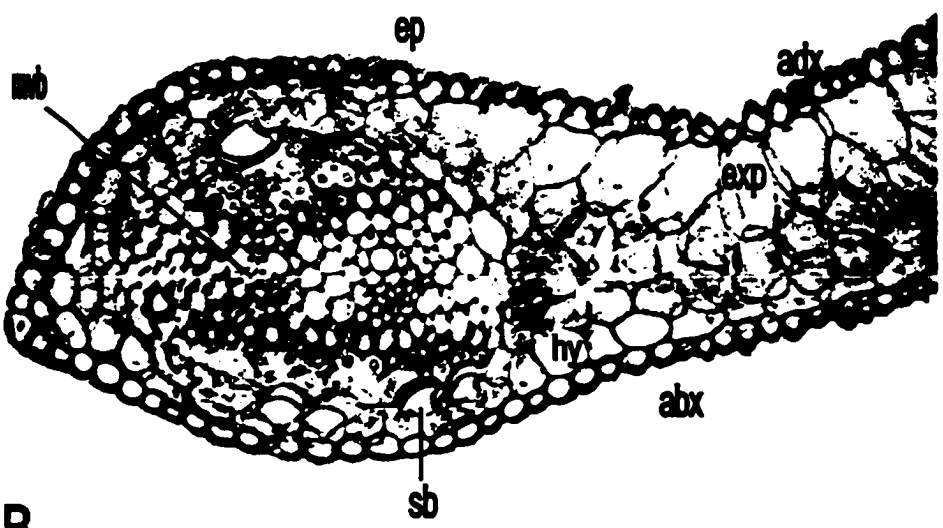
Figure 5. **A.** *Raphidophyllum histrix*, distinct coleoptile, reduced cotyledonary sheath, single scale leaf and ephemeral primary root (scale bar = 1.25 cm). **B.** *Astrocaryum alatum*, angular primary root, two cataphylls, bifid eophyll and pinnate venation (scale bar = 2.4 cm). **C.** *Corypha* sp. Persistent primary root, elongate hyperphyll, single cataphyll, entire eophyll, paralell venation and praemorse apex (scale bar = 2.5 cm). **D.** *Chamaedorea microspadix*, bifid eophyll and pinnate venation (scale bar = 3.35 cm). cat: cataphyll, cp: coleoptile, cs: cotyledonary sheath, eo: eophyll, hyp: hyperphyll, pr: primary root, sbr: shoot born roots.



.Figure 6. **A.** *Roystonea borinquena*, ʌ-shaped folding, distinct hypodermal layer, marginal vascular bundle, equidistant fibrous bundle (X 200). **B.** *Arenga hookeriana*, large marginal vascular bundle, distinct expansion cells on adaxial side, V-shapped folding, hat-shaped silica bodies around vein (X 200). abx: abaxial end, adx: adaxial end, ep: epidermal cells, exp: expansion cells, fb: fibrous bundles, hyp: hypodermimal cells, mvb: marginal vascular bundle, sb: silica bodies, st: stomata.



A



B

Figure 7. **A.** *Dictyosperma album*, rhombohedral epidermal cells, linear anticlinal walls (X 400). **B.** *Mauritia flexuosa*, rectangular epidermal cells, dentate anticlinal walls (X 400).

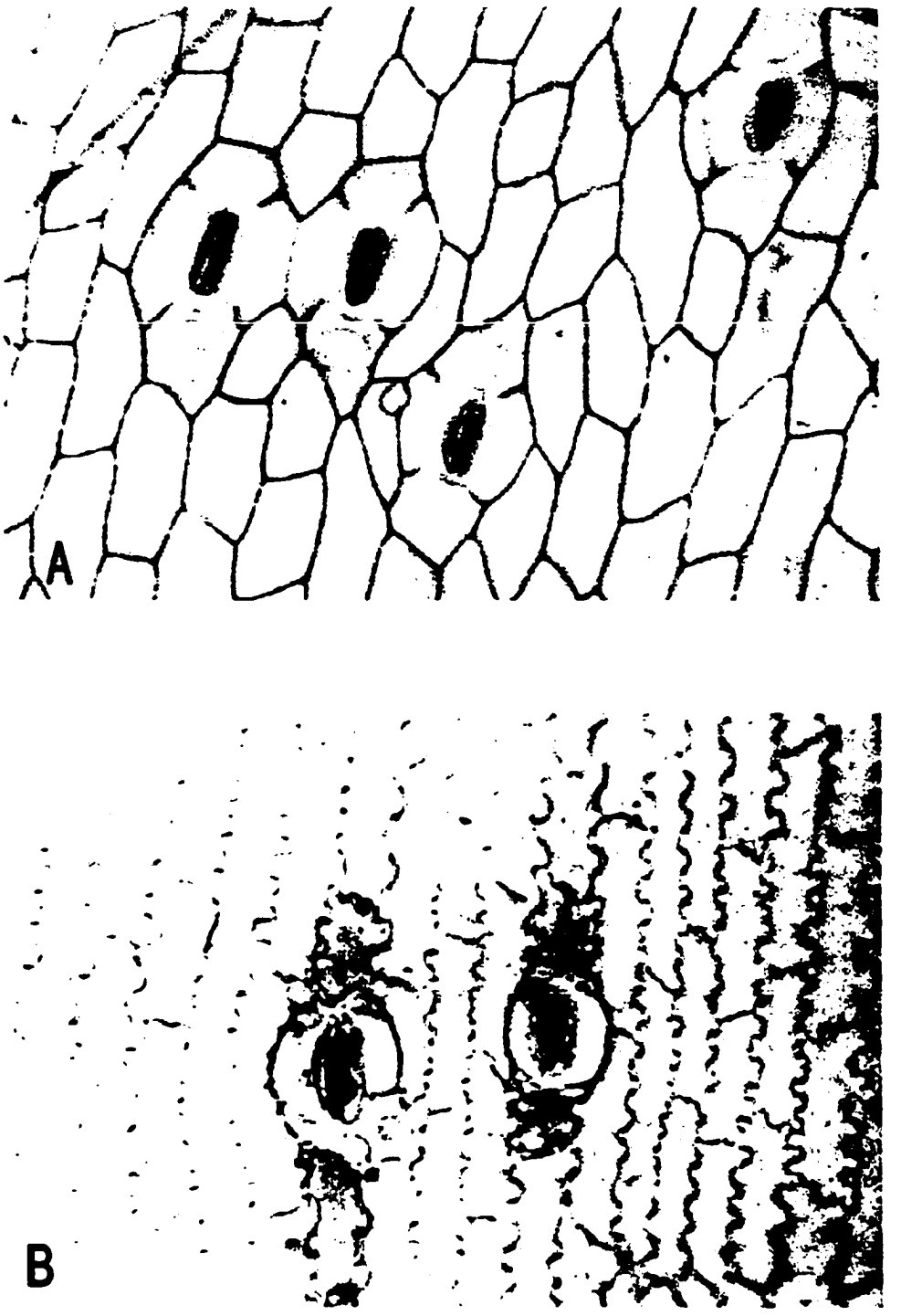


Figure 8. **A.** *Voanioala gerardii*, epidermal hair, sunken base, distinct hypodermal cells. (X 400). **B.** .*Ceroxylon* sp. Multicellular epidermal hair, base associated to vascular bundle, surrounding epidermis sunken (X 400). ep: epidermal cells, eph: epidermal hair, fbh: fibrous hypodermal layer, hyp: hypodermimal cells, vb: vascular bundle.

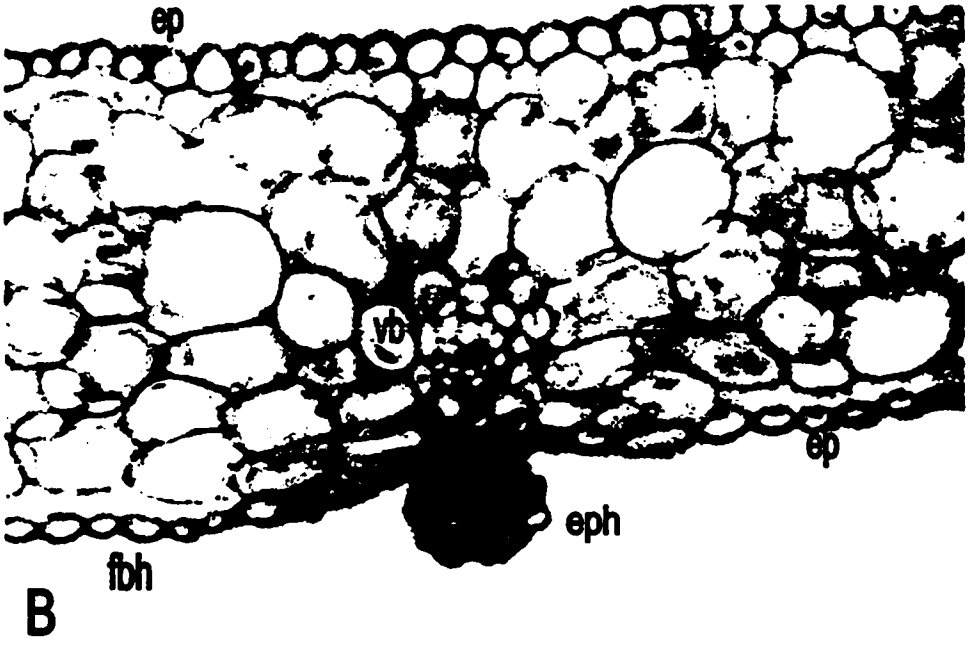
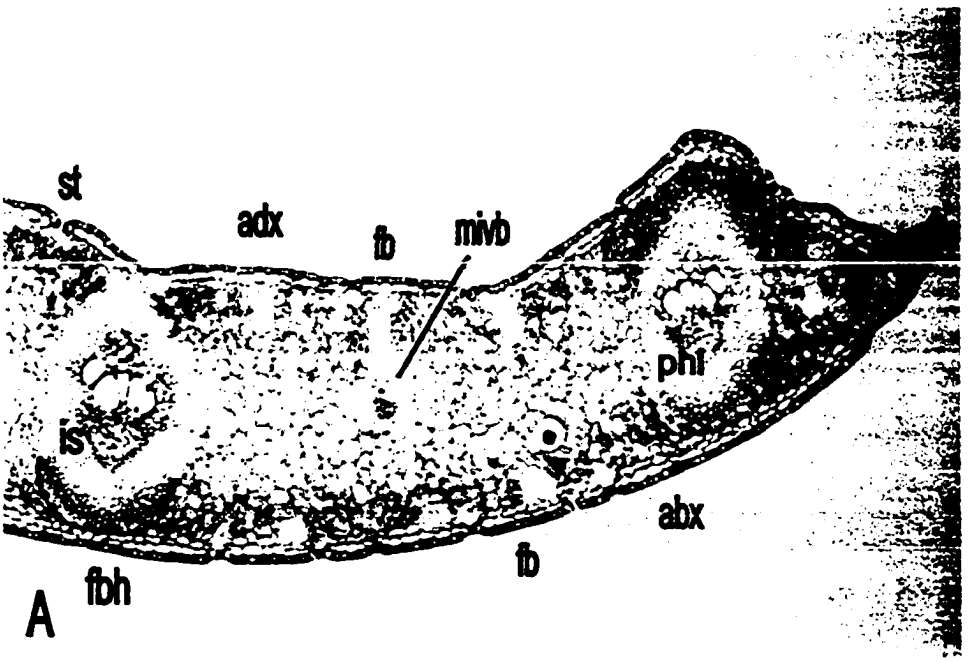


Figure 9. **A.** *Hyphaene coriacea*, sunken stomata, major vascular bundles attached to both surface layers, multilayered sclerotic IS, single phloem strand, minor veins buttressed to adaxial hypodermis and fibrous bundles at adaxial and abaxial sides (X 200). **B.** *Pseudophoenix sargentii*, marginal vascular bundle surrounded by fibrous layers, minor vascular veins equidistant from epidermal layers and two phloem strands (X 200). adx: adaxial end, abx: abaxial end, fb: fibrous bundles, fbh: fibrous hypodermal layer, is: inner sheath, mivb: minor vascular bundle, mjvb: major vascular bundle, phl: phloem, st: stomata.



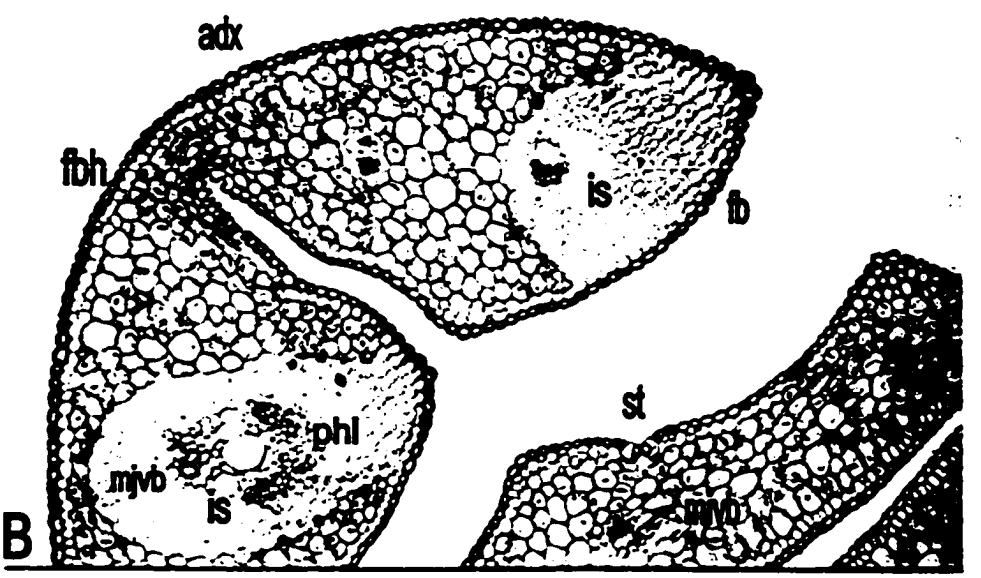
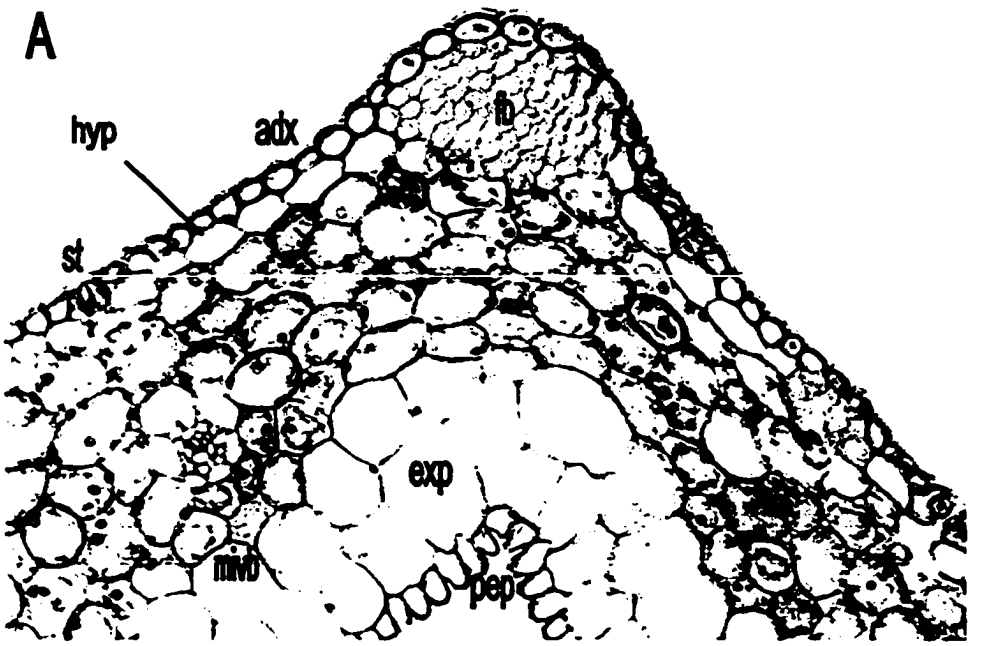
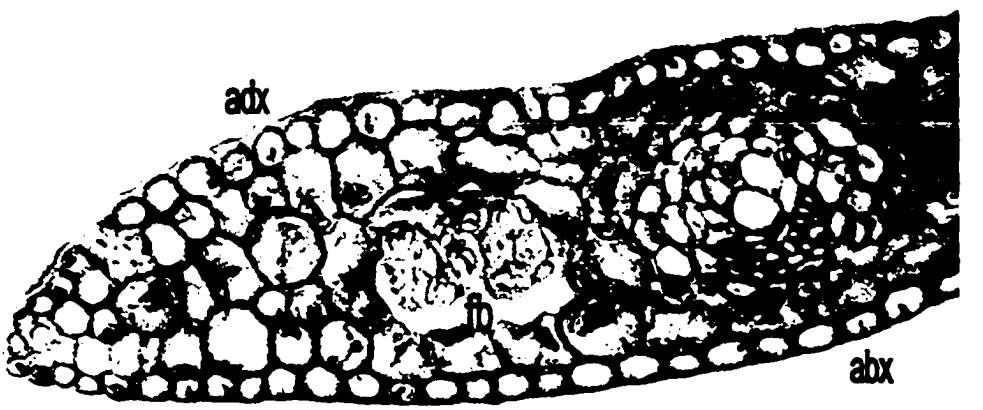


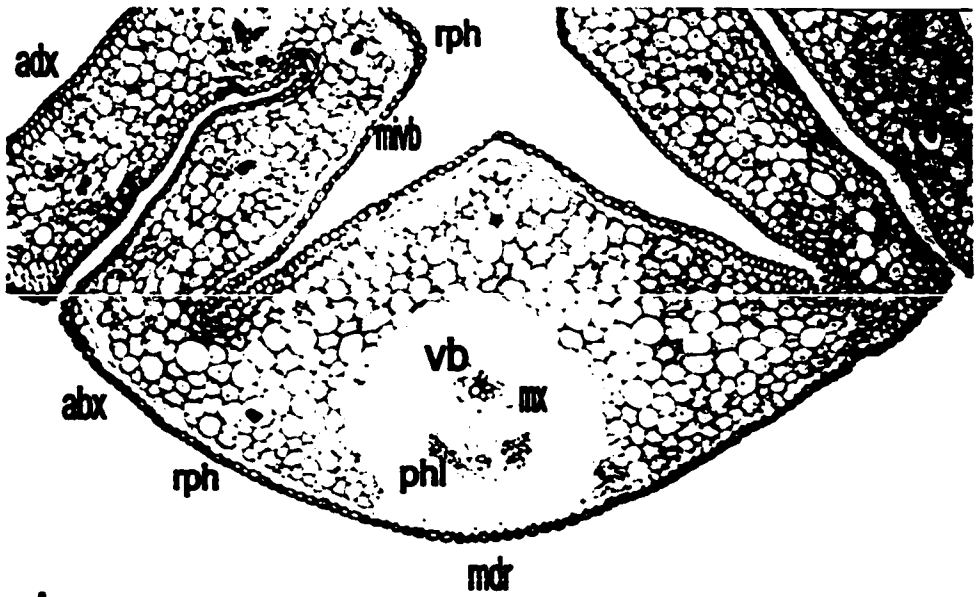
Figure 10. **A.** *Chamaerops humilis,* fibrous bundle at ridge, small bundles at adaxial hypodermis, distinct hypodermal layer, expansion cells, papilose epidermal cells and minor veins equidistant (X 200). **B.** *Calamus flagellum,* margins lacking vascular bundle, equidistant non-vascular fibrous bundle (X 200). adx: adaxial end, abx: abaxial end, exp: expansion cells, fb: fibrous bundles, hyp: hypodermal cells, mivb: minor vascular bundle, pep: papilose epidermis, st: stomata.



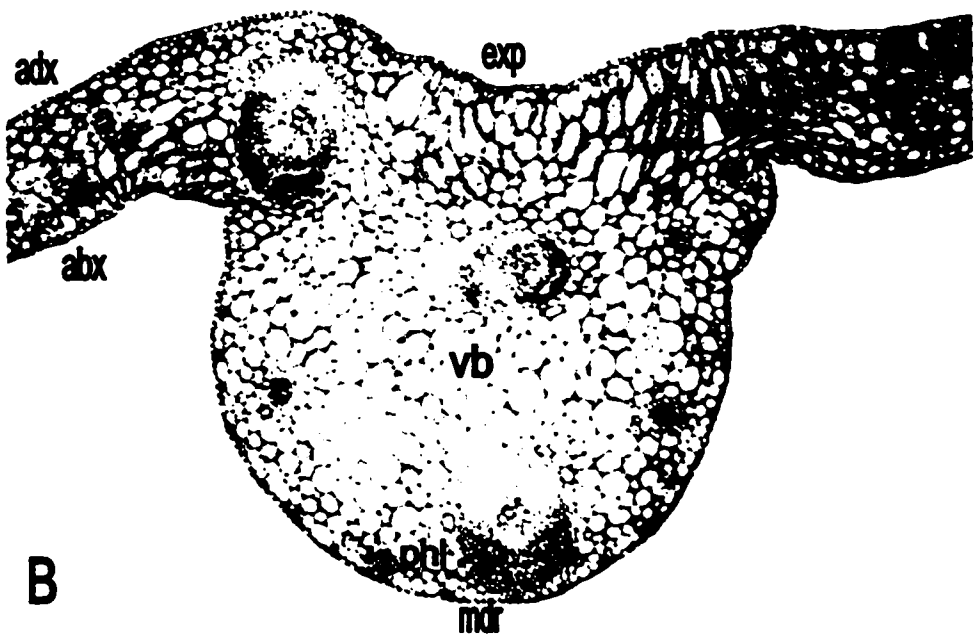


B

Figure 11. **A.** *Pseudophoenix sargentii*, midrib with single vascular bundle, two phloem strands, two metaxylem vessels, equidistant minor vascular bundles, abundant raphids (X 100). **B.** *Plectocomia* sp. Abaxially protuberant midrib, scattered vascular bundles (X 100).). adx: adaxial end, abx: abaxial end, exp: expansion cells, mdr: midrib, mx: metaxylem vessels, mivb: minor vascular bundle, phl: phloem strands, rph: raphides, vb: vascular bundles.

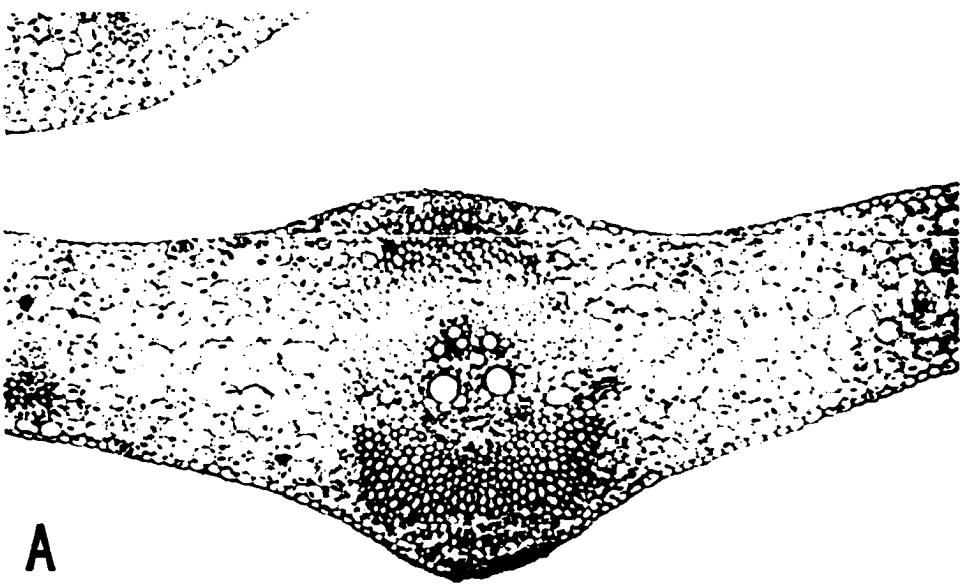


A



B

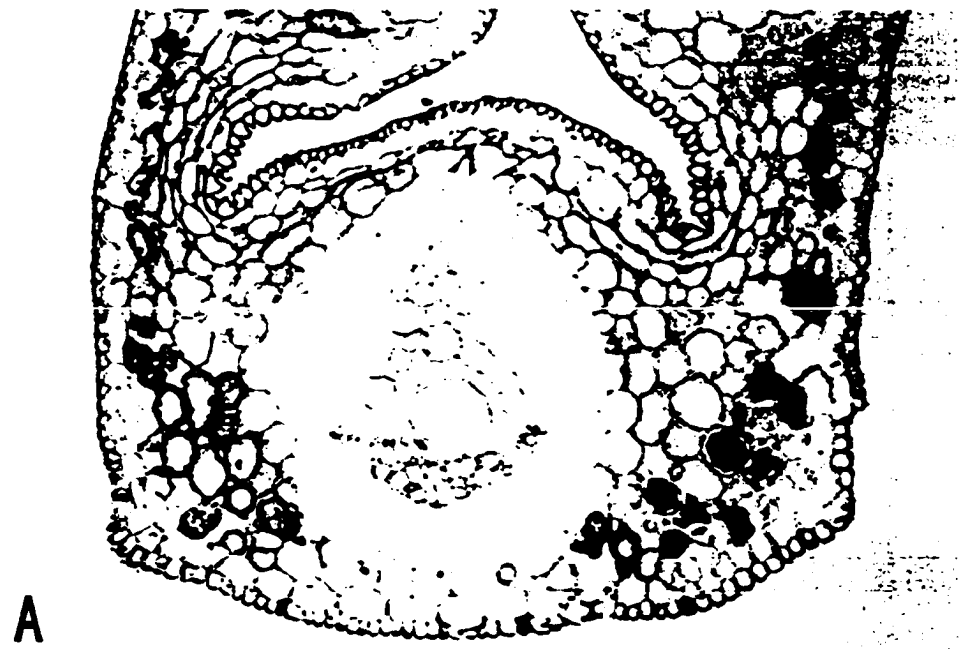
Figure 12. **A.** *Thrithrinax acanthocoma*, midrib slightly protuberant, single vascular bundle, single phloem strand, two metaxylem vessels, multilayered IS. minor veins attached to abaxial epidermis (X 100). **B.** *Nypa fruticans*, midrib protuberant to adaxial and abaxial sides; single multivascular bundle, distinct hypodermal layer, abundant minor veins oriented towards abaxial side (X 100).



A

B

Figure 13. **A.** *Borassus* sp. Protuberant midrib, single vascular bundle, single phloem strand and single metaxylem vessel, multilayered IS, tannins in full sacs (X 200). **B.** *Arenga hookeriana*, detailed view of hat-shaped silica bodies (X 400).



A

B

III RESULTS

1. Taxa description

The following are descriptions of the morphology of germination and anatomy of the eophyll. Groups are organized according to Moore's (1973) major groups. Taxa within each group are in alphabetical order.

1. CORYPHOID PALMS

Acoelorraphe wrightii (Griseb. & H. Wendl.) H. Wendl. ex Becc.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric and straight. **Primary root** stout and persistent, lacking a distinct disk collar; secondary roots simple; shoot-born roots present; root hairs present. **Hyperphyll** elongate and smooth, connected half way between cotyledonary sheath and coleoptile. **Cotyledonary sheath** distinct. **Coleoptile** opening apically, small splitting opposite to seed. **Cataphyll** one, apex acute. **Eophyll** simple, linear-lanceolate, apex acute. **Venation** pattern costa-

palmate; leaf axis reduced, midvein distinct along blade, vascular bundles convergent at apex; transverse commisures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear. **Hairs** absent. **Stomata** superficial; short terminal cell not overarching guard cells; arranged in regular lines at intercostal regions. **Hypodermis** single-layered, rounded regular cells at adaxial and abaxial sides; fibrous bundles at irregular intervals; lumen wide. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers; fibers appearing to be restricted to hypodermal layer. **Expansion cells** single-layered with scattered fibrous bundles. **Major vascular bundles** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; distinct OS. **Median vascular bundles** free, equidistant; IS single or double layered. **Minor vascular bundles** equidistant; IS single-layered; OS surrounding vascular bundle. **Midrib** adaxially prominent with a singlevascular bundle. **Marginal rib**

with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Tannins abundant in full sacs.

Chamaerops humilis L.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** Plumular/radicular axis symmetric. **Primary root** straight and persistent; secondary roots simple; shoot-born roots thick; root hairs present. **Hyperphyll** elongate and grooved. **Cotyledonary sheath** opening apically and eventually splitting lengthwise, opposite to hyperphyll. **Coleoptile** undeveloped. **Cataphyll** one. **Eophyll** simple, broadly lanceolate, apex acute; fifth leaf splitting along adaxial ridge. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, convergent at apex; transverse commisures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial

and abaxial anticlinal walls linear. **Hairs** absent. **Stomata** slightly sunken; short and occasionally elongate terminal cells overarching guard cells; more abundant in abaxial surface; scattered. **Hypodermis** single-layered, present at adaxial and abaxial sides; fibrous bundles at irregular intervals; solid bundles at ridges and grooves; lumen wide. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** single-layered, large rounded cells. **Major vascular bundles** associated with ridges, attached to adaxial and abaxial hypodermal layers; IS sclerotic multilayered; OS not distinct. **Median vascular bundles** free and equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, singlevascular bundle. **Marginal rib** with compact fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Tannins abundant, except in hypodermal and expansion cells.

Gatin (1906a) and Ginieis (1950, 1952) described germination in *Chamaerops*.

Chuniophoenix hainanensis Burret

Seed remaining above plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent;; secondary roots simple; shoot-born roots present; collar disk and collar roots present. **Hyperphyll** median length, smooth surface, slightly constricted at insertion to seed. **Cotyledonary sheath** distinct, rugulose. **Coleoptile** leathery, splitting opposite to seed. **Cataphyll** single, grooved. **Eophyll** simple, lanceolate, apex acute. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles; vascular bundles convergent at apex; transverse commisures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls slightly sinuous. **Hairs** present, few basal cells; associated to ribs. **Stomata** slightly sunken; short terminal cell not overarching guard cells; scattered.

Hypodermis single-layered; large rounded or ellipsoid cells, paralell orientation; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with with less than five layers. **Expansion cells** double layered. **Major vascular bundles** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; OS distinct. **Median vascular bundles** buttressed to adaxial side. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, singlevascular bundle. **Marginal rib lacking a vascular bundle**or fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** three. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides scattered, equidistant. Tannins scarce.

Colpothrinax cookii Read

Seed remaining above plumular/radicular node. **Plumular/radicular axis** asymmetric, forming an angle. **Primary root** persistent, disk collar distinct; secondary roots branched, pneumatophores scattered; shoot-born roots present; root hairs present.

Hyperphyll short and smooth, without grooves or furrows, attachment flat. **Cotyledonary sheath** extremely short. **Coleoptile** leathery, irregular splitting, opposite to seed. **Cataphyll** single, basal part naked and smooth, distal part rough and grooved. **Eophyll** simple, broadly lanceolate, apex acute, splitting along adaxial fold. **Venation** pattern palmate; leaf axis reduced; midvein distinct, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication with proximal** and distal marginal folds V-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear, sclerotic walls; cuticle thick. **Hairs** present, multicellular base associated or not associated to fibrous bundles. **Stomata** slightly sunken; short terminal cells overarching guard cells. **Hypodermis** single-layered, large ellipsoid, orientation paralell; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers; **Mesophyll fibers** forming compact bundles of about twenty strands, arranged at adaxial and abaxial sides; lumen small. **Expansion**

cells double layered, cells large rectangular and perpendicular; adjacent epidermal cells papillose. **Major vascular bundles** not associated with ridges; OS distinct. **Median vascular bundles** buttressed to adaxial side. **Minor vascular bundles** oriented towards abaxial side; OS surrounding vascular bundle. **Midrib** abaxially prominent; vascularized by a group of simple vascular bundles. **Marginal rib** not vascularized. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Raphides equidistant. Tannins in scattered full sacs.

Copernicia baileyana León

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** persistent, swollen collar absent; secondary roots simple; shoot-born roots absent; collar roots present; root hairs present. **Hyperphyll** elongate with a single groove in adaxial side; connection to seed swollen; attached to distal part of cotyledonary sheath. **Cotyledonary sheath** elongate, splitting

lengthwise, opposite to hyperphyll. **Coleoptile** absent. **Cataphyll** single, elongate, opening opening. **Eophyll** simple, linear-lanceolate, apex acute, with a short needle-like projection; margins spiny. **Venation** pattern palmate, leaf axis reduced, midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, elongate; adaxial and abaxial anticlinal walls linear. **Hairs** present, multicellular base associated to ribs. **Stomata** superficial; short terminal cells overarching guard cells; arranged into regular lines at intercostal regions. **Hypodermis** single-layered, present at adaxial and abaxial sides; fibrous bundles at irregular intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers; fibrous bundles at ridges. **Expansion cells** double layered; fibrous bundles scattered; lumen small. **Major vascular bundles** associated with ridges; buttressed to adaxial hypodermis; IS sclerotic multilayered; OS distinct.

Median vascular bundles free and equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** not prominent with single vascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides equidistant. Tannins abundant, in full sacs.

Corypha sp.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** straight. **Primary root** straight, stout and persistent; secondary roots branched; shoot-born roots absent; root hairs present; pneumatophores present. **Hyperphyll** elongate, grooved all around; swollen as it leaves seed. **Cotyledonary sheath** splitting lenghwise at opposite side to seed; conspicuous lenticels on cotyledonary sheath and hyperphyll. **Coleoptile** absent. **Cataphyll** single, opening apically. **Eophyll** simple, broadly oblanceolate, praemorse apex. **Venation** pattern costapalmate; leaf axis distinct; midvein distinct;

vascular bundles **diffuse** at intercostal areas; transverse commissures abundant, closelly arranged, some connect to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. Epidermal cells rectangular, adaxial anticlinal walls sinuous, abaxial walls linear. **Hairs** present, few basal cells associated to ribs. **Stomata** slightly sunken; short terminal cells overarching guard cells; lateral subsidiary cells ellipsoid. **Hypodermal** fibrous layer continuous. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** double layered; fibrous bundles scattered; lumen small. **Major vascular bundles** not associated with ridges, attached to adaxial and abaxial hypodermal layers; IS sclerotic, multilayered; OS distinct. **Median vascular bundles** free, oriented towards adaxial side, occasionally connected to transverse commisures. **Minor vascular bundles** buttressed to adaxial side; OS restricted to abaxial end, u-shaped. **Midrib** abaxially prominent, single vascular bundle. **Marginal rib** with minor vascular bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** one. **Metaxylem** single, large. **Cell**

inclusions, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Raphides, abundant, equidistant. Tannins scarce.

Gatin (1906a) described germination of *Corypha*.

Cryosophila grayumi R. Evans

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** persistent; secondary roots branched; shoot-born roots absent; root hairs absent. **Hyperphyll** moderate; single groove along adaxial side. **Cotyledonary sheath** single, longitudinally grooved; opening lengthwise, opposite to seed. **Coleoptile** absent. **Cataphyll** single, opening apical. **Eophyll** simple, broad, lanceolate, apex acute with a needle-like extension; about six or eight similar leaves born before splitted leaf, splitting side adaxial. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect some longitudinal

vascular bundles and end at intercostal areas. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear; covered by cuticle thick. **Hairs** free, few basal cells. **Stomata** slightly sunken, short and elongate terminal cells overarching guard cells, scattered. **Hypodermal** colorless layer absent, these replaced by a scatere subepidermal fibers. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers; fibrous bundles restricted to ridges and grooves; lumen wide. **Expansion cells** single-layered, ellipsoid, perpendicular; adjacent epidermal cells papillose. **Major vascular bundles** not associated with ridges; OS distinct. **Median vascular bundles** buttressed to adaxial side. **Minor vascular bundles** free, oriented towards abaxial side; OS cap-shaped. **Midrib** abaxially prominent, with single simplevascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** single. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around

vascular and fibrous bundles. Raphides abundant, equidistant. Tannins abundant.

Itaya amicorum H. E. Moore

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** straight and persistent; secondary roots simple; pneumatophores present; shoot-born roots absent; collar roots present. **Hyperphyll** extremely elongate, single groove on adaxial side; connection to seed flat. **Cotyledonary sheath** leathery; opens longitudinally, opposite to hyperphyll. **Coleoptile** absent. **Cataphyll** single, open lengthwise. **Eophyll** simple, broad, apex acute with a needle-like extension, later apex splitting into irregular segments. **Venation** pattern palmate; leaf axis reduced; midvein inconspicuous, vascular bundles convergent at apex; transverse commissures abundant, closelly arranged, connecting longitudinal or intercostal areas. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls sinuous; cuticle thick. **Hairs** present with few basal cells, not associated to

ribs. **Stomata** slightly sunken; short terminal cells overarching guard cells; scattered at intercostal regions. **Hypodermal** colorless cells absent, replaced by a continuous fibrous layer; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Expansion cells** single-layered; adjacent epidermal cells papillose. **Major vascular bundles** not associated with ridges; attached to abaxial epidermal layers; IS multilayered, sclerotic; OS distinct. **Median vascular bundles** free, towards abaxial side. **Minor vascular bundles** oriented towards abaxial side; OS surrounding vascular bundle. **Midrib** abaxially prominent, single multivascular bundle. **Marginal rib** with fibrous layers. **Petiole** not distinct. **Phloem strands** two. **Metaxylem** two. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose distributed around vascular bundles.

Livistona chinensis R. Br.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** straight and symmetric. **Primary root** straight and persistent, disk collar not distinct; secondary roots simple; shoot-born roots

present; collar roots present. **Hyperphyll** elongate, longitudinally grooved, connection to seed swollen. **Cotyledonary sheath** grooved. **Coleoptile** very short, opening apical. **Cataphyll** single, apical opening with a needle-like projection. **Eophyll** simple, broadly lanceolate, apex acute; three leaves similar to eophyll before first split leaf appears, splitting side adaxial. **Venation** pattern costapalmate; leaf axis distinct; midvein distinct, vascular bundles convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal vascular bundles and intercostal areas. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls sinuous. **Hairs** free, with few basal cells. **Stomata** superficial; short terminal cells overarching guard cells; two sets of lateral subsidiary cells. **Hypodermis** single-layered, present at adaxial and abaxial sides; fibrous bundles at irregular intervals; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibers** in scattered bundles, equidistant from surface layer or towards abaxial

side. **Expansion cells** double layered, rounded cells; fibrous bundles scattered; adjacent epidermal cells papillose. **Major vascular bundles** associated with ridges, buttressed to adaxial hypodermis; IS multilayered, sclerotic; OS distinct. **Median vascular bundles** free and equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, singlevascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions,** stegmata spherical or ellipsoid, margins spinulose; distributed around vascular bundles and fibrous bundles. Raphides equidistant.

Gatin (1906a), Zurawaska (1912), Mahabale and Kulkarni (1972), and Lothian (1959) described germination of *Livistona.*

Nannorrhops ritchiana (Griff.) Aitchson

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric. **Primary root** stout, persistent, extremely long; secondary roots simple; shoot-born roots present. **Hyperphyll** very short (ca. 1

cm. long.), smooth; connection to seed flat. **Cotyledonary sheath** not distinct, hyperphyll at base of coleoptile. **Coleoptile** elongate, apical opening. **Cataphyll** single, apex acute, apical opening, some cataphylls with ligule-like extensions. **Eophyll** simple, linear-lanceolate, apex acute with a needle-like extension. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures abundant, closely arranged, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, elongate, adaxial and abaxial anticlinal walls linear. **Hairs** present, with few basal cells. **Stomata** slightly sunken; short terminal cells overarching guard cells; scattered at intercostal regions. **Hypodermis** single-layered, rounded or ellipsoid,orientation paralell; present at adaxial and abaxial sides. **Chlorenchyma** well differentiate; palisade with two layers; spongy mesophyll with more than five layers. **Expansion cells** single-layered, slightly larger than epidermal cells. **Major vascular bundles** not associated with ridges,

attached to adaxial and abaxial hypodermis; IS multilayered, sclerotic; OS distinct. **Median vascular bundles** buttressed to adaxial hypodermis. **Minor vascular bundles** equidistant; OS surrounding vascular bundle; radial OS present. **Midrib** not prominent, vascularized by grouped simple vascular bundles. **Marginal rib** with majorvascular bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** three. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides abundant, equidistant. Tannins abundant in all cells, more concentrated on palisade cells.

Pritchardia remota (Kuntze) Becc.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent; secondary roots simple; shoot-born roots present and protruding throught cotyledonary sheath. **Hyperphyll** very short, smooth; connection to seed constricted. **Cotyledonary sheath** not distinct. **Coleoptile** leathery, opening apical, short slits opposite to hyperphyll. **Cataphylls** three, opening

lengthwise, needle-like projection at apex, second and third cataphylls bifid. **Eophyll** simple, broadly lanceolate, apex hairy, acute. **Venation** pattern costapalmate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal vascular bundles and intercostal areas. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls sinuous. **Hairs** present, few basal cells; associated to ribs. **Stomata** superficial; short terminal cells overarching guard cells; scattered at intercostal regions. **Hypodermis** single-layered, present at adaxial and abaxial sides, fibers at regular intervals; lumen wide. **Chlorenchyma** well differentiated; palisade single-layered; spongy mesophyll with more than five layers. **Expansion cells** double layered, scattered fibrous bundles. **Major vascular bundles** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS distinct. **Median vascular bundles** free and equidistant. **Minor vascular bundles**

equidistant; IS multilayered, sclerotic; OS surrounding vascular bundle; radial OS present. **Midrib** abaxially prominent, singlevascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Raphides abundant, equidistant. Tannins abundant.

Rhapidophyllum hystrix (Pursh) H. Wendl. & Drude

Seed remaining above plumular/radicular node. **Plumular/radicular axis** asymmetric angular. **Primary root** persistent, collar disk distinct; secondary roots simple; shoot-born roots protruding through cotyledonary sheath. **Hyperphyll** moderate, smooth; connection to seed constricted; attaching at mid point between cotyledonary sheath and coleoptile. **Cotyledonary sheath** leathery. **Coleoptile** elongate, slightly grooved, opening apically, eventually a short slit appears, opposite to hyperphyll. **Cataphyll** single, slightly furrowed; opening lengthwise, apex pointed. **Eophyll** simple, broadly lanceolate, apex

acute. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, connectinh some longitudinal vascular bundles and intercostal regions. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear. **Hairs** present, few basal cells; associated to ribs. **Stomata** slightly sunken; short terminal cells overarching guard cells; scattered at intercostal regions. **Hypodermis** single-layered, at adaxial and abaxial sides; fibrous bundles at irregular intervals; lumen wide. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** double layered, scattered fibrous bundles; adjacent epidermis papillose. **Major vascular bundles** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS not well differentiated. **Median vascular bundles** free and equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, single simplevascular bundle.

Marginal rib with fibrous bundles. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, large, margins spinulose, distributed around vascular bundles. Raphides present. Tannins abundant.

Clancy and Sullivan (1988) and Carpenter et al. (1993) described germination in *Rhapidophyllum*.

Sabal minor (Jacq.) Persoon

Seed remaining above plumular/radicular node. **Plumular/radicular axis** asymmetric angular. **Primary root** persistent; secondary roots branched; shoot-born roots absent. **Hyperphyll** elongate; connecting to lower part of coleoptile, forming saxophone-shape projection below the primary root and plumule connection. **Cotyledonary sheath** short or absent. **Coleoptile** with basal part curved; leathery texture, opening apical. **Cataphyll** single, apex leathery. **Eophyll** simple, lanceolate, apex acute; nine leaves similar to eophyll appearing before first segmented leaf; splitting occurs at grooves on adaxial side. **Venation pattern**

palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal vascular bundles and intercostal areas. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear. **Hairs** present, few basal cells. **Stomata** slightly sunken, short terminal cells overarching guard cells, scattered. **Hypodermis** single-layered, present at adaxial and abaxial side. **Chlorenchyma** undifferenciated; spongy mesophyll with more than five layers. **Mesophyll fibers** in bundles at ridges and grooves; lumen wide. **Expansion cells** double layered. **Major vascular bundles** not associated with ridges, attached to adaxial and abaxial epidermal layers; IS multilayered, sclerotic IS; OS distinct. **Median vascular bundles** buttressed to abaxial and adaxial sides. **Minor vascular bundles** buttressed to adaxial side; OS u-shaped. **Midrib** not prominent, square, with singlevascular bundle. **Marginal rib** with minor vascular bundles and a fibrous bundles. **Petiole** transverse section crescent-shaped. **Phloem strands**

three. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Raphides scarce, equidistant. Tannins scarce.

Germination of *Sabal* was described by Holm (1891) and Gatin (1906a).

Serenoa repens (Bartram) Small

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** stout and persistent; secondary roots simple, extremely elongate; shoot-born roots present. **Hyperphyll** moderate, smooth; as in *Sabal* connecting almost directly to radicle; attachment flat. **Cotyledonary sheath** short; hyperphyll attached to lower part. **Coleoptile** opening apically with two opposite slits. **Cataphyll** single, opening lengthwise, apex with asymmetric split. **Eophyll** simple, lanceolate; seven leaves similar to eophyll appearing before first segmented leaf, splitting side adaxial. **Venation pattern** palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles,

vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear; cuticle thick and forming a continuous layer. **Hairs** present, few basal cells; associated to ribs. **Stomata** superficial; short terminal cells overarching guard cells; scattered at intercostal regions. **Hypodermis** single-layered, at adaxial and abaxial sides, fibers at irregular intervals. **Palisade layer** distinct; spongy mesophyll with more than five layers. **Mesophyll fibrous bundles** restricted to grooves; lumen wide. **Expansion cells** double layered, ellipsoid, transversally arranged. **Major vascular bundles** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS distinct. **Median vascular bundles** free, oriented towards abaxial side. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** not prominent, single bundle. **Marginal rib** with fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem**

single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Tannins abundant, scattered, mostly concentrated on palisade parenchyma.

Germination of *Serenoa* has been described by Fisher and Tomlinson (1973) and Hilmon (1968.

Thrinax excelsa Lodd. ex Griseb.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight, **Primary root** persistent; secondary roots simple. **Hyperphyll** moderate, with a single adaxial groove, connection to seed constricted. **Cotyledonary sheath** opening with a small slit at distal end. **Coleoptile** absent. **Cataphyll** single, opening apical, apex acute. **Eophyll** simple, linear-lanceolate, apex acute with needle-like projection; five leaves similar to eophyll before first split leaf appears, splitting side adaxial. **Venation** pattern palmate; leaf axis reduced; midvein present along blade, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular

bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular to slightly rhombohedral, adaxial and abaxial anticlinal walls linear. **Hairs** present, few basal cells. **Stomata** superficial; elongate terminal cells overarching guard cells, arranged in single files at intercostal regions. **Hypodermis** single-layered, present at adaxial and abaxial sides; fibrous bundles at regular intervals; lumen wide. **Chlorenchyma Palisade layer** distinct; spongy mesophyll with less than five layers. **Expansion cells** double layered, short perpendicular rectangular cells, scattered fibrous bundles. **Major vascular bundles** not associated with ridges; IS multilayered, sclerotic; OS distinct. **Median vascular bundles** not distinct from major vascular bundles. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** not prominent, simplevascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** single. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides abundant, equidistant.

Trithrinax brasiliensis (Mart.)

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** stout and persistent, collar disk swollen; secondary roots branched; shoot-born roots present; collar roots present. **Hyperphyll** elongate, single groove in adaxial side, connection to seed flat. **Cotyledonary sheath** opening lengthwise to node, splitting opposite to hyperphyll. **Coleoptile** undeveloped. **Cataphyll** single, plicate, apex acute. **Eophyll** simple, lanceolate, apex concave with sharp acuminate projection. **Venation** pattern palmate; leaf axis reduced; vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear. **Hairs** absent. **Stomata** slightly sunken; short and elongate terminal cells overarching guard cells; scattered at intercostal regions. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with

more than five layers. **Mesophyll fibers** in bundles restricted to ridges and grooves; lumen wide. **Expansion cells** single-layered, slightly larger than epidermal cells, rounded, more conspicuous on distal portion of lamina. **Major vascular bundles** not associated with ridges, attached to adaxial and abaxial epidermal layers; IS multilayered, sclerotic; OS distinct. **Median vascular bundles** buttressed to both abaxial and adaxial sides. **Minor vascular bundles** abaxially buttressed; OS cap-shaped. **Midrib** not prominent, single simplevascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** single. **Metaxylem** two. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides equidistant. Tannins scarce.

Trachycarpus sp.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** stout and persistent; secondary roots simple. **Hyperphyll** moderate, covered by tegument, connection to seed flat. **Cotyledonary sheath** grooved, leathery,

opening lengthwise down to node. **Coleoptile** absent. **Cataphyll** single, apex acute. **Eophyll** simple, lanceolate, apex acute with needle-like projection. **Venation** pattern costapalmate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular or slightly rhombohedral, adaxial and abaxial anticlinal walls linear. **Hairs** multicellular, few basal cells. **Stomata** slightly sunken; elongate terminal cells overarching guard cells; scattered at intercostsl regions. **Hypodermis** single-layered, at adaxial and abaxial sides, occasionally interrupted by fibrous bundles. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibers** in bundles restricted to ridges and grooves; lumen wide. **Expansion cells** double layered. **Major vascular bundles** not associated with ridges, attached to adaxial epidermis and abaxial hypodermis; IS multilayered, sclerotic; OS distinct, **Median vascular**

bundles buttressed to both abaxial and adaxial sides. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, rounded; single multivascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions,** stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides present. Tannins in full sacs scattered.

Gatin (1906a) and Depoux (1968, 1969) described germination of *Trachycarpus*.

Washingtonia filifera (Linden) H. Wendl.

Seed remaining above plumular/radicular node. **Plumular radicular axis** symmetric, straight. **Primary root** stout and persistent, distinct swollen collar; secondary roots simple; shoot-born roots; collar roots present; root hairs present. **Hyperphyll** short, smooth, attached to lower part of coleoptile; connection to seed flat. **Cotyledonary sheath** not distinct. **Coleoptile** opening apically. **Cataphyll** single, opening apically, apex acute. **Eophyll** simple, linear-

lanceolate, apex acute with needle-like projection; nine or ten eophyll like leaves born before first split leaf, split along adaxial side. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures abundant, closely arranged, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear. **Hairs** absent. **Stomata** slightly sunken; short terminal cells overarching guard cells; scattered al intercostal regions. **Hypodermis** single-layered, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Non Vascular fibers** in layers, restricted to grooves; lumen wide. **Expansion cells** double layered, large, ellipsoid; perpendicular. **Major vascular bundles** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic IS; OS distinct. **Median vascular bundles** free, oriented towards abaxial side. **Minor vascular bundles** equidistant; OS surrounding vascular bundle.

Midrib not prominent, vascularized by grouped simple vascular bundles. **Marginal rib** with small fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions,** stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides equidistant. Tannins abundant.

Gatin (1906a), Ginieis (1952b) and De Mason (1988) described germination of *Washingtonia*.

Summary for Coryphoid palms

Plumular/radicular axis straight; primary root straight and persistent, collar roots developed or do not develop; hyperphyll elongate or contracted, cotyledonary sheath opening laterally or apically, a coleoptile present or absent, cataphyll one (three in *Pritchardia*). Eophyll simple, lanceolate or linear-lanceolate, and acute or lobed at apex, eophyll has palmate or costapalmate venation and no obvious mid-vein, and V-shaped marginal folding, a series of up to 9 leaves similar to eophyll borne.

Note: In *Chamaerops, Livistona,* and *Trachycarpus* the plumular/radicular axis straight and oblique to axis of embryo, cotyledonary sheath opening apically, and a coleoptile absent. Some genera have horizontal eophylls with elongate petioles: *Cryosophila, Livistona.*

Other genera have erect eophylls with short petioles: *Trithrinax, Chamaerops, Thrinax, Coccothrinax, Sabal, Acoelorraphe, Trachycarpus.*

2. PHOENICOID PALMS

Phoenix roebelinii O' Brien

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple; collar roots present. **Hyperphyll** short; single groove at adaxial side; connection to seed flat. **Cotyledonary sheath** elongate, smooth; opening apically by a short slit; apex concave. **Coleoptile** absent. **Cataphyll** single. **Eophyll** simple, linear-lanceolate, apex with needle-like projection; seven eophyll like leaves borne before split leaf appears, splitting at adaxial side,

starts at base. **Venation** pattern costapalmate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear; wall thickened; cuticle thick. **Hairs** absent. **Stomata** slightly sunken; short terminal cells not overarching guard cells. **Hypodermis** single-layered, cells rounded, at adaxial and abaxial sides; large solid fibrous bundles at irregular intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Mesophyll fibers** in bundles at adaxial and abaxial sides; lumen small. **Expansion cells** double layered, epidermal cells papillose, with scattered fibrous bundles. **Major vascular bundles** not associated with ridges, attached to adaxial and abaxial hypodermis; IS multilayered and sclerotic; OS distinct. **Median vascular bundles** free and equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** not prominent;

simple vascular bundle not centered and adjacent to fold. **Marginal rib** with fibrous bundle. **Petiole** transverse section crescent-shaped-shaped. **Phloem strands** one. **Metaxylem** single. **Cell inclusions,** stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides present. Tannins abundant, present in all mesophyll.

Germination of *Phoenix* has been described many times, beginning with illustration of Camerarius (1588). Other descriptions those of Sachs (1862), Gatin (1906a), and Ginieis (1951, 1957).

Summary for Phoenicoid palms

summary for major group same as genus

3. BORASSOID PALMS

Borassus sp.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple, with pneumatophores at the base; collar roots born on

surface of flat collar disk. **Hyperphyll** smooth and covered by lenticels. **Cotyledonary sheath** covered by lenticels. **Coleoptile** absent. **Cataphyll** single, thick, robust; opening apically, apex curved inwards. **Eophyll** simple, broadly lanceolate, apex crenulate. **Venation** pattern costapalmate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles divergent at apex; transverse commissures abundant, closely arranged, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear; cells adjacent to ridges with thickened walls. **Hairs** absent. **Stomata** sunken; short terminal cells overarching guard cells; two lateral subsidiary cells at each side of guard cells; both sets attached to the same terminal cells. **Hypodermis** single-layered; cells large, rounded, at adaxial and abaxial sides; fibrous layers or bundles at irregular intervals. **Chlorenchyma** well differentiated; palisade with two layers; spongy mesophyll with more than five layers. **Mesophyll fibers** in bundles at adaxial and abaxial sides; lumen wide.

Expansion cells double layered, rectangular or ellipsoid, perpendicular, adjacent epidermal cells papillose; with scattered fibrous bundles. **Major vascular bundles** not associated with ridges, attached to both hypodermal layers; IS multilayered; OS distinct. **Median vascular bundles** buttressed to adaxial side. **Minor vascular bundles** buttressed to adaxial side; OS u-shaped; some vascular bundles present at grooves. **Midrib** prominent, square, with single vascular bundle. **Marginal rib** with minor vascular bundles and fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** three, one large central and two small lateral. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides equidistant. Tannins abundant, some in full sacs.

Gatin (1906a), Dassanayake and Sivakadachchan (1973), and Padmanabhan et al. (1978) have described germination of *Borassus*.

Hyphaene coriacea Gaertn.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** persistent; secondary roots with distinct pneumatophores at base; shoot-born roots absent. **Hyperphyll** elongate grooved all around; connection point to seed slightly swollen. **Cotyledonary sheath** thick, opening apically, opposite short split; abundant lenticels covering hyperphyll and cotyledonary sheath. **Coleoptile** absent. **Cataphyll** single, plicate, curved inwards. **Eophyll** simple, linear-lanceolate, apex nearly closed and pointed. **Venation** pattern costapalmate; leaf axis distict; midvein distinct, vascular bundles convergent at apex; transversecommissures widely separated from each other, connecting some longitudinal vascular bundles and intercostal areas. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear; cuticle layer thick and uniform. **Hairs** multicellular, with multicellular base. **Stomata** sunken; guard cells with distinct ledges; large substomatal chamber; in surface view short terminal cells overarching guard cells; two lateral

subsidiary cells on each side of guard cells; scattered at intercostal regions. **Hypodermis** double layered, adaxial and abaxial sides. **Chlorenchyma** well differentiated; palisade layer distinct; spongy mesophyll with more than five layers. **Mesophyll fibers** in solid rounded and ellipsoid bundles of approximately 14 strands; distributed at adaxial and abaxial sides; lumen wide. **Expansion cells** double layered; adjacent epidermis papillose; scattered fibrous bundles. **Major vascular bundles** not associated with ridges; OS distinct. **Median vascular bundles** buttressed to both abaxial and adaxial sides. **Minor vascular bundles** buttressed at adaxial side and abaxial sides; OS u-shaped or cap-shaped; some vascular bundles present at grooves. **Midrib** prominent at adaxial and abaxial sides; vascularized by grouped simple vascular bundles. **Marginal rib** with minor vascular bundles and fibrous layers. **Petiole** transverse section crescent-shaped-shaped. **Phloem strands** three, large central and two small lateral. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides abundant, equidistant.

Latania loddegesii Mart.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple, pneumatophores at the base; root hairs present. **Hyperphyll** elongate, grooved all around; attachment to seed swollen. **Cotyledonary sheath** opening lengthwise; lenticels cover hyperphyll, cotyledonary sheath and primary root. **Coleoptile** absent. **Cataphyll** single, plicate, apex acute. **Eophyll** palmate, linear segments, spiny margins, splitting side adaxial. **Venation** pattern palmate; leaf axis reduced; midvein present in each segment, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear. **Hairs** present, multicellular base. **Stomata** sunken; guard cells with conspicuous ledges; short terminal cells overarching guard cells; two lateral subsidiary cells on each side of guard cells.

Hypodermis single-layered, ellipsoid, orientation paralell; present at adaxial and abaxial sides. **Chlorenchyma** well differentiated; palisade with two to three layers; spongy mesophyll with more than five layers, ca. 12 on wider portion. **Mesophyll fibers** restricted to mesophyll, arranged in solid rounded bundles, at adaxial and abaxial sides; lumen wide. **Expansion cells** double layered; adjacent epidermis papillose; with scattered fibrous bundles. **Major vascular bundles** not associated with ridges; buttressed to adaxial and abaxial hypodermal layers; IS multilayered, sclerotic and fibrous; OS distinct. **Median vascular bundles** buttressed to adaxial side; IS multilayered, sclerotic and fibrous. **Minor vascular bundles** buttressed to adaxial side; OS u-shaped; some associated to grooves. **Midrib** prominent at adaxial and abaxial sides, vascularized by grouped simple vascular bundles. **Marginal rib** with fibrous bundle. **Petiole** transverse section crescent-shaped-shaped. **Phloem strands** three, large central and two small lateral. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around

vascular bundles. Raphides abundant, equidistant. Tannins scarce.

Gatin (1906a) has described germination of *Latania*.

Summary for Borassoid palms

Plumular/radicular axis straight; primary root straight and persistent, collar roots developed or do not develop; hyperphyll elongate (up to 4 m in *Lodoicea*, Tomlinson, 1990), cotyledonary sheath opening laterally, a coleoptile absent, cataphylls one, eophyll simple or palmate, apex acute. Eophyll has palmate venation, and V-shaped marginal plication. Note: Some coryphoids (*Livistona, Trachycarpus, Chamaerops*), all phoenicoids, all Borassoids, and all caryotoids have similar germination.

4. CALAMOID PALMS

Calamus flagellum Griff.

Seed attached above plumular/radicular node. **Plumular/radicular** axis asymmetric, forming an angle. **Primary root** straight, vertical, persistent; collar

disk distinct and swollen; secondary roots branched, abundant; collar roots and root hairs absent. **Hyperphyll** inconspicuous, attachment surface flat; attached to base of coleoptile. **Cotyledonary sheath** not well developed. **Coleoptile** present, splitting longitudinally at opposite side of seed; texture rugulose. **Cataphylls** two, opening lengthwise, apex acute. **Eophyll** bifid, splitting along grooved side; segments sigmoid; petiole and leaf margins spiny. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures simple and bifurcate, connected mainly to secondary vascular bundles; abundant and closely arranged. **Plication** with proximal marginal folds Λ-shaped, distal outer marginal fold Λ-shaped, inner fold V-shaped; plication slightly sinuous. **Epidermal cells** rectangular, anticlinal walls dentate; intercostal cells slightly narrow and elongate than costal cells. **Hairs** present with few basal cells. **Stomata** superficial; arranged in regular files at intercostal regions on both surfaces, more abundant in abaxial surface; terminal cells short and overarching

guard cells. **Hypodermal** parenquimatous layer replaced by fibrous bundles at irregular intervals, forming an almost continuous fibrous layer at adaxial side. **Chlorenchyma** not differentiated; spongy mesophyll with large cells, arranged in less than five layers; **Mesophyll fibers** arranged in large solid bundles of more than ten strands, these oriented towards abaxial side; fiber lumen small. **Expansion cells** arranged in single or double layers, cells elongate, ellipsoid and rectangular; restricted to lateral flanks of major vascular bundles; fibrous bundles at outermost sides. **Major vascular bundles** associated with ridges, rounded and prominent; fibrous buttresses at adaxial side, attached to hypodermal layer; OS distinct at lateral sides of vascular bundle. **Median vascular bundles** free, oriented towards abaxial side; IS multilayered and sclerotic; OS lateral; adaxial fibrous buttress attached to hypodermal layer. **Minor vascular bundles** free, oriented towards abaxial side, not associated to grooves on abaxial folds; IS single-layered, surrounding vascular bundle; OS restricted to the adaxial end forming a cap-shaped layer. **Midrib** abaxially prominent, distinct only at proximal

section, adaxial side irregular, abaxial side rounded; highly vascularized by simple vascular bundles. **Marginal rib** occupied by subepidermal fibrous layers. **Petiole** rounded abaxially. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Tannins scattered.

Germination of *Calamus* was described by Gatin (1906a), Ginieis (1965), and Ilangovan and Padmanabhan (1993).

Mauritia flexuosa L. f.

Seeds remaining above plumular/radicular node. **Plumular/radicular** axis asymmetric, angular. **Primary root** persistent, collar disk distinct and swollen; shoot-born roots abundant, emerging above and below collar node; secondary roots branched; collar roots and root hairs absent. **Hyperphyll** not distinct. **Cotyledonary sheath** absent. **Coleoptile** distinct, shorter than cataphylls; ventral and lateral splitting; conspicuous tongue-like projections at lateral sides. **Cataphylls** two, opening lengthwise;

second cataphyll elongate with a closed sheath, apex acute. **Eophyll** palmate, segments linear-lanceolate, apex acute, margins spiny; splitting at grooves along side abaxial. **Venation pattern** palmate; leaf axis inconspicuous, vascular bundles radiate from distal end of petiole; midvein distinct in each segment; vascular bundles convergent at apex; transverse vascular bundles very conspicuous, always connected to longitudinal major and minor vascular bundles, abundant, closely arranged. **Plication** with proximal marginal fold V-shaped, distal fold Λ-shaped. **Epidermal cells** rectangular, dentate lateral walls. **Hairs** present, few basal cells. **Stomata** superficial; arranged in regular rows at intercostal regions, scarse in adaxial surface; elongate terminal cells overarching guard cells. **Hypodermal** colourless parenquimatous layer replaced by fibrous bundles, arranged at irregular intervals. **Chlorenchyma** differenciate; **palisade layer** distinct; spongy mesophyll with with less than five layers. **Mesophyll fibrous bundles** oriented towards abaxial side; fiber lumina small. **Expansion cells** single or double layered, scattered fibrous bundles. **Major vascular**

bundles associated with ridges, attached to hypodermal layer; IS partially sclerotic; OS distinct, formed by small regular cells. **Median vascular bundles** free, oriented towards abaxial side; multilayered sclerotic IS. **Minor vascular bundles** not buttressed, oriented towards or attached to abaxial side; OS surrounding vascular bundleor restricted to adaxial end; radial OS present. **Midrib** abaxially prominent, triangular, vascularized by simple vascular bundles. **Marginal rib with** fibrous layers. **Petiole** transverse section terete, vascular bundles uniformelly arranged in a V-fashion. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Tannins abundant some in full sacs.

Pigafetta filaris (Gis.) Becc.

Seed remaining above plumular/radicular node. **Plumular/radicular** axis asymmetric, angular. **Primary root** oblique, persistent; disk collar distinct and swollen, not as prominent as in *Calamus*; secondary roots branched; first internode elongate with shoot-born roots; collar roots and root hairs absent.

Hyperphyll inconspicuous. **Cotyledonary sheath** absent. **Coleoptile** distinct, splitting ventral or laterally, tonge-like projection at apical end. **Cataphylls** two, apex acute. **Eophyll** bifid, segments linear-lanceolate, apex acuminate, spiny margings; splitting along grooved side. **Venation** pattern pinnate; leaf axis short, convergent at apex; midvein not distinct from other longitudinal vascular bundles; transverse commissures always connected to longitudinal vascular bundles, widely separated from each other, with less abundant than in *Calamus*. **Plication** with proximal marginal folds Λ-shaped, distal inner marginal folds V-shaped, outer marginal folds Λ-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls sinuous. **Hairs** absent. **Stomata** superficial; elongate terminal cells do not overarching guard cells; abundant on abaxial surface; arranged in regular lines at intercostal regions. **Hypodermis** not a distinct colorless layer with fibrous bundles at regular intervals; lumen widely open. **Chlorenchyma** differentiated; palisade **layer** distinct; spongy mesophyll with less than five layers lacking fibrous bundles. **Expansion cells** double layered. **Major**

vascular bundles associated with ridges, attached to adaxial and abaxial hypodermal layers; OS distinct. **Median vascular bundles** free, oriented towards abaxial sides. **Minor vascular bundles** not buttressed, oriented towards abaxial side; OS around adaxial end forming a cap-shaped layer; associated with an extra layer of radially arranged OS. **Midrib** abaxially prominent, vascularized by several simple vascular bundles. **Marginal rib** with fibrous layers. **Petiole** transverse section deeply concave. **Phloem strands** two. **Metaxylem** single, widely open. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Tannins scattered, appearing to be more concentrated on palisade parenchyma.

Germination of *Pigafetta* has been described by Davis and Kuswara (1987).

Plectocomia sp.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** asymmetric angular. **Primary root** persistent for a long period before being

replaced by shoot-born roots; distinct disk collar; secondary roots branched; shoot-born roots abundant, arising above first node; collar roots and root hairs absent. **Hyperphyll** inconspicuous. **Cotyledonary sheath** not evident. **Coleoptile** distinct opening apically, splitting side opposite to seed. **Cataphyll** single, in contrast to other member of the group; apex acute and hard. **Eophyll** simple, lanceolate, apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles; vascular bundles convergent at apex; transverse commissures always connected to longitudinal vascular bundles, widely separated from each other. **Plication** with proximal marginal folds V-shaped, distal marginal folds Λ-shaped and V-shaped. **Epidermal cells** rectangular, dentate walls. **Hairs** absent. **Stomata** superficial; elongate terminal cells overarching guard cells; arranged in regular rows at intercostal regions. **Hypodermal** layer replaced by fibrous bundles at irregular intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with with less than five layers. **Expansion cells** single or double layered. **Major vascular bundles** associated with ridges, prominent at

adaxial side, attached to adaxial and abaxial hypodermal layers; OS at lateral sides, cells smaller than surrounding mesophyll cells. **Median vascular bundles** free, oriented towards abaxial side, multilayered sclerotic IS. **Minor vascular bundles** not buttressed, oriented towards abaxial side, sometimes attached to epidermal layer; OS cap-shaped; extra layer of radially arranged OS present. **Midrib** abaxially prominent, vascularized by several simple vascular bundles. **Marginal rib** with fibrous layers. **Petiole** transverse section hemi-ellipse. **Phloem strands** two. **Metaxylem** single. **Cell inclusions,** stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Tannins abundant, some in scattered full sacs.

Summary of Calamoid palms

Plumular/radicular axis angular; primary root either straight or oblique, persistent or ephemeral, collar roots developed or do not developed; hyperphyll inconspicuous, cotyledonary sheath opening apically, a coleoptile present, 1-2 cataphylls. Eophyll bifid, pinnate, or palmate, and acute, praemorse or lobed at

apex, eophyll has palmate or pinnate venation, proximal marginal folding v-shaped, distal folding A-folding of AV folding.

Dransfield (1979, p. 16) discussed morphology of calamoid eophylls.

5. NYPOID PALMS

Nypa fruticans Wurmb

Seed remaining horizontal to plumular extension. **Plumular/radicular axis** can not be identify, plumular axis emerges horizontally, later it diverts with a negative geotropism. **Primary root** never develops into a external estructure; secondary roots simple; shoot-born roots present; collar roots and root hairs absent. Because of its unique morphology structures such as hyperphyll and cotyledonary sheath are not easily identify. **Coleoptile** opening lateral, apex with hook-like extensions. **Cataphylls** four or more, coriaceous, apex with a hook-like projection; distichous arrangement. **Eophyll** bifid or pinnate,

segments linear-lanceolate, apex acute; splitting along grooved side. **Venation** pattern pinnate; leaf axis conspicuous; midvein not distinct from other longitudinal vascular bundles; vascular bundles convergent at apex; transverse commissures always connected to longitudinal vascular bundles, widely separated from each other. **Plication** data unavailable for proximal section; pinna distal marginal folds V-shaped. **Epidermal cells** rectangular, adaxial anticlinal walls sinuous; thick cuticular layer. **Hairs** present with few basal cells. **Stomata** sunken; short terminal cells overarching guard cells. **Hypodermal** layer present at adaxial and abaxial sides; cells ellipsoid, paralell orientation, occasionally interrupted by sunken stomata cells. **Chlorenchyma** distinct; palisade layers two, distinct; spongy mesophyll with more than five layers. **Mesophyll fibers** arranged in solid circular or ellipsoid bundles, made up of more than fifteen strands, distributed at adaxial and abaxial sides; lumen wide. **Expansion cells** double layered. **Major vascular bundles** not associated with ridges; OS lateral. **Median vascular bundles** free, oriented towards abaxial side. **Minor vascular bundles**

equidistant or towards abaxial side; OS surrounding vascular bundle. **Midrib** prominent at adaxial and abaxial sides with a single multivascular bundle. **Marginal rib** with fibrous bundles. **Petiole** transverse section ellipsoid, hypodermal layers two; distinct circular intercellular spaces. **Phloem strands** single. **Metaxylem** two. **Cell inclusions, stegmata** hat-shaped, margins spinulose, distributed around vascular and fibrous bundles. Tannins abundant, scattered, full sacs, traces are found within vascular bundles and hypodermal cells.

Germination of *Nypa* has been described by Tomlinson (1971) and Fong (1986).,

Summary of Nypoid palms

Summary as for genus.

6. CARYOTOID PALMS

Arenga hookeriana (Becc.) Whitmore

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary**

root persistent; secondary roots simple; collar roots present. **Hyperphyll** with a an adaxial single groove; region connected to seed forming a swollen disk. **Cotyledonary sheath** elongate, splitting lengthwise. **Coleoptile** absent. **Cataphyll** single, tubular, opening apically, apex acute. **Eophyll** simple, broadly lanceolate, apex praemorse. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, vascular bundles not convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** fusiform, adaxial and abaxial anticlinal walls linear, papillose in transverse section; cuticle thick. **Hairs** abundant, perpendicular and elongate cells, basal cells sunken. **Stomata** superficial; inner wall of guard cells striate; short terminal cells overarching guard cells. **Hypodermis** single-layered, large, rounded; present at adaxial and abaxial sides. **Chlorenchyma** differentiated; palisade layer present; spongy mesophyll with less than five layers. **Mesophyll fibers** in equidistant bundles, few; lumen wide. **Expansion**

cells single-layered, short, rectangular. **Major vascular bundles** not associated with ridges, attached to adaxial and abaxial hypodermis; OS distinct. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS lateral; radial OS present. **Midrib** abaxially prominent, singlevascular bundle. **Marginal rib** with majorvascular bundle; OS distinct, sourrounding bundle, paralell sclerotic wall dividingvascular bundle. **Petiole** transverse section pentagonal, large vascular bundles in each corner. **Phloem strands** one. **Metaxylem** single. **Cell inclusions,** stegmata large, hat-shaped, linear margins, distributed around vascular and fibrous bundles. Raphides abundant, large, equidistant.

Caryota mitis Lour.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple; collar roots present. **Hyperphyll** short, smooth, connecting to seed by a distinct swollen disk. **Cotyledonary sheath** split lengthwise, splitting opposite to hyperphyll. **Coleoptile** absent. **Cataphyll** single, splitting

lengthwise to plumular radicular node, apex concave. **Eophyll** bifid, praemorse apex; splitting at adaxial side. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, not convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication with** proximal and distal marginal folds V-shaped. **Epidermal cells** fusiform, adaxial and abaxial anticlinal walls sinuous; cells ellipsoid; orientation paralell. **Hairs** present, basal cells sunken. **Stomata** slightly sunken; inner wall of guard cells striate; short terminal cells overarching guard cells. **Hypodermis** single-layered, ellipsoid, orientation paralell; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Expansion cells** absent. **Major vascular bundles** not associated with ridges, large multivascular, prominent at abaxial side; OS distinct. **Median vascular bundles** free, equidistant, attached to hypodermis. **Minor vascular bundles** equidistant; OS lateral; radially arrange OS layer present. **Midrib** not distinct, major vascular bundles more prominent.

Marginal rib absent. **Petiole** transverse section pentagonal, adaxial side grooved. **Phloem strands** one. **Metaxylem** single. **Cell inclusions**, stegmata hat-shaped, linear margins, distributed around vascular and fibrous bundles. Raphides abundant.

Germination of *Caryota* has been described by Gatin (1906a) and Mahabale and Shirke (1967).

Wallichia densiflora Mart.

Seed remaining above plumular/radicular node. **Plumular radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple; collar roots present; root hairs present. **Hyperphyll** short, smooth; connected to seed by a distinct swollen disk. **Cotyledonary sheath** with short apical opening, covered by diminute hairs. **Coleoptile** absent. **Cataphyll** single, tubular, apex acute, covered by diminute hairs. **Eophyll** simple, ellipsoid, lobate, praemorse apex. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles, vascular bundles not convergent at apex; transverse commissures widely separated from each

other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds V-shaped. **Epidermal cells** fusiform, adaxial and abaxial anticlinal walls linear, papillose; cuticle thick. **Hairs** perpendicular, columnar, sunken basal cells. **Stomata** slightly sunken; inner wall of guard cells striate; short and elongate terminal cells overarching guard cell. **Hypodermis** single-layered, rounded or ellipsoid; paralell orientation; present at adaxial and abaxial sides. **Chlorenchyma** differentiated; palisade layer distinct; spongy mesophyll with less than five layers. **Mesophyll fibers** in equidistant bundles; lumen wide. **Expansion cells** single-layered, cell short, square. **Major vascular bundles** not associated with ridges, large multivascular vascular bundles; OS distinct. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS lateral. **Midrib** abaxially prominent, single multivascularvascular bundle. **Marginal rib** with majorvascular bundle; paralell sclerotic wall dividingvascular bundle. **Petiole** transverse section pentagonal. **Phloem strands** one. **Metaxylem** single. **Cell inclusions**, stegmata hat-

shaped, linear margins, distributed around vascular and fibrous bundles. Raphides abundant, equidistant.

Summary for Caryotoid palms

Plumular/radicular axis; primary root straight and persistent, collar roots well developed; hyperphyll elongate, swollen at proximal end, cotyledonary sheath opening laterally, a coleoptile absent, one cataphyll. Eophyll simple or bifid, and praemorse at apex, eophyll has palmate venation, and V-shaped marginal folding.

Note: Only some coryphoids, phoenicoids, and caryotoids have plumular/radicular axis straight and parallel to axis of embryo, giving lateral sheath opening and non-coleoptile germination.

7. PSEUDOPHOENICOID PALMS

Pseudophoenix sargentii H. Wendl.

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple, with pneumatophores at base; root hairs abundant.

Hyperphyll moderate; single groove at adaxial side, connection to seed flat. **Cotyledonary sheath** grooved, splitting lengthwise opposite to hyperphyll. **Coleoptile** absent. **Cataphylls** two, plicate, opening apically, apex acute. **Eophyll** simple, lanceolate, apex acute. **Venation** pattern pinnate; leaf axis distinct; vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds Λ-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear; regular rounded cells in transverse section; walls thickened; cuticle thick. **Hairs** absent. **Stomata** sunken, epidermal layer around stomatal complex sunken; short terminal cells overarching guard cells; two sets of lateral subsidiary cells at each side of guard cells. **Hypodermal** colorless layer absent, replaced by a continuous fibrous layer; double or triple layers at ridges; lumen wide. **Chlorenchyma** differentiated; palisade layer distinct; spongy mesophyll with more than five layers. **Expansion cells** single-layered, elongate, ellipsoid; adjacent epidermal cells

papillose. **Major vascular bundles** prominent, associated to ridges, fibrous buttresses at abaxial side, attached to hypodermis; IS multilayered, sclerotic; OS distinct. **Median vascular bundles** buttressed to both abaxial and adaxial sides. **Minor vascular bundles** small, equidistant; OS surrounding vascular bundle. **Midrib** adaxially prominent, singlevascular bundle. **Marginal rib** with minorvascular bundle; IS fibrous, solid multilayer. **Petiole** transverse section heart shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions,** stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphids abundant, equidistant.

Read (1968) described germination in *Pseudophoenix*.

Summary for Pseudophoenicoid palms

As above

8. CEROXYLOID PALMS

Ceroxylon sp.

Seed horizontal, neither above or below plumular/radicular node. **Plumular/radicular** axis asymmetric, angular. **Primary root** persistent, collar disk distinct; secondary roots simple; shoot-born roots present; collar roots present. **Hyperphyll** inconspicuous, about 5-6 mm long, connection to seed flat, connected to base of coleoptile. **Cotyledonary sheath** absent. **Coleoptile** short, splitting at ventral and lateral sides, corrugated. **Cataphylls** two, elongate, opening apically, apex acute. **Eophyll** simple, broadly lanceolate, apex acute; several leaves similar to eophyll appearing before first split leaf; seventh leaf splitting along grooved side. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct, vascular bundles converge gradually to marginalvascular bundle; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal marginal folds V-shaped, distal marginal folds V-shaped and margin Λ-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls sinuous; cuticle think; abaxial epidemis sunken around hair base. **Hairs** multicellular,

ward-like, base multicellular associated to ribs; abundant at abaxial surface. **Stomata** superficial; short terminal cells overarching guard cells. **Hypodermal** colorless cells absent, replaced by a continuous fibrous layer; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Expansion cells** single-layered, rectangular, short, perpendicular; adjacent epidermis papillose. **Major vascular bundles** associated with ridges; attached to adaxial and abaxial epidermal layers; OS distinct. **Median vascular bundles** buttressed to adaxial side. **Minor vascular bundles** oriented towards abaxial side; OS cap-shaped; radially arranged OS present. **Midrib** abaxially prominent, transverse section ax-shaped; single large and several small vascular bundles grouped. **Marginal rib** with fibrous layers. **Petiole** transverse section heart shaped. **Phloem strands** single. **Metaxylem** one or two. **Cell inclusions**, stegmata irregular, margins spinulose, distributed around vascular bundles. Raphides scarse, equidistant. Tannins abundant in full sacs

Karsten (1857) described and illustrated germination of *Ceroxylon*.

Oraniopsis appendiculata (F. Bailey) Dransf., Uhl & Irvine

Seed horizontal, neither above or below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent, a disk collar is present, resembles caryotoids collar disk; secondary roots simple; shoot-born roots present. **Hyperphyll** very short around 4-5mm long, smooth, connection to seed flat, connecting at base of coleoptile. **Cotyledonary sheath** inconspicuous. **Coleoptile** short, leathery, splitting opposite to hyperphyll. **Cataphylls** two, first cataphyll opening apically, apex acute; second cataphyll elongate, opening laterally; both covered by brownish integument. **Eophyll** simple, linear-lanceolate, apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular

bundles. **Plication** with proximal marginal folds V-shaped; distal marginal folds one side V-shaped one, the other fold Λ-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear; cuticle thick. **Hairs** multicellular, multicellular base associated to ribs; abundant at abaxial surface, associated to ribs. **Stomata** superficial; short terminal cells overarching guard cells; scattered on intercostal regions. **Hypodermis** single-layered, at adaxial and abaxial sides, rounded or ellipsoid in transverse section, interrupted by small fibrous bundles at irregular intervals; more concentrated at ridges and grooves. **Chlorenchyma** undifferentiated; spongy mesophyll up to five layers. **Mesophyll fibrous bundles** at adaxial and abaxial sides; lumen wide. **Expansion cells** single-layered, large, rectangular, perpendicular; adjacent epidermal cells papillose. **Major vascular bundles** associated with ridges, buttressed to adaxial hypodermis; IS multilayered, sclerotic; OS distinct at lateral sides ofvascular bundle. **Median vascular bundles** buttressed to adaxial side. **Minor vascular bundles** oriented towards abaxial side; OS cap-shaped; radially arranged

OS present. **Midrib** abaxially prominent, triangular; with simple and multivascular vascular bundles grouped. **Marginal rib** with fibrous layers. **Petiole** transverse section rounded shaped. **Phloem strands** one. **Metaxylem** one or two. **Cell inclusions**, stegmata irregular, margins spinulose, distributed around fibrous bundle or vascular bundle.

Ravenea rivularis Jum. & H. Perrier

Seed above plumular/radicular node. **Plumular/radicular axis** symmetric, straight, **Primary root** persistent, distinct swollen disk collar; secondary roots branched; shoot-born roots present; root hairs abundant. **Hyperphyll** short and smooth, connection to seed flat. **Cotyledonary sheath** inconspicuous. **Coleoptile** short, rugulose, splitting at opposite sides. **Cataphylls** two, opening apically. **Eophyll** bifid, apex acute, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and ending at intercostal areas. **Plication** with proximal

and distal marginal fold Λ-shaped on one side, V-shaped the other. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear; uniform rounded cells in transverse section. **Hairs** present, multicellular base. **Stomata** superficial; short terminal cells overarching guard cells. **Hypodermis** single-layered, present at adaxial and abaxial sides, replaced by small fibrous bundles at regular intervals; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Expansion cells** single-layered, rectangular, perpendicular; adjacent epidermal cells papillose. **Major vascular bundles** associated with ridges, buttressed to adaxial hypodermis by multilayered fibrous IS, abaxial side attached to expansion layer; OS distinct. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, simple or multivascular bundles grouped. **Marginal rib** with fibrous layers. **Petiole** transverse section semi-ellipsoid, adaxial side ridges. **Phloem strands** one.**Metaxylem** one or two. **Cell inclusions,**

stegmata shape irregular, margins spinulose, distributed around vascular bundles. Raphides present.

Summary for Ceroxyloid palms

Plumular/radicular axis straigh or angular; primary root straight and persistent, collar roots developed or do not developed; hyperphyll elongate or contracted, cotyledonary sheath opening laterally or apically, a coleoptile present, two cataphylls, eophyll simple, bifid, or pinnate, and acute at apex, eophyll has palmate or pinnate venation, proximal marginal folding V-shaped, distal folding AV-shaped.

9. CHAMAEDOREOID PALMS

Chamaedorea microspadix Burret

Seed attachment displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent, distinct disk collar; secondary roots simple; shoot-born roots present; root hairs abundant. **Hyperphyll** undeveloped. **Cotyledonary sheath** absent. **Coleoptile** short, splitting lengthwise opposite to hyperphyll.

Cataphylls two, elongate, opening apically, apex acute. **Eophyll** bifid, segments sigmoid, apex acute, margins on pickle specimens darker than rest of lamina; splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles converging gradualy towards apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folding V-shaped, distal folds varying on each side, one margin Λ-shaped and other margin V-shaped. **Epidermal cells** rhombohedral, papillose, adaxial and abaxial anticlinal walls linear. **Stomata** superficial; short or elongate terminal cells overarching guard cells; distribution irregular, at intercostal regions. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers, with less layers at folding regions. **Expansion cells** not distinct. **Major vascular bundles** multivascular, distribution associated with ridges, attached to adaxial and abaxial hypodermis; OS restricted to lateral sides. **Median vascular bundles**

free, equidistant. **Minor vascular bundles** equidistant; OS restricted to lateral sides; radial OS present. **Midrib** abaxially prominent, spatula-shaped in transverse section; simple and multivascular bundles grouped. **Margins** lacking vascular bundles or fibrous bundles. **Petiole** heart-shaped, abaxial side deeply concave. **Phloem strands** one. **Metaxylem** two. **Cell inclusions**, stegmata hat-shaped, smaller than stegmata in Caryotoids, margins spinulose, distributed around vascular and fibrous bundles, more concentrated at adaxial and abaxial sides of bundle. Sclereids present. Tannins scattered. Raphids abundant.

Gaussia maya (O. F. Cook) Quero & Read

Seed attachment displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent, distinct disk collar present; secondary roots simple; shoot-born roots present; collar roots present; root hairs present, abundant. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, opening apically, small slit opposite to seed. **Cataphylls** two, opening apically. **Eophyll** bifid, lanceolate segments, apex

acute. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles converging towards inner vascular bundles; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal marginal outer folding V-shaped, inner folding Λ-shaped. **Epidermal cells** rectangular or rhombohedral, papillose, adaxial and abaxial anticlinal walls linear. **Stomata** superficial; short or elongate terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Expansion cells** single-layered, short, not too distinct from surrounding cells; adjacent epidermal cells papillose. **Major vascular bundles** multivascular, associated with ridges, attached to adaxial and abaxial epidermis; OS restricted to lateral sides. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS restricted to lateral sides. **Midrib** abaxially prominent, simple vascular bundles grouped. **Margins** lacking vascular bundles or fibrous bundles. **Petiole**

transverse section half-ellipsoid. **Phloem strands** one. **Metaxylem** two. **Cell inclusions**, stegmata shape hat-shaped, margins spinulose, distributed around vascular bundles. Sclereids present. Raphides equidistant. Tannins scattered.

Synecanthus fibrosus (H. Wendl.) H. Wendl.

Seed attachment displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent; disk collar distinct and swollen; shoot-born roots present; collar roots present; root hairs abundant. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, rugulose; opening apically opposite to seed. **Cataphylls** two, elongate, opening apically, apex acute or splitted and leathery. **Eophyll** bifid, lanceolate segments, apex acute, splitting side abaxial; short fibers visible in leaf clearings. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal

marginal folds V-shaped, distal outer marginal folding V-shaped, inner marginal folding Λ-shaped. **Epidermal cells** rhombohedral, adaxial and abaxial anticlinal walls linear, papillose in transverse section. **Hairs Stomata** superficial; short or elongate terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Expansion cells** single-layered, conspicuous near major vascular bundles and midrib. **Major vascular bundles** multivascular, associated with ridges, attached to adaxial and abaxial epidermis; OS not distinct. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle; radial OS present. **Midrib** abaxially prominent, rounded-sinuous; simple bundles grouped. **Margins** lacking vascular bundles or fibrous bundles. **Petiole** semi-elliosoid; adaxial side flat, abaxial side ellipsoid. **Phloem strands** single. **Metaxylem** two. **Cell inclusions**, stegmata hat-shaped, margins spinulose, distributed around vascular and fibrous bundles. Sclereids present. Raphides equidistant. Tannins abundant.

Summary for Chamaedoreoid palms

Plumular/radicular axis angular; primary root either straight or oblique, persistent or ephemeral, collar roots developed or do not developed; hyperphyll absent, cotyledonary sheath opening apically, rugulose (resembling *Plectocomia* (Calamoid), coleoptile present, two cataphylls, eophyll bifid or pinnate and acute at apex, proximal marginal folds V-shaped, distal margins AV-shaped.

10. IRIARTEOID PALMS

Iriartea deltoidea R. & P.

Seed horizontal, neither above or below plumular/radicular node. **Plumular radicular axis** asymmetric, angular. **Primary root** ephemeral, collar disk distinct, with wide flat surface; secondary roots branched, pneumatophores present; shoot-born roots thicker than primary root. **Hyperphyll** undeveloped. **Cotyledonary sheath** absent. **Coleoptile** short, splits opposite to seed. **Cataphylls** two, opening apically, apex acute, leathery. **Eophyll** simple, ellipsoid, apex praemorse. **Venation** pattern pinnate; leaf axis

distinct; midvein present, vascular bundles not convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal marginal folds V-shaped, distal margins Λ-shaped. **Epidermal cells** shape rhombohedral, adaxial and abaxial anticlinal walls linear, papillose in transverse section. **Hairs** conical, few basal cells, abundant; conspicuous in surface view. **Stomata** superficial; short or elongate terminal cells overarching guard cells; distribution irregular. **Hypodermis** single-layered, squared cells; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibers** forming solid equidistant bundles; lumen small. **Expansion cells** single-layered, double-layered when flanking midrib. **Major vascular bundles** multivascular, prominent at abaxial surface; not associated with ridges, attached to hypodermis in both sides; distinct OS. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, square-shaped; simple and multivascular

bundles grouped. **Marginal rib** with compact fibrous bundle. **Petiole** transverse section semi-circular. **Phloem strands** one. **Metaxylem** one or two. **Cell inclusions**, stegmata hat-shaped, linear margins, distributed around vascular and fibrous bundles. Sclereids present. Raphides equidistant.

Iriartella setigera (Mart.) H. Wendl.

Seed attachment horizontal, neither above or below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral; secondary roots shoot-born roots collar roots. **Hyperphyll** undeveloped. **Cotyledonary sheath** absent. **Coleoptile** present. **Cataphylls XXX**. **Eophyll** simple, praemorse apex (need herbarium sample). **Venation** pinnate; leaf axis distinct; midvein present, vascular bundles not convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds Λ-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear, cuticle thick. **Hairs** conical, few basal cells. **Stomata** superficial; short or

elongate terminal cells overarching guard cells. **Hypodermis** single-layered, large ellipsoid cells arranged paralell; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibrous bundles** abundant, small, equidistant; lumen small. **Expansion cells** single-layered, scattered fibrous bundles. **Major vascular bundles** prominent at abaxial side, not associated with ridges, attached to both hypodermis; OS distinct. **Median vascular bundles** free, oriented towards abaxial sides. **Minor vascular bundles** oriented towards abaxial side; OS cap-shaped; radial OS present. **Midrib** abaxially prominent, single multivascular bundle. **Marginal rib** with non-vascular bundle. **Petiole** semi-circular. **Phloem strands** one. **Metaxylem** single. **Cell inclusions**, stegmata shape hat-shaped, margins smooth, distributed around fibrous bundles. Sclereids present. Tannins abundant in full sacs.

Socratea exorrhiza (Mart.) H. Wendl.

Seed attachment horizontal, neither above or below plumular/radicular node. **Plumular/radicular axis**

asymmetric, angular. **Primary root** ephemeral, disk collar large, flat with callous contourn; secondary roots simple, pneumatophores present; shoot-born roots thicker than radicle. **Hyperphyll** inconspicuous. **Cotyledonary sheath** absent. **Coleoptile** distinct, splitting apically. **Cataphylls** four, these increasing size gradually, fourth cataphyll elongate; apex bifid. **Eophyll** bifid, segments broad, margins and apex crenulate, spliting along grooved side. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles not convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal marginal folds V-shaped, distal marginal folds Λ-shaped. **Epidermal cells** rhombohedral, adaxial and abaxial anticlinal walls linear, abaxial cells papillose in transverse section. **Hairs** conical, abundant in both surfaces, few basal cells. **Stomata** superficial; short terminal cells overarching guard cells. **Hypodermis** single-layered, squared cells, at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five

layers. **Mesophyll fibers** in equidistant bundles; lumen small. **Expansion cells** single-layered, mainly associated to sides midvein or major vascular bundles; adjacent epidermal cells papillose. **Major vascular bundles** multivascular, not associated with ridges, attached to adaxial hypodermis and abaxial epidermis; prominent at abaxial surface; IS multilayered and sclerotic; OS not distinct. **Median vascular bundles** free, oriented towards abaxial side. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, rounded, simple and multivascular bundles grouped. **Marginal rib** with fibrous bundle. **Petiole** transverse section heart-shaped. **Phloem strands** one. **Metaxylem** one or two. **Cell inclusions**, stegmata hat-shaped, linear margins, distributed around vascular and fibrous bundles. Sclereids present. Tannins abundant some in full sacs.

Summary for Iriarteoid palms

Plumular/radicular axis angular; primary root oblique and ephemeral, collar roots developed or do not develop; cotyledonary sheath opening apically, a coleoptile present, 2-4 cataphylls, eophyll bifid

(simple in *Iriartea* and *Iriartella*), and praemorse at apex, eophyll has pinnate venation and reduplicate margins.

11. PODOCOCCOID PALMS

Podococcus barteri Mann & H. Wendl.

Seed horizontal, neither above or below plumular/radicular node. **Plumular/radicular axis** asymmetric. **Primary root** ephemeral; **Hyperphyll** undeveloped. **Cotyledonary sheath** absent. **Coleoptile** present.. **Eophyll** simple, rhombohedral, crenulate margin. **Venation** pattern pinnate; leaf axis distinct; midvein?, vascular bundles not convergent at apex. **Plication** with proximal marginal A-shaped, distal marginal folds Λ-shaped. **Epidermal cells** shape rhombohedral, adaxial and abaxial anticlinal walls linear, irregular and papillose in transverse section. **Hairs** conical, basal cells superficial. **Stomata** superficial; elongate terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibers** abundant, compact, small,

equidistant bundles; lumen small. **Expansion cells** absent. **Major vascular bundles** not associated with ridges, sclerotic IS, distinct OS, attached to both epidermal layers. **Median vascular bundles** free, equidistant; OS lateral and large single cells. **Minor vascular bundles** equidistant; OS restricted to lateral sides. **Midrib** prominent at both adaxial and abaxial sides, single multivascular bundle. **Margins** lacking ribs. **Petiole** transverse section heart shaped. **Phloem strands** one. **Metaxylem** single. **Cell inclusions, stegmata** spherical or ellipsoid, margins spinulose, around vascular and fibrous bundles. Tannins abundant, some in full sacs.

Summary for Podococcoid palms

Summary as for genus

12. ARECOID PALMS

Archontophoenix alexandrae (F. Muell.) H. Wendl. & Drude

Seed attachment displaced below plumular/radicular node. **Plumular/radicular axis**

asymmetric, angular. **Primary root** ephemeral; secondary roots branched; shoot-born roots several, protruding thought coleoptile base. **Hyperphyll** absent. **Cotyledonary sheath** not distinct. **Coleoptile** lateral split, apex acute, texture granitic. **Cataphylls** two, apex splitting into several sections. **Eophyll** bifid, lanceolate segments, apex acute, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present, vascular bundles not convergent at apex; transverse commissures widely separated from each other, some vascular bundles connect longitudinal vascular bundles, some end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal marginal outer folding V-shaped and inner folding Λ-shaped, apex irregular. **Epidermal cells** rhombohedral, adaxial and abaxial anticlinal walls linear. **Hairs** present, few basal cells, polyhedral in transverse section. **Stomata** superficial; short terminal cells overarching guard cells, scattered. **Hypodermis** single-layered, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers, cells orientation paralell. **Mesophyll fibers** as equidistant

bundles; lumen small. **Expansion cells** single-layered. **Major vascular bundles** prominent at both surfaces, associated with ridges, attached to adaxial and abaxial epidermis; OS distinct. **Median vascular bundles** free, equidistant; OS distinct; radial OS present. **Minor vascular bundles** distribution abaxial side; OS surrounding vascular bundle; radially arranged OS present. **Midrib** abaxially prominent, irregular ax-shaped in transverse section, vascularized by grouped simple vascular bundles. **Marginal rib** with minor vascular bundles. **Petiole** transverse section semi-ellipsoid. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Tannins abundant. Raphides equidistant.

Gatin (1906a) and Ginieis (1953a, 1953b) studied germination of *Archontophoenix*.

Dictyosperma album (Bory) H. Wendl. & Drude

Seed attachment displaced below plumular/radicular node. **Plumular/radicular axis**

asymmetric, angular. **Primary root** ephemeral, distinct swollen collar; secondary roots branched, pneumatophores present; shoot-born roots few, emerge throughout coleoptile base, as thick as radicle. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, apex acute, splitting laterally opposite to seed. **Cataphylls** two, apex acute and sharp. **Eophyll** bifid, segments linear-lanceolate, apex acute, splitting side along grooved side. **Venation** pattern pinnate; leaf axis distinct; midvein present, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal marginal folds Λ-shaped. **Epidermal cells** rhombohedral, adaxial and abaxial anticlinal walls linear, polyhedral cells in transverse section. **Hairs** present, multicellular base. **Stomata** superficial; short terminal cells overarching guard cells, abundant in abaxial surface, scattered arrangement. **Hypodermis** not distinct, fibrous bundles present as a discontinuous layer; lumen wide. **Chlorenchyma** undifferentiated; spongy mesophyll with

more than five layers. **Expansion cells** single-layered. **Major vascular bundles** prominent at both surfaces, associated with ridges, distinct OS, attached to adaxial and abaxial epidermis. **Median vascular bundles** free, equidistant. **Minor vascular bundles** distribution abaxial side; OS surrounding vascular bundle; radially arranged OS present. **Midrib** abaxially prominent, simple and multivascular bundles grouped. **Marginal rib** with fibrous layers. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides equidistant. Tannins abundant.

Germination of *Dictyosperma* was described by Gatin (1906a).

Dypsis lutescens (H. Wendl.) Beentje & J. Dransf.

Seed attachment displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral, disk collar not swollen; secondary roots simple, pneumatophores present; shoot-born roots distinct.

Hyperphyll absent. **Cotyledonary sheath** absent. **Coleoptile** short, splitting opposite to hyperphyll. **Cataphylls** two, opening apically, apex acute. **Eophyll** bifid, linear-lanceolate segments, apex acute, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal marginal folds Λ-shaped. **Epidermal cells** rhombohedral, adaxial and abaxial anticlinal walls linear, rounded in transverse section. **Hairs** present, multicellular base. **Stomata** superficial; short terminal cells overarching guard cells, scattered arrangement, more concentrated at abaxial surface. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Mesophyll fibers** in equidistant bundles; lumen wide. **Expansion cells** double layered, elongate rectangles, perpendicular, adjacent epidermal cells papillose. **Major vascular bundles** associated with ridges; OS distinct. **Median vascular bundles** free,

equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle; radially arranged OS present. **Midrib** abaxially prominent, rounded, vascularized by grouped simple vascular bundles. **Marginal rib** with minorvascular bundle. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides equidistant. Tannins abundant in full sacs, some in OS.

Euterpe precatoria Mart.

Seed attachment displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral; secondary roots branched, pneumatophores scattered; shoot-born roots present; collar present; root hairs present. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, splitting opposite to seed. **Cataphylls** two, opening apically, apex acute, plicate. **Eophyll** pinnate, linear-lanceolate segments, apex acute, split leaf first, split along grooved side. **Venation** pattern pinnate; leaf axis distinct; midvein

present, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal outer margin V-shaped, inner margin Λ-shaped. **Epidermal cells** rectangular or fusiform, adaxial anticlinal walls linear, abaxial anticlinal walls sinuous. **Hairs** present, multicellular base. **Stomata** superficial; elongate terminal cells overarching guard cells, scattered. **Hypodermis** not distinct, fibrous strands present as a discontinuous layer; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers, rectangular, horizontal orientation. **Expansion cells** single-layered, few cells, elongate and perpendicular. **Major vascular bundles** prominent at adaxial and abaxial surfaces, associated with ridges; IS multilayered and sclerotic; OS distinct. **Median vascular bundles** buttressed, attached to both epidermal layers; OS large lateral cells. **Minor vascular bundles** equidistant; OS lateral. **Midrib** adaxially prominent, vascularized by grouped simple vascular bundles. **Marginal rib** with majorvascular

bundle; IS multilayered at marginal end. **Petiole** transverse section rounded, adaxial side slightly concave. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles.

Germination of *Euterpe* has been described by Belin-Depoux & de Queiroz (1971b).

Hyospathe elegans Mart.

Seed displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral, collar disk distinct; secondary roots branched; shoot-born roots thicker than radicle. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, apex acute, splitting opposite to seed. **Cataphylls** two, splitting lengthwise, apex acute. **Eophyll** bifid, lanceolate segments, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present, vascular bundles not convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas.

Plication with proximal marginal folds V-shaped, distal margin Λ-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear, polyhedral in transverse section. **Hairs** present, multicellular base. **Stomata** slightly sunken, short or elongate terminal cell not overarching guard cells, scattered distribution, more concentrated at abaxial surface. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers, rectangular, horizontal orientation. **Expansion cells** single-layered, distributed at lateral sides of major vascular bundles. **Major vascular bundles** abaxially prominent, associated with ridges, distinct OS. **Median vascular bundles** free, equidistant. **Minor vascular bundles** at abaxial side; OS surrounding vascular bundle; radially arranged OS present. **Midrib** adaxially prominent, singlevascular bundle. **Marginal rib** with minor vascular bundles present. **Petiole** transverse section heart shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Raphides equidistant. Tannins abundant, scattered in every cell.

Neonicholsonia watsonii Dammer

Seed horizontal, neither above or below the plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral, swollen collar present; secondary roots branched, pneumatophores present. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, splitting ventral. **Cataphylls** two, apex acute. **Eophyll** pinnate, segments lanceolate, apex acute, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal margins one Λ-shaped the other V-shaped. **Epidermal cells** rectangular or fusiform, adaxial and abaxial anticlinal walls linear or sinuous. **Hairs** absent. **Stomata** superficial; elongate terminal cells overarching guard cells, scattered. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibers** abaxial and adaxial bundles;

lumen wide. **Expansion cells** single-layered, flanking major vascular bundles. **Major vascular bundles** prominent adaxially, associated with ridges; OS distinct. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** adaxially prominent, singlevascular bundle. **Marginal rib** with majorvascular bundle; IS multilayered and fibrous at marginal end. **Petiole** transverse section heart shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Tannins scattered, some in full sacs.

Nephosperma vanhoutteanum (H. Wendl.) Balfour

Seed displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral, swollen disk collar; secondary roots simple; shoot-born roots thicker than radicle, born on flat surface of collar. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, ventral splitting. **Cataphylls** three, longer than coleoptile, apex acute. **Eophyll** pinnate, lanceolate segments, apex

acute, splitting at abaxial side. **Venation** pattern pinnate; leaf axis distinct; midvein present, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal margins one Λ-shaped, the other V-shaped. **Epidermal cells** rhombohedral, adaxial and abaxial anticlinal walls linear. **Hairs** present, few basal cells. **Stomata** superficial; short terminal cells overarching guard cells. **Hypodermis** not distinct, fibrous bundles and layers present; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** double layered, elongate, ellipsoid. **Major vascular bundles** associated with ridges; OS distinct, attached to adaxial epidermal layer and abaxial expansion cells. **Median vascular bundles** free, equidistant. **Minor vascular bundles** oriented towards abaxial side; OS cap-shaped; radially oriented OS present. **Midrib** abaxially prominent, rounded, vascularized by grouped simple vascular bundles. **Marginal rib** with fibrous layers. **Petiole** transverse section heart shaped. **Phloem**

strands two. **Metaxylem** single. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Tannins abundant.

Orania regalis Zipp.

Seed displaced above plumular/radicular node. **Plumular/radicular axis** slighly assymetric, angular. **Primary root** persistent, collar not distinct; secondary roots branched, pneumatophores present; shoot-born roots abundant; collar roots present. **Hyperphyll** elongate, single apical groove, texture of epidermis in hyperphyll smooth in contrast to sheath, connection to seed swollen. **Cotyledonary sheath** thick, rugulose and wrinkled, opening laterally opposite to hyperphyll. **Coleoptile** absent. **Cataphylls** two, thick, covered by dense tegument. **Eophyll** bifid, segments broadly lanceolate, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present, vascular bundles not convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal marginal folds V-shaped, distal margins Λ-shaped. **Epidermal cells** polyhedral; abaxial

epidermis papillose in transverse section. **Hairs** large, bicellular, few basal cells. **Stomata** superficial. **Hypodermis** not distinct. **Chlorenchyma** differentiated; palisade with distinct two layers; spongy mesophyll with more than five layers. **Mesophyll fibers** in equidistant bundles. **Expansion cells** double layered. **Major vascular bundles** multivascular, associated with ridges, distinct OS. **Median vascular bundles** free, toward abaxial side. **Minor vascular bundles** oriented towards abaxial side; OS surrounding vascular bundle, some associate with grooves. **Midrib** abaxial squared protuberance, simple and multivascular bundles grouped. **Marginal rib** with minorvascular bundle. **Petiole** transverse section heart shaped. **Phloem strands** three. **Metaxylem** single. **Cell inclusions, stegmata** spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Tannins scattered.

Phoenicophorium borsigianum (K. Koch) Stuntz

Seed displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral, distinct flat disk collar present;

secondary roots branched, pneumatophores present; shoot-born roots few, thicker than radicle. **Hyperphyll** very short. **Cotyledonary sheath** absent. **Coleoptile** short, splitting opposite to seed. **Cataphylls** two, opening lengthwise, apex with acute projection, covered by large trychomes. **Eophyll** simple, lanceolate, apex acuminate, split leaf third, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal margins Λ-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls sinuous. **Hairs** present, few basal cells. **Stomata** superficial; short or elongate terminal cells overarching guard cells, scattered. **Hypodermis** not a distinct, fibrous bundles present as a discontinuous layer; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** single-layered, scattered fibers. **Major vascular bundles** associated with ridges, adaxial buttresses

attached to epidermis and abaxial expansion cells, multilayered IS, distinct OS. **Median vascular bundles** free, towards abaxial side. **Minor vascular bundles** towards abaxial side; OS surrounding vascular bundle; radially arranged OS present. **Midrib** abaxially prominent, single bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section heart shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions, stegmata** spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Raphides equidistant. Tannins scattered.

Roystonea borinquena O. F. Cook

Seed horizontal, neither above or below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral; disk collar distinct and swollen; secondary roots simple; shoot-born roots; collar roots present; root hairs present. **Hyperphyll** short, appearing continuous to primary root with plumule erupting at adaxial side. **Cotyledonary sheath** absent. **Coleoptile** short, slight slit opposite to seed. **Cataphylls** two, elongate, first opening apically, second split length wise, extremely

apex acute. **Eophyll** simple, broadly lanceolate, apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein distinct, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds V-shaped, distal margins Λ-shaped. **Epidermal cells** rectangular or fusiform, adaxial and abaxial anticlinal walls linear, papillose in transverse section. **Hairs** present, few basal cells. **Stomata** superficial; elongate terminal cells overarching guard cells, scattered distribution, more concentrated at abaxial surface. **Hypodermis** single-layered, large rounded cells, at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibrous bundles** solid with around 10 strands, equidistant; lumen wide. **Expansion cells** single-layered, scattered fibrous bundles. **Major vascular bundles** not associated with ridges, distinct OS, attached to adaxial and abaxial hypodermis. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** adaxially prominent, single,

largevascular bundle. **Marginal rib** with minor vascular bundles present. **Petiole** transverse section heart shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions, stegmata** hat-shaped, margins spinulose, distributed around vascular and fibrous bundles. Raphides equidistant. Tannins scattered.

Germination of *Roystonea* was described by Gatin (1906a).

Veitchia montgomeryana H. E. Moore

Seed horizontal, neither above or below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral, collar disk distinct; secondary roots branched, scattered pneumatophores; shoot-born roots abundant, arousing around primary root and through base of coleoptile. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, splitting at lateral sides. **Cataphylls** three, displaying diverse splitting forms, apex acute and slightly split. **Eophyll** bifid, segments broadly lanceolate, apex praemorse, abundant rounded spots present on lamina, splitting along grooved side.

Venation pattern pinnate; leaf axis distinct; midvein not a distinct, vascular bundles not convergent at apex; transverse commissures widely separated from each other, connect some longitudinal vascular bundles and end at intercostal areas. **Plication** with proximal marginal folds Λ-shaped, distal outer margin Λ-shaped, inner margin V-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear or sinuous. **Hairs** present, multicellular base. **Stomata** slightly sunken, short and elongate terminal cells overarching guard cells, scattered. **Hypodermis** single-layered, rounded cells, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated, spongy mesophyll with less than five layers. **Mesophyll fibrous bundles** at adaxial and abaxial sides; lumen small. **Expansion cells** double layered, ellipsoid or rectangular. **Major vascular bundles** associated with ridges, attached to adaxial hypodermis and abaxial epidermis; OS distinct; radial OS present. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle; radial OS present. **Midrib** abaxially prominent, ax-shaped, vascularized by grouped simple vascular

bundles. **Marginal rib** with minor vascular bundles present. **Petiole** transverse section heart shaped. **Phloem strands** two. **Metaxylem** one or two. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles. Sclereids present. Raphides adaxial. Tannins abundant, some in full sacs.

Summary for Arecoid palms

Plumular/radicular axis asymmetric, angular; primary root either straight or oblique, persistent or ephemeral, collar roots developed or do not develop; cotyledonary sheath opening apically, a coleoptile present, there two or more cataphylls, eophyll bifid, rarely simple or pinnate, and usually acute at apex (sometimes praemorse), eophyll has pinnate venation, and reduplicate inner margins and induplicate outer margins.

13. COCOSOID PALMS

Allagoptera leucocalyx (Mart.) Kuntze

Seed remaining above plumular/radicular node. **Plumular/radicular** axis symmetric, straight. **Primary root** stout and persistent, collar disk not distinct; secondary roots simple, short, pneumatophores present; collar roots present. **Hyperphyll** elongate, grooved all around, connection to seed flat. **Cotyledonary sheath** grooved, splitting lengthwise, opposite to hyperphyll. **Coleoptile** absent. **Cataphylls** two, apex acute and curved. **Eophyll** simple, linear-lanceolate, apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein distinct, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal and distal marginal folds varying on each side, one margin Λ-shaped, other margin V-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear; regular and uniform in transverse section. **Hairs** present, few basal cells. **Stomata** slightly sunken; short and elongate terminal cells overarching guard cells; arranged in rows at intercostal regions; more abundant on abaxial surface. **Hypodermis** single-layered, present at adaxial and abaxial sides. Fibrous

bundles present at irregular intervals; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Mesophyll fibers** as subepidermal bundles present at ridges. **Expansion cells** single-layered. **Major vascular bundles** associated with ridges; OS distinct. **Median vascular bundles** buttressed to abaxial and adaxial sides. **Minor vascular bundles** buttressed to abaxial side; OS cap-shaped; some vascular bundles associate to abaxial grooves. **Midrib** abaxially prominent, with simple and multivascular vascular bundles grouped. **Marginal rib** with minor vascular bundles. **Petiole** transverse section crescent-shaped. **Phloem strands** two to four. **Metaxylem** single. **Cell inclusions**, stegmata irregular, margins spinulose, distributed around vascular bundles

Astrocaryum alatum Loomis

Seed displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral; shoot-born roots abundant; secondary roots stout, branched, pneumatophores present; shoot-born roots present. **Hyperphyll** inconspicuous. **Cotyledonary sheath** absent. **Coleoptile** short,

splitting side opposite to seed; spiny. **Cataphylls** two, splitting lengthwise. **Eophyll** bifid, splitting side abaxial; margins spiny. **Venation** pattern pinnate; leaf axis distinct; midvein distinct, vascular bundles convergent near apex. transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal marginal folds V-shaped, distal outer marginal folds V-shaped, inner fold Λ-shaped. **Epidermal cells** fusiform, adaxial and abaxial walls linear; papillose in transverse section; wax layer thick. **Hairs** present, few basal cells. **Stomata** sunken; short terminal cell overarching guard cells; occluded by wax layer. **Hypodermis** single-layered, cells ellipsoid, orientation paralell; present at adaxial and abaxial sides. **Chlorenchyma** with differentiated layers; palisade layer present; spongy mesophyll with less than five layers. **Mesophyll fibers** as compact bundles, abundant, scattered; small lumen. **Expansion cells** double layered, fibrous bundles scattered. **Major vascular bundles** abaxially prominent, associate with ridges, attached to adaxial and abaxial epidermis; OS not distinct, usually flanked by expansion cells.

Median vascular bundles free, equidistant. **Minor vascular bundles** at abaxial side, not associated to grooves; OS surrounding vascular bundle. **Midrib** abaxially prominent, rounded, simple and multivascular vascular bundles grouped. **Marginal rib** with minor vascular bundlepresent. **Petiole** tranverse section heart shaped. **Phloem strands** four. **Metaxylem** single. **Cell inclusions**, stegmata hat-shaped, margins spinulose, distributed around nonvascular bundles. Tannins scattered.

Bactris killippii Burret

Seed displaced below plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** ephemeral; secondary roots simple; shoot-born roots stout, thicker than radicle. **Hyperphyll** absent. **Cotyledonary sheath** inconspicuous. **Coleoptile** short, splitting opposite to seed. **Cataphylls** two, opening apical, apex acute. **Eophyll** bifid, linear-lanceolate segments, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct, vascular bundles gradually convergent towards the apex; transverse commissures widely separated from each other, always

connected to longitudinal vascular bundles. **Plication** with proximal marginal folds V-shaped; distal outer fold V-shaped, inner fold Λ-shaped. **Epidermal cells** fusiform, adaxial and abaxial anticlinal walls linear, papillose in transverse section; cuticle thick. **Hairs** present, few basal cells. **Stomata** superficial; short or elongate terminal cell not overarching guard cells; guard cells with large ledges. **Hypodermis** single-layered, present at adaxial and abaxial sides; orientation paralell. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibrous bundles** compact, equidistant, surrounded by distinct tanning filled outer sheath; lumen small. **Expansion cells** single-layered. **Major vascular bundles** adaxially prominent, associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS distinct **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, rounded, simple and multivascular vascular bundles grouped. **Marginal rib** with fibrous bundle. **Petiole** transverse section heart-shaped. **Phloem strands** four. **Metaxylem** single. **Cell**

inclusions, stegmata hat-shaped, spinulose margins, distributed around fibrous bundles. Tannins scattered in mesophyll, abundant in OS.

Elaeis guineensis Jacq.

Seed above plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent; secondary roots branched, pneumatophores present; shoot-born roots present; collar disk swollen, collar roots present. **Hyperphyll** short, almost inconspicuous. **Cotyledonary sheath** absent. **Coleoptile** short, non split. **Cataphylls** two, elongate, apex acute, opening lengthwise. **Eophyll** simple, broadly lanceolate, apex acute; five leaves similar to eophyll before first split leaf appearing, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein distinct, vascular bundles convergent gradually to midvein; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal marginal folds V-shaped, distal folds AV-shaped. **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls

linear; polyhedric in transverse section. **Hairs** present, few basal cells. **Stomata** slightly sunken; short terminal cells overarching guard cells; scattered at intercostal regions. **Hypodermis** single-layered, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibers** in equidistant bundles; lumen wide. **Expansion cells** single-layered. **Major vascular bundles** adaxially prominent, displaced from ridge; attached to epidermal layers; OS not distinct. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle; radial OS present. **Midrib** abaxially prominent, squared protuberance, simple and multivascular vascular bundles grouped. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** four. **Metaxylem** single. **Cell inclusions**, stegmata shape irregular, stegmata margins smooth, stegmata distribution around fibrous bundle or vascular bundle. Sclereids present. Raphides equidistant. Tannins, abundant full sacs.

Yampolsky (1922) and Rees (1960) described germination of *Elaeis guineensis* Jacq.

Jubaea chilensis (Molina) Baillon

Seed remaining above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** stout and persistent, disk collar slightly swollen; secondary roots simple, very short; collar roots present. **Hyperphyll** short, smooth, connection to seed flat. **Cotyledonary sheath** short, splitting apically. **Coleoptile** opening apically, splitting opposite to seed. **Cataphylls** two, opening laterally, apical extensions bifid with distinct protuberant transverse lines. **Eophyll** simple, lanceolate, apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein distinct, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal marginal and distal folds varying on each side, one marginal fold Λ-shaped and other fold V-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear; cuticle thick. **Hairs** present; few basal cells.

Stomata slightly sunken; terminal cells short and elongate overarching guard cells; scattered. **Hypodermis** single-layered, rounded cells; present at adaxial and abaxial sides; compact fibrous bundles at irregular intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Mesophyll fibers** in bundles at aaxial side, distinct bundles at ridges; lumen wide. **Expansion cells** double layered; adjacent epidermis papillose. **Major vascular bundles** not associated with ridges, buttressed to adaxial and abaxial epidermis; IS multilayered, sclerotic; OS not distinct. **Median vascular bundles** buttressed to abaxial and adaxial sides, solid buttresses. **Minor vascular bundles** abaxially buttressed; OS not distinct. **Midrib** abaxially prominent, squared, simple and multivascular vascular bundles grouped. **Marginal rib** with minorvascular bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** four. **Metaxylem** single. **Cell inclusions**, spherical or ellipsoid, margins spinulose, around vascular bundles. Tannins abundant.

Gatin (1906a) described germination of *Jubaea*.

Syagrus coronata (Mart.) Becc.

Seed above plumular/radicular node. **Plumular/radicular axis** symmetric, straight. **Primary root** stout and persistent, disk collar swollen; secondary roots simple and short, pneumatophores present; collar roots present. **Hyperphyll** elongate, grooved all around, connection to seed flat. **Cotyledonary sheath** splitting lengthwise, deeply grooved. **Coleoptile** absent. **Cataphylls** two, elongate, apex acute. **Eophyll** simple, linear-lanceolate, apex acute. **Venation** pattern pinnate, leaf axis distinct, midvein distinct, vascular bundles convergent at apex; transverse commissures widely separated from each other, connect longitudinal vascular bundles sporadically. **Plication** with proximal and distal marginal folds V-shaped and Λ-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear. **Hairs** with few basal cells. **Stomata** sunken; short and elongate terminal cells overarching guard cells; scattered, abundant in both surfaces. **Hypodermis** single-layered, present at adaxial and abaxial sides; fibrous bundles or layers at regular

intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Mesophyll fibers** in bundles at ridges; lumen small. **Expansion cells** double layered, elongate, ellipsoid; adjancent epidermis papillose. **Major vascular bundles** not associated with ridges, attached to both epidermis; OS not distinct. **Median vascular bundles** buttressed to both adaxial and abaxial sides. **Minor vascular bundles** buttressed to abaxial side; OS cap-shaped; some vascular bundles associate to grooves. **Midrib** abaxially prominent, triangular; single large multivascularvascular bundle. **Marginal rib** with minorvascular bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** two and four. **Metaxylem** single. **Cell inclusions**, stegmata irregular, margins spinulose, around vascular bundles. Raphides equidistant. Tannins scattered.

Gatin (1906a) described germination of *Syagrus australis* (as *Cocos australis*) and *S. campestris* (as *Cocos campestris*).

Voanioala gerardii J. Dransf.

Seed characters not recorded. **Plumular/radicular axis** symmetric. **Primary root** persistent, collar disk distinct; secondary roots simple; shoot-born roots present. **Hyperphyll** elongate, connection to seed flat. **Cotyledonary sheath** rugulose, opening lengthwise. **Coleoptile** not seen. **Cataphylls** two. **Eophyll** simple, lanceolate, apex acute with long linear extension; third leaf splitting at abaxial side. **Venation** pattern pinnate; leaf axis distinct; midvein distinct, vascular bundles convergent at apex; transverse commissures abundant, very close from each other, connecting longitudinal vascular bundles or intercostal regions sporadically. **Plication** with proximal and distal marginal folds Λ-shaped and V-shaped. **Epidermal cells** rectangular or rhombohedral, adaxial and abaxial anticlinal walls linear; small and polyhedric in transverse section; cuticle thick. **Hairs** present, sunken base, few cells. **Stomata** sunken, at hypodermal layer; short terminal cells overarching guard cells; scattered. **Hypodermis** single-layered, at adaxial and abaxial sides. **Chlorenchyma** differentiated; palisade layer distinct; spongy mesophyll up to five layers. **Mesophyll fibers** in

bundles at adaxial side; lumen wide. **Expansion cells** double layered, elongate, rectangular; adjacent epidermis papillose. **Major vascular bundles** associated with ridges, attached to adaxial hypodermis and abaxial expansion layer; OS not distinct. **Median vascular bundles** free, equidistant. **Minor vascular bundles** oriented towards abaxial side; OS cap-shaped. **Midrib** abaxially prominent, squared; simple and multivascular vascular bundles grouped. **Marginal** rib not vascularized. **Petiole** transverse section terete. **Phloem strands** two to four. **Metaxylem** single. **Cell inclusions**, stegmata irregular, margins spinulose, distributed around vascular bundles.

* only one sample in an advance stage of developmental was available for study.

Summary for Cocosoid palms

Summary for non-spiny cocosoids:

Plumular/radicular axis may be straight or curved; primary root straight and persistent, collar roots developed, hyperphyll elongate or contracted, cotyledonary sheath opening apically or laterally, a coleoptile present or absent, two cataphylls, eophyll

simple, rarely pinnate, and acute at apex, eophyll has pinnate venation, and reduplicate and induplicate margins.

Summary for spiny cocosoids:

Plumular/radicular axis may be straight or curved; primary root either straight or oblique, persistent or ephemeral, collar roots developed or do not develop; cotyledonary sheath opening apically, a coleoptile present, two cataphylls, eophyll bifid, rarely simple and acute at apex; eophyll has pinnate venation, and outer margins induplicate and inner margins reduplicate.

14. GEONOMOID PALMS

Geonoma interrupta (R. & P.) Mart.

Seed above plumular/radicular node. **Plumular/radicular axis** asymmetric, angular; primary root persistent; disk collar distinct; secondary roots branched; shoot-born roots outgrowing radicle. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, not split. **Cataphylls** two, elongate,

opening lengthwise, apex acute split. **Eophyll** bifid, segments sigmoid, apex acute, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication** with proximal marginal folds V-shaped, distal outer margin V-shaped, inner margin Λ-shaped. **Epidermal cells** rhombohedral, adaxial and abaxial anticlinal walls linear; large and regular in transverse section; costal cells shorter than intercostal cells. **Hairs** unicellular, globose with few basal cells. **Stomata** superficial; short terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibrous bundles** equidistant. **Expansion cells** single-layered, large cuneate cells adjacente to midrib. **Major vascular bundles** prominent at abaxial and abaxial sides, associated with ridges, attached to epidermal layers; IS multicellular, sclerotic; OS distinct, at lateral sides ofvascular bundle, filled with tannins. **Median vascular bundles**

free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle, filled with tannins. **Midrib** abaxially prominent, simple and multivascular bundles grouped. **Margins** lacking ribs. **Petiole** croissand-shaped. **Phloem strands** two. **Metaxylem** single. **Cell inclusions, stegmata** hat-shaped, margins spinulose, around vascular bundle. Raphides equidistant. Tannins in full sacs, large.

Welfia regia H. Wendl.

Seed above plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent; secondary roots branched; shoot-born roots abundant. **Hyperphyll** extremely short. **Cotyledonary sheath** absent. **Coleoptile** very short, opening apically, not split. **Cataphylls** two, opening lengthwise, with apex split. **Eophyll** bifid, broad-sigmoid segments, apex acute, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein distinct from other longitudinal vascular bundles, vascular bundles gradually converging at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular

bundles. **Plication** with proximal marginal folds V-shaped, distal outer margin V-shaped, inner margin Λ-shaped. **Epidermal cells** rhombohedral, adaxial and abaxial anticlinal walls linear, papillose in transverse section, cuticle present. **Hairs** unicellular, globular, few basal cells. **Stomata** superficial; short terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Mesophyll fibrous bundles** equidistant. **Expansion cells** single-layered. **Major vascular bundles** associated with ridges, distinct OS. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, rounded, simple and multivascular bundles grouped. **Margins** lacking ribs. **Petiole** transverse section heart-shaped. **Phloem strands** one. **Metaxylem** single. **Cell inclusions, stegmata** irregular, margins spinulose, around vascular bundle. Raphides scarce. Tannins abundant, full sacks, present in vascular bundle and mesophyll cells.

Summary for Geonomoid palms

Plumular/radicular axis curved; primary root either straight or oblique; primary root persistent or ephemeral, collar roots developed or do not develop; cotyledonary sheath opening apically, a coleoptile present, two cataphyll, eophyll bifid and acute at apex, eophyll has pinnate venation and reduplicate margins.

15. PHYTELEPHANTOID PALMS

Phytelephas seemanii O. F. Cook

Seed above plumular/radicular node. **Plumular/radicular axis** asymmetric, angular. **Primary root** persistent; secondary roots branched, pneumatophores present; shoot-born roots present; collar roots present. **Hyperphyll** elongate, smooth, attachment to seed slightly swollen. **Cotyledonary sheath** very short. **Coleoptile** opening apically, dentate all around. **Cataphylls** three, apex acute, thick claw-like, ligular fibrous extensions. **Eophyll** pinnate, lanceolate segments, apex acute, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal

vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication**, proximal section not available, distal marginal folds Λ-shaped one margin, the other margin V-shaped. **Epidermal cells** rectangular, elongate, adaxial and abaxial anticlinal walls linear. **Hairs** present, few basal cells. **Stomata** superficial; short terminal cells overarching guard cells, arranged in rows at intercostal regions. **Hypodermis** with fibers at irregular intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** double layered, flanking major vascular bundles. **Major vascular bundles** multivascular, not associated with ridges, attached to both epidermal layers; IS multilayered; OS not distinct. **Median vascular bundles** free, equidistant. **Minor vascular bundles** equidistant; OS surrounding vascular bundle. **Midrib** prominent at both adaxial and abaxial sides, single multivascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section terete. **Phloem strands** two. **Metaxylem** two. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around

vascular bundles. Raphides equidistant, large. Tannins abundant, some in full sacs.

Phytelephas tenuicaulis (Barfod) Henderson

Seed above plumular/radicular node. **Plumular/radicular axis** asymmetric. **Primary root** persistent; secondary roots branched; shoot-born roots present, pneumatophores present. **Hyperphyll** elongate, smooth, attachment to seed slightly swollen. **Cotyledonary sheath** short. **Coleoptile** short, opening apically. **Cataphylls** three, acute and bifid apices. **Eophyll** pinnate, linear-lanceolate segments, apex acute, splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal vascular bundles, vascular bundles convergent at apex; transverse commissures widely separated from each other, always connected to longitudinal vascular bundles. **Plication**, proximal section not available, distal marginal folds Λ-shaped one margin, the other margin V-shaped. **Epidermal cells** rectangular, adaxial and abaxial anticlinal walls linear, rounded and papillose in transverse section. **Hairs** present, few basal cells. **Stomata** superficial;

short terminal cells overarching guard cells, arranged in row at intercostal regions. **Hypodermis** with fibers at irregular intervals. **Chlorenchyma** undifferentiated; palisade **layers** Spongy mesophyll with more than five layers. **Expansion cells** single layered. **Major vascular bundles** not associated with ridges, attached to epidermis; IS multilayered and sclerotic; OS not distinct. **Median vascular bundles** free, equidistant; OS surrounding vascular bundle. **Minor vascular bundles** very small, equidistant; OS surrounding vascular bundle. **Midrib** prominent at both adaxial and abaxial sides, single large multivascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section terete. **Phloem strands** two. **Metaxylem** two. **Cell inclusions**, stegmata spherical or ellipsoid, margins spinulose, distributed around vascular bundles. Tannins abundant, some in full sacs.

Summary of Phytelephantoid palms

Plumular/radicular axis may be straight or curved, primary root straight and persistent, collar roots developed or do not develop, hyperphyll elongate, cotyledonary sheath opening apically, a

coleoptile present, two cataphylls, eophyll pinnate, and acute at apex, eophyll has pinnate venation, and reduplicate.

2. Cladistic Analysis

Analysis I. Seedling data using the calamoids as the outgroup

The seedling data matrix (Table 4) had a total of 2.14% missing characters, 6.38% inapplicable, and 2.33% polymorphic. The cladistic analysis using the calamoids as outgroup recovered one most parsimonious tree (MPT) (Fig. 14) of 356 steps. The consistency index (C.I.) is 20, and the retention index (R.I.) is 66.

The tree is poorly resolved. The ceroxyloids form a monophyletic basal clade. The arecoids are polyphyletic, with *Nephrosperma, Dictyosperma* and *Phoenicophorium* forming a clade. *Euterpe* is sister to a clade formed by *Archontophoenix, Hyospathe, Dypsis* and *Veitchia*. The chamaedoreoids form a clade, and the geonomoids form a clade that include the cocosoids

Astrocaryum and *Bactris*. Next is an unresolved clade with *Neonicholsonia* (arecoid), *Nypa*, and the iriarteoids with *Podococcus*. Next is a clade containing *Elaeis*, the phytelephantoids, and the remaining cocosoids (*Jubaea*, *Allagoptera*, and *Syagrus*), and *Pseudophoenix*. The remaining taxa are grouped into three clades with *Trachycarpus* as sister taxon. The first of these clades comprises some members of the coryphoids, *Sabal* and *Corypha*, next to the borassoids; the second comprises the caryotoids forming a monophyletic clade with *Nannorrhops* as sister taxon, together with three coryphoids (*Trithrinax*, *Cryosophila*, and *Itaya*). The third clade comprises *Phoenix* (phoenicoid) and the remaining coryphoids.

Analysis II. Seedling data using *Nypa* as the outgroup

The same matrix was run using *Nypa* as outgroup. The analysis recovered 1 MPT (Fig. 15) of 356 steps (C.I. = 20, R.I. = 66). The basal clade contains the iriarteoids with *Podococcus* next to *Iriartella*. The arecoids are again polyphyletic, with *Roystonea*, *Neonicholsonia*, and *Dypsis* basal. The first clade

comprises *Veitchia, Nephrosperma, Dictyosperma, Phoenicophorium* and *Euterpe* (arecoid), *Ceroxylon* and *Oraniopsis* (ceroxyloid) and the four taxa of the calamoids. The second clade clade contains *Archontophoenix* and *Hyospathe* (arecoid), the chamaedoreoids (forming a clade), and *Geonoma* and *Welfia* (not forming a clade). *Astrocaryum* and *Bactris* form a separate clade from *Elaeis* and *Voanioala* (cocosoids) and *Ravenea* (ceroxyloid). *Orania,* the phytelenphantoids, *Pseudophoenix* the remaining cocosoids (*Jubaea, Allagoptera and Syagrus*), and *Trachycarpus* are basal to two other clades. The first of these comprises some of the coryphoids and *Phoenix,* the second the remaining coryphoids with the borassoids forming a monophyletic clade with *Corypha* a sister taxon, and the third, the remaining coryphoids and the caryotoids forming a clade with *Nannorrhops* as sister taxon.

Seedling character support

Eophyll anatomical characters supported most of the major groups. The ceroxyloids are supported by

three character states: hypodermal layer (25), single phloem strand (44), and irregular silica body (47), but all these are homoplasious. The chamaedoreoids are supported by four character states: lack of epidermal hairs (21), lack of fibrous bundles (29), presence of a second OS with radially oriented cells (39), and two metaxylem vessels (45). Again, all these are homoplasious. *Astrocaryum* and *Bactris* occur independently from the other cocosoid taxa, and this relationship is supported by three character states: fusiform epidermal cells (18), distinct hypodermis (25) and silica bodies around non-vascular bundles (48). Fusiform epidermal cells occur elsewhere in the family. Distribution of silica bodies occurs as a multiple character in several taxa, but the occurrence of silica bodies around the non-vascular bundles is a synapomorphy for *Astrocaryum* and *Bactris*. In both seedling trees *Podococcus* is placed next to the iriarteoids, and this relationship is supported by four character states: non-convergent veins (15), rhombohedral epidermal cells (18), single conical epidermal hair (22), and fiber lumina small (32). Only character state 22 is a synapomorphy for the clade.

Sabal and Corypha (coryphoid) are resolved as sister taxa to the borassoids, supported by two characters. One of these is a synapomorphy, minor vein towards adaxial side (36). The other, buttressed minor veins (40), is a synapomorphy for the borassoids. The caryotoids resolve within the coryphoids next to *Nannorrhops*, and this is supported by seven homoplasious characters.

Analysis III. Combined analysis of seedling data and adult data using the calamoids as the outgroup

This matrix had 1.74% missing characters, 4.58% inapplicable, and 1.35% polymorphic characters. The combined analysis using the calamoids as outgroup resulted in one MPT (Fig. 16), with a length of 356, a C.I. of 23, a R.I. of 66. The overall tree topology resolved into five major clades. The ceroxyloids and chamaedoreoids, both monophyletic, form a basal clade. The second clade comprises the geonomoids next to the cocosoids, both monophyletic. The third clade comprises most of the arecoids. These form a paraphyletic group, with the second branch comprising

the remaining arecoids, *Nypa*, the iriarteoids, and *Podococcus*. The phytelenphantoids and *Pseudophoenix* are basal to the remaining clade. The caryotoids are sister to this clade. One branch contains some coryphoids and the borassoids, the second branch the remaining coryphoids and *Phoenix*.

Analysis IV. Combined analysis of seedling data and adult data using *Nypa* as the outgroup

Using *Nypa* as outgroup, the heuristic search found one MPT (Fig. 17) of 356 steps, with a C.I. of 23 and a R.I. of 66. The phytelenphantoids are basal to the rest of the palms. The first clade comprises the calamoids, the ceroxyloids, and the chamaedoreoids, each forming monophyletic groups. *Euterpe* and *Neonicholsonia* are sisters to the second clade formed by most of the arecoids, iriarteoids, and *Podococcus*. The third clade resolves the geonomoids next to the cocosoids. *Orania* (arecoid) and *Pseudophoenix* are unresolved. The caryotoids form a monophyletic clade sister to the fourth clade that comprises part of the coryphoids and the borassoids.

The fifth clade resolves *Chamaerops* (coryphoid) as sister taxon to the remaining coryphoids and *Phoenix* (phoenicoid).

Combined analysis character support

The supporting statistics in the combined analysis (Analysis IV) are higher than the analyses using seedling characters alone. The ceroxyloids and chamaedoreoids form clades supported by one seedling anatomical character and one adult character: single phloem strand (44) and stigmatic remains basal to lateral (82), although both characters are homoplasious. The ceroxyloids share four character states: one anatomical, distinct hypodermal layer (25), and three adult characters, incomplete prophyll (62), flowers opening precociously (69) and hemianatropous ovules (76). An incomplete prophyll is a synapomorphy for the group, but precocious flower opening occurs in *Nypa, Socratea,* and the phytelephantoids. The chamaedoreoids are supported by four characters, three of them seedling characters: angular plumular/radicular axis (0), lack of epidermal hairs (21), absence of hypodermal fibers (26), and one

adult character: developed crownshaft (60). All four character states are homoplasious. The geonomoids resolve as sister group to the cocosoids, supported by two characters: irregular silica body (46) and staminodial ring absent (72). *Geonoma* and *Welfia* form a monophyletic group supported by rhombohedral epidermal cells (18) and basal stigmatic remains (83), although both character states are homoplasious. Four characters support the cocosoid group: sunken stomata (24), distinct hypodermis (25), four phloem strands (44), and three endocarp pores (80). Phloem strands and endocarp pores are synapomorphies for the group. All the arecoids are in the same paraphyletic clade, which includes *Nypa, Podococcus* and the iriarteoids. This clade is supported by four character states: angular plumular/radicular axis (0), ephemeral primary root (1), developed crownshaft (60), and pseudomonomery (75). The angular plumular radicular axis also occurs in the chamaedoreoids. Ephemeral primary root and pseudomonomery are synapomorphies for the group with the exception of *Orania*. *Nypa* resolves as sister to the iriarteoids plus *Podococcus*, and this relationship is supported by four character states:

marginal rib with a non-vascular bundle (43), single phloem strand (44), smooth marginal silica body (47), and absence of pseudomonomery (75). All these character states are homoplasious. Iriarteoids and *Podococcus* form a clade supported by six character states: non-convergent veins (15), rhombohedral epidermal cells (18), single conical hair (22), fiber lumina small (32), praemorse pinnae (56), and several peduncular bracts (64). Praemorse pinnae also occur in the caryotoids, formerly placed near the iriarteoids by Uhl & Dransfield (1987) and in the arecoid *Orania*. The caryotoids are supported by thirteen homoplasious character states. The clade including the coryphoids, borassoids, and phoenicoids is supported by four character states: adaxial fibrous bundle (30), hastula (53), absence of a winged rachis (55), and apocarpus gynoecium (74). Absence of a winged rachis is a synapomorphy for the group.

Analysis V. Combined analysis of seedling data and adult data using the monocot family Dasypogonaceae as the outgroup

The analysis resulted in 6 MPTs (Fig. 18) of 549 steps, with a C.I. of 22 and a R.I of 66. Nine of the major groups are monophyletic. The phoenicoids are resolved as a basal clade next to a paraphyletic coryphoid group (Fig. 19). The caryotoids are monophyletic, supported by 8 seedling character states: flat hyperphyll connection (4), longitudinal veins non-convergent (15), epidermal cells fusiform (18), hypodermal cells absent (26), minor veins OS incomplete (39), phloem strands 2 (45), silica body hat-shaped (47), silica body margins smooth (48); and 5 adult character states: pinnae praemorse (55), flowering hapaxanthic (60), flowers in triads (65), plants monoecious (67) and atectate pollen wall (85). The calamoids are supported by 4 seedling character states: adaxial and abaxial wall of epidermal cells dentate (19)(20), longitudinal median veins at abaxial side (35), minor vein at abaxial side (37), and 5 adult character states: tubular bracts subtending flower clusters (64), flowers in diads (65), staminodial ring present (71), micropyle not oriented toward center (77), scaly pericarp (78). The ceroxyloids formed a sister clade to the

chamaedoreoids. The monophyly of the ceroxyloids is supported by a single seedling character state: hypodermal layer present (25) and 3 adult character states: prophyll incomplete (61), flowers open precociously (68) and ovules hemianatropous (76). The chamaedoreoids are supported by 3 seedling character states: plumular/radicular axis angular (0), lack of epidermal hairs (21), hypodermal fibers absent (26), and a single adult character state: developed crownshaft (59). The ceroxyloids and chamaedoreoids have a single phloem strand (59) and the stigmatic remains are basal to lateral (82). The geonomoids are resolved as sister to the cocosoids. The geonomoids share rhombohedral epidermal cells (18) and basal to lateral stigmatic remains (82). The cocosoids are supported by 3 seedling character states: sunken stomata (24), hypodermal layer present (25), four phloem strands (45), and a single adult character state: endocarp with three pores (79). Geonomoids and cocosoids share midribs with a group of vascular bundles (43), irregular silica bodies (47) and the presence of a staminodial ring (71). *Podococcus* is nested among the iriarteoids in the basal arecoid

clade, this clade is supported by 4 seedling character states: non-convergent veins (15), rhombohedral epidermal cells (18), unicellular, conical trychoma (22), fiber lumina small (32), and 2 adult character states: praemorse pinnae (55), and several peduncular bracts (63).

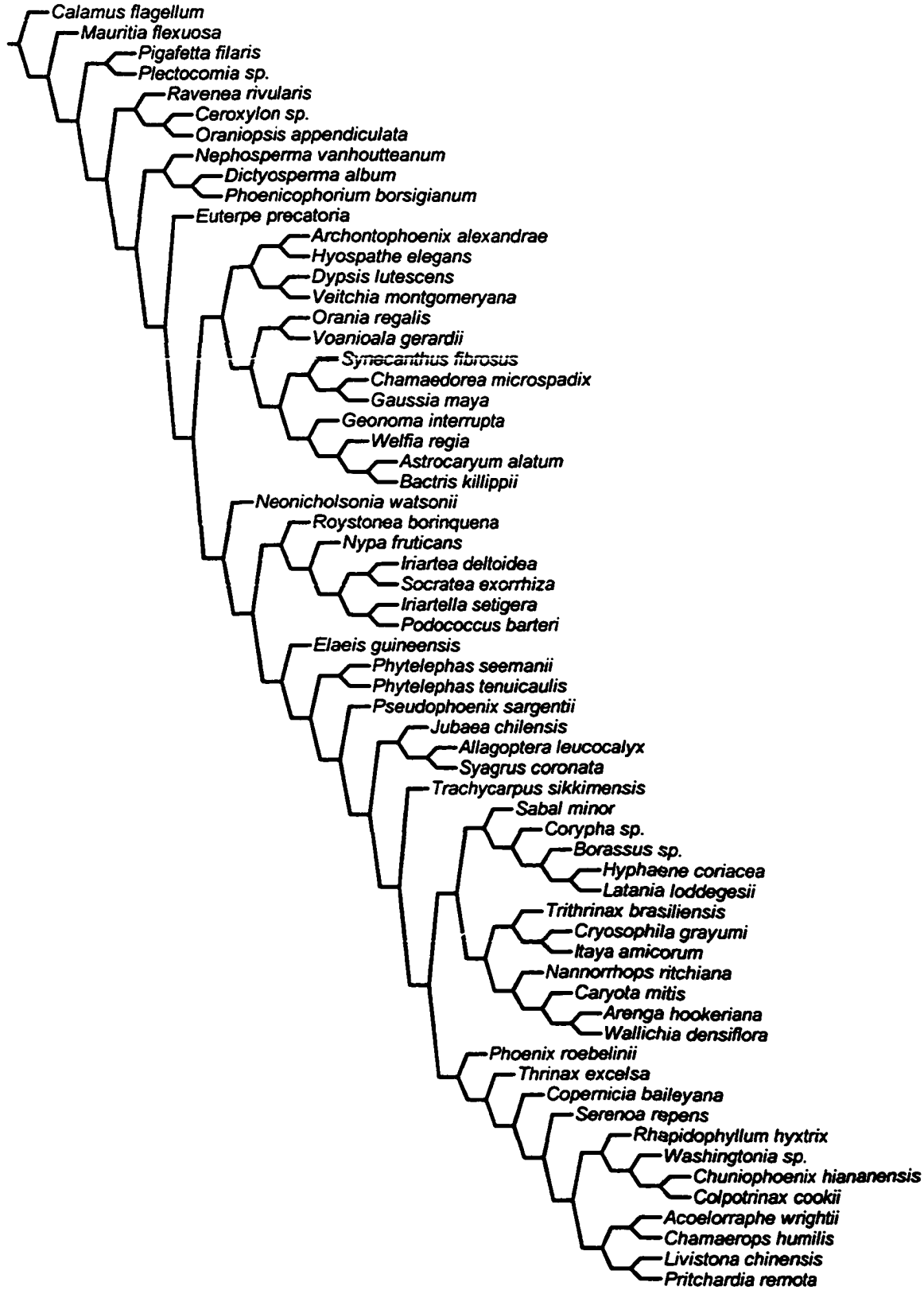


Figure 14. MPT using the calamoids as the outgroup, length= 356, CI = 22, RI = 66

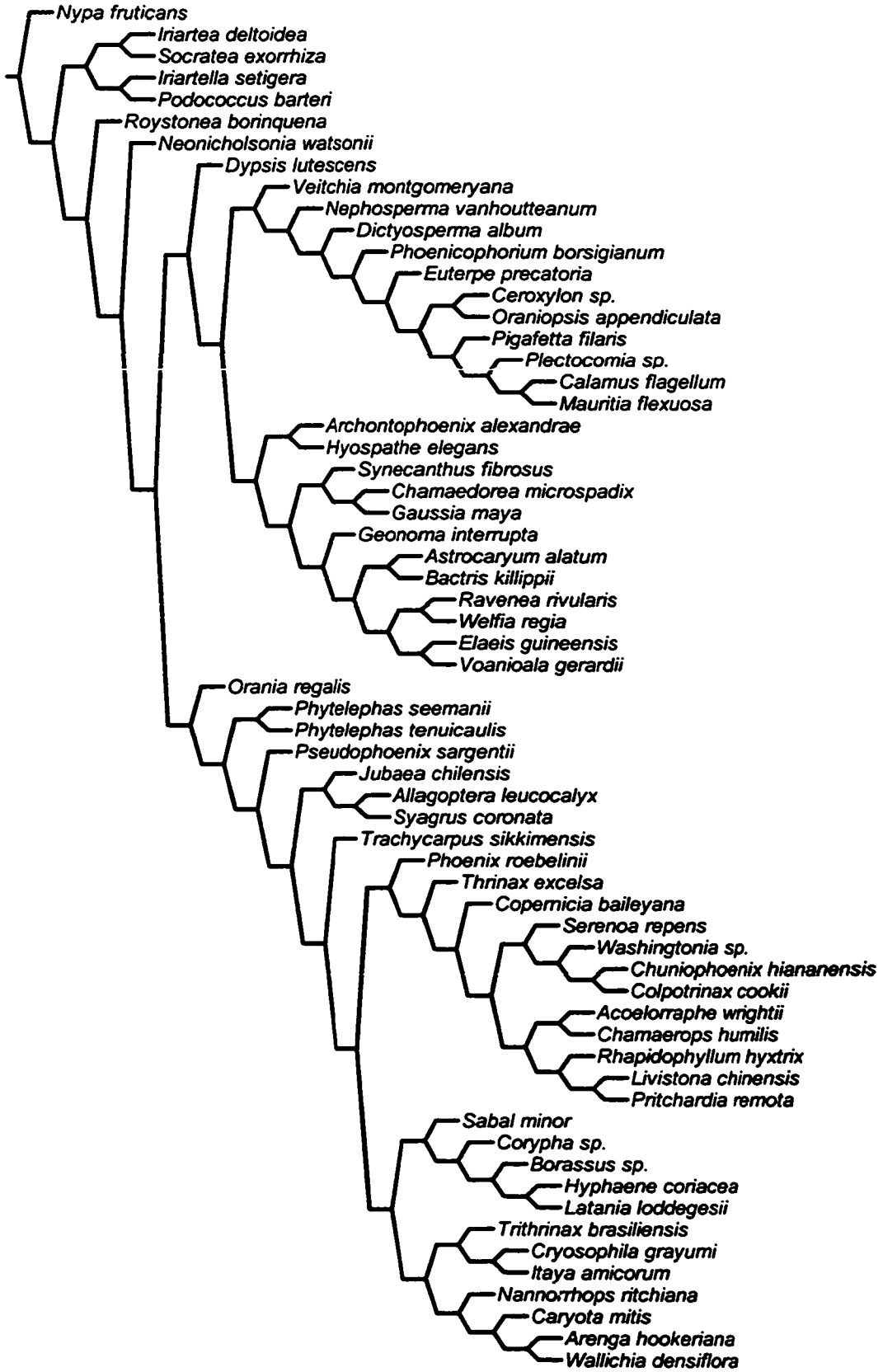


Figure 15. MPT using *Nypa* as outgroup, length = 356, CI = 22, RI = 66

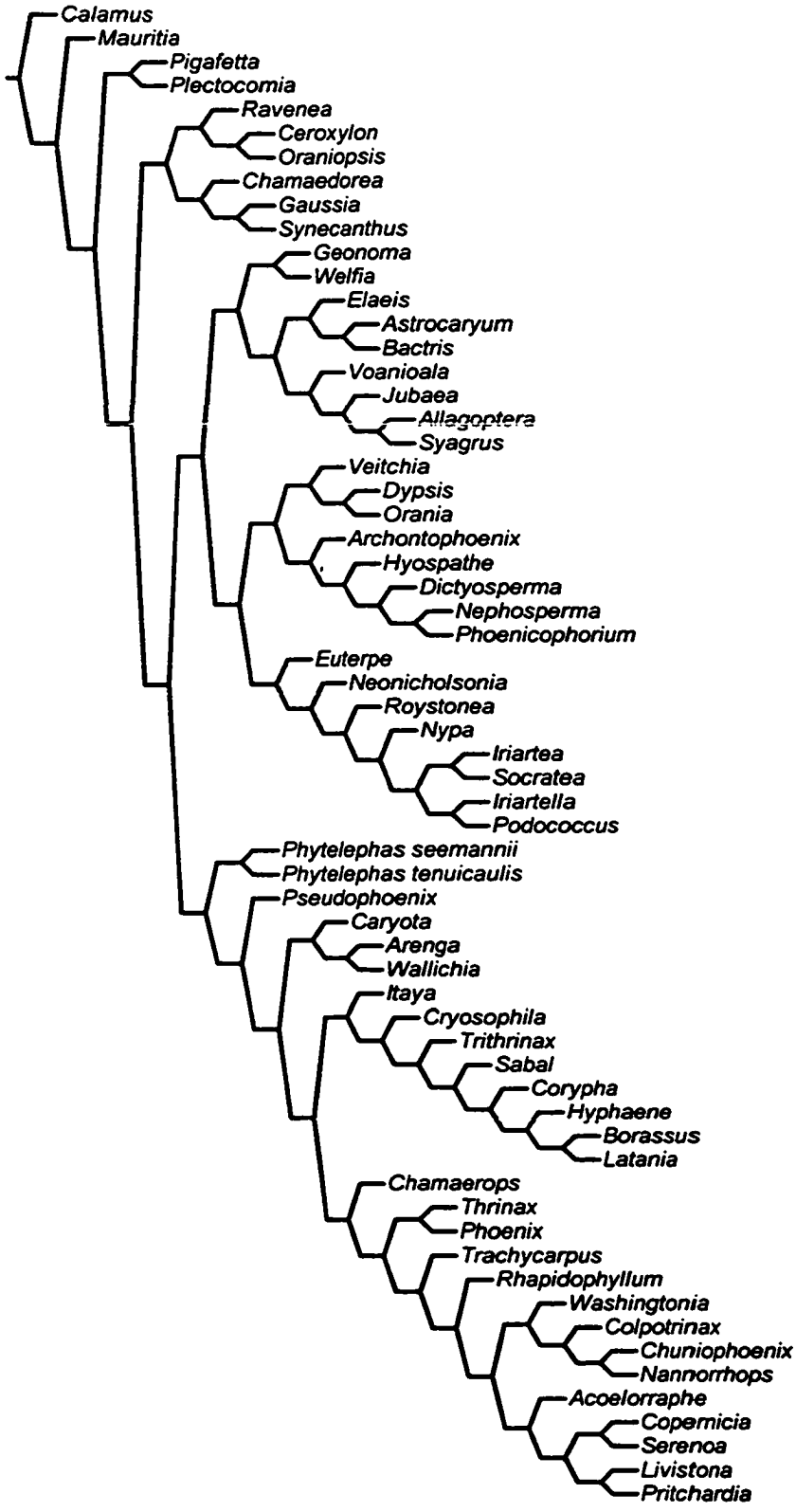


Figure 16. MPT of combined analysis using calamoids as the outgroup, length = 356, CI = 22, RI = 66.

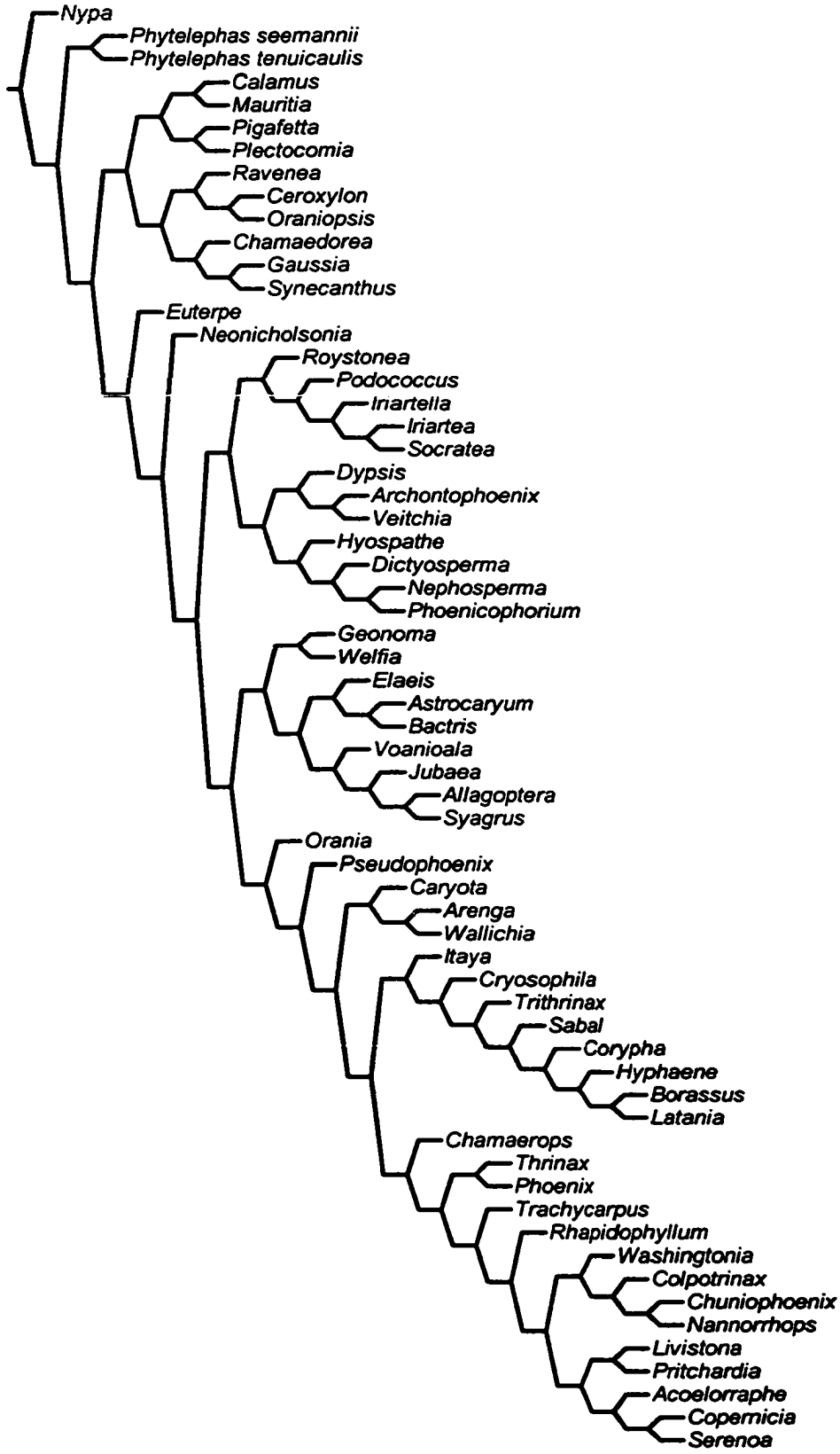


Figure 17. MPT of combined analysis using *Nypa* as outgroup, length = 356, Ci= 22, RI = 66

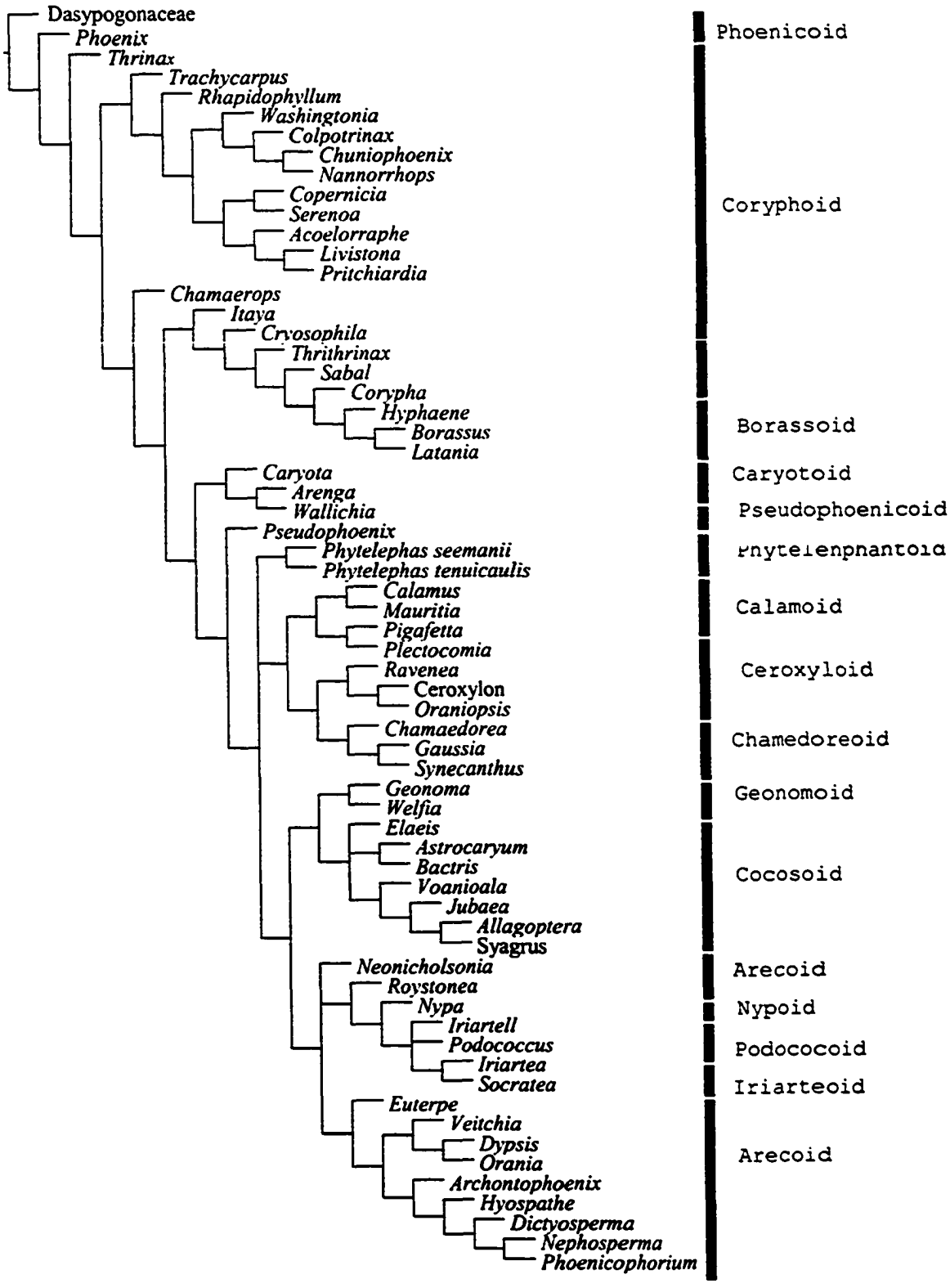


Figure 18. MPT of 6 using Dasypogonaceae as the outgroup. Tree length = 549, CI = 22, RI = 66

Figure 19. Branches showing supporting character states.

Figure 19. continue

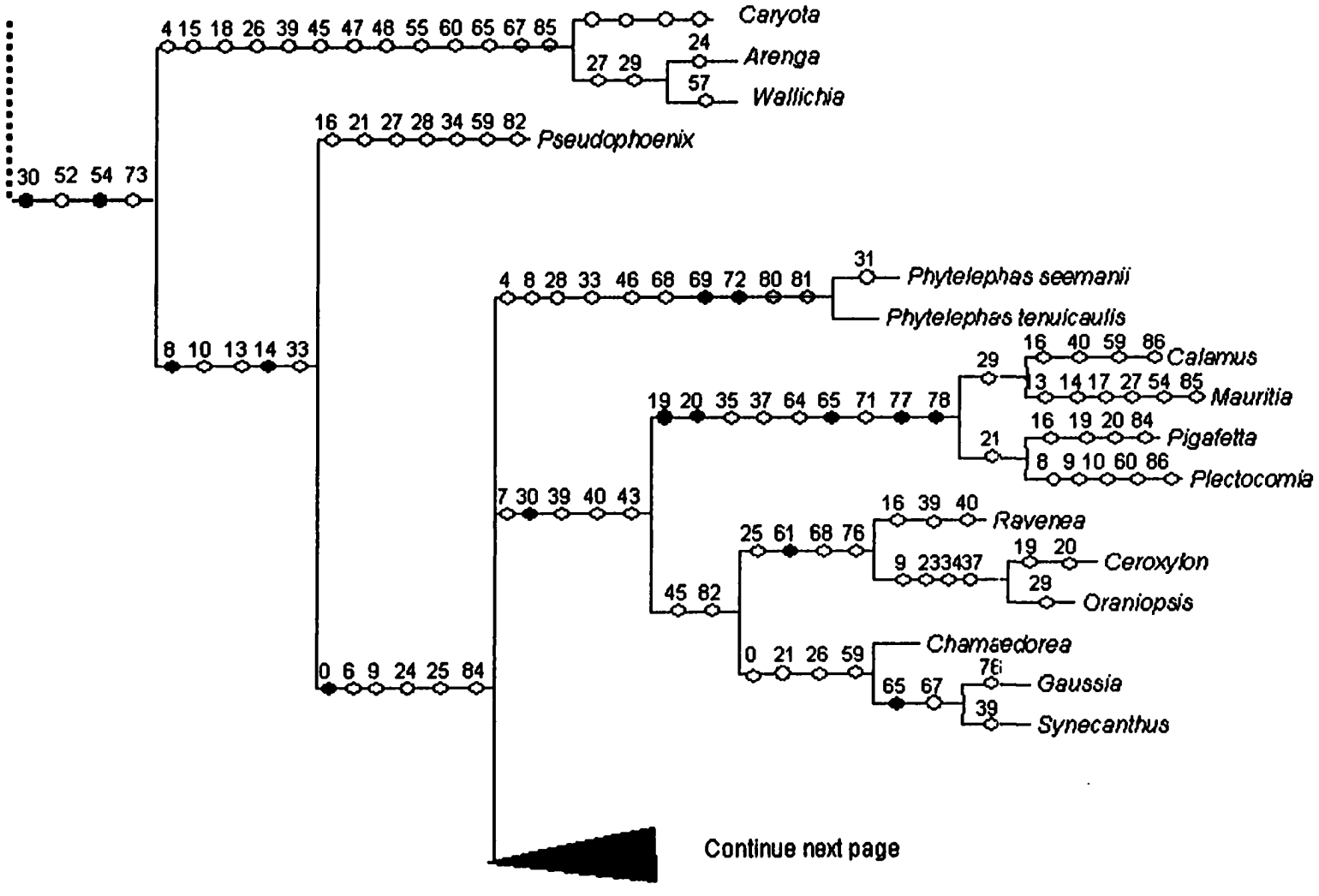
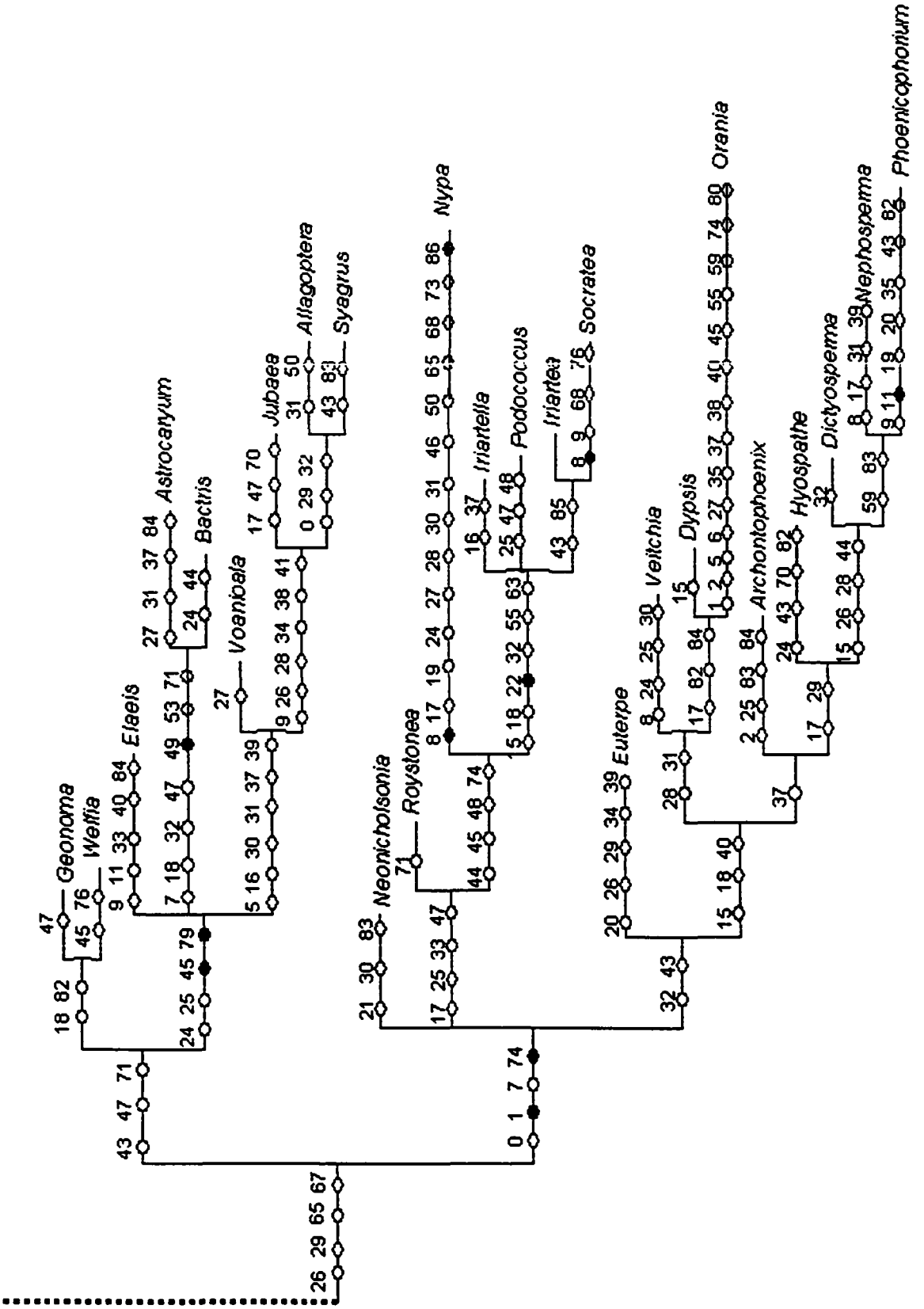


Figure 19. continue



V DISCUSSION AND CONCLUSIONS

Germination types

The three germination types proposed by Martius (1823-50) are not supported by the present study. The seedling cannot be classified based on the length of the hyperphyll and presence of the coleoptile alone. The hyperphyll length is a not a discrete character. This structure can extend different distances from the seed, from a few millimeters e.g. *Arenga hookeriana* (Fig. 2a), *Nannorrhops ritchiana* (Fig. 3b), to several centimeters, e.g. *Chryosophyla grayumii* (Fig. 2d), *Chamaerops humilis* (Fig. 4a) and *Corypha* sp. (Fig. 5c). The variation is difficult to describe without using a quantitative measure.

The second feature considered by Martius was the presence of a coleoptile (ocrea or ligule). This structure is also highly variable. The length of the coleoptile is dependent on the point of attachment with the hyperphyll and the hypocotyl. If the hyperphyll is inserted at the base or directly at the plumular/radicular node, the coleoptile is distinct (Fig. 3d). In some taxa the hyperphyll is inserted

(Fig. 3d). In some taxa the hyperphyll is inserted halfway to the hypocotyl leaving a visible cotyledonary sheath and a short coleoptile (Fig. 4c). If the hyperphyll is connected to the distal end of the sheath, the coleoptile does not develop further (Fig. 2a). A coleoptile does not develop if the cotyledonary sheath is split (the tubular type of Martius) (Fig. 2d).

The primary root appears to be the structure that provides substantial information. Even though primary roots are present for a short period of time and are soon replaced by adventitious roots, they are present during the development of the eophyll. The primary root can be vertically oriented (Fig. 2a), diagonally oriented (Fig. 2b) or horizontally oriented (Fig. 2c and 2d), thus forming different angles in relation to the plumular/radicular axis.

Seedling developmental patterns in palms are at a lower evolutionary level, according to Tillich (2000). This assumption is based on the presence of cataphylls. Slow developers have fewer cataphylls than faster developers (e.g., the iriarteoids). The number of cataphylls appears to be of diagnostic value, and it

varies from one in several coryphoids to four or seven in *Socratea* (iriarteoid) (Fig. 2c) and *Nypa*.

The number of cataphylls is related to eophyll shape. For example, single cataphylls are associated with simple eophylls (Fig. 5c) and seedlings with more than one cataphyll generally have bifid (Fig. 5b), palmate or pinnate eophylls. The more cataphylls the seedling has, the more complex the morphology of the eophyll. For example, *Socratea* (iriarteoid) has four to seven cataphylls, the eophyll is bifid, with pinnate venation, non-convergent longitudinal vascular bundles, and a crenate apex. *Nypa* has more than four cataphylls, and the eophyll is either bifid or pinnate.

After a series of cataphylls, the first photosynthetic leaf, the eophyll (Tomlinson, 1971) emerges. It exhibits a range of shapes from simple (Fig. 5c) in most coryphoids, borassoids, phoenicoids, and some cocosoids to bifid (Figs. 5b and 5d), in most arecoids, ceroxyloids, geonomoids and some calamoids, to palmate in *Mauritia* (calamoid), *Latania* (borassoid), to pinnate in *Phytelephas* (phytelephantoid) and *Nypa*.

Taxa with simple eophylls develop a variable number of eophyll-like leaves before the first split leaf appears. The leaf axis or future rachis is reduced or short, the venation in this type of eophyll is parallel. Bifid eophylls have a distinct axis running between the two segments, pinnate venation, eg. calamoids, arecoids, and cocosoids. An exception to this is the bifid eophyll of *Caryota,* which, unlike the arecoids, the "apical" pinna does not split basally, but, the segments or pinnae are formed before their emergence.

A series of eophyll-like leaves follow the eophyll, before the final adult shape. Bifid eophylls are effectively the apical pair of pinnae of an adult leaf, new pinnae are added basally on successively older leaves. In palms with simple eophylls (except *Phoenix*) several successive leaves precede the segmented stage. In other words, in bifid eophylls, development is speeded up and in simple eophylls a developmental stage is missing.

Plication in palms is the result of differential growth (Kaplan et al., 1982). This character separates palms leaves into two groups. Palms with reduplicate

leaves (∧-shaped) (Fig. 6a), and palms with induplicate leaves (V-shaped) (Fig. 6b). Simple eophylls have the same folding pattern that runs along the whole length of margin of the lamina. The exception to this rule is the bifid cocosoid eophyll, where each margin exhibits a different folding type; the proximal end V-shaped and the inner distal end of the segment ∧-shaped. Another observation in relation to plication is that some eophylls seem to be strongly plicate, such as some coryphoids, while others do not show plication, e.g., caryotoids. Others are more sinuous than plicate.

Anatomical features have proven to be of diagnostic value (Tomlinson, 1961). In seedlings most of the anatomical structures are in the early stages of development, but some features are of diagnostic value. Epidermal cell walls are generally thin, and in surface view anticlinal walls are either linear (Fig. 7a), sinuous or dentate (Fig. 7b).

Stomata are superficial (Fig. 10a) or sunken (Figs. 9a and 9b). Some groups have distinct epidermal hairs, for example the iriarteoids with large basal cells and unicellular trichomes. Hair bases in some

borassoids, arecoids, ceroxyloids, and chamaedoreoids are multicellular and sclerotic. A hypodermal layer is present in most taxa, generally appearing as a colorless layer, with the cells larger than epidermal cells (Figs. 8a and 10a). They may be single-layered or two-layered. In some cases the hypodermal layer is replaced by fibers that are solitary, arranged in bundles (Fig. 10a), or even forming a continuous layer as in *Borassus* (borassoid), *Corypha* and *Itaya* (coryphoid), and *Pseudophoenix* (pseudophoenicoid) (Fig.9b).

The mesophyll layers are rarely well differentiated into distinct palisade and spongy parenchyma. However, taxa with distinct palisade parenchyma are common among caryotoids and borassoids. Mesophyll fibrous non-vascular bundles are common among mesophyll cells, forming compact bundles arranged in an orderly fashion. There seems to be a pattern in the distribution of non-vascular fibers. These are distributed in either the sub-epidermis or among the mesophyll layer. Taxa with both types of fibers bundles are rare, e.g., in *Livistona, Borassus, Calamus, Mauritia, Oraniopsis* and *Jubaea* (Fig. 25 and 26).

In the vascular tissue, the sclerotic parenchyma forms a protective sheath surrounding the vascular tissue (inner sheath - IS). The vascular bundles are differentiated into three categories. Major vascular bundles are the larger vascular bundles in the mesophyll, these are usually connected to the epidermal or hypodermal layers both adaxially and abaxially. These vascular bundles are either associated or not associated with folds are either free or buttressed by fibrous strands. Median vascular bundles are an intermediate type between major and minor vascular bundles. They are not easy to distinguish and their distribution is usually among the mesophyll cells and they are attached to either the adaxial or the abaxial epidermal layers, or are independent. Minor vascular bundles can be equidistant from the abaxial and adaxial layers, or displaced toward or buttressed abaxial or adaxially.

The midrib can be prominent or flat, symmetric or asymmetric, or with single or multiple vascular bundles. The margin of the eophyll may or may not have vascular tissue. Some groups have distinct vascular bundles, others have fibrous layers or bundles, and

other have regular parenchyma tissue. *Arenga, Wallichia* (caryotoid) and *Socratea* and *Iriartea* (iriarteoid) have a distinct large vascular bundle protubers both abaxial and adaxially. The vascular bundles are surrounded by several layers of sclerotic tissue. The eophyll of the caryotoids is simple or bifid, with palmate venation, and a praemorse apex; while the eophyll of the iriarteoids is simple or bifid, with pinnate venation, and a praemorse apex.

The number of phloem strands in major vascular bundles of adult leaves is a distinct feature. They are generally single or double (Tomlinson 1961; Uhl & Dransfield, 1987). Eophylls follow the general adult leaf pattern, with some exceptions. Three phloem strands were detected in various taxa. The arrangement consisted of a large central strand and two small lateral strands, for example in the borassoids and *Chuniophoenix, Nannorrhops,* and *Sabal* (coryphoids). Vascular bundles with four strands were also found in the cocosoids, and the sclerotic partitions in this latter case were irregular. It is possible that the sclerotic partitions are ephemeral at this stage of development, and eventually vascular bundles with three

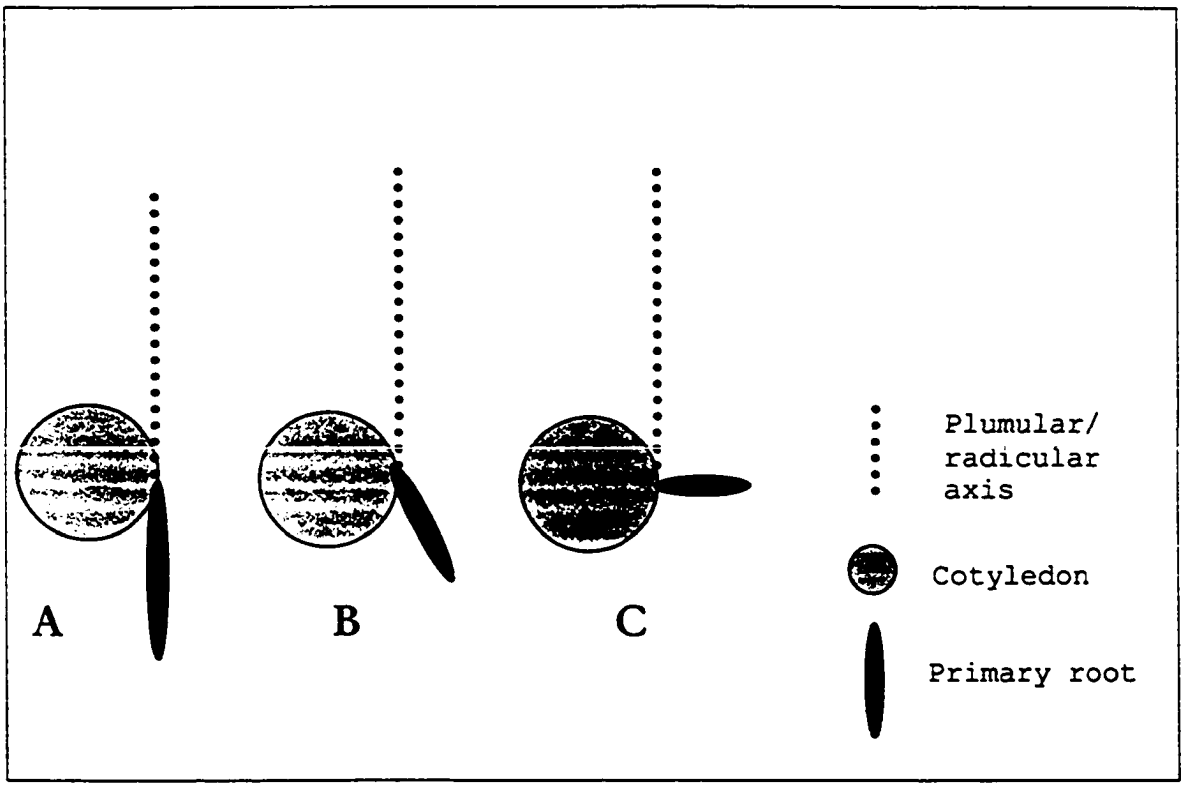


Figure. 20. Primary root in palm seedlings display three distinct orientation planes: **A.** Straight primary root, in the same plane as the plumular axis, usually stout and persistent. **B.** Diagonal primary root, oblique with reference to the plumular axis, persistent for a short period of time. **C.** Horizontal primary root, perpendicular to the plumular axis, ephemeral and soon replaced by shoot-born roots.

phloem strands will fuse into a single one, and vascular bundles with four strands will fuse into two strands.

Cell inclusions (idioblasts) are various and common in most eophylls; but only the distinct shapes of stegmata (silica bodies) offer taxonomic

information. The most common silica body shapes are spherical, ellipsoid, and hat-shaped, of which the last shape is present in caryotoids, iriarteoids, nypoids, chamaedoreoids, some cocosoids, and *Roystonea* arecoid). In some cocosoids and ceroxyloids stegmata are small and of irregular shape, and they resemble silica sand. Earlier workers have explained the presence of silica bodies as a defense mechanism against herbivores (Tomlinson, 1961, 1990). Their abundance in seedlings justifies this hypothesis, considering that young individuals are an easy target for herbivores.

Palm seedlings can be arranged into three groups based on the orientation of the primary root with reference to the seedling's main axis, and other distinctive features (Fig. 20). The first group is composed of seedlings with vertically oriented, stout, persistent primary roots, and straight plumular/radicular axis. These features are almost constantly associated with features such as a single cataphyll, simple eophyll, reduced eophyll axis, parallel or palmate venation, V-shaped plication, epidermal cells rectangular or sometimes rhombohedral, major vascular bundles associated or not associated

with ridges, phloem strands 1-3, and metaxylem vessels 1-2. Taxa with these features are found in the coryphoids, borassoids, phoenicoids, pseudophoenicoids, caryotoids groups and *Allagoptera* and *Syagrus* (cocosoid).

The second group is composed of seedlings with diagonally oriented and persistent primary roots that form an angular plumular/radicular axis. Features associated with this type are: two or more cataphylls, coleoptile present, divided eophyll, eophyll axis, pinnate or palmate venation, proximal plication V-shaped, distal plication AV-shaped, epidermal cells rectangular, major vascular bundles associated with ridges, phloem strands 1-2, and metaxylem vessels 1-2. Taxa with these features are found in the phytelephantoid, calamoid, ceroxyloid, geonomoid, and *Astrocaryum, Bactris, Elaeis* and *Jubaea* (cocosoids).

The third group conprises seedlings with ephemeral horizontally oriented primary roots, and an angular plumular/radicular axis. Features associated with this type are: two or more cataphylls, coleoptile present, bifid eophyll, distinct axis, pinnate venation, proximal plication V-shaped, distal

plication ʌ-shaped at one margin and V-shaped at the other, epidermal cells rhombohedral, rectangular, or rectangular-fusiform, major vascular bundle associated or not associated with ridges, phloem strands 2 or 4, and metaxylem vessels single. Taxa with these features are found in the chamaedoreoids, iriarteoids and arecoids.

Phylogenetic analysis

Seedlings provide few but consistent morphological and anatomical characters. Some major groups are resolved and the results are similar to the phylogenies based on molecular data. The caryotoids form a monophyletic clade separate from the coryphoids, as found by Asmussen and Chase (2001) and Hahn (2002). The cocosoids are polyphyletic in contrast to all previous studies, which demonstrated the monophyly of the group. Obviously, seedling data alone are not adequate for subdividing this group.

A straight plumular/radicular axis is a common feature for palms in the basal lineages, such as borassoids, coryphoids, phoenicoids, and caryotoids.

Oblique axes are present in groups such as calamoids, ceroxyloids and phytelephantoids. An angular axis is present in the arecoids, geonomoids, chamaedoreoids, and iriarteoids (Fig. 21). Persistent primary roots (Fig. 22) are present in basal groups including calamoids and ceroxyloids; in intermediate groups such as chamaedoreoids and geonomoids; and two independent taxa, *Orania* of the arecoids and *Voanioala* of the cocosoids. These last two taxa have exceptional morphological features within their groups.

With few exceptions, the cotyledonary sheath separates the palms into two groups; the basal groups, including the calamoids, ceroxyloids, arecoids, chamaedoreoids, iriartoiods, and *Nypa*. *Orania* and *Voanioala* lack a distinct cotyledonary sheath. In contrast, the phytelephantoid, pseudophoenicoid, cocosoid, coryphoid, caryotoid, phoenicoid have a distinct cotyledonary sheath. Cataphyll number per seddling varies; a single cataphyll distinguishes the basal clades, and variable numbers of cataphylls are scattered among the remaining clades.

The reduplicate and induplicate plication types are not as distinct as in adult leaves. Some taxa have

induplicate (V-shaped) folding at both margins, others reduplicate (∧-shaped) folding at both margins. A third type has induplicate folding at one margin and redupliate at the other margin (Fig. 23). Venation patterns of eophylls (Fig.24) are pinnate in all bifid eophylls and in the simple eophylls of cocosoids. All the remaining groups are non-pinnate category because the variation in axis (rachis) length. *Mauritia* of the calamoids has a palmate eophyll that differs from the palmate eophylls of the coryphoid palms, in that the longitudinal vascular bundles radiate uniformily from a well difined but reduced rachis; in contrast, the longitudinal vascular bundles of the coryphois originate at different points of an obscure rachis, or radiate irregularly from a anastomosed major bundle. This character can be subdivided further if the number of taxa is expanded. Hypodermal fibers have a selective distribution, they occur at the mesophyll layer or/and among the mesophyll layers, with some exceptions (Figs. 25 and 26).

The inclusion of adult morphological data and a monocot outgroup increased resolution. In the resulting tree (Fig. 18) from the combined analysis

most of the groups are resolved except for the arecoids and coryphoids.

Phoenix branches first, followed by *Thrinax*. These two taxa have appeared together in most clades, as in previous analyses, e.g. (Hahn 2002). The ceroxyloids appear next to phytelephantoids in molecular studies, but here they form a clade with the chamaedoreoids. Martius (1823-50) put *Pseudophoenix* and *Phytelephas* together, and these two taxa are resolved as sister taxa in most trees. Molecular analyses place the caryotoids as sister to the borassoids. Here, the borassoids appear nested among the coryphoids while the caryotoids appear as sister to the all taxa except the coryphoids. *Roystonea* resolves as sister to the chamaedoreoids in molecular analyses, here it resolves among the arecoids as sister to *Nypa* and the iriarteoids. *Podococcus* appears nested among the iriarteoids sister to *Iriartella*. *Pseudophoenix* has been defined as a "floater" in Uhl & Dransfield (1995) but here it appears consistently as sister to the phytelephantoids, calamoids, ceroxyloids, geonomoids, cocosoids and arecoids.

The two palm outgroups *Nypa* and Calamoids are not basal as in molecular analyses. The calamoids form a clade with the ceroxyloids and chamaedoreoids. *Nypa* is nested among the arecoids, sister to the iriarteoids and *Podococcus*.

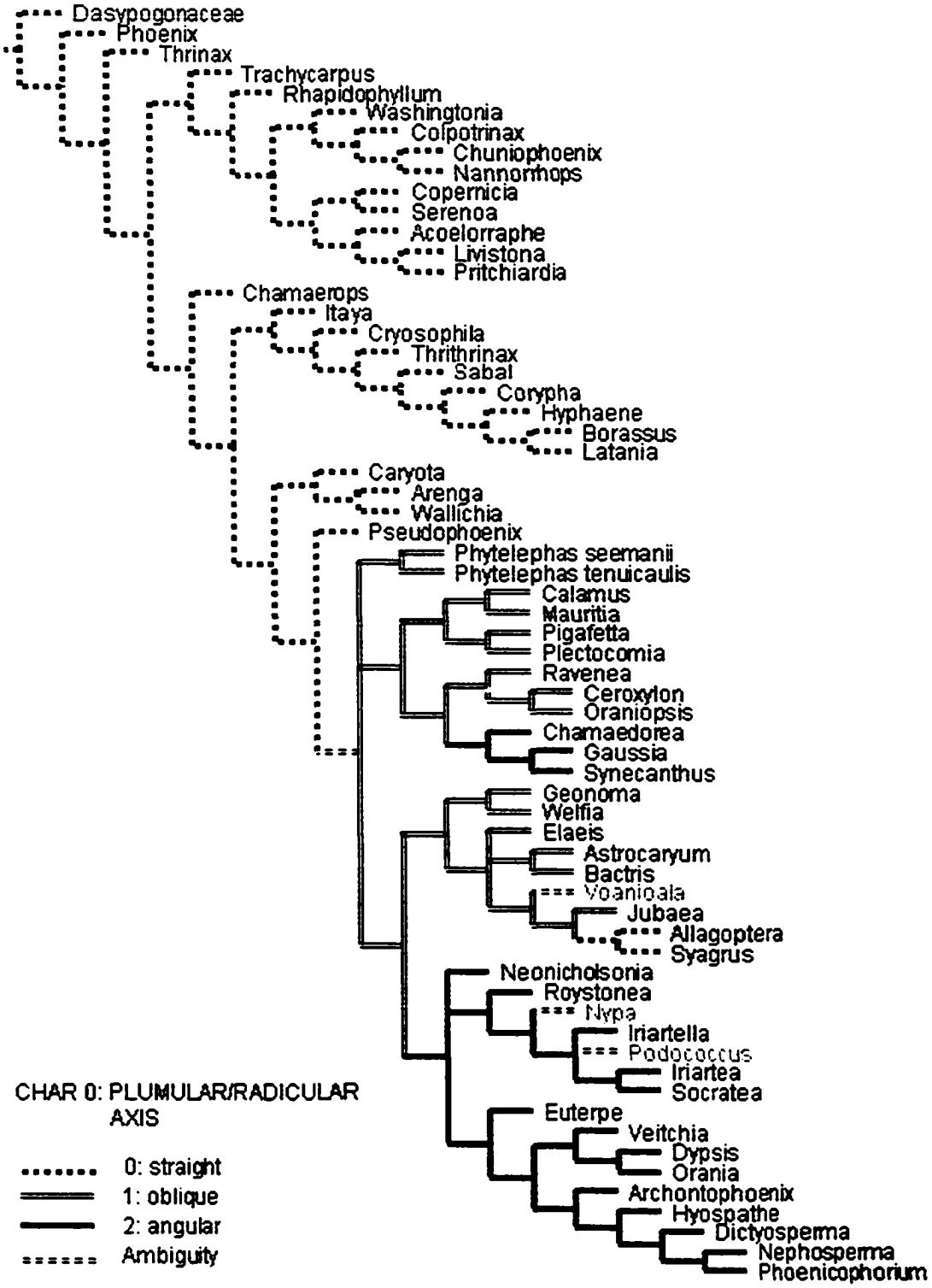


Figure 21. Seedling character distribution. Plumular/radicular axis.

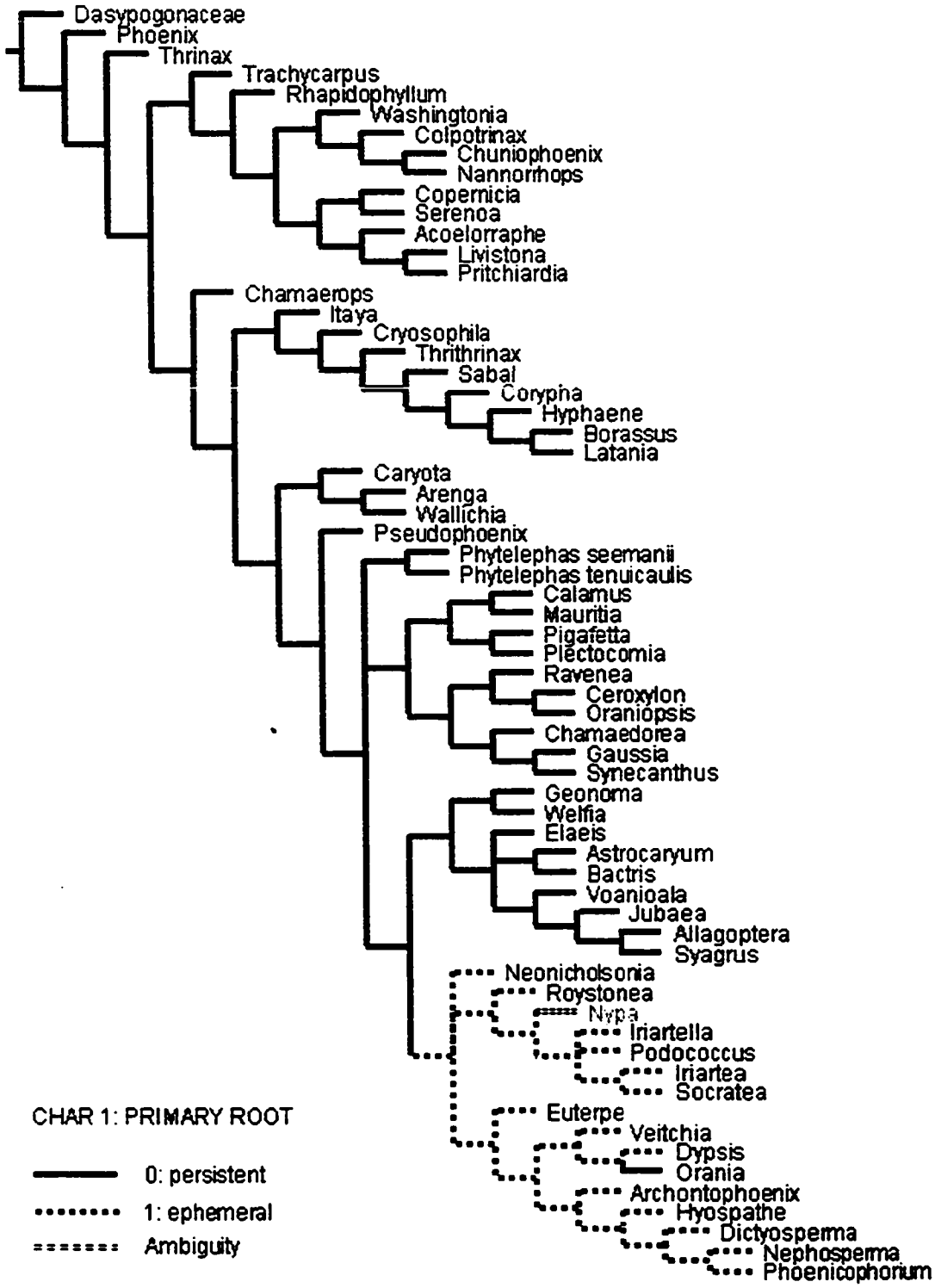


Figure 22. Seedling morphological character distribution. Primary root.

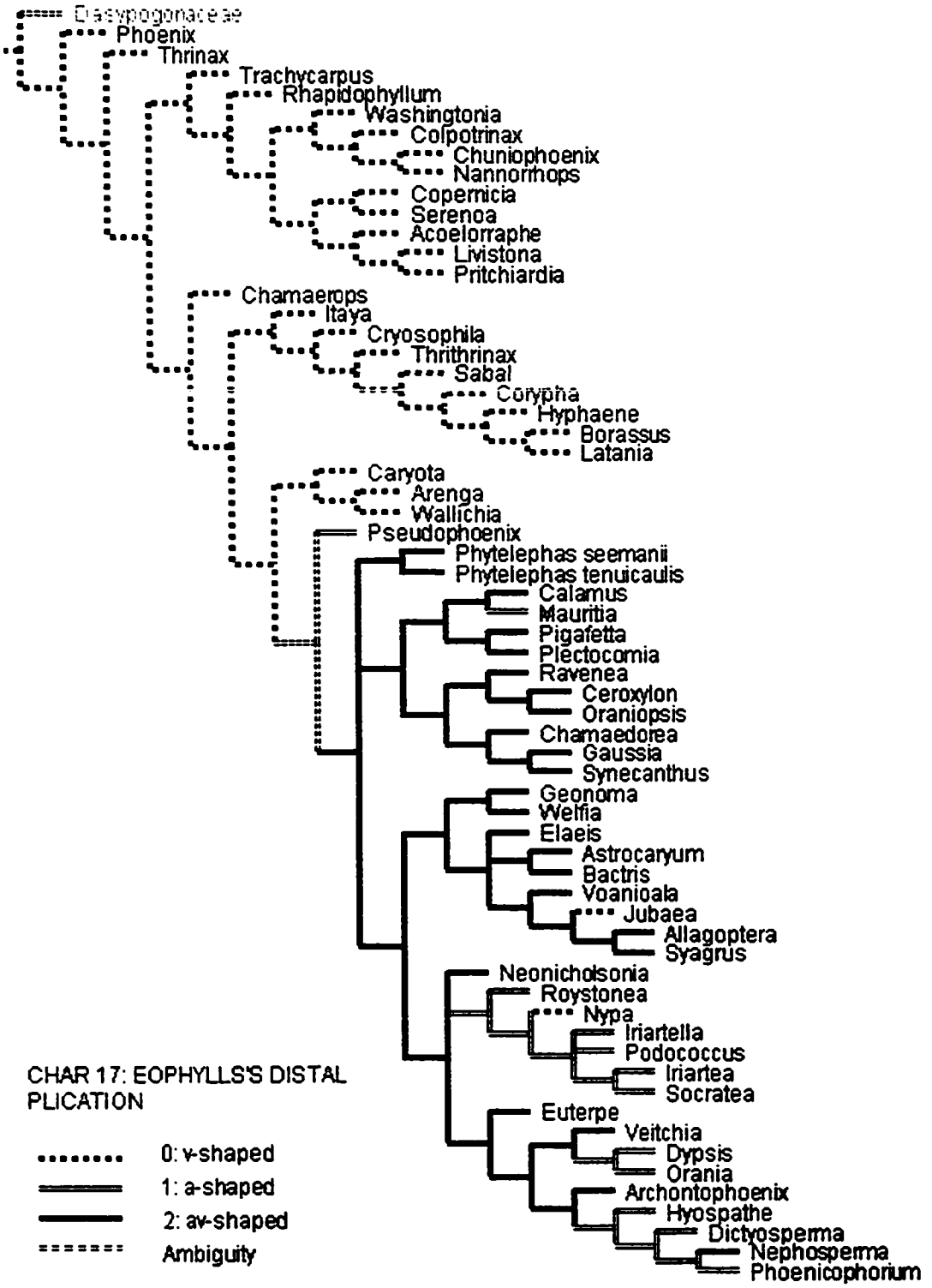


Figure 23. Eophyll character distribution. Eophyll distal plication.

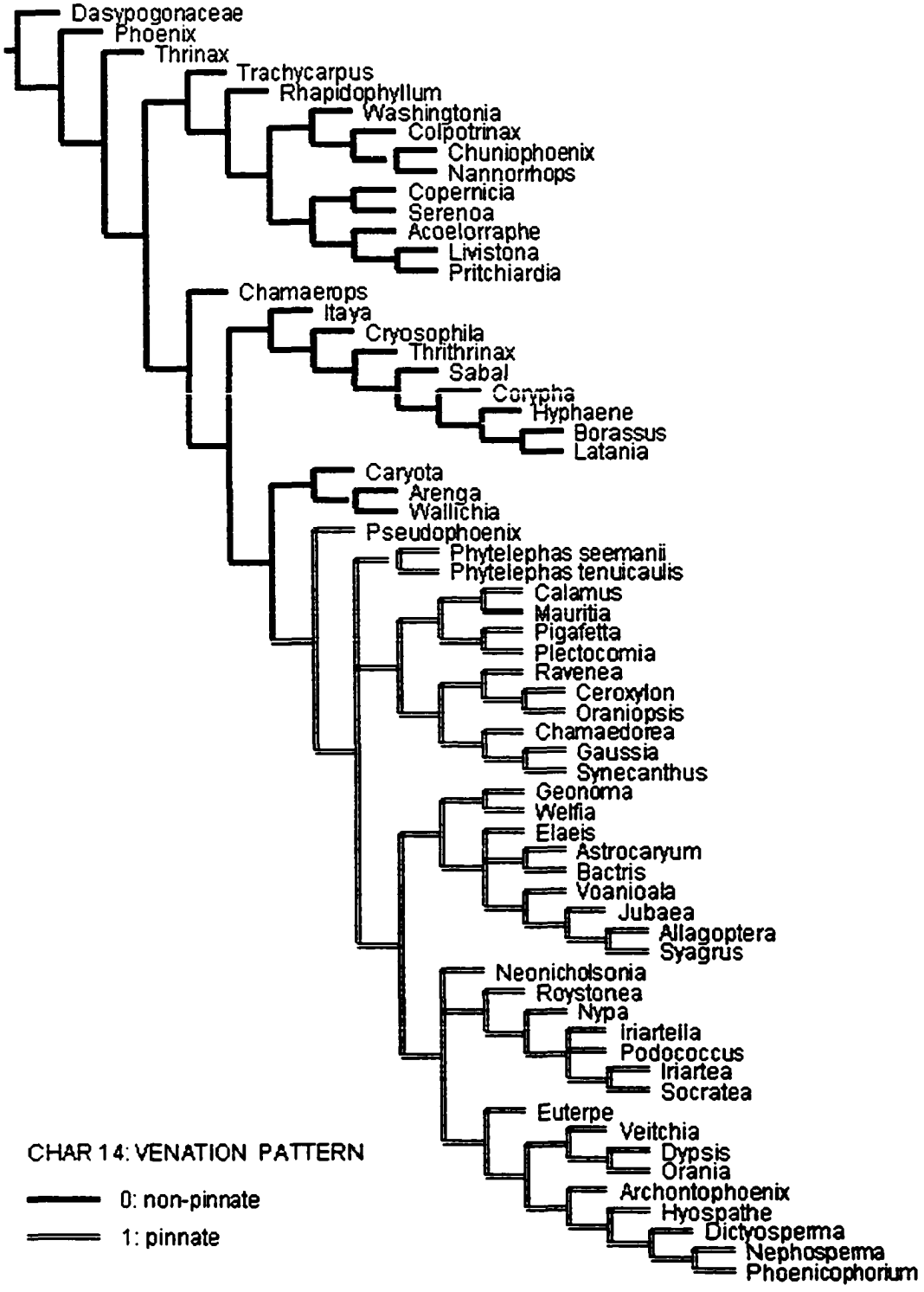


Figure 24. Eophyll character distribution. Eophyll venation pattern.

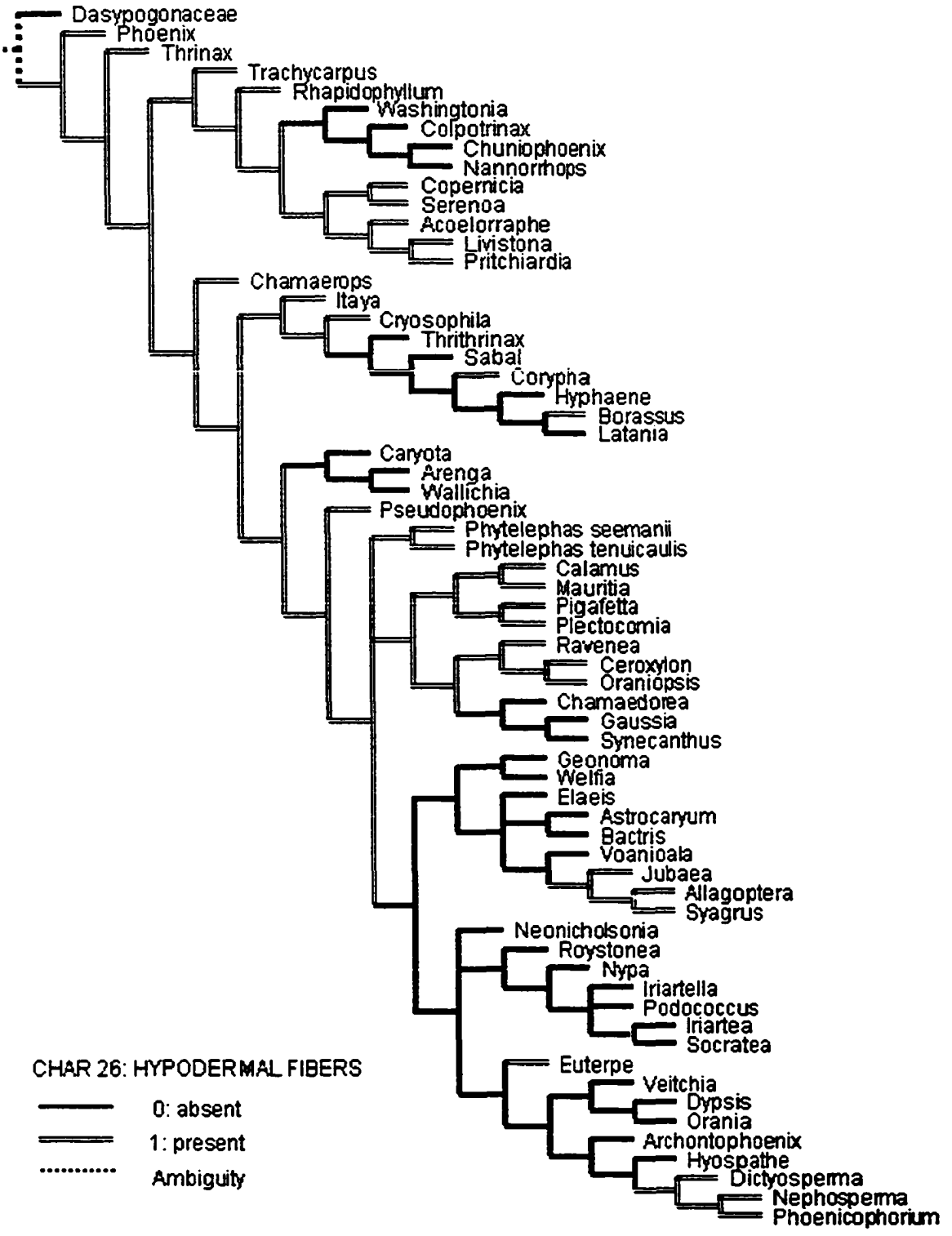


Figure 25. Eophyll anatomical character distribution. Hypodermal fibers.

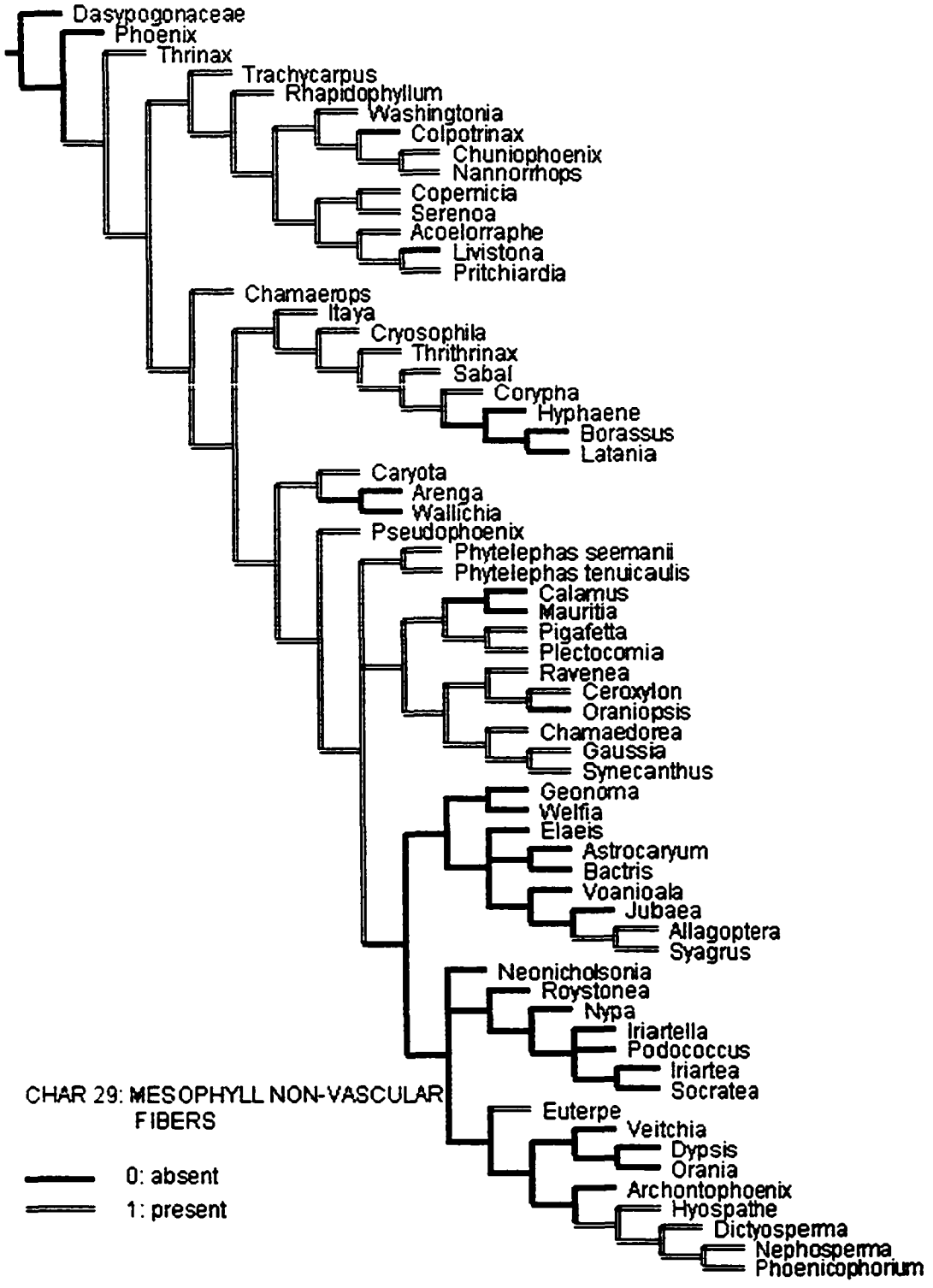


Figure 26. Eophyll anatomical character distribution. Mesophyll non-vascular fiber.

A P P E N D I C E S

Appendix 1

Glossary *

Admote germination = in which there is no extension of the hyperphyll (usually called adjacent).

Cataphylls = first leaves after the cotyledon which lack blades and consist only of a sheath (sometimes called scale leaves).

Coleoptile = a tubular extension of the sheath above the point of insertion of the hyperphyll (usually called a ligule, sometimes called an ocrea).

Collar = the first node, between base of cotyledonary sheath and radicle (sometimes called the cotyledonary node).

Collar roots = roots developing from the collar (sometimes called nodal roots).

Cotyledon = the first leaf, consisting of haustorium, middle part, and cotyledonary sheath.

Cotyledonary sheath = first leaf sheath, which may be open laterally or apically; if apically it may or may not have a coleoptile.

Eophyll = first photosynthetic, expanded leaf which may be simple, bifid, pinnate with a short rachis, or pinnate with a long rachis (sometimes called primary leaf).

Embryo = the rudimentary plant within the seed consisting mostly of a single cotyledon, a plumule, and a root apex.

Epicotyl = axis of the embryonic plant above the cotyledon, terminating in the apical meristem, sometimes bearing scale leaves.

Appendix 1. continue

Haustorium = leaf blade (or at least distal part of it) of the first leaf, confined to the seed and acting as an absorptive organ.

Hyperphyll = part of cotyledon connecting haustorium to sheath. It is very short in plants with admote germination, but may be elongate or contracted in plants with remote germination (sometimes called middle part of cotyledon, cotyledonary petiole or apocole).

Hypogeal = germination in which the most distal part of the cotyledon is not expanded and photosynthetic, but confined to the seed and absorbent.

Induplicate = folding of eophyll and later leaves in which the cross-section of a fold is V-shaped.

Plumule = shoot apical meristem and leaf primordia in the embryo. The embryonic plumular-radicular axis may be straight or curved; if straight it may be parallel or oblique to the axis of the embryo.

Primary root = first root, which may be vertical and persistent, or oblique and ephemeral (also called the radicle).

Reduplicate folding = occur in eophylls and later leaves; cross-section of lamina folding is ʌ-shaped.

Remote = germination in which there is an extension or elongation of the hyperphyll.

Shoot-born roots = sometimes called adventitious roots these roots developed endogenously in contrast to the primary root that develops exogenously.

* Mostly taken from Tillich (1995)

Appendix 2

Embedding

Paraffin-Toluene series (samples in each solution for at least 30 min.)

EtOh	Toluene
70%	-
95%	-
100%	-
90%	10%
70%	30%
50%	50%
30%	70%
10%	90%
	100% (overnight)
	100% (overnight)

- Add paraffin chips until saturated at room temperature.
- Put vials on warming plate, add more paraffin chips, leave lids on (at least 24 hours)
- Transfer to oven (60-65°C). Replace 1/2 solution with melted paraffin, take lid off. Repeat step every 24 hours, until there are no traces of toluene is left.

Appendix 3.

Sectioning

- Trim paraffin block in cubes and Mount cubes on supporting wooden stubs.
- Expose selected sectioning edge and leave the block on softening solution* for a minimun period of two weeks.
- Section softened blocks.
- Spread a thin layer of Haupt's adhesive** on glass slide, allow to dry.
- Add few drops of formalin 4% as floating media.
- Using a razor blade, transfer sections to the slide, remove any excess of formalin using absorbent tissue.
- Leave the slides on warming plate at 42°C during 24 hours.

** Haupt's adhesive

1g gelatin
100 ml distilled water
2g phenol crystals
15 ml glycerin

Dissolve gelatin in distilled water at 30°C, add phenol crystals and glycerin, stir well and filter. Keep refrigerated.

* Softening solution

10 ml Glycerin
60 ml EtOH 70%

Homogenized.

Appendix 4

Staining

Safranin* 1% and Astra Blue staining series** (samples in solutions 1 to 5 for at least 30 min.)

1. Xylene 100%
2. Xylene 100%
3. EtOH 100%
4. EtOH 95%
5. EtOH 70%
6. Safranin 1% (minimum 12 hours)
7. Rinse excess of safranin with ionized water until no more red stain dissolves from slides.
8. Astra blue 30 min.
9. EtOH 70% dip quickly 3-5 times
10. EtOH 95% 5 sec
11. EtOH 100% 10 sec
12. EtOH 50%/ Hemo-De 50% 10 sec
13. Hemo-De 10 min
14. Hemo-De 10 min

<u>Safranin 1%</u> *

2g safranin
100 ml distilled water
100 ml 95% ethanol
Mix the solution until safranin powder dissolves completely.

<u>Astra blue</u> **

1g astra blue
4g tartaric acid
200 ml distilled water
2-3 drops phenol
Mix astra blue, tartaric acid, and water. Heat slightly until powder dissolves. Add phenol, and store in dark bottle

Appendix 5

Epidermal peels

- Trim samples to desire size (appr. 2 cm), leaving one margin intact. Put samples in glass vials with lids on.
- Add Jeffrey's solution*, change the solution if it becomes very dark (usually after 24-48 hours).
- Wash samples at least 3 times in dionized water, using a pipette to extract and add water.
- Add 0.5% aqueous safranin enough to cover sample, leave to stain overnight.
- Transfer the sample to a petri dish with water. Using a paint brush transfer the samples through a dehydration series.
    1. Water 100%
    2. Water 50%, EtOH 50%
    3. EtOH 100%
    4. EtOH 50%/Hemo-De 50%
    5. Hemo-De 100%
    6. Hemo-De 100%
- Leave the sample for a couple of minutes in each solution.
- Mount samples in Permount, and leave in a warming plate 47°C for at least one week.

Jeffrey's solution*

Solution A: 10% aqueous nitric acid

Solution B: 10% aqueous chromic acid (10g chromic tetroxide in 100ml water).

Mix solutions A and B just before using it.

Appendix 6

Leaf Clearing

1. NaOH 10% during 3 days, change to
2. 5% NaOH when the solution becomes dark (more than six days is not recommended).
3. Rinse in dionize water several times, using paintbrush to handle the samples.

Staining

1. 1% safranin during 30 min.
2. EtOH 50%
3. EtOH 70%
4. EtOH 95%
5. EtOH 100%
6. EtOH 50%/ Hemo-De 50%
7. Hemo-De 100%
8. Hemo-De 100%

Leave sample in each solution during five minutes.

Mounting

- Prepare glass sheaths to fit size of the sample.
- Mount samples in Permount, secure the 4 corners of the glass sheaths with binder clips.
- Leave slides in a warming plate 47°C for at least two weeks, them, move samples to conventional oven until Permount is dry. This depends on the size and thickness of the eophyll from four weeks to two years.

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