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Morphology and Anatomy of Palm Seedlings

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Abstract

A historical survey of studies of seedling morphology and anatomy in the palm family is given. The traditional three germination types—adjacent ligular, remote ligular, and remote tubular—that have been commonly recognized are reevaluated. The study includes seedlings of 63 species, representing the six subfamilies of palms. Morphological characteristics of germination patterns and the anatomy of the eophyll are described. The results of this survey show that germination types determined by the length of the hyperphyll (cotyledonary petiole) are not completely valid. Instead, a combination of characters such as primary root orientation, coleoptile length, number of cataphylls, and eophyll plication correspond to the most recent classification of the family, and represent a better way of describing germination.

Introduction

The palm family (Palmae or Arecaceae) is one of the largest families of monocotyledons. The most recent estimate is that it contains 190 genera and 2364 species (Govaerts & Dransfield, 2005). These are widespread in tropical areas throughout the world, with

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the greatest concentration of species in America and Southeast Asia. Palms are usually very abundant in tropical ecosystems, especially in lowland and montane moist forests.

The Palmae are 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 (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 representing the six subfamilies of palms are described. 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 (1823–1850). Martius recognized distinct types of germination in palms: "germinatio admotiva," in which the seedling develops adjacent to the seed, and "germinatio remotiva," in which the seedlings develop at some distance from the seed. This latter type was again divided into "germinatio remotiva tubulosa," in which the tubular cotyledonary sheath is open (e.g., *Arenga*, *Phoenix*) and "germinatio remotiva ocreata," in which the cotyledonary sheath extends, forming an ocrea (e.g., *Brahea*, *Chamaerops*). These three types of germination described by Martius have served as the basis for all future discussions of palm seedlings (Fig. 1) Mohl (in Martius, 1823–1850) described and illustrated in great detail the anatomy of embryos and germination of palm seeds.

Micheels (1889) proposed three germination types based on the attachment of the "embracing region" (cotyledonary sheath). His results, based on 33 taxa, are basically similar to the types of Martius, although he assigned new names: "*Phoenix* type" palms, with the sheath at the base of the cotyledonary stalk; "*Sabal* type" palms, with a tubular sheath; and "*Dictyosperma* type" palms, with a short sheath. Micheels' anatomical studies include a detailed description of the primary root (radicle), hyperphyll, and first and second cataphylls.

The most comprehensive historical review of germination studies in palms is that of Gatin (1906a), which includes information from the early works of Pliny and Theophrastus and 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 the germination of *Phoenix* and *Archontophoenix*. He then surveyed 33 other genera and 58 species of palms. He observed a relation between the internal structure of the embryo and the germination pattern. The embryo can take one of three forms: the plumular-radicular axis can be straight or curved; the plane or orientation of the straight plumular-radicular axis can be parallel or oblique with respect to the axis of the embryo; and a straight plumular-radicular axis gives rise to nonligulate germination,

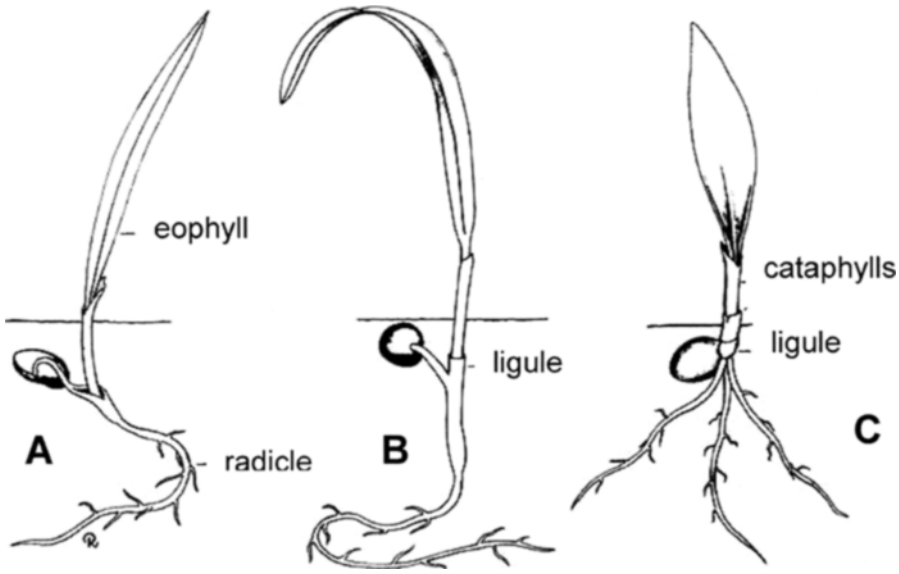

Fig. 1. Germination types proposed by Gatin (1904a). **A**. Remote tubular (*Phoenix*). **B**. Remote ligular (*Sabal*). **C**. Adjacent ligular (*Phoenicophorium*). Source: Uhl & Dransfield, 1987.

whereas a curved plumular-radicular axis gives rise to ligulate (ocreate) germination. Gatin surveyed many aspects of palm seedlings (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 of his work in a comprehensive book on palms (Gatin, 1912).

Several other studies followed the germination types of Martius and Gatin without discussion. Significant contributions to the field were made by several researchers, including Zurawska (1912), who gave extensive morphological descriptions of germination and seedlings of 24 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 vascular tissues of the cotyledon, plumule, and roots, and described briefly the lamina of *Cocos capitata* (= *Butia capitata*).

In 1950, the French botanist Ginieis began a 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 (nonligular) germination are primitive, that admotive ligular palms are phylogenetically younger groups, and that remote ligular palms are intermediate between old remote tubular and early admotive ligular. He also suggested that morphological features of germination blur or disappear after the emergence of the second or third leaves.

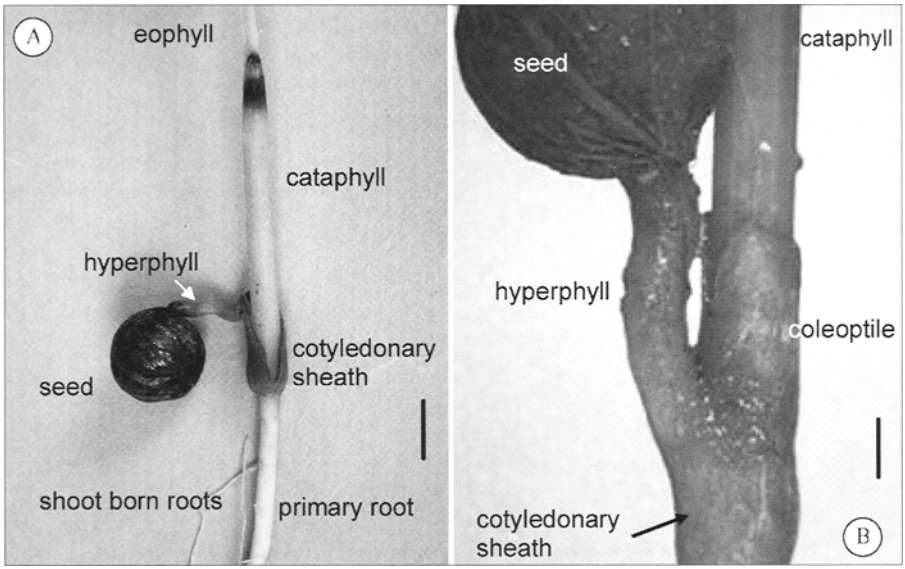

Fig. 2. Seedling morphology. **A.** *Acoelorraphe wrightii* (scale bar = 22 mm). **B.** *Chryosophyla grayumii* (scale bar = 1 cm).

Tomlinson (1960a, 1990) reviewed germination and seedling morphology, including illustrations and examples. He followed Martius's three germination types, but suggested that both *Nypa* and *Phytelephas* may have different patterns of germination. He discussed specialized germination types in *Lodoicea, Cocos*, *Nypa*, and *Pigafetta*.

Moore and Uhl (1973) attempted to use germination characteristics to understand phylogeny. They considered remote-tubular and remote-ligular germination types to be less-specialized groups, and the genus *Livistona*, which has remote-ligular germination, to be the most advanced of the Corypheae. The adjacent-ligular type corresponded to advanced groups, among them the Areceae.

Low (1976), in an extensive but overlooked work on palm phylogeny, reviewed seedling morphology of 84 species in 82 genera of palms. He made several original observations on morphological characteristics of germination. He listed several seedling characteristics and emphasized the number of cataphylls as a diagnostic characteristic.

Uhl and Dransfield (1987) provided information on germination type and eophyll shape for most genera of palms. They followed Martius's basic germination types with a variation in the terminology: remote tubular (= germination remotiva tubulosa), remote ligular (= germinatio remotiva ocreata), and adjacent (= germination admotiva).

Tillich (1995) reviewed seedling morphology in all monocotyledons and demonstrated the usefulness of seedling characteristics 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 his terminology is used here (Fig. 2, Appendix). Tillich (2000) stressed the importance of the cotyledon 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 character-

ized 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 to be a key characteristic for detection of phylogenetic relationships.

Materials and Methods

Plant material (seeds and seedlings) representing all of the subfamilies were gathered from various sources, such as botanical gardens, private gardens, personal contacts, and fieldwork in Bolivia and Peru. Two taxa, *Podococcus barteri* and *Iriartella setigera,* were examined from herbarium specimens. The seeds were germinated and grown under standard conditions of light, temperature, and humidity. Identification of the source material was made in situ. Each sample consisted of several seedlings at different stages of development. Sixty-two genera representing all subfamilies were evaluated. Voucher specimens were made and are deposited at The New York Botanical Garden (Table I). Seedlings with the eophyll fully expanded were collected and fixed in FPA (formalin:proprionic acid:acetic acid, 5:5:90) and stored in 70% ethanol.

Seedling morphology was studied by direct observation using a hand lens 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 follow Martens and Uhl (1984). Segments of 2 cm2 from near the base and apex of the lamina and petiole were processed through a dehydration series of absolute ethanol and toluene. Blocks were sectioned on an AO Spence 820 rotary microtome at 12–17 mm and stained with safranin and astra blue. Segments for epidermal peels were obtained from the upper side of the lamina. Images of anatomical features were taken with a Nikon FX-35 camera attached to the microscope. For morphological features, a Nikon Coolpix 990 digital camera was used. Images were processed in Adobe PhotoShop.

Results

Each sample consists of a complete seedling, eophyll transverse sections of proximal and distal sections, an eophyll epidermal peel, and eophyll clearing. The taxa descriptions within each subfamily and tribe (Uhl & Dransfield, 1987) are arranged in alphabetical order.

I. CORYPHOIDEAE

1. Corypheae

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

Seed remaining above plumular-radicular node. **Plumular-radicular axis** straight in the same plane. **Primary root** stout and persistent, smooth; secondary roots simple; shoot-borne roots present; root hairs present. **Hyperphyll** elongate and smooth, connected halfway between cotyledonary sheath and coleoptile. **Cotyledonary sheath** distinct. **Coleoptile** apically open, short split opposite to seed. **Cataphyll** single; apex acute. **Eophyll** entire, linear-lanceolate; apex acute. **Venation** pattern costapalmate; leaf axis reduced; midvein distinct along blade; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins. **Plica-**

Table I
List of material examined

Taxa	Voucher specimen*
I. CORYPHOIDEAE	
1. Corypheae	
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 grayumii 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
Trachycarpus sp.	Chávez 902
Trithrinax brasiliensis (Mart.)	Chávez 967
Washingtonia filifera (Linden) H. Wendl.	Chávez 930
2. Phoeniceae	
Phoenix roebelinii O'Brien	Chávez 904
3. Borasseae	
Borassus sp.	Chávez 968
Hyphaene coriacea Gaertn.	Chávez 969
Latania loddegesii Mart.	Chávez 957
II. CALAMOIDEAE	
1. Calameae	
Calamus flagellum Griff.	Chávez 945
Pigafetta filaris (Gis.) Becc.	Chávez 944
Plectocomia sp.	Chávez 946
2. Lepidocaryeae	
Mauritia flexuosa L. f.	Chávez 948
III. NYPOIDEAE	
Nypa fruticans Wurmb	Chávez 949
IV. CEROXYLOIDEAE	
1. Cyclospatheae	
Pseudophoenix sargentii H. Wendl.	Chávez 971
2. Ceroxyleae	
Ceroxylon sp.	Henderson 3019
Oraniopsis appendiculata (F. Bailey) Dransf., Uhl & Irvine	Henderson 3070
Ravenea rivularis Jum. & H. Perrier	Chávez 972
3. Hyophorbeae	
*Chamaedorea microspadix*Burret	Chávez 937
Gaussia maya (O. F. Cook) Quero & Read	Chavez 978
Synecanthus fibrosus (H. Wendl.) H. Wendl.	Chávez 938

Table I *(continued)*

Taxa	Voucher specimen*
V. ARECOIDEAE	
1. Caryoteae	
Arenga hookeriana (Becc.) Whitmore	Chávez 907
Caryota mitis Lour.	Chávez 916
Wallichia densiflora Mart.	Chávez 905
2. Iriarteeae	
Iriartea deltoidea R. & P.	Henderson 3015
Iriartella setigera (Mart.) H. Wendl.	Henderson 647
Socratea exorrhiza (Mart.) H. Wendl.	Chávez 935
3. Podococceae	
Podococcus barteri Mann & H. Wendl.	Reitsma 2840
4. Areceae	
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
Phoenicophorium borsigianum (K. Koch) Stuntz	Henderson 2063
Roystonea borinquena O. F. Cook	Chávez 927
Veitchia montgomeryana H. E. Moore	Chávez 977
5. Cocoeae	
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
6. Geonomeae	
Geonoma interrupta (R. & P.) Mart.	Henderson 30
Welfia regia H. Wendl.	Henderson 301
VI. PHYTELEPHANTOIDEAE	
Phytelephas seemanii O. F. Cook	Chávez 950
Phytelephas tenuicaulis (Barfod) Henderson	Chávez 951

* All vouchers are deposited at The New York Botanical Garden.

tion proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls linear. **Hairs** absent. **Stomata** superficial, arranged in regular lines at intercostal regions; short terminal cells not overarching guard cells. **Hypodermis** single-layered, rounded regular cells at adaxial and abaxial sides; fibrous bundles at irregular intervals; fiber lumen wide. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers; fibers appear to be restricted to hypodermal layer. **Expansion cells** single-layered with scattered fibrous bundles. **Major veins** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; distinct outer sheath (OS). **Median veins** free, equidistant; inner sheath (IS) single- or double-layered. **Minor veins** equidistant; IS single-layered; OS surrounding vascular bundle. **Midrib** adaxially prominent; single large vascular bundle. **Marginal rib** occu-

pied by fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessel** single. **Cell inclusions**: silica bodies 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** on the same plane. **Primary root** straight and persistent; secondary roots simple; shoot-borne roots thick; root hairs present. **Hyperphyll** elongate, grooved lengthwise. **Cotyledonary sheath** apical opening, eventually splitting lengthwise, opposite to hyperphyll. **Coleoptile** undeveloped. **Cataphyll** single. **Eophyll** entire, broadly lanceolate; apex acute; fifth successional leaf splitting along adaxial ridge (Fig. 3A). **Venation** pattern palmate, convergent at apex; leaf axis reduced; midvein not distinct from other longitudinal veins; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls linear. **Hairs** absent. **Stomata** slightly sunken, scattered on adaxial surface, abundant on abaxial surface; terminal cells short, occasionally elongate and overarching guard cells. **Hypodermis** single-layered, present at adaxial and abaxial sides; fibrous bundles at irregular intervals; solid bundles at ridges and grooves; lumen wide (Fig. 4A). **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** single-layered; large rounded cells. **Major veins** associated with ridges, attached to adaxial and abaxial hypodermal layers; IS sclerotic, multilayered; OS not distinct. **Median veins** free and equidistant. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent; single large vascular bundle. **Marginal rib** with compact fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; tannins abundant, except in hypodermal and expansion cells.

Gatin (1906a) and Ginieis (1950, 1952a) have 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-borne roots present; collar disk and collar roots present. **Hyperphyll** medium length, smooth surface, slightly constricted at insertion to seed. **Cotyledonary sheath** distinct; texture rugulose. **Coleoptile** leathery, splitting opposite to seed. **Cataphyll** single, grooved. **Eophyll** entire, lanceolate; apex acute. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal vascular bundles; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls slightly sinuous. **Hairs** present; few basal cells, associated with ribs. **Stomata** slightly sunken, scattered; short terminal cells not overarching guard cells. **Hypodermis** single-layered; large rounded or ellipsoid cells; parallel orientation; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Expansion cells** double-layered. **Major veins** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; OS distinct. **Median veins** buttressed to adaxial side. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent; single vascular bundle. **Marginal rib** lacking a vascular bundle or fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** three. **Metaxylem vessels** single. **Cell inclusions:** sil-

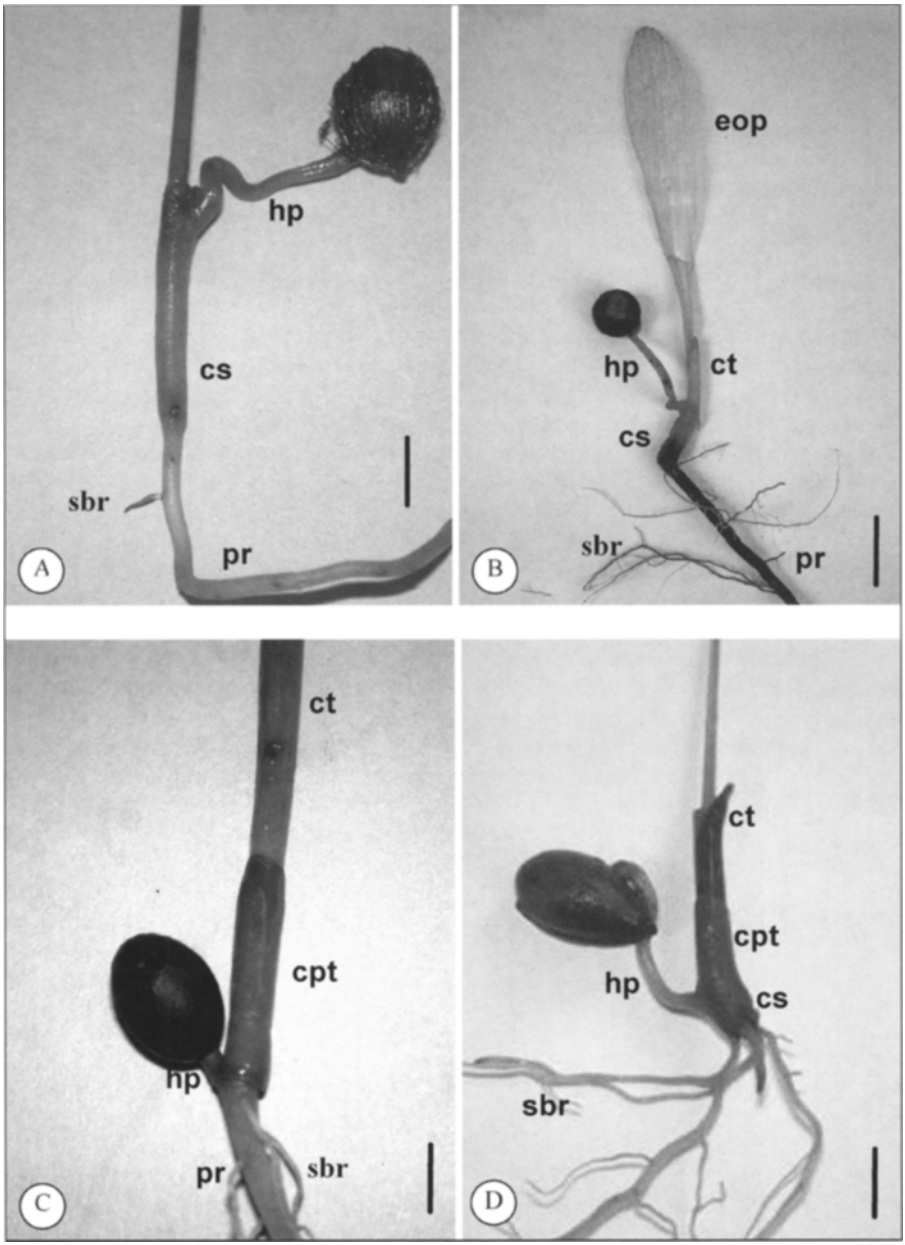

Fig. 3. Seedling morphological characteristics. **A**. *Chamaerops humilis*: primary root straight and hyperphyll attached to distal end of cotyledonary sheath (scale bar = 70 mm). **B**. *Corypha* sp.: primary root persistent; hyperphyll elongate; cataphyll single; eophyll entire, venation parallel, apex praemorse (scale bar = 2.5 cm). **C**. *Nannorrhops ritchiana*: primary root straight and persistent; coleoptile distinct; hyperphyll attached to base of coleoptile (scale bar = 6 mm). **D**. *Rapidophyllum histrix*: primary root ephemeral; coleoptile distinct; cotyledonary sheath reduced; cataphyll single (scale bar = 1.25 cm). cpt, coleoptile; cs, cotyledonary sheath; ct, cataphyll; eop, eophyll; hp, hyperphyll; pr, primary root; sbr, shoot-borne roots.

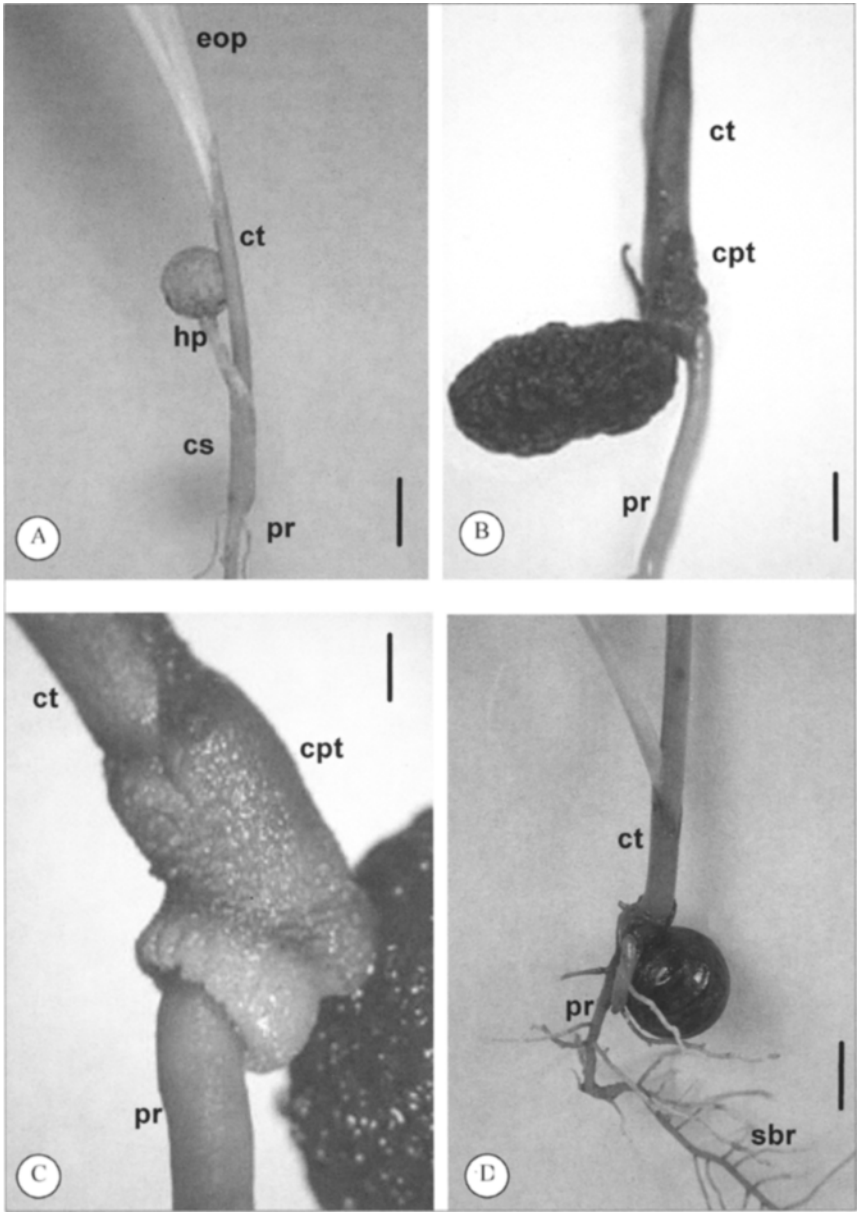

Fig. 4. Seedling morphological characteristics. **A**. *Thrinax excelsa*: primary root straight and persistent; cotyledonary sheath well developed (scale bar = 5 mm). **B**. *Calamus flagellum*: primary root persistent; coleoptile short (scale bar = 6 mm). **C**. *Calamus flagellum*: primary root collar swollen; collar roots lacking (scale bar = 25 mm). **D**. *Ceroxylon* sp.: primary root diagonally oriented; shoot-borne roots abundant; coleoptile short, split (scale bar = 1 cm). cpt, coleoptile; cs, cotyledonary sheath; ct, cataphyll; eop, eophyll; hp, hyperphyll; pr, primary root; sbr, shoot-borne roots.

ica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids 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-borne roots present; root hairs present. **Hyperphyll** short and smooth, without grooves or furrows; attachment area 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** entire, broadly lanceolate; apex acute; splitting along adaxial fold. **Venation** pattern palmate; leaf axis reduced; midvein distinct; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls linear; sclerotic walls; cuticle thick. **Hairs** present; multicellular base, associated or not associated with fibrous bundles. **Stomata** slightly sunken; short terminal cells overarching guard cells. **Hypodermis** single-layered, large ellipsoid cells; orientation parallel; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers; mesophyll fibers forming compact bundles of about 20 strands, arranged at adaxial and abaxial sides; lumen small. **Expansion cells** double-layered cells, large, rectangular, and perpendicular; adjacent epidermal cells papillose. **Major veins** not associated with ridges; OS distinct. **Median veins** buttressed to adaxial side. **Minor veins** oriented toward abaxial side; OS surrounding vascular bundle. **Midrib** abaxially prominent, vascularized by grouped simple vascular bundles. **Marginal rib** not vascularized. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; raphids 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-borne 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. **Eophyll** entire, linear-lanceolate; apex acute, forming a short needle-like projection; margins spiny. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular, elongate; adaxial and abaxial anticlinal walls linear. **Hairs** present; multicellular base associated with ribs. **Stomata** superficial, arranged into regular lines at intercostal regions; short terminal cells overarching guard cells. **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 veins** associated with ridges; buttressed to adaxial hypodermis; IS sclerotic, multilayered; OS distinct. **Median veins** free and equidistant. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** not prominent,

vascular bundle single. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids 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-borne roots absent; root hairs present; pneumatophores present. **Hyperphyll** elongate, grooved all around, swollen as it leaves seed. **Cotyledonary sheath** splitting lengthwise at side opposite to seed; conspicuous lenticels on cotyledonary sheath and hyperphyll. **Coleoptile** absent. **Cataphyll** single; opening apical. **Eophyll** entire, broadly oblanceolate; praemorse apex (Fig. 3B). **Venation** pattern costapalmate; leaf axis distinct; midvein distinct; veins diffuse at intercostal areas; transverse commissures abundant, closely arranged, some connect to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. Epidermal cells rectangular; adaxial anticlinal walls sinuous; abaxial walls linear. **Hairs** present; few basal cells associated with 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 veins** not associated with ridges, attached to adaxial and abaxial hypodermal layers; IS sclerotic, multilayered; OS distinct. **Median veins** free; oriented toward adaxial side, occasionally connected to transverse commissures. **Minor veins** 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 vessels** single; large. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; raphids, abundant, equidistant; tannins scarce.

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

Cryosophila grayumii R. Evans

Seed remaining above plumular-radicular node. **Plumular-radicular axis** symmetric, straight. **Primary root** persistent; secondary roots branched; shoot-borne 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** entire, broad, lanceolate; apex acute with a needle-like extension; about six or eight similar leaves borne before the segmented leaf; splitting side adaxial. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular, covered by thick cuticle; adaxial and abaxial anticlinal walls linear. **Hairs** free; few basal cells. **Stomata** slightly sunken, scattered; short and elongate terminal cells overarching guard cells. **Hypodermal** colorless layer absent, replaced by a layer of scattered 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 veins** not associated with ridges; OS distinct. **Median veins** buttressed to adaxial side. **Minor veins** free; oriented toward abaxial side; OS

cap-shaped. **Midrib** abaxially prominent; vascular bundle single, simple. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** single. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; raphids 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-borne 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** entire, broad; apex acute with a needle-like extension; later apex splitting into irregular segments. **Venation** pattern palmate; leaf axis reduced; midvein inconspicuous; veins convergent at apex; transverse commissures abundant, closely arranged, connecting longitudinal or intercostal areas. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls sinuous; cuticle thick. **Hairs** present; basal cells few, not associated with ribs. **Stomata** slightly sunken, scattered at intercostal regions; 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; adjacent epidermal cells papillose. **Major veins** not associated with ridges, attached to abaxial epidermal layers; IS multilayered, sclerotic; OS distinct. **Median veins** free, toward abaxial side. **Minor veins** oriented toward abaxial side; OS surrounding vascular bundle. **Midrib** abaxially prominent; single multivascular bundle. **Marginal rib** with fibrous layers. **Petiole** not distinct. **Phloem strands** two. **Metaxylem vessels** two. **Cell inclusions:** silica bodies 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-borne roots present; collar roots present. **Hyperphyll** elongate, longitudinally grooved; connection to seed swollen. **Cotyledonary sheath** grooved. **Coleoptile** very short; apical opening. **Cataphyll** single; apical opening with a needle-like projection. **Eophyll** entire, 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; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and intercostal areas. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls sinuous. **Hairs** free; basal cells few. **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 toward abaxial side. **Expansion cells** double-layered; rounded cells; fibrous bundles scattered; adjacent epidermal cells papillose. **Major veins** associated with ridges, buttressed to adaxial hypodermis; IS multilayered, sclerotic; OS distinct. **Median veins** free and equidistant. **Minor veins** equi-

distant; OS surrounding vascular bundle. **Midrib** abaxially prominent; single vascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose; distributed around vascular bundles and fibrous bundles; raphids equidistant.

Gatin (1906a), Zurawaska (1912), Mahabale and Kulkarni (1972), and Lothian (1959) have 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-borne 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 coleoptile-like extensions. **Eophyll** entire, linear-lanceolate; apex acute with a needle-like extension (Fig. 3C). **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures abundant, closely arranged, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular, elongate; adaxial and abaxial anticlinal walls linear. **Hairs** present; basal cells few. **Stomata** slightly sunken; scattered at intercostal regions; short terminal cells overarching guard cells. **Hypodermis** single-layered, rounded or ellipsoid cells; orientation parallel; present at adaxial and abaxial sides. **Chlorenchyma** well differentiated; palisade with two layers; spongy mesophyll with more than five layers. **Expansion cells** single-layered; slightly larger than epidermal cells. **Major veins** not associated with ridges, attached to adaxial and abaxial hypodermis; IS multilayered, sclerotic; OS distinct. **Median veins** buttressed to adaxial hypodermis. **Minor veins** equidistant; OS surrounding vascular bundle; radial OS present. **Midrib** not prominent, vascularized by grouped simple vascular bundles. **Marginal rib** with major vascular bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** three. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids abundant, equidistant; tannins abundant in all cells, more concentrated in palisade cells.

Pritchardia remota (Kuntze) Becc.

Seed remaining above plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** persistent; secondary roots simple; shoot-borne roots present, protruding through 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** entire, broadly lanceolate; apex hairy, acute. **Venation** pattern costapalmate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and intercostal areas. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls sinuous. **Hairs** present; few basal cells, associated with ribs. **Stomata** superficial, scattered at intercostal regions; short terminal cells overarching guard cells. **Hypodermis** single-layered, present at adaxial and abaxial sides; fibers at regular intervals; lumen wide. **Chlorenchyma** well differentiated; pal-

isade single-layered; spongy mesophyll with more than five layers. **Expansion cells** double-layered; scattered fibrous bundles. **Major veins** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS distinct. **Median veins** free and equidistant. **Minor veins** equidistant; IS multilayered, sclerotic; OS surrounding vascular bundle; radial OS present. **Midrib** abaxially prominent; single vascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; raphids 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-borne roots protruding through cotyledonary sheath. **Hyperphyll** moderate, smooth; connection to seed constricted, attaching at midpoint between cotyledonary sheath and coleoptile. **Cotyledonary sheath** leathery. **Coleoptile** elongate, slightly grooved; apical opening, a short slit eventually appearing, opposite to hyperphyll. **Cataphyll** single, slightly furrowed; opening lengthwise; apex pointed. **Eophyll** entire, broadly lanceolate; apex acute (Fig. 3D). **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and intercostal regions. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls linear. **Hairs** present; few basal cells, associated with ribs. **Stomata** slightly sunken, scattered at intercostal regions; short terminal cells overarching guard cells. **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 veins** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS not well differentiated. **Median veins** free and equidistant. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent; single simple vascular bundle (Fig. 5A). **Marginal rib** with fibrous bundles. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, large, margins spinulose distributed around vascular bundles; raphids present; tannins abundant.

Clancy and Sullivan (1988) and Carpenter et al. (1993) have 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-borne roots absent. **Hyperphyll** elongate, connecting to lower part of coleoptile, forming saxophone-shaped 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** entire, 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 veins; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and intercostal areas. **Plica-**

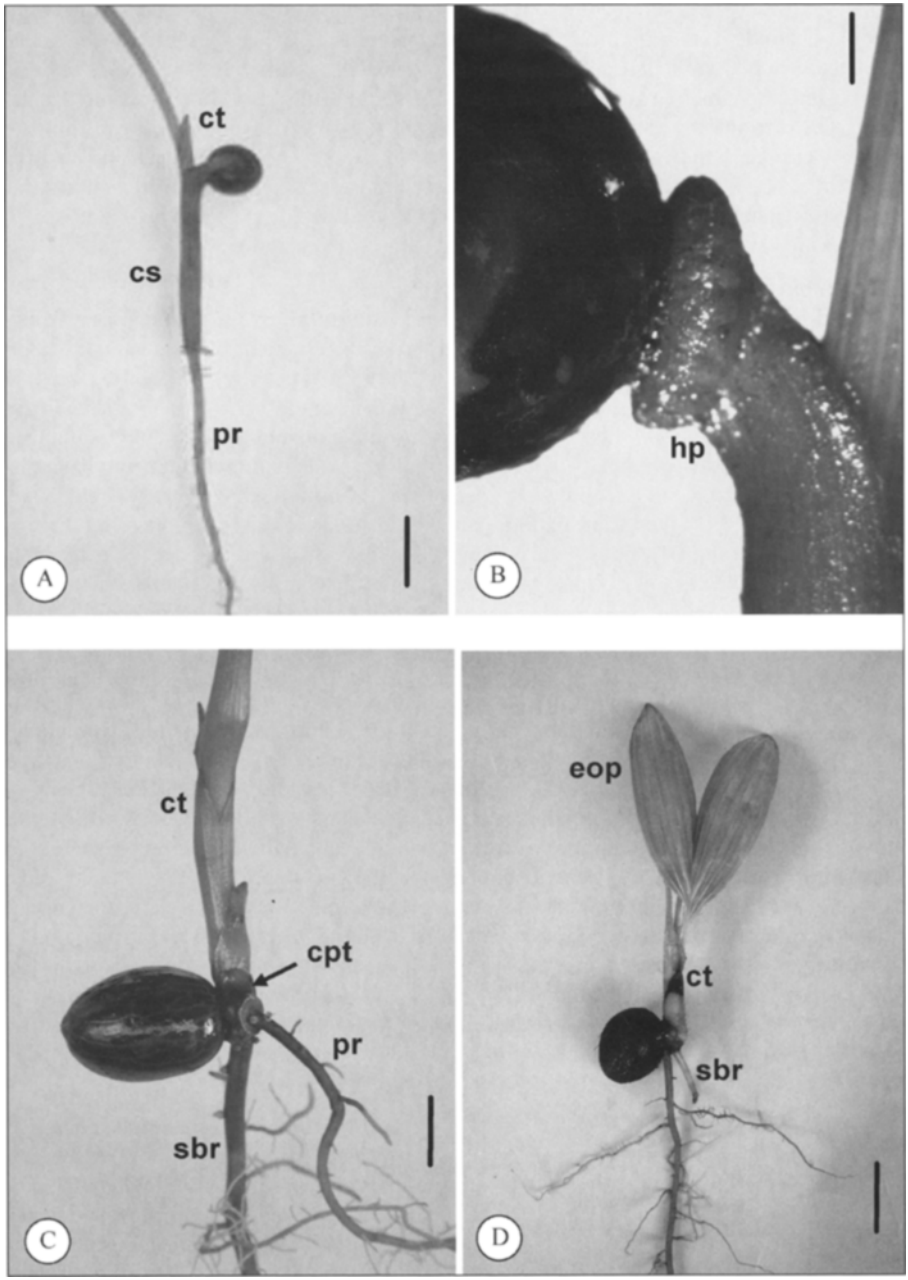

Fig. 5. Seedling morphological characteristics. **A**. *Arenga hookeriana*: primary root persistent; collar roots present; cotyledonary sheath well developed; cataphyll single (scale bar = 1.25 cm). **B**. *Caryota mitis*: hyperphyll swollen (scale bar = 15 mm). **C**. *Socratea exorrhiza*: primary root persistent, horizontally oriented; hyperphyll absent; cataphylls four (scale bar = 9 mm). **D**. *Astrocaryum alatum*: primary

tion with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls linear. **Hairs** present; few basal cells. **Stomata** slightly sunken, scattered; short terminal cells overarching guard cells. **Hypodermis** single-layered, present at adaxial and abaxial side. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers; fibers in bundles at ridges and grooves; lumen wide. **Expansion cells** double-layered. **Major veins** not associated with ridges, attached to adaxial and abaxial epidermal layers; IS multilayered, sclerotic IS; OS distinct. **Median veins** buttressed to abaxial and adaxial sides. **Minor veins** buttressed to adaxial side; OS u-shaped. **Midrib** not prominent, squared; vascular bundle single (Fig. 5B). **Marginal rib** with minor vascular bundles and fibrous bundles. **Petiole** transverse section crescent-shaped. **Phloem strands** three. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; raphids scarce, equidistant; tannins scarce.

Germination of *Sabal* has been 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-borne roots present. **Hyperphyll** moderate, smooth; as in *Sabal* connecting almost directly to primary root; attachment flat. **Cotyledonary sheath** short; hyperphyll attached to lower part. **Coleoptile** apical opening with two opposite slits. **Cataphyll** single; opening lengthwise; apex with asymmetric split. **Eophyll** entire, 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 veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls linear; cuticle thick and forming a continuous layer. **Hairs** present; few basal cells, associated with ribs. **Stomata** superficial, scattered at intercostal regions; short terminal cells overarching guard cells. **Hypodermis** single-layered, at adaxial and abaxial sides; fibers at irregular intervals. **Palisade layer** distinct; spongy mesophyll with more than five layers; fibrous bundles restricted to grooves; lumen wide. **Expansion cells** double-layered, ellipsoid, transversally arranged. **Major veins** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS distinct. **Median veins** free, oriented toward abaxial side. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** not prominent; single bundle. **Marginal rib** with fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; tannins abundant, scattered, mostly concentrated on palisade parenchyma.

Fisher and Tomlinson (1973) and Hilmon (1968) have described germination of *Serenoa*.

Fig. 5, *continued*
root horizontally oriented; cataphylls two; eophyll bifid, pinnate venation (scale bar = 2.4 cm). cpt, coleoptile; cs, cotyledonary sheath; ct, cataphyll; eop, eophyll; hp, hyperphyll; pr, primary root; sbr, shoot-borne roots.

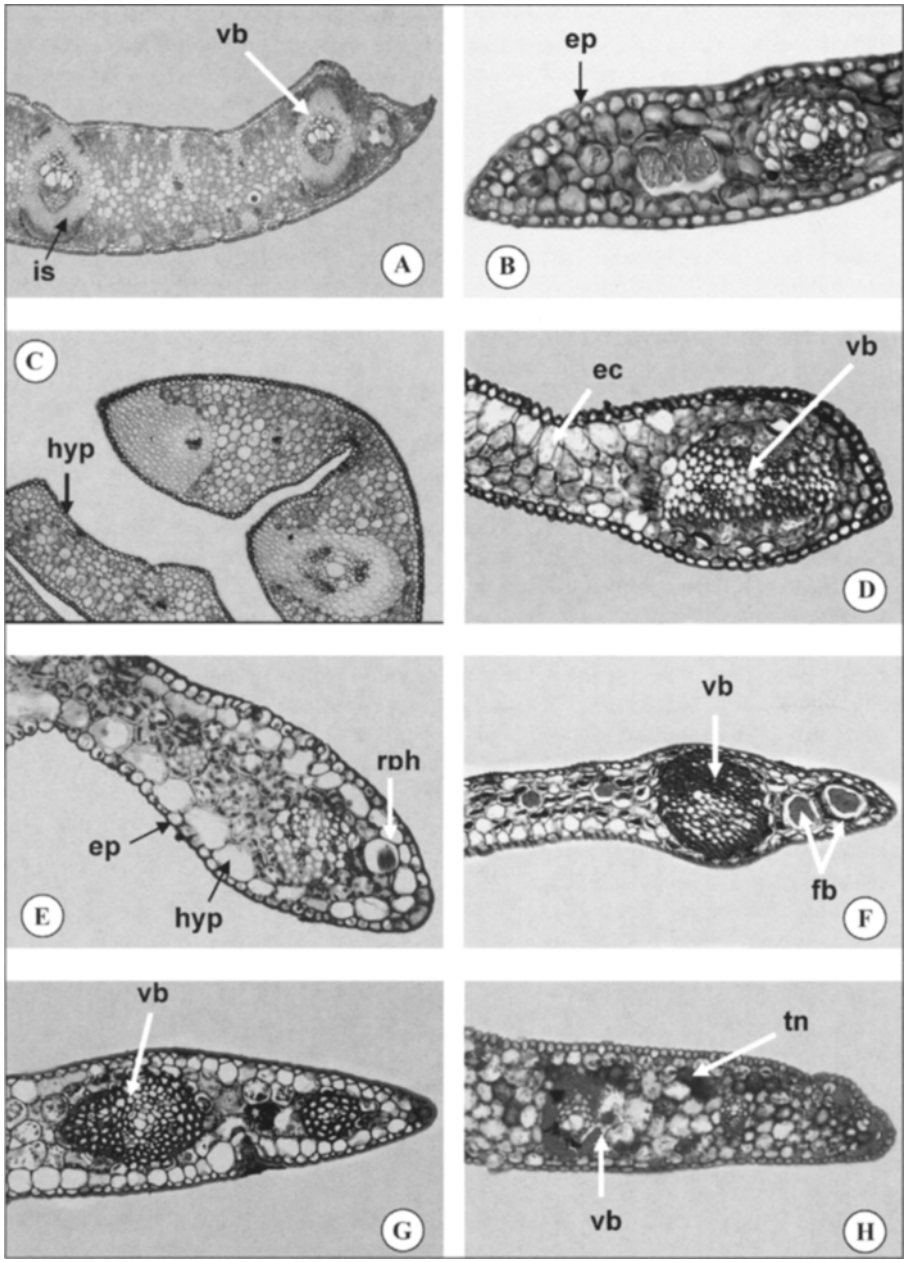

Fig. 6. Eophyll margins. **A.** *Hyphaene coriacea*: stomata sunken; major veins attached to both surface layers; inner sheath multilayered, sclerotic; phloem strand single; minor veins buttressed to adaxial hypodermis; fibrous nonvascular bundles at adaxial and abaxial sides (×100). **B.** *Calamus flagellum*: vascular bundle absent at margin; fibrous bundles equidistant from adaxial and abaxial surfices (×200). **C.** *Pseudophoenix sargentii*: marginal vascular bundle surrounded by fibrous layers; major veins with two

Thrinax excelsa Lodd. ex Griseb.

Seed remaining above plumular-radicular node. **Plumular-radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple. **Hyperphyll** moderate; 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** entire, linear-lanceolate; apex acute with needle-like projection; five leaves similar to eophyll before first split leaf appears; splitting side adaxial (Fig. 6A). **Venation** pattern palmate; leaf axis reduced; midvein present along blade; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular to slightly rhombohedral; adaxial and abaxial anticlinal walls linear. **Hairs** present; few basal cells. **Stomata** superficial, arranged in single files at intercostal regions; elongate terminal cells overarching guard cells. **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 veins** not associated with ridges; IS multilayered, sclerotic; OS distinct. **Median veins** not distinct from major veins. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** not prominent; simple vascular bundle. **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** single. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids abundant, equidistant.

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** entire, lanceolate; apex acute with needle-like projection. **Venation** pattern costapalmate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular or slightly rhombohedral; adaxial and abaxial anticlinal walls linear. **Hairs** multicellular; few basal cells. **Stomata** slightly sunken, scattered at intercostal regions; elongate terminal cells overarching guard cells. **Hypodermis** single-layered, at adaxial and abaxial sides, occasionally interrupted by fibrous-

Fig. 6, *continued*
phloem strands; median veins buttressed to abaxial epidermis; minor veins equidistant from epidermal layers (×200). **D.** *Arenga hookeriana*: marginal vascular bundle large; folding induplicate; expansion cells on adaxial side; silica bodies abundant, hat-shaped, distributed around vascular bundle (×200). **E.** *Roystonea borinquena*: reduplicate folding; hypodermis distinct; marginal median vein; fibrous bundles equidistant (×200). **F.** *Bactris killippii*: hypodermis distinct in abaxial surface; marginal fibrous bundles; vascular bundle surrounded by fibrous inner sheath (×200). **G.** *Voanioala gerardii*: hypodermis distinct in margins of both adaxial and abaxial surfaces, with median and major vascular bundles; epidermal hairs large, sunken (×200). **H.** *Phytelephas tenuicaulis*, hypodermis small, occupied by small fibrous bundles; vascular bundle at some distance from the margin; tannins abundant (×200). ec, expansion cells; ep, epidermis; fb, fibrous bundles; hyp, hypodermis; IS, inner sheath; rph, raphids; tn, tannins; vb, vascular bundle.

bundles. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers; fibers in bundles restricted to ridges and grooves; lumen wide (Fig. 4B). **Expansion cells** double-layered. **Major veins** not associated with ridges, attached to adaxial epidermis and abaxial hypodermis; IS multilayered, sclerotic; OS distinct. **Median veins** buttressed to both abaxial and adaxial sides. **Minor veins** 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 vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids present; tannins in full sacs scattered.

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

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-borne roots present; collar roots present. **Hyperphyll** elongate; single groove on adaxial side; connection to seed flat. **Cotyledonary sheath** opening lengthwise to node; splitting opposite to hyperphyll. **Coleoptile** undeveloped. **Cataphyll** single, plicate; apex acute. **Eophyll** entire, lanceolate; apex concave with sharp acuminate projection. **Venation** pattern palmate; leaf axis reduced; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls linear. **Hairs** absent. **Stomata** slightly sunken, scattered at intercostal regions; short and elongate terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers; 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 veins** not associated with ridges, attached to adaxial and abaxial epidermal layers; IS multilayered, sclerotic; OS distinct. **Median veins** buttressed to both abaxial and adaxial sides. **Minor veins** abaxially buttressed; OS cap-shaped. **Midrib** not prominent; vascular bundle single, simple (Fig. 5C). **Marginal rib** with fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** single. **Metaxylem vessels** two. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids equidistant; tannins scarce.

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-borne 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 apical. **Cataphyll** single; apical opening; apex acute. **Eophyll** entire, linear-lanceolate; apex acute with needle-like projection; nine or ten eophyll-like leaves borne before first split leaf; splitting along adaxial side. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures abundant, closely arranged, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls linear. **Hairs**

absent. **Stomata** slightly sunken, scattered al intercostal regions; short terminal cells overarching guard cells. **Hypodermis** single-layered, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Nonvascular fibers** in layers, restricted to grooves; lumen wide. **xpansion cells** double-layered, large, ellipsoid, perpendicular. **Major veins** associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS distinct. **Median veins** free, oriented toward abaxial side. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** not prominent, vascularized by grouped simple vascular bundles (Fig. 5D). **Marginal rib** with small fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids equidistant; tannins abundant.

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

SUMMARY FOR CORYPHEAE

Plumular-radicular axis straight; primary root straight and persistent; collar roots developed or not developed; hyperphyll elongate or contracted; cotyledonary sheath opening laterally or apically; coleoptile present or absent; cataphyll single in most taxa (three in *Pritchardia*); eophyll entire, lanceolate or linear-lanceolate, acute or lobed at apex; induplicate folding; venation palmate or costapalmate without obvious midvein. In *Chamaerops*, *Livistona,* and *Trachycarpus,* the plumular-radicular axis is straight and oblique to the axis of the embryo; the cotyledonary sheath opens apically; and a coleoptile is absent. Some genera have horizontally oriented eophylls with elongate petioles, for example, *Cryosophila* and *Livistona.* Other genera have erect eophylls with short petioles, as in *Trithrinax, Chamaerops, Thrinax, Coccothrinax, Sabal, Acoelorraphe,* and *Trachycarpus.*

2. Phoeniceae

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; apical opening by a short slit; apex concave. **Coleoptile** absent. **Cataphyll** single. **Eophyll** entire, linear-lanceolate; apex with needle-like projection; seven eophyll-like leaves borne before split leaf appears; splitting at adaxial side, starting at proximal end. **Venation** pattern costapalmate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **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, at adaxial and abaxial sides; cells rounded; large solid fibrous bundles at irregular intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers; fibers in bundles at adaxial and abaxial sides; lumen small. **Expansion cells** double-layered; epidermal cells papillose; scattered fibrous bundles. **Major veins** not associated with ridges, attached to adaxial and abaxial hypodermis; IS multilayered and sclerotic; OS distinct. **Median veins** free and equidistant. **Minor veins** equidistant; OS

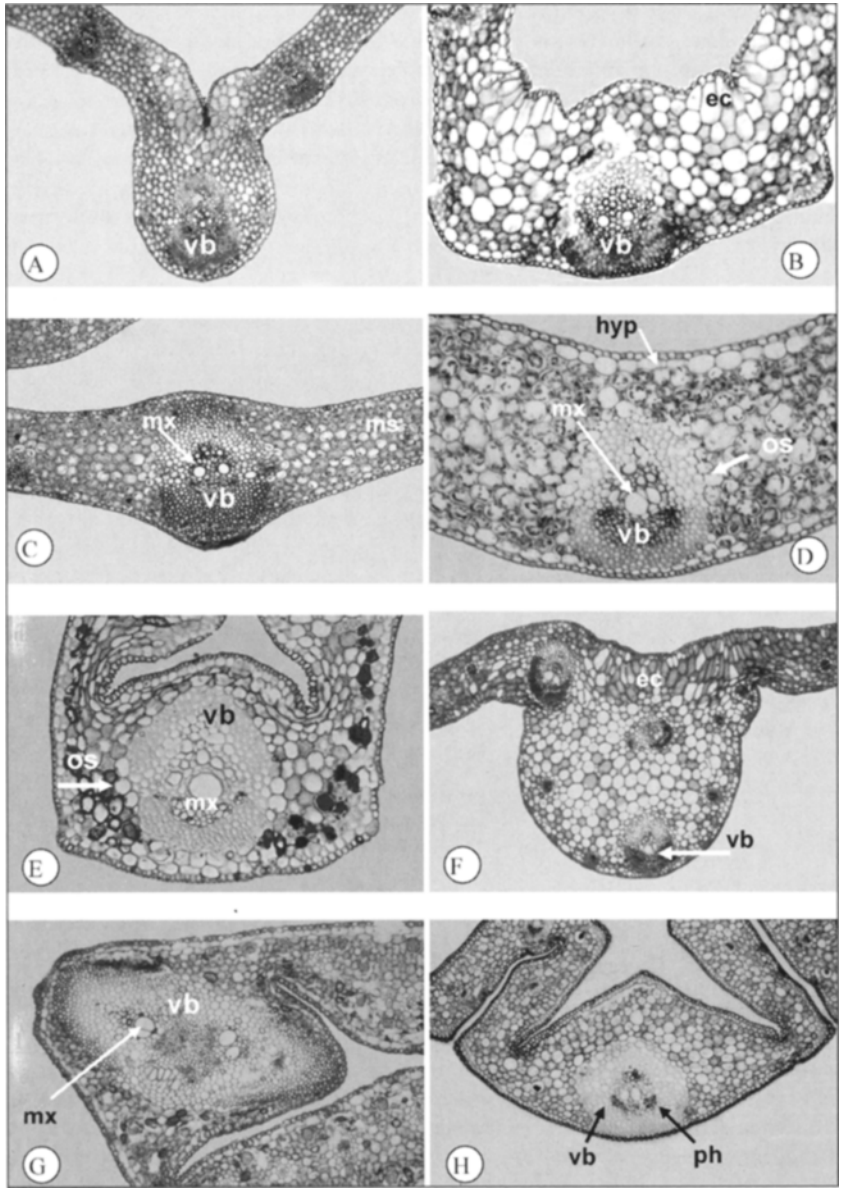

Fig. 7. Eophyll midribs. **A**. *Rhapidophyllum hystrix*: folding distinctly induplicate; midrib rounded; vascular bundle large, single (×40). **B**. *Sabal minor*: midrib flat at the abaxial end; vascular bundle single, metaxylem vessels two (×20). **C**. *Trithrinax brasiliensis*: midrib slightly protuberant; vascular bundle single, phloem strand single, metaxylem vessels two; minor veins attached to adaxial epidermis, inner sheath multilayered (×20). **D**. *Washingtonia filifera*: midrib slightly folded; vascular bundle single, large (×40). **E**. *Borassus* sp.: midrib protuberant, angular; vascular bundle single, phloem strand single, metaxylem vessel single, inner sheath multilayered; tannins in full sacs (×30). **F**. *Plectocomia* sp.:

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 vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids present; tannins abundant, present in all mesophyll.

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

SUMMARY FOR PHOENICEAE

Plumular-radicular axis symmetric, straight; primary root persistent; hyperphyll short, single groove at adaxial side; cotyledonary sheath present, elongate, split lengthwise; coleoptile not developed; cataphyll single; eophyll entire, linear-lanceolate, apex with needle-like projection; costapalmate, induplicate.

3. Borasseae

Borassus sp.

Seed remaining above plumular-radicular node. **Plumular-radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple; pneumatophores at the base; collar roots borne on surface of flat collar disk. **Hyperphyll** smooth and covered by lenticels. **Cotyledonary sheath** covered by lenticels. **Coleoptile** absent. **Cataphyll** single, thick, robust; apical opening; apex curved inwards. **Eophyll** entire, broadly lanceolate; apex crenulated. **Venation** pattern costapalmate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins divergent at apex; transverse commissures abundant, closely arranged, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls linear; cells adjacent to ridges with thickened walls (Fig. 7A). **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; 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 veins** not associated with ridges, attached to both hypodermal layers; IS multilayered; OS distinct. **Median veins** buttressed to adaxial side. **Minor veins** buttressed to adaxial side; OS u-shaped; some vascular bundles present at grooves. **Midrib** prominent, squared; vascular bundle single (Fig. 5E). **Marginal rib**

Fig. 7, *continued*

midrib abaxially protuberant; vascular bundles scattered (×20). **G.** *Nypa fruticans*: midrib protuberant at adaxial and abaxial sides; multivascular bundle single; hypodermal layer distinct; minor veins abundant, oriented toward abaxial side (×20). **H.** *Pseudophoenix sargentii*: midrib slightly rounded at abaxial side and pointed at adaxial side; vascular bundle single, phloem strands two, metaxylem vessels two; minor veins equidistant; raphids abundant (×20). ec, expansion cells; hyp, hypodermis; ms, mesophyll; mx, metaxylem; os, outer sheath; ph, phloem; vb, vascular bundle.

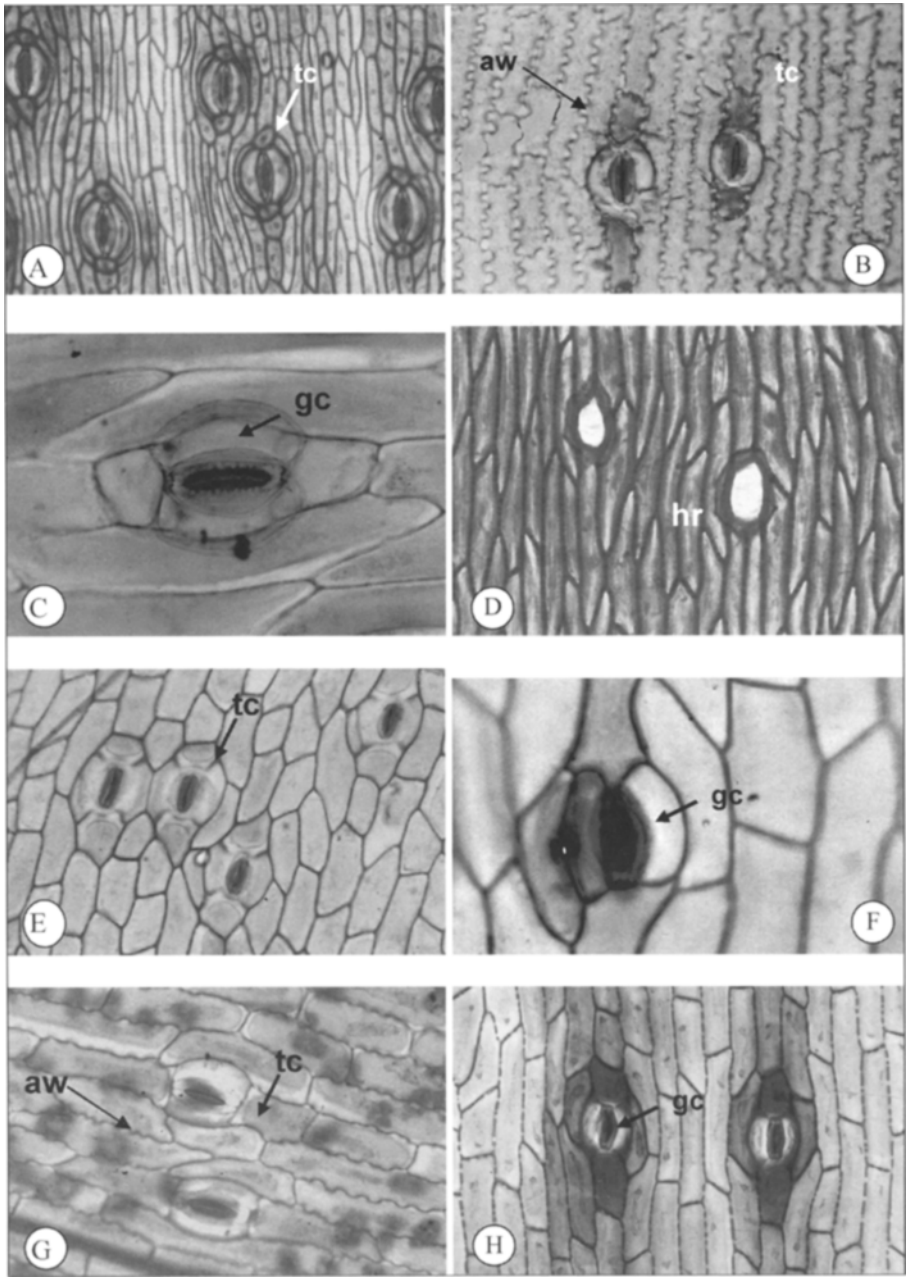

Fig. 8. Epidermal peels. **A.** *Borassus* sp.: abaxial epidermis, stomata abundant, companion cells elongate, terminal cells small (×40). **B.** *Mauritia flexuosa*: abaxial epidermis, epidermal cells rectangular; anticlinal walls dentate (×50). **C.** *Caryota mitis*: stomata slightly sunken; inner wall of guard cells striate; terminal cells short, overarching guard cells (×400). **D.** *Iriartea deltoidea*: epidermal cells

with minor veins and fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** three, one large central flanked by two smaller strands. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids equidistant; tannins abundant, some in full sacs.

Gatin (1906a) and Dassanayake and Sivakadachchan (1973) 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-borne roots absent. **Hyperphyll** elongate, grooved all around; connection point to seed slightly swollen. **Cotyledonary sheath** thick; apical opening; opposite short split; abundant lenticels covering hyperphyll and cotyledonary sheath. **Coleoptile** absent. **Cataphyll** single, plicate, curved inwards. **Eophyll** entire, linear-lanceolate; apex nearly closed and pointed. **Venation** pattern costapalmate; leaf axis distinct; midvein distinct; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and intercostal areas. **Plication** with proximal and distal marginal folds induplicate (Fig. 8A). **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls linear; cuticle layer thick and uniform. **Hairs** multicellular, with multicellular base. **Stomata** sunken, scattered at intercostal regions; 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. **Hypodermis** double-layered, at adaxial and abaxial sides. **Chlorenchyma** well differentiated; palisade layer distinct; spongy mesophyll with more than five layers; 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 veins** not associated with ridges; OS distinct. **Median veins** buttressed to both abaxial and adaxial sides. **Minor veins** 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 veins and fibrous layers. **Petiole** transverse section crescent-shaped. **Phloem strands** three; large central flanked by two smaller strands. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids 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 abundant, covering hyper-

Fig. 8, *continued*
fusiform; hair base (×50). **E.** *Dictyosperma album*: epidermal cells rhombohedral; anticlinal walls linear (×50). **F.** *Hyospathe elegans*: stomata slightly sunken; terminal cells elongate, not overarching guard cells (×400). **G.** *Neonicholsonia watsonii*: anticlinal wall dentate; stomata superficial; terminal cells elongate, overarching guard cells (×50). **H.** *Syagrus coronata*: stomata sunken; terminal cells short or elongate, overarching guard cells. aw, anticlinal wall; gc, guard cell; hr, hair; tc, terminal cell.

phyll, 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; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **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 cells; orientation parallel; present at adaxial and abaxial sides. **Chlorenchyma** well differentiated; palisade with two to three layers; spongy mesophyll with more than five layers, about 12 layers on wider portion; 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 veins** not associated with ridges, buttressed to adaxial and abaxial hypodermal layers; IS multilayered, sclerotic, and fibrous; OS distinct. **Median veins** buttressed to adaxial side; IS multilayered, sclerotic, and fibrous. **Minor veins** buttressed to adaxial side, some associated with grooves; OS u-shaped. **Midrib** prominent at adaxial and abaxial sides, vascularized by grouped simple vascular bundles. **Marginal rib** with fibrous bundle. **Petiole** transverse section crescent-shaped. **Phloem strands** three; large central flanked by two smaller. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids abundant, equidistant; tannins scarce.

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

SUMMARY FOR BORASSEAE

Plumular-radicular axis straight; primary root straight and persistent; collar roots developed or not developed; hyperphyll elongate; cotyledonary sheath opening laterally; coleoptile absent; cataphyll single; eophyll entire or palmate; apex acute; venation palmate; marginal plication induplicate. Some Corypheae (*Livistona, Trachycarpus, Chamaerops*) and all Phoeniceae, all Borasseae, and all Caryoteae have similar germination patterns.

II. CALAMOIDEAE

1. Calameae

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 (Fig. 6B, 6C). **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures simple and bifurcate, connected mainly to secondary veins, abundant, and closely arranged. **Plication** with proximal marginal folds reduplicate; distal outer marginal fold redupli-

cate; inner fold induplicate; plication slightly sinuous (Fig. 8B). **Epidermal cells** rectangular; anticlinal walls dentate; intercostal cells slightly narrower and more elongate than costal cells. **Hairs** present; basal cells few. **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** layer occupied by fibrous bundles arranged 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; fibers arranged in large solid bundles of more than ten strands, these oriented toward abaxial side; fiber lumen small. **Expansion cells** arranged in single or double layers; cells elongate, ellipsoid, and rectangular, restricted to lateral flanks of major veins; fibrous bundles at outermost sides. **Major veins** associated with ridges, rounded and prominent; fibrous buttresses at adaxial side, attached to hypodermal layer; OS distinct at lateral sides of vascular bundle. **Median veins** free, oriented toward abaxial side; IS multilayered and sclerotic; OS lateral; adaxial fibrous buttress attached to hypodermal layer. **Minor veins** free, oriented toward abaxial side, not associated with 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 vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; tannins scattered.

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

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-borne roots; collar roots and root hairs absent. **Hyperphyll** inconspicuous. **Cotyledonary sheath** absent. **Coleoptile** distinct, splitting ventrally or laterally; tongue-like projection at apical end. **Cataphylls** two; apex acute. **Eophyll** bifid; segments linear-lanceolate; apex acuminate; spiny margins; splitting along grooved side. **Venation** pattern pinnate, convergent at apex; leaf axis short; midvein not distinct from other longitudinal veins; transverse commissures always connected to longitudinal veins, widely separated from each other, less abundant than in *Calamus*. **Plication** with proximal marginal folds reduplicate; distal inner marginal folds induplicate; outer marginal folds reduplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls sinuous. **Hairs** absent. **Stomata** superficial, abundant on abaxial surface, arranged in regular lines at intercostal regions; elongate terminal cells do not overarch guard cells. **Hypodermis** an indistinct 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 veins** associated with ridges, attached to adaxial and abaxial hypodermal layers; OS distinct. **Median veins** free, oriented toward abaxial sides. **Minor veins** not buttressed, oriented toward abaxial side; OS around adaxial end, forming a cap-shaped layer; an extra layer of radially arranged OS is present. **Midrib** abaxially prominent, vascularized by several simple vascular bundles. **Marginal rib** with fibrous layers. **Peti-**

ole transverse section deeply concave. **Phloem strands** two. **Metaxylem vessels** single, widely open. **Cell inclusions:** silica bodies 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-borne roots; distinct disk collar; secondary roots branched; shoot-borne roots abundant, arising above first node; collar roots and root hairs absent. **Hyperphyll** inconspicuous. **Cotyledonary sheath** not evident. **Coleoptile** distinct apical opening; splitting side opposite to seed. **Cataphyll** single. **Eophyll** entire, lanceolate; apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures always connected to longitudinal veins, widely separated from each other. **Plication** with proximal marginal folds induplicate; distal marginal folds reduplicate and induplicate. **Epidermal cells** rectangular; dentate walls. **Hairs** absent. **Stomata** superficial, arranged in regular rows at intercostal regions; elongate terminal cells overarching guard cells. **Hypodermal** layer replaced by fibrous bundles at irregular intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with less than five layers. **Expansion cells** single- or double-layered. **Major veins** 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 veins** free, oriented toward abaxial side; multilayered sclerotic IS. **Minor veins** not buttressed, oriented toward 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 (Fig. 5F). **Marginal rib** with fibrous layers. **Petiole** transverse section hemi-ellipse. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; tannins abundant, some in scattered full sacs.

SUMMARY OF CALAMEAE

Plumular-radicular axis angular; primary root either straight or oblique, persistent or ephemeral; collar roots developed or not developed; hyperphyll inconspicuous; cotyledonary sheath apical opening; coleoptile present; cataphylls 1–2; acute and hard apex in *Plectocomia*; eophyll bifid, pinnate, acute, praemorse or lobed at apex; venation pinnate.

Dransfield (1979) has discussed the morphology of Calameae eophylls.

2. Lepidocaryeae

Mauritia flexuosa L. f.

Seeds remaining above plumular-radicular node. **Plumular-radicular** axis asymmetric, angular. **Primary root** persistent; collar disk distinct and swollen; shoot-borne 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 abaxial side. **Venation pattern** palmate; leaf axis inconspicuous; veins radiate from distal end of petiole; midvein distinct in each segment; veins convergent at apex; transverse veins very conspicuous, connected to longitudinal major and minor veins, abundant, closely arranged. **Plication** with proximal marginal fold induplicate; distal fold reduplicate. **Epidermal cells** rectangular; dentate lateral walls (Fig. 7B). **Hairs** present; few basal cells. **Stomata** superficial, arranged in regular rows at intercostal regions, scarce in adaxial surface; elongate terminal cells overarching guard cells. **Hypodermal** colorless parenchyma layer replaced by fibrous bundles arranged at irregular intervals. **Chlorenchyma** differentiated; palisade layer distinct; spongy mesophyll with less than five layers; fibrous bundles oriented toward abaxial side; fiber lumen small. **Expansion cells** single- or double-layered; scattered fibrous bundles. **Major veins** associated with ridges, attached to hypodermal layer; IS partially sclerotic; OS distinct, formed by small regular cells. **Median veins** free, oriented toward abaxial side; multilayered sclerotic IS. **Minor veins** not buttressed, oriented toward or attached to abaxial side; OS surrounding vascular bundle or 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 uniformly arranged in a V-fashion. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; tannins abundant some in full sacs.

SUMMARY FOR LEPIDOCARYEAE

Plumular-radicular axis angular; primary root persistent; hyperphyll not distinct; cotyledonary sheath absent; coleoptile distinct, shorter than cataphylls; cataphylls two; eophyll palmate; plication with proximal marginal fold induplicate, distal fold reduplicate.

III. NYPOIDEAE

Nypa fruticans Wurmb

Seed remaining horizontal to plumular extension. **Plumular-radicular axis** not identifiable; plumular axis emerges horizontally, later diverts with a negative geotropism. **Primary root** never develops into an external structure; secondary roots simple; shoot-borne roots present; collar roots and root hairs absent. Because of its unique morphology, structures such as hyperphyll and cotyledonary sheath are not easily identified. **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 veins; veins convergent at apex; transverse commissures always connected to longitudinal veins, widely separated from each other. **Plication** data unavailable for proximal section; pinnae distal marginal folds induplicate. **Epidermal cells** rectangular; adaxial anticlinal walls sinuous; thick cuticular layer. **Hairs** present; basal cells few. **Stomata** sunken; short terminal cells overarching guard cells. **Hypodermal** layer present at adax-

ial and abaxial sides; cells ellipsoid; parallel orientation, occasionally interrupted by sunken stomata cells. **Chlorenchyma** distinct; palisade layers two, distinct; spongy mesophyll with more than five layers; fibers arranged in solid circular or ellipsoid bundles, made up of more than 15 strands, distributed at adaxial and abaxial sides; lumen wide. **Expansion cells** double-layered. **Major veins** not associated with ridges; OS lateral. **Median veins** free, oriented toward abaxial side. **Minor veins** equidistant or toward abaxial side; OS surrounding vascular bundle. **Midrib** prominent at adaxial and abaxial sides with a single multivascular bundle (Fig. 5G). **Marginal rib** with fibrous bundles. **Petiole** transverse section ellipsoid; hypodermal layers two; distinct circular intercellular spaces. **Phloem strands** single. **Metaxylem vessels** two. **Cell inclusions:** silica bodies 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), Fong (1986), and Bacon (2001).

SUMMARY OF NYPOIDEAE

Plumular axis emerges horizontally; primary root does not emerge from seed; secondary roots simple; shoot-borne roots present; hyperphyll and cotyledonary sheath are not easily identified; 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.

IV. CEROXYLOIDEAE

1. Cyclospatheae

Pseudophoenix sargentii H. Wendl.

Seed remaining above plumular-radicular node. **Plumular-radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple; 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; apical opening; apex acute. **Eophyll** entire, lanceolate; apex acute. **Venation** pattern pinnate; leaf axis distinct; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds reduplicate (Fig. 8C). **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 stomata 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 veins** prominent, associated with ridges; fibrous buttresses at abaxial side, attached to hypodermis; IS multilayered, sclerotic; OS distinct. **Median veins** buttressed to both abaxial and adaxial sides. **Minor veins** small, equidistant; OS surrounding vascular bundle. **Midrib** adaxially prominent; single vascu-

lar bundle (Fig. 5H). **Marginal rib** with minor vein; IS fibrous, solid, multilayered. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids abundant, equidistant.

Read (1968) has described germination in *Pseudophoenix*.

SUMMARY FOR CYCLOSPATHEAE

Plumular-radicular axis straight; primary root persistent; secondary roots simple; pneumatophores present; root hairs abundant; hyperphyll moderate size; cotyledonary sheath grooved; coleoptile absent; cataphylls two, plicate, apex acute; eophyll entire, lanceolate, apex acute; venation pattern pinnate; leaf axis distinct; plication with proximal and distal marginal folds reduplicate.

2. Ceroxyleae

Ceroxylon sp.

Seed horizontal, neither above nor below plumular-radicular node. **Plumular-radicular** axis asymmetric, angular. **Primary root** persistent; collar disk distinct; secondary roots simple; shoot-borne 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; apical opening; apex acute. **Eophyll** entire, broadly lanceolate; apex acute; several leaves similar to eophyll appearing before first split leaf; seventh leaf splitting along grooved side (Fig. 6D). **Venation** pattern pinnate; leaf axis distinct; midvein not distinct; veins converge gradually to marginal vein; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate, distal marginal folds induplicate and margin reduplicate. **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls sinuous; cuticle think; abaxial epidermis sunken around hair base. **Hairs** multicellular, wart-like, abundant at abaxial surface; base multicellular, associated with ribs (Fig. 4C). **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 fewer than five layers. **Expansion cells** single-layered, rectangular, short, perpendicular; adjacent epidermis papillose. **Major veins** associated with ridges, attached to adaxial and abaxial epidermal layers; OS distinct. **Median veins** buttressed to adaxial side. **Minor veins** oriented toward 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 vessels** single or double. **Cell inclusions:** silica bodies irregular, margins spinulose, distributed around vascular bundles; raphids scarce, equidistant; tannins abundant in full sacs

Karsten (1847) has described and illustrated germination of *Ceroxylon*.

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

Seed horizontal, neither above nor below plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** persistent; disk collar present, resembling Caryoteae collar disk; secondary roots simple; shoot-borne roots present. **Hyperphyll**

very short, around 4–5 mm 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 apical opening; apex acute; second cataphyll elongate, opening laterally; both covered by brownish integument. **Eophyll** entire, linear-lanceolate; apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal marginal folds, one induplicate, the other reduplicate. **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls linear; cuticle thick. **Hairs** multicellular, abundant at abaxial surface, associated with ribs; multicellular base associated with ribs. **Stomata** superficial, scattered on intercostal regions; short terminal cells overarching guard cells. **Hypodermis** single-layered, at adaxial and abaxial sides; rounded or ellipsoid cells 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; fibrous bundles at adaxial and abaxial sides; lumen wide. **Expansion cells** single-layered, large, rectangular, perpendicular; adjacent epidermal cells papillose. **Major veins** associated with ridges, buttressed to adaxial hypodermis; IS multilayered, sclerotic; OS distinct at lateral sides of vascular bundle. **Median veins** buttressed to adaxial side. **Minor veins** oriented toward 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 in shape. **Phloem strands** one. **Metaxylem vessels** single or double. **Cell inclusions:** silica bodies 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-borne roots present; root hairs abundant. **Hyperphyll** short, smooth, connection to seed flat. **Cotyledonary sheath** inconspicuous. **Coleoptile** short, rugulose, splitting at opposite sides. **Cataphylls** two; apical opening. **Eophyll** bifid; apex acute; splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present; veins convergent at apex; transverse commissures widely separated from each other, connecting to some longitudinal veins and ending at intercostal areas. **Plication** with proximal and distal marginal fold reduplicate on one side, induplicate on 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 fewer than five layers. **Expansion cells** single-layered, rectangular, perpendicular; adjacent epidermal cells papillose. **Major veins** associated with ridges, buttressed to adaxial hypodermis by multilayered fibrous IS; abaxial side attached to expansion layer; OS distinct. **Median veins** free, equidistant. **Minor veins** 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 vessels** single or double. **Cell inclusions:** silica bodies shape irregular, margins spinulose, distributed around vascular bundles; raphids present.

SUMMARY FOR CEROXYLEAE

Plumular-radicular axis straight or angular; primary root straight and persistent; collar roots developed or not developed; hyperphyll elongate or contracted; cotyledonary sheath opening laterally or apically; coleoptile present; cataphylls two; eophyll entire, bifid or pinnate; apex acute; venation palmate or pinnate; proximal marginal folding induplicate; distal folding induplicate.

3. Hyophorbeae

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-borne roots present; root hairs abundant. **Hyperphyll** undeveloped. **Cotyledonary sheath** absent. **Coleoptile** short, splitting lengthwise opposite to hyperphyll. **Cataphylls** two, elongate; apical opening; apex acute. **Eophyll** bifid; segments sigmoid; apex acute; splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins converging gradually toward apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folding induplicate; distal folds varying on each side, one margin reduplicate and the other induplicate. **Epidermal cells** rhombohedral, papillose; adaxial and abaxial anticlinal walls linear. **Stomata** superficial, distribution irregular at intercostal regions; short or elongate terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fewer layers at folding regions. **Expansion cells** not distinct. **Major veins** multivascular; distribution associated with ridges; attached to adaxial and abaxial hypodermis; OS restricted to lateral sides. **Median veins** free, equidistant. **Minor veins** equidistant; OS restricted to lateral sides; radial OS present. **Midrib** abaxially prominent, spatula-shaped in transverse section; simple and multivascular bundles grouped. **Margins** lacking veins or fibrous bundles. **Petiole** heart-shaped; abaxial side deeply concave. **Phloem strands** one. **Metaxylem vessels** two. **Cell inclusions:** silica bodies hat-shaped, smaller than silica bodies in the Caryoteae, margins spinulose, distributed around vascular and fibrous bundles, more concentrated at adaxial and abaxial sides of bundle; 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-borne roots present; collar roots present; root hairs present, abundant. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short; apical opening; small slit opposite to seed. **Cataphylls** two; apical opening. **Eophyll** bifid; segments lanceolate; apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins converging toward inner veins; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate; distal marginal outer folding induplicate; inner folding reduplicate. **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 fewer than five layers.

Expansion cells single-layered, short, not too distinct from surrounding cells; adjacent epidermal cells papillose. **Major veins** multivascular, associated with ridges, attached to adaxial and abaxial epidermis; OS restricted to lateral sides. **Median veins** free, equidistant. **Minor veins** 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 vessels** two. **Cell inclusions:** silica bodies hat-shaped, margins spinulose, distributed around vascular bundles; raphids 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-borne roots present; collar roots present; root hairs abundant. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, rugulose; apical opening opposite to seed. **Cataphylls** two, elongate; apical opening; apex acute or split and leathery. **Eophyll** bifid; segments lanceolate; apex acute; splitting side abaxial; short fibers visible in leaf clearings. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal outer marginal folding induplicate; inner marginal folding reduplicate. **Epidermal cells** rhombohedral; adaxial and abaxial anticlinal walls linear; papillose in transverse section. **Hairs** absent. **Stomata** superficial; short or elongate terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers. **Expansion cells** single-layered, conspicuous near major veins and midrib. **Major veins** multivascular, associated with ridges, attached to adaxial and abaxial epidermis; OS not distinct. **Median veins** free, equidistant. **Minor veins** 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-ellipsoid; adaxial side flat; abaxial side ellipsoid. **Phloem strands** single. **Metaxylem vessels** two. **Cell inclusions:** silica bodies hat-shaped, margins spinulose, distributed around vascular and fibrous bundles; raphids equidistant; tannins abundant.

SUMMARY FOR HYOPHORBEAE

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

V. ARECOIDEAE

1. Caryoteae

Arenga hookeriana (Becc.) Whitmore

Seed remaining above plumular-radicular node. **Plumular-radicular axis** symmetric, straight. **Primary root** persistent; secondary roots simple; collar roots present; root hairs absent. **Hyperphyll** with an adaxial single groove; region connected to seed, form-

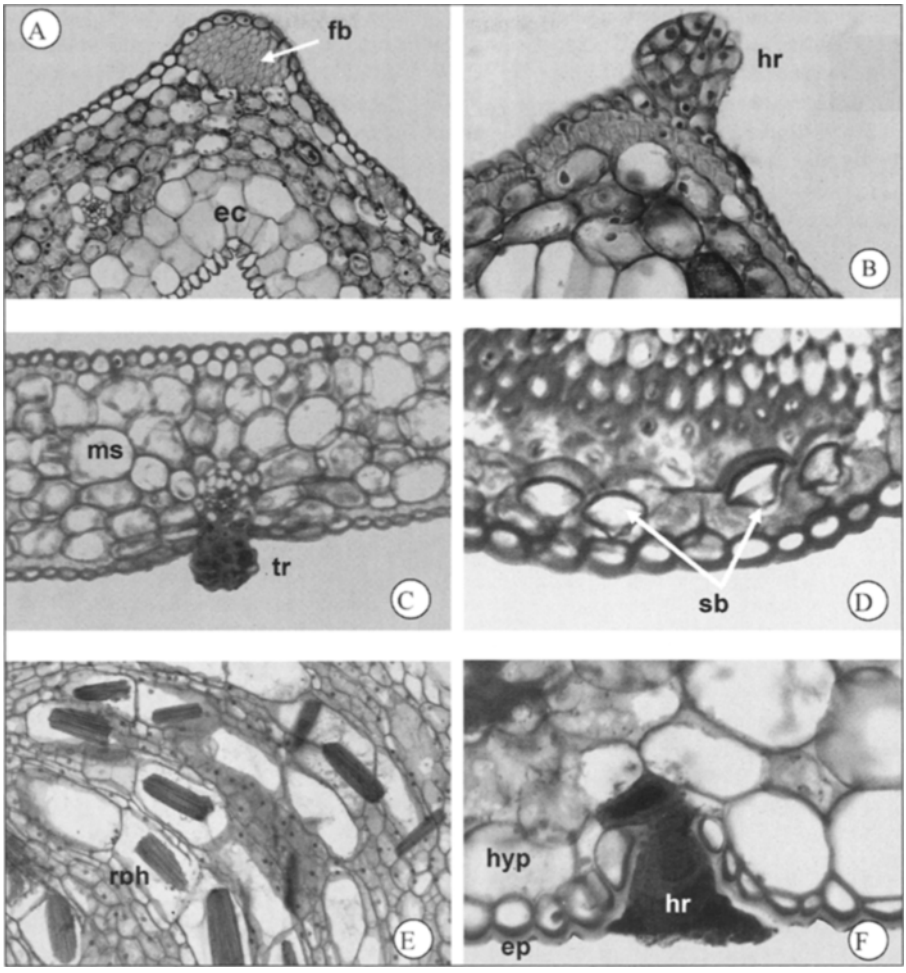

Fig. 9. Various interesting anatomical features. **A.** *Chamaerops humilis*: nonvascular fibrous bundle at ridge; small bundles at adaxial hypodermis; epidermal cells at groove papillose; hypodermal layer distinct; expansion cells columnar; minor veins equidistant (×200). **B.** *Trachycarpus* sp.: fibrous bundles restricted to ridges; hair multicellular. **C.** *Ceroxylon* sp.: hair multicellular, base associated with vascular bundle, surrounding epidermis sunken (×200). **D.** *Arenga hookeriana*: hat-shaped silica bodies (×400). **E.** *Caryota mitis*: abundant raphids (×400) **F.** *Voanioala gerardii*: epidermal hair with sunken base; hypodermal cells large. (×400). ec, expansion cells; ep, epidermis; fb, fibrous bundle; hr, hair; hyp, hypodermis; ms, mesophyll; rph, raphid; sb, silica body.

ing a swollen disk. **Cotyledonary sheath** elongate, splitting lengthwise. **Coleoptile** absent. **Cataphyll** single, tubular; apical opening; apex acute. **Eophyll** entire, broadly lanceolate; apex praemorse (Fig. 9A). **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal veins; veins not convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate (Fig. 8D). **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 cells; present at adaxial and abaxial sides. **Chlorenchyma** differentiated; palisade layer present; spongy mesophyll with fewer than five layers; fibers in equidistant bundles, few; lumen wide. **Expansion cells** single-layered, short, rectangular. **Major veins** not associated with ridges, attached to adaxial and abaxial hypodermis; OS distinct. **Median veins** free, equidistant. **Minor veins** equidistant; OS lateral; radial OS present. **Midrib** abaxially prominent; single vascular bundle. **Marginal rib** with major vascular bundle; OS distinct, surrounding bundle; parallel sclerotic wall dividing vascular bundle. **Petiole** transverse section pentagonal; large vascular bundles in each corner. **Phloem strands** one. **Metaxylem vessels** single. **Cell inclusions:** silica bodies large, hat-shaped, linear margins, distributed around vascular and fibrous bundles (Fig. 4D); raphids 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 (Fig. 9B). **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal veins; veins not convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** fusiform; adaxial and abaxial anticlinal walls sinuous; cells ellipsoid; orientation parallel (Fig. 7C). **Hairs** present; basal cells sunken. **Stomata** slightly sunken; inner wall of guard cells striate; short terminal cells overarching guard cells. **Hypodermis** single-layered, ellipsoid cells; orientation parallel; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers. **Expansion cells** absent. **Major veins** not associated with ridges; large, multivascular, prominent at abaxial side; OS distinct. **Median veins** free, equidistant, attached to hypodermis. **Minor veins** equidistant; OS lateral; radially arranged OS layer present. **Midrib** not distinct; major veins more prominent. **Marginal rib** absent. **Petiole** transverse section pentagonal; adaxial side grooved. **Phloem strands** one. **Metaxylem vessels** single. **Cell inclusions:** silica bodies hat-shaped, linear margins, distributed around vascular and fibrous bundles; raphids abundant (Fig. 4E).

Germination of *Caryota* has been described by Gatin (1906a), Mahabale and Shirke (1967), and Sento (1971).

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 short hairs. **Coleoptile** absent. **Cataphyll** single, tubular, covered by short hairs; apex acute. **Eophyll** entire, ellipsoid; praemorse apex. **Venation** pattern palmate; leaf axis reduced; midvein not distinct from other longitudinal veins; veins not convergent at apex; transverse

commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds induplicate. **Epidermal cells** fusiform, papillose; adaxial and abaxial anticlinal walls linear; 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 cells; parallel orientation; present at adaxial and abaxial sides. **Chlorenchyma** differentiated; palisade layer distinct; spongy mesophyll with fewer than five layers; fibers in equidistant bundles; lumen wide. **Expansion cells** short, square, single-layered. **Major veins** not associated with ridges; large multivascular vascular bundles; OS distinct. **Median veins** free, equidistant. **Minor veins** equidistant; OS lateral. **Midrib** abaxially prominent; single multivascular vascular bundle. **Marginal rib** with major vein; parallel sclerotic wall dividing vein. **Petiole** transverse section pentagonal. **Phloem strands** one. **Metaxylem vessels** single. **Cell inclusions:** silica bodies hat-shaped, linear margins, distributed around vascular and fibrous bundles; raphids abundant, equidistant.

SUMMARY FOR CARYOTEAE

Plumular-radicular axis; primary root straight and persistent; collar roots well developed; hyperphyll elongate, swollen at proximal end; cotyledonary sheath opening laterally; coleoptile absent; one cataphyll; eophyll entire or bifid, apex praemorse; palmate; induplicate marginal folding.

2. Iriarteeae

Iriartea deltoidea R. & P.

Seed horizontal, neither above nor below plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** ephemeral; collar disk distinct; wide flat surface; secondary roots branched; pneumatophores present; shoot-borne roots thicker than primary root. **Hyperphyll** undeveloped. **Cotyledonary sheath** absent. **Coleoptile** short, splitting opposite to seed. **Cataphylls** two, leathery; apical opening; apex acute. **Eophyll** entire, ellipsoid; apex praemorse. **Venation** pattern pinnate; leaf axis distinct; midvein present; veins not convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal margins reduplicate. **Epidermal cells** shape rhombohedral; adaxial and abaxial anticlinal walls linear; papillose in transverse section. **Hairs** abundant, conical, conspicuous in surface view; few basal cells (Fig. 7D). **Stomata** superficial, distribution irregular; short or elongate terminal cells overarching guard cells. **Hypodermis** single-layered, squared cells, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibers forming solid equidistant bundles; lumen small. **Expansion cells** single-layered; double-layered when flanking midrib. **Major veins** multivascular, prominent at abaxial surface, not associated with ridges, attached to hypodermis on both sides; distinct OS. **Median veins** free, equidistant. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** abaxially prominent, square-shaped; simple and multivascular bundles grouped. **Marginal rib** with compact fibrous bundle. **Petiole** transverse section semicircular. **Phloem strands** one. **Metaxylem vessels** single or double. **Cell inclusions:** silica bodies hat-shaped, linear margins, distributed around vascular and fibrous bundles; raphids equidistant.

Iriartella setigera (Mart.) H. Wendl.

Seed attachment horizontal, neither above nor below plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** ephemeral; secondary roots, shoot-borne roots, collar roots, and root hairs absent. **Hyperphyll** undeveloped. **Cotyledonary sheath** absent. **Coleoptile** present. **Eophyll** entire; praemorse apex. **Venation** pinnate; leaf axis distinct; midvein present; veins not convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds reduplicate. **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 parallel; present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibrous bundles abundant, small, equidistant; lumen small. **Expansion cells** single-layered; scattered fibrous bundles. **Major veins** prominent at abaxial side, not associated with ridges, attached to both hypodermal layers; OS distinct. **Median veins** free, oriented toward abaxial sides. **Minor veins** oriented toward abaxial side; OS cap-shaped; radial OS present. **Midrib** abaxially prominent; single multivascular bundle. **Marginal rib** with nonvascular bundle. **Petiole** semicircular. **Phloem strands** one. **Metaxylem vessels** single. **Cell inclusions:** silica bodies hat-shaped, margins smooth, distributed around fibrous bundles; tannins abundant in full sacs.

Socratea exorrhiza (Mart.) H. Wendl.

Seed attachment horizontal, neither above nor below plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** ephemeral; disk collar large, flat with callous contour; secondary roots simple; pneumatophores present; shoot-borne roots thicker than primary root. **Hyperphyll** inconspicuous. **Cotyledonary sheath** absent. **Coleoptile** distinct, splitting apically. **Cataphylls** four; fourth cataphyll elongate; apex bifid. **Eophyll** bifid; segments broad; margins and apex crenulated; splitting along grooved side (Fig. 9C). **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins not convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate, distal marginal folds reduplicate. **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 fewer than five layers; fibers in equidistant bundles; lumen small. **Expansion cells** single-layered, mainly associated to midvein or major veins; adjacent epidermal cells papillose. **Major veins** multivascular, not associated with ridges, attached to adaxial hypodermis and abaxial epidermis, prominent at abaxial surface; IS multilayered and sclerotic; OS not distinct. **Median veins** free, oriented toward abaxial side. **Minor veins** 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 vessels** single or double. **Cell inclusions:** silica bodies hat-shaped, linear margins, distributed around vascular and fibrous bundles; tannins abundant, some in full sacs.

SUMMARY FOR IRIARTEEAE

Plumular-radicular axis angular; primary root oblique and ephemeral; collar roots develop or do not develop; cotyledonary sheath apical opening; a coleoptile present; cataphylls 2–4; eophyll bifid in *Socratea* and simple in *Iriartea* and *Iriartella*; apex praemorse; venation pinnate; reduplicate.

3. Podococceae

Podococcus barteri Mann & H. Wendl.

Seed horizontal, neither above nor below plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** ephemeral. **Hyperphyll** undeveloped. **Cotyledonary sheath** absent. **Coleoptile** present. **Cataphylls** were not easy to evaluate from herbarium samples. **Eophyll** entire, rhombohedral; crenulated margin. **Venation** pattern pinnate; leaf axis distinct; midvein; veins not convergent at apex. **Plication** with proximal marginal reduplicate; distal marginal folds reduplicate. **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 fewer than five layers; fibers abundant, compact, small; equidistant bundles; lumen small. **Expansion cells** absent. **Major veins** not associated with ridges, attached to both epidermal layers; sclerotic IS; distinct OS. **Median veins** free, equidistant; OS lateral and large single cells. **Minor veins** 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 vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, around vascular and fibrous bundles; tannins abundant, some in full sacs.

SUMMARY FOR PODOCOCCEAE

Plumular-radicular axis angular; primary root ephemeral; hyperphyll undeveloped. cotyledonary sheath absent; coleoptile present; eophyll entire, rhombohedral, crenulated margin; venation pinnate; reduplicate.

4. Areceae

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-borne roots protruding through coleoptile base. **Hyperphyll** absent. **Cotyledonary sheath** not distinct. **Coleoptile** lateral split; apex acute; texture granular. **Cataphylls** two; apex splitting into several sections. **Eophyll** bifid; segments lanceolate; apex acute; splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present; veins not convergent at apex; transverse commissures widely separated from each other; some veins connect longitudinal veins; some end at intercostal areas. **Plication** with proximal marginal folds induplicate; distal marginal outer folding induplicate and inner folding reduplicate. **Epidermal cells** rhombohedral; adaxial and abaxial anticlinal walls linear.

Hairs present, polyhedral in transverse section; few basal cells. **Stomata** superficial, scattered; short terminal cells overarching guard cells. **Hypodermis** single-layered, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; cells oriented parallel; fibers as equidistant bundles; lumen small. **Expansion cells** single-layered. **Major veins** prominent at both surfaces, associated with ridges, attached to adaxial and abaxial epidermis; OS distinct. **Median veins** free, equidistant; OS distinct; radial OS present. **Minor veins** distribution abaxial side; OS surrounding vascular bundle; radially arranged OS present. **Midrib** abaxially prominent, irregularly ax-shaped in transverse section, vascularized by grouped simple vascular bundles. **Marginal rib** with minor veins. **Petiole** transverse section semi-ellipsoid. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; tannins abundant; raphids equidistant.

Gatin (1906a) and Ginieis (1953a, 1953b) have 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-borne roots emerging throughout coleoptile base, thick as the primary root. **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; axis distinct; midvein present; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate, distal marginal folds reduplicate. **Epidermal cells** rhombohedral; adaxial and abaxial anticlinal walls linear; polyhedral cells in transverse section (Fig. 7E). **Hairs** present; multicellular base. **Stomata** superficial, abundant in abaxial surface, arrangement scattered; short terminal cells overarching guard cells. **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 veins** prominent at both surfaces, associated with ridges, attached to adaxial and abaxial epidermis; distinct OS. **Median veins** free; equidistant. **Minor veins** distribution abaxial side; OS surrounding vascular bundle; radially arranged OS present. **Midrib** abaxially prominent, simple; multivascular bundles grouped. **Marginal rib** with fibrous layers. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids equidistant; tannins abundant.

Germination of *Dictyosperma* has been 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-borne roots distinct. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, splitting opposite to hyperphyll. **Cataphylls** two; apical opening; apex acute. **Eophyll** bifid; linear segments lanceolate; apex acute;

splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein present; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate; distal marginal folds reduplicate. **Epidermal cells** rhombohedral, rounded in transverse section; adaxial and abaxial anticlinal walls linear. **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; fibers in equidistant bundles; lumen wide. **Expansion cells** double-layered; rectangular; perpendicular; adjacent epidermal cells papillose. **Major veins** associated with ridges; OS distinct. **Median veins** free, equidistant. **Minor veins** equidistant; OS surrounding vascular bundle; radially arranged OS present. **Midrib** abaxially prominent, rounded, vascularized by grouped simple vascular bundles. **Marginal rib** with minor vein. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids 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-borne roots present; collar present; root hairs present. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, splitting opposite to seed. **Cataphylls** two; apical opening; apex acute; plicate. **Eophyll** pinnate; linear-segments lanceolate; apex acute; split leaf first; split along grooved side. **Venation** pattern pinnate; leaf axis distinct; midvein present; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate; distal outer margin induplicate; inner margin reduplicate. **Epidermal cells** rectangular or fusiform; adaxial anticlinal walls linear; abaxial anticlinal walls sinuous. **Hairs** present; multicellular base. **Stomata** superficial, scattered; elongate terminal cells overarching guard cells. **Hypodermis** not distinct; fibrous strands present as a discontinuous layer; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers, rectangular, with a horizontal orientation. **Expansion cells** single-layered, elongate, perpendicular; few cells. **Major veins** prominent at adaxial and abaxial surfaces, associated with ridges; IS multilayered and sclerotic; OS distinct. **Median veins** buttressed, attached to both epidermal layers; OS large lateral cells. **Minor veins** equidistant; OS lateral. **Midrib** adaxially prominent, vascularized by grouped simple vascular bundles. **Marginal rib** with major vein; IS multilayered at marginal end. **Petiole** transverse section rounded; adaxial side slightly concave. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles.

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

Hyospathe elegans Mart.

Seed displaced below plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** ephemeral; collar disk distinct; secondary roots branched; shoot-borne roots thicker than primary root. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short; apex acute; splitting opposite to seed. **Cataphylls** two; splitting lengthwise; apex acute. **Eophyll** bifid; segments lanceolate; splitting side abaxial. **Venation**

pattern pinnate; leaf axis distinct; midvein present; veins not convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate; distal margin reduplicate. **Epidermal cells** rectangular or rhombohedral, polyhedral in transverse section; adaxial and abaxial anticlinal walls linear (Fig. 7F). **Hairs** present; multicellular base. **Stomata** slightly sunken; short or elongate terminal cells not overarching guard cells; scattered distribution, more concentrated at abaxial surface. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers, rectangular, with horizontal orientation. **Expansion cells** single-layered, distributed at lateral sides of major veins. **Major veins** abaxially prominent, associated with ridges; distinct OS. **Median veins** free, equidistant. **Minor veins** at abaxial side; OS surrounding vascular bundle; radially arranged OS present. **Midrib** adaxially prominent; single vascular bundle. **Marginal rib** with minor veins present. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids equidistant; tannins abundant, scattered in every cell.

Neonicholsonia watsonii Dammer

Seed horizontal, neither above nor 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; veins convergent at apex; transverse commissures widely separated from each other, connecting longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate; distal margins, one reduplicate the other induplicate. **Epidermal cells** rectangular or fusiform; adaxial and abaxial anticlinal walls linear or sinuous (Fig. 7G). **Hairs** absent. **Stomata** superficial, scattered; elongate terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibers in abaxial and adaxial bundles; lumen wide. **Expansion cells** single-layered, flanking major veins. **Major veins** prominent adaxially, associated with ridges; OS distinct. **Median veins** free, equidistant. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** adaxially prominent; single vascular bundle. **Marginal rib** with major vein; IS multilayered and fibrous at marginal end. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies 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-borne roots thicker than primary root, borne on flat collar surface **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short; ventral splitting. **Cataphylls** three, longer than coleoptile; apex acute. **Eophyll** pinnate; segments lanceolate; apex acute; splitting at abaxial side. **Venation** pattern pinnate; leaf axis distinct; midvein present; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate; distal margins, one reduplicate, the other induplicate. **Epider-**

mal 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 veins** associated with ridges, attached to adaxial epidermal layer and abaxial expansion cells; OS distinct. **Median veins** free, equidistant. **Minor veins** oriented toward 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 vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; tannins abundant.

Orania regalis Zipp.

Seed displaced above plumular-radicular node. **Plumular-radicular axis** slightly asymmetric, angular. **Primary root** persistent; collar not distinct; secondary roots branched; pneumatophores present; shoot-borne roots abundant; collar roots present. **Hyperphyll** elongate; single apical groove; 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; veins not convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal margins reduplicate. **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; fibers in equidistant bundles. **Expansion cells** double-layered. **Major veins** multivascular, associated with ridges; distinct OS. **Median veins** free, toward abaxial side. **Minor veins** oriented toward abaxial side, some associated with grooves; OS surrounding vascular bundle. **Midrib** abaxial squared protuberance; simple and multivascular bundles grouped. **Marginal rib** with minor vein. **Petiole** transverse section heart-shaped. **Phloem strands** three. **Metaxylem vessels** single. **Cell inclusions:** silica bodies 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-borne roots few, thicker than primary root; collar roots; root hairs. **Hyperphyll** very short. **Cotyledonary sheath** absent. **Coleoptile** short; splitting opposite to seed. **Cataphylls** two; opening lengthwise; apex with acute projection; covered by large trichoma. **Eophyll** entire, lanceolate; apex acuminate; split leaf third; splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate; distal margins reduplicate. **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls sinuous. **Hairs** present; few basal cells. **Stomata** superficial, scattered; short or elongate terminal cells overarching guard cells. **Hypodermis** not distinct; fibrous bundles present as a discon-

tinuous layer; lumen small. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** single-layered; scattered fibers. **Major veins** associated with ridges; adaxial buttresses attached to epidermis and abaxial expansion cells; multilayered IS; distinct OS. **Median veins** free; toward abaxial side. **Minor veins** toward 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 vessels** single. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; raphids equidistant; tannins scattered.

Roystonea borinquena O. F. Cook

Seed horizontal, neither above nor below plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** ephemeral; disk collar distinct and swollen; secondary roots simple; shoot-borne roots absent; 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 apical opening; second split lengthwise; extremely acute apex. **Eophyll** entire, broadly lanceolate; apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein distinct; veins convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds induplicate; distal margins reduplicate (Fig. 8E). **Epidermal cells** rectangular or fusiform, papillose in transverse section; adaxial and abaxial anticlinal walls linear. **Hairs** present; few basal cells. **Stomata** superficial scattered distribution, more concentrated at abaxial surface; elongate terminal cells overarching guard cells. **Hypodermis** single-layered, large rounded cells, at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibrous bundles solid with around 10 strands, equidistant; lumen wide. **Expansion cells** single-layered; scattered fibrous bundles. **Major veins** not associated with ridges, attached to adaxial and abaxial hypodermis; distinct OS. **Median veins** free, equidistant. **Minor veins** equidistant; OS surrounding vascular bundle. **Midrib** adaxially prominent; single, large vascular bundle. **Marginal rib** with minor veins present. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies hat-shaped, margins spinulose, distributed around vascular and fibrous bundles; raphids equidistant; tannins scattered.

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

Veitchia montgomeryana H. E. Moore

Seed horizontal, neither above nor below plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** ephemeral; collar disk distinct; secondary roots branched; scattered pneumatophores; shoot-borne roots abundant, arising around primary root and through base of coleoptile; collar roots and root hairs absent. **Hyperphyll** absent. **Cotyledonary sheath** absent. **Coleoptile** short, splitting laterally. **Cataphylls** three, displaying diverse splitting forms; apex acute, 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 distinct; veins not convergent at apex; transverse commissures widely separated from each other, connecting some longitudinal veins and ending at intercostal areas. **Plication** with proximal marginal folds reduplicate; distal outer margin reduplicate; inner

margin induplicate. **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls linear or sinuous. **Hairs** present; multicellular base. **Stomata** slightly sunken, scattered; short and elongate terminal cells overarching guard cells. **Hypodermis** single-layered, rounded cells, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibrous bundles at adaxial and abaxial sides; lumen small. **Expansion cells** double-layered, ellipsoid or rectangular. **Major veins** associated with ridges, attached to adaxial hypodermis and abaxial epidermis; OS distinct; radial OS present. **Median veins** free, equidistant. **Minor veins** equidistant; OS surrounding vascular bundle; radial OS present. **Midrib** abaxially prominent, ax-shaped, vascularized by grouped simple vascular bundles. **Marginal rib** with minor veins present. **Petiole** transverse section heart-shaped. **Phloem strands** two. **Metaxylem vessels** one or two. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular and fibrous bundles; raphids adaxial; tannins abundant, some in full sacs.

SUMMARY FOR ARECEAE

Plumular-radicular axis, angular; primary root either straight or oblique, persistent or ephemeral; collar roots develop or do not develop; cotyledonary sheath apical opening; coleoptile present; cataphylls 2–3; eophyll bifid, rarely simple or pinnate, and usually acute at apex (sometimes praemorse); reduplicate inner margins and induplicate outer margins.

5. Cocoeae

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** entire, linear-lanceolate; apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein distinct; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal and distal marginal folds varying on each side, one margin reduplicate, the other induplicate. **Epidermal cells** rectangular or rhombohedral, regular and uniform in transverse section; adaxial and abaxial anticlinal walls linear. **Hairs** present; few basal cells. **Stomata** slightly sunken, arranged in rows at intercostal regions, more abundant on abaxial surface; short and elongate terminal cells overarching guard cells. **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; fibers as subepidermal bundles present at ridges. **Expansion cells** single-layered. **Major veins** associated with ridges; OS distinct. **Median veins** buttressed to abaxial and adaxial sides. **Minor veins** buttressed to abaxial side; OS cap-shaped; some vascular bundles associated with abaxial grooves. **Midrib** abaxially prominent, with simple and multivascular vascular bundles grouped. **Marginal rib** with minor veins. **Petiole** transverse section crescent-shaped. **Phloem strands** two to four. **Metaxylem vessels** single. **Cell inclusions:** silica bodies 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-borne roots abundant; secondary roots stout, branched; pneumatophores present; shoot-borne 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 (Fig. 9D). **Venation** pattern pinnate; leaf axis distinct; midvein distinct; veins convergent near apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal outer marginal folds induplicate; inner fold reduplicate. **Epidermal cells** fusiform, papillose in transverse section; adaxial and abaxial walls linear; wax layer thick. **Hairs** present; few basal cells. **Stomata** sunken, occluded by wax layer; short terminal cells overarching guard cells. **Hypodermis** single-layered; cells ellipsoid; orientation parallel; present at adaxial and abaxial sides. **Chlorenchyma** with differentiated layers; palisade layer present; spongy mesophyll with fewer than five layers; fibers as compact bundles, abundant, scattered; small lumen. **Expansion cells** double-layered; fibrous bundles scattered. **Major veins** abaxially prominent, associated with ridges, attached to adaxial and abaxial epidermis, usually flanked by expansion cells; OS not distinct. **Median veins** free, equidistant. **Minor veins** 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 vein present. **Petiole** transverse section heart-shaped. **Phloem strands** four. **Metaxylem vessels** single. **Cell inclusions:** silica bodies 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-borne roots stout, thicker than primary root. **Hyperphyll** absent. **Cotyledonary sheath** inconspicuous. **Coleoptile** short, splitting opposite to seed. **Cataphylls** two; opening apical; apex acute. **Eophyll** bifid; linear segments lanceolate; splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; veins gradually convergent toward the apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal outer fold induplicate; inner fold reduplicate (Fig. 8F). **Epidermal cells** fusiform, papillose in transverse section; adaxial and abaxial anticlinal walls linear; cuticle thick. **Hairs** present; few basal cells. **Stomata** superficial; short or elongate terminal cells not overarching guard cells; guard cells with large ledges. **Hypodermis** single-layered, present at adaxial and abaxial sides, orientation parallel. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibrous bundles compact, equidistant, surrounded by distinct tannin-filled OS; lumen small. **Expansion cells** single-layered. **Major veins** adaxially prominent, associated with ridges, attached to adaxial hypodermis and abaxial expansion cells; IS multilayered, sclerotic; OS distinct. **Median veins** free, equidistant. **Minor veins** 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 vessels** single. **Cell inclusions:** silica bodies 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-borne roots present; collar disk swollen; collar roots present. **Hyperphyll** short, almost inconspicuous. **Cotyledonary sheath** absent. **Coleoptile** short, not split. **Cataphylls** two, elongate; apex acute; opening lengthwise. **Eophyll** entire, 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; veins convergent gradually to midvein; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal folds induplicate. **Epidermal cells** rectangular or rhombohedral, polyhedral in transverse section; adaxial and abaxial anticlinal walls linear. **Hairs** present; few basal cells. **Stomata** slightly sunken, scattered at intercostal regions; short terminal cells overarching guard cells. **Hypodermis** single-layered, present at adaxial and abaxial sides. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibers in equidistant bundles; lumen wide. **Expansion cells** single-layered. **Major veins** adaxially prominent, displaced from ridge, attached to epidermal layers; OS not distinct. **Median veins** free, equidistant. **Minor veins** 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 vessels** single. **Cell inclusions:** silica bodies irregular, margins smooth, distribution around fibrous bundle or vascular bundle; raphids equidistant; tannins, abundant full sacs.

Yampolsky (1922) has 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** apical opening; splitting opposite to seed. **Cataphylls** two, opening laterally; apical extensions bifid with distinct protuberant transverse lines. **Eophyll** entire, lanceolate; apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein distinct; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal and distal folds varying on each side; one marginal fold reduplicate and the other induplicate. **Epidermal cells** rectangular or rhombohedral; adaxial and abaxial anticlinal walls linear; cuticle thick. **Hairs** present; few basal cells. **Stomata** slightly sunken, scattered; terminal cells short and elongate overarching guard cells. **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; fibers in bundles at abaxial side; distinct bundles at ridges; lumen wide. **Expansion cells** double-layered; adjacent epidermis papillose. **Major veins** not associated with ridges, buttressed to adaxial and abaxial epidermis; IS multilayered, sclerotic; OS not distinct. **Median veins** buttressed to abaxial and adaxial sides; solid buttresses. **Minor veins** abaxially buttressed; OS not distinct. **Midrib** abaxially prominent, squared; simple and multivascular vascular bundles grouped. **Marginal rib** with minor vein. **Petiole** transverse section crescent-shaped.

Phloem strands four. **Metaxylem vessels** single. **Cell inclusions:** spherical or ellipsoid, margins spinulose, around vascular bundles; tannins abundant.

Gatin (1906a) has 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** entire, linear-lanceolate; apex acute. **Venation** pattern pinnate; leaf axis distinct; midvein distinct; veins convergent at apex; transverse commissures widely separated from each other, connecting longitudinal veins sporadically. **Plication** with proximal and distal marginal folds induplicate and reduplicate. **Epidermal cells** rectangular; adaxial and abaxial anticlinal walls linear (Fig. 7H). **Hairs** basal cells few. **Stomata** sunken, scattered, abundant in both surfaces; short and elongate terminal cells overarching guard cells. **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; fibers in bundles at ridges; lumen small. **Expansion cells** double-layered, elongate, ellipsoid; adjacent epidermis papillose. **Major veins** not associated with ridges, attached to both epidermal layers; OS not distinct. **Median veins** buttressed to both adaxial and abaxial sides. **Minor veins** buttressed to abaxial side; OS cap-shaped; some vascular bundles associated with grooves. **Midrib** abaxially prominent, triangular; single, large multivascular bundle. **Marginal rib** with minor vein. **Petiole** transverse section crescent-shaped. **Phloem strands** two and four. **Metaxylem vessels** single. **Cell inclusions:** silica bodies irregular, margins spinulose, around vascular bundles; raphids equidistant; tannins scattered.

Gatin (1906a) has 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-borne roots present. **Hyperphyll** elongate, connection to seed flat. **Cotyledonary sheath** rugulose, opening lengthwise. **Coleoptile** not seen. **Cataphylls** two. **Eophyll** entire, lanceolate; apex acute with long linear extension; third leaf splitting at abaxial side. **Venation** pattern pinnate; leaf axis distinct; midvein distinct; veins convergent at apex; transverse commissures abundant, very close to each other, connecting longitudinal veins or intercostal regions sporadically. **Plication** with proximal and distal marginal folds reduplicate and induplicate (Fig. 8G). **Epidermal cells** rectangular or rhombohedral, small and polyhedral in transverse section; adaxial and abaxial anticlinal walls linear; cuticle thick. **Hairs** present, with few cells; sunken base (Fig. 4F). **Stomata** sunken, scattered at hypodermal layer; short terminal cells overarching guard cells. **Hypodermis** single-layered, at adaxial and abaxial sides. **Chlorenchyma** differentiated; palisade layer distinct; spongy mesophyll up to five layers; fibers in bundles at adaxial side; lumen wide. **Expansion cells** double-layered, elongate, rectangular; adjacent epidermis papillose. **Major veins** associated with ridges, attached to adaxial hypodermis and abaxial expansion layer; OS not distinct. **Median veins** free, equidistant. **Minor veins** oriented toward 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 vessels** single. **Cell inclusions:** silica bodies irregular, margins spinulose, distributed around vascular bundles (only one sample in an advanced stage of development was available for study).

SUMMARY FOR COCOEAE

Plumular-radicular axis may be straight or angular; primary root straight and persistent or oblique and ephemeral; collar roots developed or not developed; hyperphyll short or elongated; cotyledonary sheath opening apically or laterally; coleoptile present or absent; cataphylls two; eophyll entire or bifid; apex acute; bifid eophyll with pinnate venation; margins either reduplicate on both sides or induplicate on one and reduplicate on the other.

6. Geonomeae

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-borne roots outgrowing primary root. **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 veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal outer margin induplicate; inner margin reduplicate. **Epidermal cells** rhombohedral, large and regular in transverse section; adaxial and abaxial anticlinal walls linear; costal cells shorter than intercostal cells. **Hairs** unicellular; globose basal cells few. **Stomata** superficial; short terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibrous bundles equidistant. **Expansion cells** single-layered; large cuneate cells adjacent to midrib. **Major veins** prominent at abaxial and abaxial sides, associated with ridges, attached to epidermal layers; IS multicellular, sclerotic; OS distinct, at lateral sides of vascular bundle, filled with tannins. **Median veins** free, equidistant. **Minor veins** equidistant; OS surrounding vascular bundle, filled with tannins. **Midrib** abaxially prominent; simple and multivascular bundles grouped. **Margins** lacking ribs. **Petiole** crescent-shaped. **Phloem strands** two. **Metaxylem vessels** single. **Cell inclusions:** silica bodies hat-shaped, margins spinulose, around vascular bundle; raphids equidistant; tannins abundant, large, in full sacs.

Welfia regia H. Wendl.

Seed above plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** persistent; secondary roots branched; shoot-borne roots abundant; collar roots and root hairs absent. **Hyperphyll** extremely short. **Cotyledonary sheath** absent. **Coleoptile** very short; apical opening; 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

veins; veins gradually converging at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** with proximal marginal folds induplicate; distal outer margin induplicate; inner margin reduplicate. **Epidermal cells** rhombohedral, papillose in transverse section; adaxial and abaxial anticlinal walls linear; cuticle present. **Hairs** unicellular, globular; few basal cells. **Stomata** superficial; short terminal cells overarching guard cells. **Hypodermis** not distinct. **Chlorenchyma** undifferentiated; spongy mesophyll with fewer than five layers; fibrous bundles equidistant. **Expansion cells** single-layered. **Major veins** associated with ridges; distinct OS. **Median veins** free, equidistant. **Minor veins** 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 vessels** single. **Cell inclusions:** silica bodies irregular, margins spinulose, around vascular bundle; raphids scarce; tannins abundant, full sacks, present in vascular bundle and mesophyll cells.

SUMMARY FOR GEONOMEAE

Plumular-radicular axis curved; primary root either straight or oblique, persistent or ephemeral; collar roots develop or do not develop; cotyledonary sheath apical opening; coleoptile present; cataphylls two; eophyll bifid, apex acute; venation pinnate; margins reduplicate.

VI. PHYTELEPHANTOIDEAE

Phytelephas seemanii O. F. Cook

Seed above plumular-radicular node. **Plumular-radicular axis** asymmetric, angular. **Primary root** persistent; secondary roots branched; pneumatophores present; shoot-borne roots present; collar roots present. **Hyperphyll** elongate, smooth; attachment to seed slightly swollen. **Cotyledonary sheath** very short. **Coleoptile** apical opening; dentate all around. **Cataphylls** three; apex acute; thick claw-like ligular fibrous extensions. **Eophyll** pinnate; segments lanceolate; apex acute; splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** proximal section not available; distal marginal folds, one margin reduplicate, the other margin induplicate. **Epidermal cells** rectangular, elongate; adaxial and abaxial anticlinal walls linear. **Hairs** present; few basal cells. **Stomata** superficial, arranged in rows at intercostal regions; short terminal cells overarching guard cells. **Hypodermis** with fibers at irregular intervals. **Chlorenchyma** undifferentiated; spongy mesophyll with more than five layers. **Expansion cells** double-layered, flanking major veins. **Major veins** multivascular, not associated with ridges, attached to both epidermal layers; IS multilayered; OS not distinct. **Median veins** free, equidistant. **Minor veins** 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 vessels** two. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; raphids 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-borne roots present; pneumatophores present; collar roots and root hairs absent. **Hyperphyll** elongate, smooth; attachment to seed slightly swollen. **Cotyledonary sheath** short. **Coleoptile** short; apical opening. **Cataphylls** three; acute and bifid apices. **Eophyll** pinnate; linear segments lanceolate; apex acute; splitting side abaxial. **Venation** pattern pinnate; leaf axis distinct; midvein not distinct from other longitudinal veins; veins convergent at apex; transverse commissures widely separated from each other, connected to longitudinal veins. **Plication** proximal section not available; distal marginal folds, one margin reduplicate, the other induplicate (Fig. 8H). **Epidermal cells** rectangular, rounded and papillose in transverse section; adaxial and abaxial anticlinal walls linear. **Hairs** present; few basal cells. **Stomata** superficial, arranged in rows at intercostal regions; short terminal cells overarching guard cells. **Hypodermis** with fibers at irregular intervals. **Chlorenchyma** undifferentiated; palisade layers; spongy mesophyll with more than five layers. **Expansion cells** single-layered. **Major veins** not associated with ridges, attached to epidermis; IS multilayered and sclerotic; OS not distinct. **Median veins** free, equidistant; OS surrounding vascular bundle. **Minor veins** 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 vessels** two. **Cell inclusions:** silica bodies spherical or ellipsoid, margins spinulose, distributed around vascular bundles; tannins abundant, some in full sacs.

SUMMARY OF PHYTELEPHANTOIDEAE

Plumular-radicular axis angular; primary root straight and persistent; collar roots develop or do not develop; hyperphyll elongate; cotyledonary sheath apical opening; coleoptile present; cataphylls two; eophyll pinnate, apex acute; venation pinnate; reduplicate.

Discussion

Seedling hyperphyll was the characteristic used by Martius (1823–1850) to separate palm seedlings into three groups. The present study shows that palm seedlings have variable length hyperphylls, which can extend to various degrees from the seed, from a few millimeters (e.g., *Jubaea chilensis*, *Colpotrinax cookii*, *Nannorrhops ritchiana*, *Pritchiardia remota*) to several centimeters (e.g., *Corypha*, *Borassus*, *Phytelephas*).

Another relevant characteristic for the cited classification was the presence of a coleoptile (also called ligule or ocrea), which was used to divide palms with remote germination into ligulate and nonligulate seedlings. Coleoptile presence and length is 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 into the plumular-radicular node, the coleoptile is very distinct (e.g., *Nannorrhops ritchiana*). In some taxa, the hyperphyll is inserted halfway into the hypocotyl, leaving a short but visible cotyledonary sheath and a short coleoptile (e.g., *Raphidophyllum hyxtrix*). If the hyperphyll is connected to the distal end of the sheath, the coleoptile

does not develop further (e.g., *Chamaerops humilis*). A coleoptile does not develop if the cotyledonary sheath is split.

The number of cataphylls appears to be distinct for every tribe, and it varies from one in several Corypheae to four or seven in *Socratea* and *Nypa*. The number of cataphylls is related to eophyll shape. For example, seedlings with single cataphylls can be associated with entire eophylls, and seedlings with more than one cataphyll generally have bifid, palmate, or pinnate eophylls. The more cataphylls the seedling has, the more complex is the morphology of the eophyll. *Socratea* has four to seven cataphylls, and the eophyll is bifid, with pinnate venation, nonconvergent longitudinal veins, and 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 entire in most Corypheae, Borasseae, Phoeniceae, and some Cocoeae to bifid in most Areceae, Ceroxyleae, Geonomeae, and some Calameae, to palmate in *Mauritia* (Lepidocaryeae), *Latania* (Borasseae), to pinnate in *Phytelephas* (Phytelephantoideae) and *Nypa*.

Taxa with entire 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, and venation in this type of eophylls is parallel. Bifid eophylls have a distinct axis running between the two segments, and pinnate venation, as in the Calameae, Areceae, and Cocoeae. An exception is the bifid eophyll of *Caryota*. Unlike in the Areceae, the "apical" pinnae does not split basally, but completely formed pinnae are borne on an elongate petiole well below the apical pinnae. A series of eophyll-like leaves follow the eophyll, before the final adult shape. Bifid eophylls are effectively the apical pair of pinnae of the adult leaf; new pinnae are added basally on successively older leaves. In palms with entire eophylls (except *Phoenix*), several succeeding leaves precede the segmented stage. In other words, in bifid eophylls, development is speeded up, and in entire eophylls, a developmental stage is missing.

Plication in palms is the result of differential growth (Kaplan et al., 1982). This character separates palms into two groups—palms with reduplicate (L-shaped) folding and palms with induplicate (V-shaped) folding. Entire eophylls have the same folding pattern, which runs along the whole length of the margins of the lamina. The exceptions to this are bifid Cocoeae eophylls, where each margin exhibits a different folding type; the proximal end is induplicate, and the inner distal end of the segment is reduplicate. This anomaly requires further study. Another observation in relation to plication is that some eophylls seem to be strongly plicate, such as some Corypheae, while others do not show plication, for example, Caryoteae. Others are rather sinuous than plicate.

Stomata are superficial or sunken. Some groups have distinct epidermal hairs; for example, the Iriarteeae have large basal cells and unicellular trichoma. Hair bases in some Borasseae, Areceae, Ceroxyleae, and Hyophorbeae 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. They may be single-layered or two-layered. In some cases, the hypodermal layer is replaced by fibers, solitary or arranged in bundles at regular intervals; in other cases the fibers can form a continuous layer, as in *Borassus* (Borasseae), *Corypha* and *Itaya* (Corypheae), and *Pseudophoenix* (Cyclospatheae).

The mesophyll layers are rarely well differentiated into distinct palisade and spongy parenchyma. However, taxa with distinct palisade parenchyma are common among Caryoteae and Borasseae. Mesophyll fibrous bundles are common among mesophyll cells, forming compact bundles arranged in an orderly fashion. There seems to be a pat-

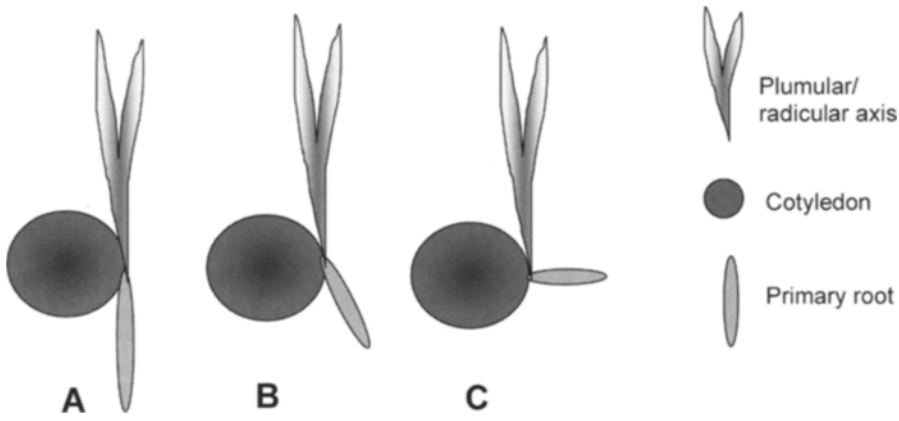

Fig. 10. Primary root orientation planes. **A**. Vertically oriented, not forming an angle with the main axis. **B**. Obliquely orientated, forming an obtuse angle with the main axis. **C**. Horizontally oriented, forming a right angle with the main axis.

tern to the distribution of nonvascular fibers. These are distributed either in the subepidermal layers or among the mesophyll layers. Taxa with both types of fibers in the same eophyll are rare (*Livistona, Borassus, Calamus, Mauritia, Oraniopsis,* and *Jubaea*).

The vascular bundles are in general protected by a sclerotic layer, which is present as a protective inner sheath (IS) surrounding the vascular tissue. These vascular bundles are differentiated into three categories. Major veins (those that occupy the mesophyll) are separate from epidermal or hypodermal layers at the adaxial and abaxial ends. These veins are either associated or not associated with folds; they are free or buttressed by fibrous strands. Median veins are an intermediate type between major and minor veins. They are not easy to differentiate, and their distribution is usually among the mesophyll cells. They are attached to either adaxial or abaxial layers, or they are independent. Minor veins have a distinct distribution among layers. They can be equidistant from the abaxial and adaxial layers, or toward or buttressed to either side.

The midrib can be prominent or flat, symmetric or asymmetric, and 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 others have regular parenchyma tissue. *Arenga* and *Wallichia* (Caryoteae), and *Socratea* and *Iriartea* (Iriarteeae) have a distinct large vein that appears protuberant at both sides of the marginal end. Vascular bundles are surrounded by several layers of sclerotic tissue. Externally, the eophyll of the Caryoteae is entire or bifid with palmate venation and praemorse apex, while the eophyll of the Iriarteeae is entire or bifid but with pinnate venation and a praemorse apex.

The number of phloem strands in adult leaves is a diagnostic feature of palms. 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 Borasseae and in *Chuniophoenix, Nannorrhops,* and *Sabal* (Corypheae). Vascular bundles with four strands were also found in the Cocoeae,

and the sclerotic partitions in this latter case were irregular. It is possible that the sclerotic partitions are ephemeral at this stage of development; eventually, vascular bundles with three phloem strands may fuse into a single one, and vascular bundles with four strands may fuse into two strands. This aspect needs further study.

Cell inclusions (ideoblasts) are various and common in most eophylls. Only the silica bodies offer taxonomic information, and these have distinct shapes. The most common shapes are spherical, ellipsoid, and hat-shaped; the last shape is present in Caryoteae, Iriarteeae, Nypoideae, Hyophorbeae, some Cocoeae, and *Roystonea* (Areceae). In some Cocoeae and Ceroxyleae, silica bodies are small and of irregular shape. They resemble silica sand. Earlier workers have explained the presence of silica bodies as a defense mechanism against predators (Tomlinson, 1961, 1990).

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. 10). The first group is composed of seedlings with vertically oriented, stout, and persistent primary roots, with a straight plumular-radicular axis. These features are associated with almost constant features such as a single cataphyll, coleoptile present or absent, entire eophyll, reduced axis, parallel or palmate venation, induplicate plication, epidermal cells rectangular or sometimes rhombohedral, major veins associated or not associated with ridges, phloem strands 1–3, and metaxylem vessels 1–2.

The second group is composed of seedlings with diagonally oriented and persistent primary roots, forming an angular plumular-radicular axis. The features associated with this type are two or more cataphylls, coleoptile present, segmented eophyll, distinct axis, pinnate or palmate venation, proximal plication induplicate, distal plication induplicate, epidermal cells rectangular, major veins associated with ridges, phloem strands 1–2, and metaxylem 1–2.

The third group is composed of seedlings with a horizontally oriented primary root, forming a 90° angle with reference to the main axis. The features associated with this type are two or more cataphylls, coleoptile present, segmented eophyll, distinct axis, pinnate venation, reduplicate, epidermal cells rectangular, phloem strands 2, metaxylem 1–2.

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Appendix

GLOSSARY

The following terms used to describe germination in palms are taken mostly from Tillich (1995).

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 the cotyledonary sheath and primary root (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.

Haustorium Leaf blade (or at the 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).

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 of eophyll and later leaves in which the cross section of a fold is Λ-shaped.

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

Shoot-borne roots Sometimes called adventitious roots, these roots develop endogenously, in contrast to the primary root, which develops exogenously.