

The Palms

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The uniqueness of palms

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Palms build tall trees entirely by primary growth in a way that limits their growth habit, but not their capacity for continued stem development. They achieve massive primary stature because of distinctive features of leaf development, stem vasculature and anatomical properties. They exhibit several record features of leaf and seed, and inflorescence size and leaves of great complexity. A marked ability to generate new roots allows them to be transplanted easily. As climbing plants they develop the longest unrooted stems in which there are, paradoxically, anomalous features of vascular construction compared with tree palms. It is here claimed that they are the world's longest lived trees because stem cells of several kinds remain active in differentiated tissues throughout the life of the palm. Absence of physiological dormancy may be related to this property, together with inability to withstand freezing temperatures that would cause irreversible cavitation of tracheary elements. This largely restricts them to the tropics, for which they are emblematic organisms. In these biological features palms are indeed unique organisms. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, **151**, 5–14.

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INTRODUCTION

Palms are distinctive tropical plants with an easily recognized physiognomy. In this article, I explore the relationship between their 'gestalt' and their unique biological features. For extensive background information, Tomlinson (1990) and Uhl & Dransfield (1987) are used as references to earlier literature; only more recent and relevant articles are cited. From an evolutionary perspective, all groups of organisms are genetically unique as independent lineages. However, palms are distinctive in that they can make tall and long lived trees entirely by primary developmental processes (Fig. 1), i.e. all tissues are the direct result of continually active root and shoot apical meristems. Intercalary meristems do play an important role, but there is no secondary addition of vascular tissues such

as occurs in other lignophytes, represented in modern floras by conifers and dicotyledonous flowering plants. The success of palms in their tree making abilities arises, in part, because they escape some of the ecological limitations of trees with a peripheral secondary vascular cambium. This includes fire and pathogen resistance, and minimal susceptibility to wind damage. One constraint of the palm habit is its seeming inability to undergo dormant periods, so that palms are inevitably almost restricted to tropical and subtropical regions. On the other hand, palms have fully explored the developmental possibilities inherent in monocotyledonous construction, most significantly in their vasculature, as was early appreciated by von Mohl, (1849). Here, I will try to explain how the palm is able to function as an integrated whole. The palm behaves, in a sense, more like an organism with unitary (animal-like) construction rather than with a plant-like modular construction. Palms also function in time and space according to elementary principles of body size and allometry, i.e. according to the empir-

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Figure 1. *Jubaea chilensis* cultivated in the Temperate House at the Royal Botanic Gardens, Kew. The palm, now 163 years old, was raised from seed in 1843. It is said to be the largest and oldest single stemmed palm cultivated under glass outside its natural habitat. Photo: RBG Kew.

ical generalizations known, respectively, as Cope's "Law" and Corner's "Rules".

COPE'S LAW

In many lineages of living organisms there is a phyletic trend toward increasing body size, an observation first made by Cope (1887). Although stated in a zoological context, it applies well to plants and is implicit in the evolution of the tree habit in all major clades of vascular plants. That it is also well exemplified as a tropical phenomenon has been emphasized by Hallé (1993) in using the term 'giantism.' This secondary adaptive radiation, whereby trees originating from herbaceous ancestors has occurred, presumably independently, in several groups of monocotyledons (e.g. bamboos, palms, pandans and Zingiberales, all with-

out secondary growth, as well as several with a novel form of secondary growth, e.g. *Cordyline* and *Draacaena*). The competitive advantage of increasing height in photosynthetic plants is self evident, but it can also bring advantages in terms of dispersal of spores, pollen and seeds. The tropical forest itself can be seen as the ultimate expression of Cope's Law. However, the generalization is not consistently unidirectional as adaptive radiation in any lineage can also involve 'dwarfism'; duckweeds versus *Eucalyptus regnans* F. Muell. are brought to mind.

CORNER'S RULES

A second set of generalizations is specifically applicable to plants and, although intuitively obvious, was first clearly formulated by Corner (1949) and has been emphasized in the description of tree architecture (Hallé, Oldeman & Tomlinson, 1978: 82). Palms exhibit the rules well and, despite their lack of secondary growth, record dimensions can be achieved. In condensed form Corner's Rules are as follows.

(1) *Axial conformity*: i.e. thicker axes produce thicker appendages. It is self evident that a narrow axis can support, neither mechanically nor hydraulically, an axis wider than itself. This is easily observed in most palm inflorescences but, more significantly, it is seen in the establishment growth of all monocotyledons, most obviously in palms, in which the seedling axis becomes progressively wider with age and, in proportion, its appendages (roots and leaves) also become successively larger (Tomlinson, 1990, 1995).

(2) *Diminution on ramification*: i.e. branch or appendage diameter becomes progressively narrower with increase in branch order number. This may be seen as a simple outcome of the first rule; it is permanently expressed, most obviously in axes without secondary growth and notably in palm inflorescences.

PALMS AS RECORD MAKERS

In part because of their trend toward giantism, palms would be well represented in any botanical record book. The following are some well established examples.

Widest stems built by primary growth: The champion is probably *Jubaea chilensis* (Molina) Baill. (Fig. 1) in which well grown specimens can exceed trunk diameters of 1 m. It is important to emphasize that the shoot apex from which all aerial tissues are ultimately derived starts its activity within an embryo 3–4 mm in diameter. The bulking up to the mature axis is achieved by extensive establishment growth (Tomlin-

son, 1990). Any wide axis in palms becomes the basis for deployment of Corner's first rule.

Largest self-supporting leaves: The record length for a pinnate leaf is held by *Raphia regalis* Becc., as measured at 25.11 m by Hallé (1977). The largest palmately compound leaf occurs in *Corypha umbraculifera* L. with a blade up to 8 m in diameter and a proportionately champion petiole of c. 5 m in length. *Lodoicea maldivica* (J.F. Gmel.) Pers. ex H. Wendl. approaches these dimensions (blade 6 × 4 m, petiole 4 m). Such large appendages are, of course, supported by a wide trunk.

Longest unrooted aerial stem: The measured record is held by climbing palms of the rattan genus *Calamus* at c. 172 m, but unmeasured examples may have reached 200 m (Burkill, 1966). This is a length more than twice the height of the tallest orthodox trees, but the stem is not self supporting and winds through to the forest canopy. The conductive requirements of these narrow stems are the most extensive of any vascular plant, but include paradoxical features discussed below.

Largest inflorescence: The hapaxanthic palm *Corypha umbraculifera* holds this record because the terminal panicle inflorescence develops from the previously vegetative trunk. Each first order branch is then equivalent to the 'lateral inflorescence unit' of a pleoanthic palm (Tomlinson, 1990). The total height of the inflorescence may exceed 8 m on a trunk 20 m tall (Blatter, 1926). There are up to four branch orders, with all axes ending in a narrow rachilla c. 6 mm in diameter and with flowers borne in clusters of eight. Total flower number is estimated at 23.9 million (Fisher, Saunders & Edmonson, 1987). From calculations based on these authors' measurements, the total length of all rachillae is 8821 m, to which may be added a total length of first and second order branches of 476 m for a total of over 9 km. This huge value leads to a corresponding large total fruit weight, although individual fruits are small because each is supported only by a narrow rachilla (cf. Tomlinson & Soderholm, 1975). Such values can be determined with considerable accuracy because all parts are primary and all axes are determinate. *Metroxylon* provides a similar but smaller example (Tomlinson, 1971). Both palms illustrate Corner's second rule precisely.

Largest seed: This record is familiarly held by *Lodoicea maldivica* (double coconut), with seeds of the order of 10–25 kg. Since the fruit may contain up to three seeds, its weight can reach 45 kg. How the seeds of this palm could ever migrate uphill is unknown because no careful observations have been made.

Mostly easily transplanted living trees: This property relates to root development, stem anatomy and cell physiology. The palm trunk stores considerable quantities of available water (Holbrook & Sinclair, 1992) and, most importantly, has a seemingly unlimited capability to generate new adventitious roots at the stem base. These features become the foundation for horticultural practices, which allow the transplanting of large palms (e.g. *Washingtonia*, *Sabal* and *Roystonea* in Florida; *Phoenix* in California) and instant landscaping. Mature palms can be moved from a nursery, after root pruning, to the planting site, producing the effect of a long established tree. New adventitious roots are developed in a totally unknown way.

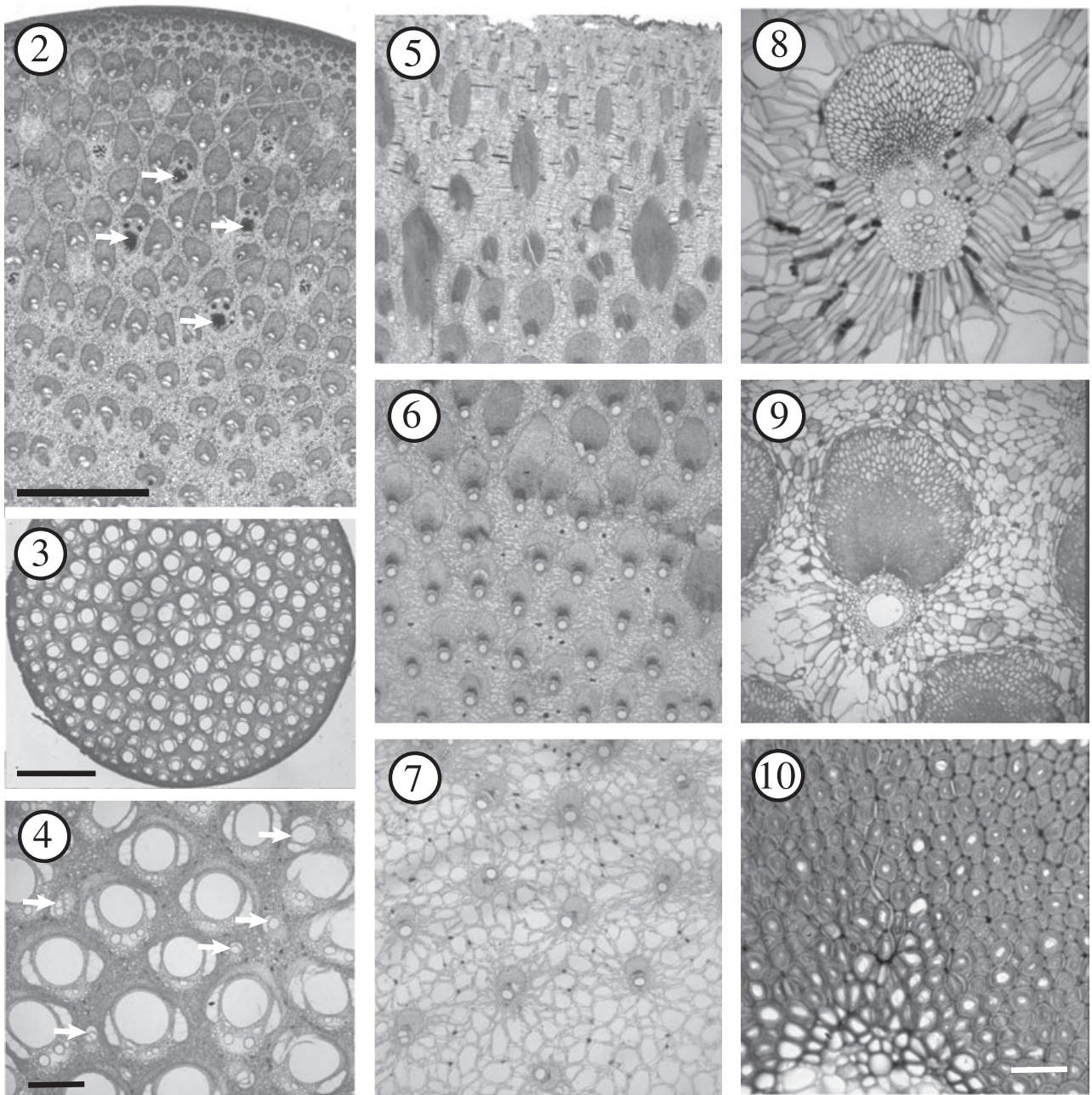
Other records: It is tempting to describe palms as the most ecologically diverse of tropical families. In wet habitats they occur in mangroves, freshwater swamps and in seasonally inundated forests (varzea). They occur at all levels in lowland tropical rain forests, from understory treelets to emergent climbing palms. In tropical montane regions they may be the most conspicuous growth form and are also outstanding in dry forests, savannah and at desert oases. Possibly *Nannorrhops* is the only true desert palm. The few extratropical taxa show a surprising diversity of habitat; fire-climax pinelands in Florida (*Serenoa*), mild temperate forest in New Zealand (*Rhopalostylis*), montane (*Trachycarpus*) in the Himalayas, understory shrubs (*Rhapidophyllum*) in south-eastern United States and in maquis-type vegetation in north Africa and Europe (*Chamaerops*). In summary, palms exist in a complete range of hydroseres but are virtually excluded from environments with freezing temperatures. As will be explained, this is a result of inherent physiological attributes that have a structural basis.

Agriculture: A disputed claim might be that, agronomically, they are the most prolific producers of vegetable oil, most obviously from oil palm and coconut.

The emphasis has to be made on those structural features that relate most directly to the uniqueness of palms, of which the vascular system is the most obvious.

STEM ANATOMY

In recent decades our understanding of the vascular system of monocotyledons has advanced to the extent that we can abandon its meaningless description as an 'atactostele' or as consisting of 'scattered vascular bundles' because it is structurally and developmentally well ordered (Tomlinson, 1990). The pattern of development and its structural consequences are consistent but admit a wide variation in histological appearance, as illustrated in Figures 2–7. The stems of smaller



Figures 2–10. Transverse sections of palm stems. Fig. 2. *Geonoma* sp., leaf traces (arrows) with occluded (tanniniferous) xylem. Fig. 3. *Calamus* sp., from a commercial cane. Fig. 4. *Calamus* sp., detail of Fig. 1 with basal bundle ends (arrows). Figs 5–7. *Roystonea regia* (Kunth) O.F. Cook. Three regions of the incompletely mature stem. Fig. 5. Including cortex and outer part of central cylinder. Fig. 6. Crowded immature vascular bundles near the periphery of the central cylinder; fibres largely with immature cell walls. Fig. 7. Stem centre with lacunose ground tissues; fibres of vascular bundle sheath immature; tannin cells (black) remain unextended. Fig. 8. *Archontophoenix alexandrae* (F. Muell.) H. Wendl. & Drude, central stem vascular bundle (leaf trace) with divergent axial bundle to right; ground tissue cells, around vascular bundle, horizontally extended and often septate; fibrous cap immature. Fig. 9. *Oenocarpus bataua* var. *oligocarpa* (Griseb. & H. Wendl.) A.J. Hend., axial bundle with incompletely differentiated fibrous cap, the enlarged outer fibres still thin walled. Fig. 10. *Cocos nucifera* L., lamellate fibres from bundle sheath. Scale bars: Fig. 2, 1.5 mm; Figs 3, 5, 6, 3 mm; Figs 4, 8, 9, 350 μ m; Fig. 10, 100 μ m.

palms, which have been most suited to vascular analysis, have a relatively uniform and compact distribution of central vascular bundles with unspecialized but usually lignified ground tissue (Fig. 2). Rattans show the greatest departure from the usual pattern, with a very narrow cortex, uniform distribution of vascular bundles and wide vessels (Figs 3, 4). Developmentally they are distinctive, as explained later.

In larger palms, illustrated by the immature stem of *Roystonea* (Figs 5–7), the histological variation at any one level is considerable. There is a fibrous cortex only penetrated by departing leaf traces (Fig. 5). The peripheral crowded bundles of the central cylinder with large fibre caps ultimately provide most of the mechanical strength of the stem (Fig. 6), whereas the stem centre is highly lacunose, with widely separated vascular bundles and spongy, unligified ground tissue (Fig. 7). These textural changes occur only gradually and imply functional differences related to biochemical changes, as explained later.

The palm stem is mechanically efficient, and by establishment growth and continued primary thickening growth, together with gradual lignification of fibrous and parenchymatous tissue, the tree habit can be realized.

VASCULATURE

In contrast with the dicotyledonous tree, the monocotyledonous tree has compensatory benefits ultimately related to their unique vasculature. The stem is totally occupied by functioning vascular bundles, with phloem and xylem in close juxtaposition. There is no heartwood, representing nonconducting tissue. There is no superficial meristematic cambium vulnerable to fire, pathogens and trauma. Axial supply and leaf connection are made by regular branching of leaf traces as they depart the axis. Interconnection between axial bundles by vascular bridges is extensive, so that interlinking is complete and sectoriality is minimized. Traces that supply inflorescences are readily derived by the same mechanism that produces axial bundles. Continuous development of xylem over the extended period of leaf maturation and through functioning intercalary meristems results in the leaf being irrigated solely by protoxylem (Zimmermann & Sperry, 1983; Tomlinson & Vincent, 1984). The axial hydraulic system is protected against xylem dysfunction, and leaves are disposed of in order of their age (Fig. 2). The hydrosystem is massive in terms of water storage capacity, both in parenchyma and axial metaxylem, which remains permanently functional (Holbrook & Sinclair, 1992). This property is another benefit to the landscaper in transplanting large palms. No one of these features is inherent in the primary vascular system of conifers and dicotyledons, which is limited to

the surface of a cylinder and is therefore essentially two-dimensional. The vascular system of a palm is clearly three-dimensional and at any level, continuously functional.

The contrast between the vascular anatomy of other lignophytes versus palms explains why palms can reach giant primary diameters. As coniferous and dicotyledonous trees increase in primary diameter, i.e. become pachycaulous, vasculature can only increase as the square of the diameter but in palms, the increase is by the cube of the diameter.

On the other hand, the constraints of the monocotyledonous vascular system are also clear and have been well described (Schoute, 1903; Holttum, 1955; Tomlinson, 1995). Once the crown size becomes fixed at the end of establishment growth, transport capacity becomes fixed. The stem is necessarily overbuilt at first, in terms of transport, because it must anticipate the later increase in stem height. Crown size is fixed, as palms rarely show aerial branches. This constraint does not necessarily apply to the adventitious root system, as demonstrated by the viability of transplanted palms, nor does it apply to mechanical tissues, as will be described later as one of the unique developmental properties of the palm stem.

The palm is thus an inherently self regulated organism. It is an engineering structure built by continually adding appendages of fixed dimensions to a central axis. Proportions are fixed within the simple allometric principles implied in Corner's rules. The same development principles produce axes of widely varying diameter in different species. It is therefore suggested that in its constructional plan ('bauplan'), the palm resembles the closed (unitary) growth of most animals rather than the open (modular) growth of most plants. The units are fixed but repeated continually.

SIZE CORRELATIONS

Corner's rules explain most of the record morphological features of palms, but developmental features add considerably to their uniqueness. Given a large primary axis of up to 1 m in diameter, appendages can be large, as in the record sized leaves of *Corypha* and *Raphia*. Again, given a wide primary axis combined with hapaxanthly, in *Corypha* a much branched panicle can be produced with large numbers of flowers, but only small ones, because they only occur on the ultimate narrow axes, according to Corner's second rule. In this genus fruits are inevitably small because they occur on the narrow rachilla. In contrast, the record fruit and seed size of *Lodoicea* is achieved via Corner's first rule, because female reproductive axes remain unbranched but massive in relation to a wide parent vegetative axis, and are thus capable of nourishing a giant fruiting structure.

The large size (but always in proportion to stem diameter) of palm leaves has resulted in unique structural features, first in the method of development of the leaf blade and second, in the often mechanically elaborate structure of the leaf base. The multiplicate palm leaf is developed by differential growth within the solid blade primordium, resulting in a folded structure except for a solid marginal strip of tissue that is evident in most palm leaves as they unfold (e.g. Kaplan, Dengler & Dengler, 1982a, b). This method of developing a segmented structure is unique in vascular plants and presumably results by evolutionary modification of a hypothetical linear leaf blade in ancestral monocotyledons. Other monocotyledons with multiplicate leaves (e.g. *Cyclanthus*) show no marginal strip. The palm leaf becomes segmented by partial or complete separation along primary folds of the plicate blade. In simple terms, fan-shaped blades (palmate) versus feather-shaped blades (pinnate) result from differences in the degree of extension of the leaf rachis, with a somewhat intermediate costapalmate condition in some taxa. The corrugation of the initial blade primordium becomes mechanically efficient at maturity in the palmate type, with induplicate versus reduplicate leaflet folding in pinnate leaves as a simple difference in position of splits (in upper versus lower folds, respectively). In fan leaves the unsegmented portion of the blade varies considerably. Giantism, then, can be expressed as a mechanism to produce leaves of record size.

A concomitant structural feature is the highly specialized leaf sheath (Tomlinson, 1990), which has undergone structural diversification in both anatomy and morphology (vasculature and leaf abscission). In many palms the sheath vascular system consists of contra-rotating vascular and fibrous helices (Tomlinson, 1964). Otherwise, the vascular system is linear and leaves abscise cleanly via ventral vertical splits (as in most arecoid palms) combined with circumferential nodal separation. Much of this structural variation refers to the mechanics of the mature leaf, but because the palm leaf sheath is always a closed tube, progressive growth accommodation is necessary as the leaf sheath is subject to the expansive forces of stem primary growth. The palm leaf remains one of the most complicated of plant vegetative organs when viewed in space and time. Its frequent massive proportions reflect sound mechanical construction even though it is a somewhat ephemeral structure.

LONGEVITY OF PALMS

All the structural champions that have been listed and accounted for in mechanical and developmental terms ultimately depend on a palm's ability, shared by all large monocotyledons, to produce and sustain a long

lived vascular system (Tomlinson, 1995). To this may be added a further claim that palms retain the longest lived differentiated cells in their stems, leading to the further statement that palms are the longest lived trees. How does this come about?

It is self evident by structural examination that palm stems produce no secondary vascular tissues, and that both xylem and phloem tissues (tracheary elements, sieve tubes and companion cells) are histologically identical to those of other angiosperms. In contrast to the conducting elements of dicotyledons, however, palm vascular elements retain their conductive ability throughout the total life span of the tree. The age of a palm can only be determined accurately from knowledge of its seed planting date. An iconic example is the famous specimen of *Jubaea chilensis* in the Temperate House at Kew, planted in 1843 (Fig. 1) Other examples, as summarized in Uhl & Dransfield (1987), are based on extrapolated values that range from 100 to 740 years. In trees traditionally thought to be thousands of years old, as in conifers [e.g. *Pinus longaeva* D.K. Bailey, *Sequoiadendron giganteum* (Lindl.) J. Bucholz], most of the tree's tissue is nonliving and phloem cells remain conducting for quite short periods. Palms are histologically astounding because their sieve cells and associated companion cells must remain indefinitely functional, those at the stem base being the oldest. For sieve tubes, this is remarkable considering that at functional maturity they are enucleate, but they can live for at least 200 years!

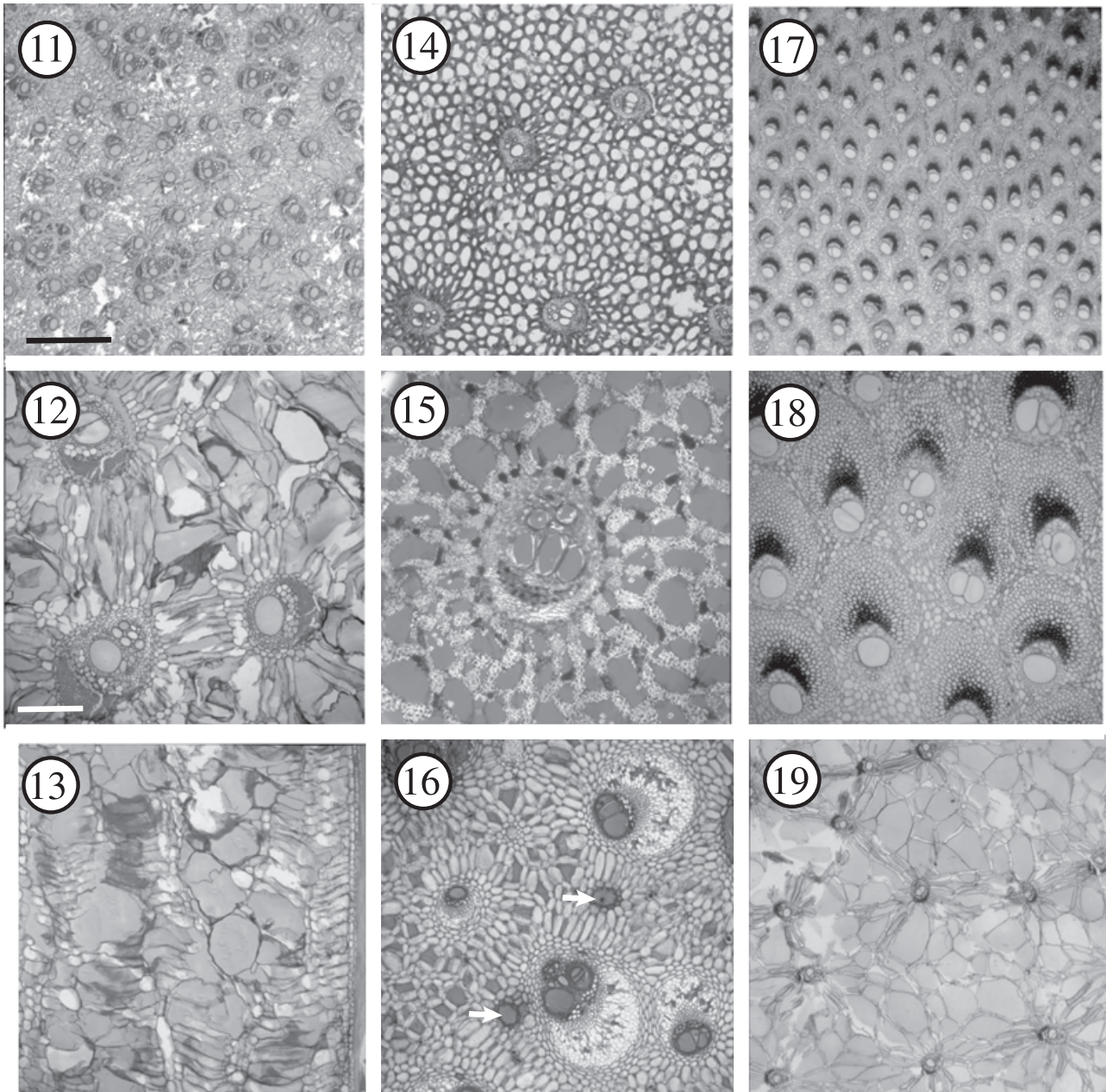
LONGEVITY OF STEM CELLS

Within the palm stems, both the sheathing fibres of the vascular bundles and the parenchyma cells of the ground tissue retain metabolic activity seemingly throughout the life of the palm (Figs 2–10, 11–19). This is exhibited in continuous cell changes throughout the palm stem, those cells at the base of the trunk being oldest. This leads to a distinctive secondary diffuse thickening that is measurable (Schoute, 1912). Metabolic activity is demonstrated structurally in several different ways.

Cytology: The microscopic demonstration of nucleated protoplasts in both fibres and parenchyma (Parthasarathy & Klotz, 1976).

Mitotic activity: This is most obvious in the formation of new primary cell walls in existing ground tissue cells, as in Figure 8, where septae are formed in horizontally extended cells radiating from the vascular bundles.

Cell expansion: A common feature of many palms is the enlargement of stem cells, sometimes accompanied



Figures 11–19. Sections of palm stems, all TS except for Fig. 13 (LS). Figs 11–13. *Euterpe precatoria* var. *longivaginata* (Mart.) A.J. Hend. Fig. 11. TS immature (distal) stem with early enlargement of ground tissue. Fig. 12. Mature stem, centre, with differentially enlarged ground tissue cells. Fig. 13. The same in LS, bundle sheath fibres to right. Figs 14, 15. *Metroxylon sagu* Rottb. Fig. 14. Stem centre with lacunose ground tissue. Fig. 15. Detail under polarized light to show abundant birefringent starch (displaced grains in the lacunae are an artifact). Fig. 16. *Aiphanes minima* (Gaertn.) Burret. Stem bundles separated by lacunose ground tissue, arrows indicate mucilage canals; most fibres of vascular bundles remain undifferentiated. Figs 17, 18. *Socratea exorrhiza* (Mart.) H. Wendl., crowded axial bundles at the periphery of the central cylinder. Fig. 18. Detail to show fibres of vascular bundles only fully differentiated near the phloem. Fig. 19. *Iriartea deltoidea* Ruiz & Pav. Stem centre; the widely separated vascular bundles appear suspended in the lacunose ground tissue by radiating plates of narrow cells. Scale bars: Figs 11, 14, 17, 19, 3 mm; Figs 12, 13, 15, 16, 18, 350 μ m.

by cell division (Figs 11–13). Cortical ground tissue cells show this in most large palms (Fig. 5). Cells do not necessarily undergo uniform expansion (Figs 12, 13) and the pattern of change may be diagnostic for certain palms. A common result is that intercellular spaces are enlarged and a highly lacunar ground tissue can develop (Figs 7, 14). These changes can be seen by comparing top and bottom of a single stem, although a more precise analysis would be to compare the tissue at the same level in a single trunk at different ages, a technically difficult operation. In the extreme condition, central vascular bundles are widely separated and appear as if suspended by narrow plates of horizontally elongated cells (Fig. 19). It is not always easy to distinguish collapsed plates of cells from the walls of individual enlarged cells (Figs 12, 13).

Cell wall thickening: In all palms, fibres of the vascular bundles, especially those in the crowded peripheral regions (Fig. 17), are thin walled at the completion of initial stem expansion, but progressively develop thicker walls with age (Figs 8, 9, 18). The fewer fibres of central bundles are also initially thin walled. (Fig. 16). Wall material is added to fibres in all regions, almost always starting first in the region of the metaphloem and continuing in a centrifugal direction within the bundle sheath (Figs 8, 9). Wall material is typically laid down as concentric lamellae (Fig. 10), a situation comparable with that known for many bamboos. Progressive lignification also takes place, increasing the mechanical stiffness of the axis overall (e.g. Rich, 1987). This ability, to continually increase the mechanical ability of primary tissues so that the stem grows stronger as it increases in height, is an unusual property for a tree trunk and is one factor responsible for the palm's capacity to withstand wind storms, possibly accompanied by greater flexibility of younger tissues. In conventional trees wood mechanical properties do not change significantly with age. The process in a demographic context has been described in detail by Waterhouse & Quinn (1978).

Storage properties: The ability of palm trunks to store large quantities of water suggests that the water is retained within the vacuoles of living cells (Holbrook & Sinclair, 1992). That the water is not stored in intercellular spaces is demonstrated by cutting into the trunk. Water does not flow freely when an incision is made. Starch is common in ground parenchyma cells of many palms, but is particularly notable in hapaxanthic taxa because it forms the energy on which final reproduction largely depends. It is commercially important in the sago palm (*Metroxylon sagu*), which is harvested before flowering. Here, the ground tissue is very lacunose (Fig. 14) with abundant cellular starch (Fig. 15). This material is made available as the

palm flowers, demonstrating metabolic activity of such cells. Continued metabolic ability is the ultimate foundation for the palm's property of being easily transplanted. Other metabolic processes involve tannin and calcium oxalate formation. In taxa with mucilage canals, these may function indefinitely (e.g. Fig. 16).

STEM LENGTH

Rattan stems have been claimed as the longest unrooted axes in vascular plants; their overall length can considerably exceed the overall height of the world's largest free-standing trees (Burkill, 1966). Since such stems are narrow and cane like, the ability of the vascular system of the rattan to sustain conducting function demonstrates acutely the extreme efficiency of the palm stem. The crown of a rattan wilts rapidly when its stem is cut. However, a paradoxical observation is that the vascular system is strangely disconnected (Figs 3, 4). First, protoxylem and metaxylem within stem vascular bundles are, in general, not contiguous (Tomlinson & Fisher, 2000). In this sense there is no 'vascular insertion', as defined by Zimmermann & Sperry (1983). Second, and most significantly, there is no axial continuity established by branching of the leaf trace, as is usual in tree palms (Tomlinson *et al.*, 2001). The leaf trace at its departure from the stem supplies no axial bundle or bridges that would allow axial translocation and water transport. Individual axial bundles differentiate *de novo* within the developing crown without obvious reference to other bundles; their topographic beginnings, or basal portions, are seen as narrow bundles throughout the stem (Fig. 4, arrows). Any transport between axial bundles can only occur via transverse commissures, which are late developing narrow strands of xylem and phloem (Tomlinson & Spangler, 2002). How this distinctive condition may have arisen is suggested by a typological reduction series, beginning with *Rhapis* and continuing, via *Desmoncus* and *Daemonorops*, to the extreme condition represented by *Calamus* (Tomlinson & Zimmermann, 2003; Tomlinson, in press). Rattan canes show the characteristics of lianescent stems in possessing wide (and long) vessels demonstrating hydraulic efficiency but limited vascular continuity may relate more to the persistence of a system that has no mechanism for self repair and yet must function virtually indefinitely.

CONCLUSIONS

The uniqueness of palms in being able to produce trees, often of massive proportions, resides in a constellation of structural and developmental features, all of which are the exclusive result of primary growth

(von Mohl, 1824). The palms have thus exploited the inherent properties of the monocotyledonous vascular system in ways that have led to free-standing trees that compete well with trees of conventional construction, represented by conifers and hardwoods. Palms also grow as climbing plants that can exceed the aerial linear dimensions of all tropical lianes. This success is based on simple rules of allometric construction and the ability of a vascular system to function indefinitely without replacement. Perhaps the most distinctive property of palm stems is the ability of mature differentiated stem cells to retain their viability for centuries. Even though the claim that this makes palms the 'longest lived' of all trees may seem extravagant, in a strictly biological context, it seems appropriate and certainly must justify the continued examination of palms as unique biological objects. However, these unique metabolic stem properties seemingly cannot be sustained in cold climates. As highly integrated organisms with all stem cell types physiologically active, palms cannot undergo dormancy; in this characteristic they are indeed the icons of the tropics.

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