Even the Russians like to strike a romantic note with palms on postage stamps, and they have issued about a dozen just to show how balmy and languorous life can be on the shores of the Black Sea. The United States, which has never been any great shakes with palm stamps, has barely matched Russia's dozen. This pittance seems extreme when compared with the lavish hundreds issued by the African nations, for the United States can boast of almost as many different palm species as may be found on the whole continent of Africa; and if there are any native species in Russia, this reviewer has not yet heard of them. Said reviewer has in mind to illustrate in later issues of PRINCIPES, if Heaven wills it and the editor falls for it, groups of palm stamps picturing men climbing palms, palms at waterfalls, dusky maidens not overclothed languishing beneath palms, etc., all for the edification of palmophiles. Another object would be to show that the whole world is palm-conscious, and very, whether aware of it or not.

Essays on the Morphology of Palms

P. M. TOMLINSON
Fairchild Tropical Garden, Miami 56, Florida

IV. THE LEAF

Adult palm leaves are amongst the largest developed by plants. There is, however, an enormous range in their size. The largest are probably those of some *Raphia* species and often exceed a length of 50 feet. The fan palm *Corypha umbraculifera* has leaf blades up to 12 feet in diameter. At the other end of the range are several species of *Chamaedorea* with leaves only two or three feet long. In addition to this great range in size there is also a considerable range of form. It is the purpose of this article not only to try and indicate this diversity, but also to show that it is less complex and more easily understood than a glance at a collection of living palms would first suggest. All palm leaves have a fundamentally similar structure which suggests that they have been derived from one basic type.

In the earlier essay on seedling leaves (Tomlinson, 1961) it was indicated that the palm leaf could be regarded as being made up in the same way as many monocotyledonous leaves. The blade or lamina is supported by a long slender axis. The axis consists of three distinct regions; a basal leaf sheath extending above into a long or short naked petiole which is continued into the rachis. It is convenient to distinguish the rachis from the petiole as that part of the leaf axis on which the blade is inserted. In many monocotyledons a scale-like organ, the ligule, is present at the mouth of the sheath but this is rarely present in palms. Sometimes it is only visible in immature leaves as in *Bactris*.

Although the palm leaf is an organic whole it is convenient to describe its various parts separately.

Leaf Sheath

In some palms, as in most members of the arecoid groups, the leaf sheath is an obvious closed tube. Otherwise, as in the larger fan palms, it is a short, less well defined region at the base of the petiole and clasps the stem. The former tubular type of leaf sheath is long and particularly conspicuous in the climbing palms of the lepidocaryoid group because adjacent sheaths are persistent and overlap only slightly. The exposed part of the sheath in these palms is commonly armed with sharp prickles, the arrangement of which is constant and fairly diagnostic for each species. Also the mouth of each sheath is often prolonged beyond the insertion of the petiole as a tubular projection. This organ corresponds to the ligule of other monocotyledons. In several species of *Korthalsia* this projection is swollen and normally occupied by ants.

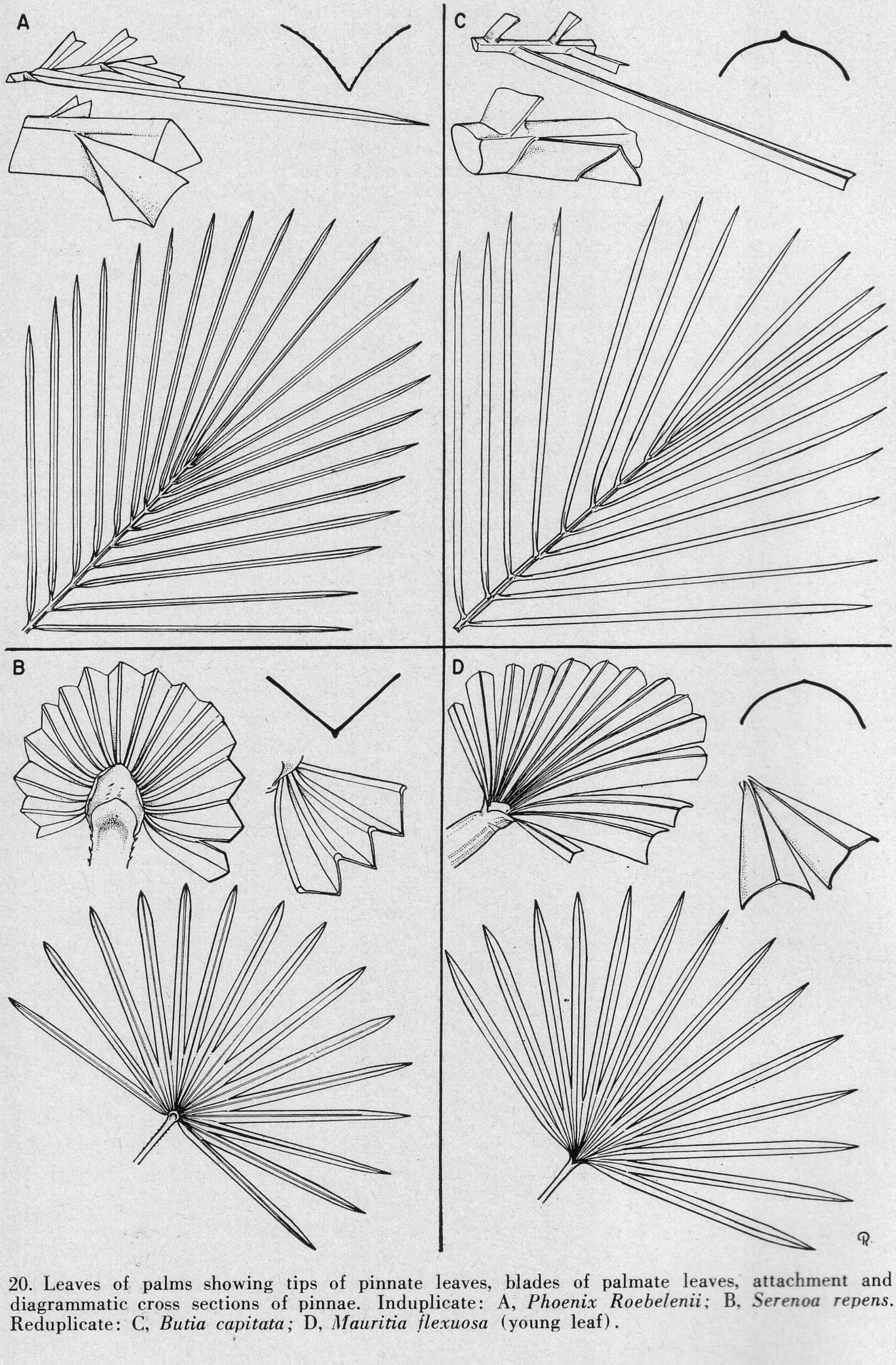
In the larger palms belonging to the arecoid, chamaedoroid, and iriartoid alliances the tubular leaf sheath is smooth and green, that of the oldest leaf being conspicuous below the terminal crown of leaves as the outside of a structure to which L. H. Bailey gave the name of crownshaft. The crownshaft of the royal palm serves as a familiar example. In these palms the leaves fall as a single unit, each abscissing cleanly at the node. Consequently the stem below the crownshaft is always smooth and may be described as self-cleaning. In other palms the leaves persist, wholly or partly, in various ways, and the stem is often obscured by their remains. In the larger fan palms in which the leaf base is not tubular, the woody leaf sheath splits vertically down its back, largely as a result of expansion of the stem within. These split leaf bases form a very regular criss-cross pattern and persist for many years, as in *Corypha* and *Sabal.* In other palms the leaf base may have a different appearance as it dries out. In *Copernicia* for example, the leaf bases persist as woody stumps. In *Cocos* and *Livistona* part of the persistent leaf base has the consistency and appearance of coarse sacking. Commonly the leaf base shreds into its constituent fibres which may persist as a shaggy coat throughout the life of the palm, as in *Arenga* and especially in *Trachycarpus.* In *Zombia* the fibrous remains form sharp protective spines. The "skirts" of whole persistent dried leaves which clothe the stems of mature *Washingtonias* are a familiar sight to Californians.

The Petiole

This region is defined as that part of the leaf axis above the leaf sheath which carries no leaflets. Usually it is very long and conspicuous as in the larger fan palms and in *Raphia.* In some climbing palms and in some of the cocoid alliance, however, it is virtually absent since the first leaflets are inserted on the leaf axis immediately above the leaf sheath. *Copernicia Torreana* is a fan palm which always attracts attention in cultivation because the leaves closely encircle the stem, each leaf having only a very short petiole. The petiole is usually grooved above and rounded below, but in many fan palms the groove disappears distally so that in cross-section the petiole just below the insertion of the leaf blade is almost diamond-shaped. In *Nypa* the petiole is almost round in cross-section throughout much of its length. The petiole margin in some fan palms is beset with numerous teeth, thus does the saw-palmetto *(Serenoa repens)* get its name. Other palms may have prickles scattered over the petiole surface.

The Rachis

This is distinguished from the petiole merely as the region of the leaf axis on which the leaf blade is inserted. In the feather palms it is rounded below but above it bears conspicuous lateral grooves on either side of a central ridge, the leaflets being inserted in the



20. Leaves of palms showing tips of pinnate leaves, blades of palmate leaves, attachment and diagrammatic cross sections of pinnae. Induplicate: A, *Phoenix Roebelenii*; B, *Serenoa repens*. Reduplicate: C, *Butia capitata*; D, *Mauritia flexuosa* (young leaf).

grooves. A true fan leaf has no rachis since the leaflets are inserted together at the end of the petiole but as is indicated below, the fan leaf can be regarded as a feather leaf with a condensed rachis.

The Blade

It has been convenient throughout this series of articles to refer to fan leaves and feather leaves as objects familiar to the non-specialist since they are self-explanatory descriptive terms. In some botanical writings they are accorded considerable prominence, it being suggested that palms can be divided into two groups according to whether they have leaves which are fan-shaped (palmate, Fig. 20, B, D.) or feather-shaped (pinnate, Fig. 20, A, C.). Although this subdivision is a useful one, it is not a natural one.

On the other hand, a more fundamental basis for subdivision depends on the way in which the leaflets or leaf segments are folded. This basic subdivision has been clearly described by Moore (1960) in his article on the Caryotoideae and I reproduce with Dr. Moore's permission the illustrations which clearly indicate these features (Fig. 20). If the leaflets of a palm leaf are examined carefully they will be found to be, in transverse section, either V-shaped, i.e. induplicate or folded upwards (Fig. 20 A, B) or Λ-shaped i.e. reduplicate or folded downwards (Fig. 20 C, D). This feature is often difficult to establish in flattened leaflets, but it can always be elucidated by examining the insertion of the leaflets. We can now, therefore, distinguish two major groups of palms—the induplicate-leaved palms and the reduplicate-leaved palms. The former group includes most of the fan-leaved genera and a few feather-leaved genera. The latter group is almost entirely feather-leaved except for three fan-leaved genera.

Induplicate (V-folded) Palm Leaves

Phoenix has feather leaves which are a good example of this type (Fig. 20 A). The leaflets are sharply folded and each ends in a stiff spine whilst the basal leaflets are reduced to spines. It is noticeable that there is always an odd terminal leaflet, i.e. the leaf is imparipinnate (see Tomlinson, 1961) and this is a fundamental property of such leaves. Moore (1960) has shown that the caryotoid palms, which are the other feather-leaved members of this group, also have fundamentally imparipinnate leaves, but this can usually be established with certainty only in juvenile leaves. *Caryota* itself is specialized and unique because its leaves are not once—but twice-pinnate.

The remaining induplicate - leaved palms all have fan leaves (Fig. 20 B) and comprise the sabaloid and borassoid groups. These have palmate leaves, i.e. the leaf blade segments are arranged like the fingers of a hand. In some species of *Licuala* and in *Teysmannia* the blade is virtually unsegmented but the ribs have the typical palmate arrangement. Otherwise distinct segments or "fingers" are visible extending out of the "palm" of the blade. Rarely the splits between the segments extend to the base of the blade and there is no "palm". Usually the segmentation is very regular, as in *Serenoa* (Fig. 20 B), but it may be quite irregular, as in *Rhapis* and species of *Licuala.* At first sight there does not seem to be much in common between the feather leaf of *Phoenix* and the typical sabaloid fan leaf (Fig. 20 A and B) but Eames (1953) has recently shown that a fan leaf is equivalent to a feather leaf in which the rachis is so condensed that the leaf segments are inserted at much the same level on the end of the petiole. The chief evidence for this conclusion is that in many palms of the borassoid and sabaloid groups leaves intermediate between true palmate and true pinnate leaves occur. L. H. Bailey termed these leaves costapalmate since they superficially resemble palmate leaves but have a conspicuous rachis. *Sabal* is a good example and its leaves are well illustrated on the cover of PRINCIPES, Vol. 4, No. 3. Having emphasized previously the correlation between the type of pinnation and folding of the leaflets it may be asked if a solitary terminal leaflet can ever be recognized in fan palms. Because of congestion of the rachis the terminal leaflet seems always to be displaced and it is never obvious except occasionally in some juvenile leaves. One other characteristic structure of fan leaves deserves mention. This is the hastula which is visible as a scale-like organ at the apex of the petiole (Fig. 20 B). A hastula may be present on the upper and sometimes also the lower surface of the petiole of a typical palmate leaf.

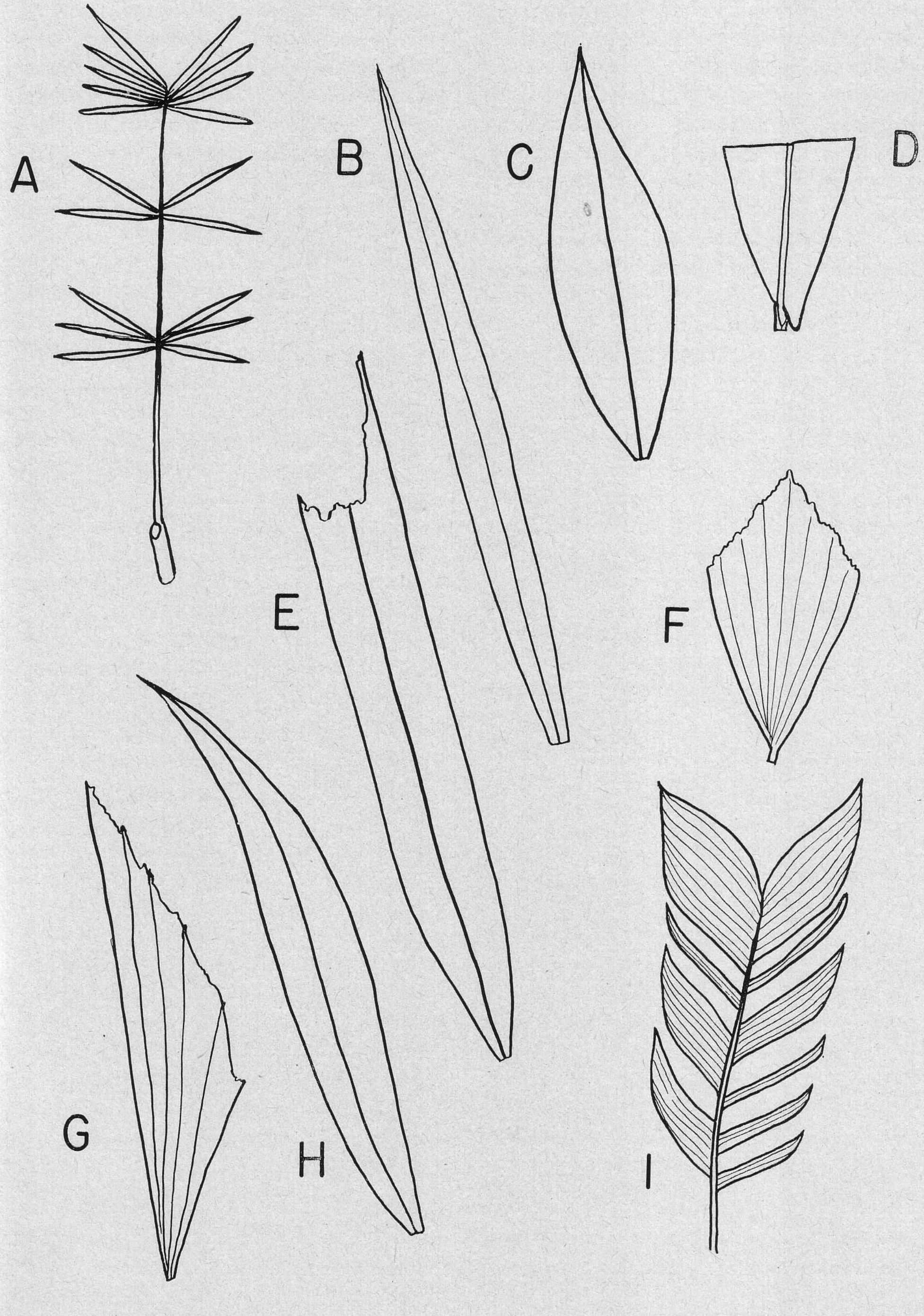
Reduplicate (A-folded) Palm Leaves

Most members of this group have feather leaves which are paripinnate, i.e. they have an equal pair of terminal leaflets (Fig. 20 C). This feature is usually fairly obvious in adult leaves of members of the arecoid, chamaedoroid and iriartoid groups, as well as in seedling leaves. In many of the lepidocaryoid palms and especially in the cocoid palms there is usually an irregular arrangement of veins at the leaf apex resulting in an inconstant arrangement of apical leaflets so that the paripinnate nature of the leaf is not evident. Three genera of reduplicate-leaved palms, *Lepidocaryum, Mauritia* and *Mauritiella* have developed fan leaves. They show no hastula (Fig. 20 D).

Elsewhere I have dealt in greater detail with the fundamental morphology of the palm leaf and tried to explain some of its peculiarities on an evolutionary basis (Tomlinson, 1960).

The above brief outline indicates the fundamental construction of palm leaves but conveys little of their diversity. The most regular and symmetrical of palm leaves, exemplified by those of the coconut, have equal pinnae which are lanceolate (lance-shaped, Fig. 21 B), distributed regularly along the rachis and all equally pendulous. More usually, however, they show varying degrees of irregularity in their spacing. The most striking irregularity is that in which the leaflets are borne in clusters, separated by long naked portions of the rachis (Fig. 21 A). This arrangement occurs in species of *Calamus* and in a less striking fashion in many palms. Often the leaflets do not all extend in the same plane but project sideways at varying angles, as is common in *Phoenix*. Leaflet shape also varies considerably from its typical lanceolate form. The outline may be ovate (Fig. 21 C) rhombohedral (Fig. 21 F) or even slightly sigmoid (Fig. 21 H). Certain groups of palms are characterized by leaflets with irregularity torn apices (Fig. 21 E). These include the ptychospermate palms, the iriartoid palms and, most strikingly many caryotoid palms. The common

21. Leaf and leaflet morphology in palms. A, leaf of *Calamus poensis* with clustered leaflets. B-H, leaflets. B, *Bactris Gasipaes* (lanceolate); C, *Desmoncus* sp. (ovate); D, *Arenga Ambong* (leaflet base, auriculate); E. *Ptychosperma Macarthurii* (leaflet apex praemorse); F, *Korthalsia scaphigera* (rhombohedral); G, *Caryota mitis* (triangular); *H, Chamaedorea* sp. (sigmoid). I, leaf of *Geonoma* sp. with unequal segments.


A
B
C
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name, fishtail palms from the irregular flabellate outline of the leaflets, is a particularly appropriate name for the genus *Caryota* (Fig. 21 G). *Caryota* itself is outstanding amongst all palms in having bipinnate leaves, the primary leaflets themselves being split into secondary segments. The insertion of the leaflets on the rachis is usually broad but it is constricted in *Korthalsia* (Fig. 21 F), while in *Arenga* and a few other palms the leaflets often have an auriculate base, i.e. the base extends backwards beyond the level of insertion, as a small ear (Fig. 21 D). Commonly also, the leaflets are not of uniform width on each side of the leaf. This is characteristic of many species of *Astrocaryum* and *Geonoma* in which the wider leaflets have many prominent ribs, while narrow leaflets on the same leaf may have only one rib (Fig. 21 I).

The above notes on the palm leaf do not indicate its most peculiar feature. Since, however, this feature is shown by the leaf only in its early development it is not striking or easily observed. The initial stages of leaf development corresponds to those in other monocotyledons but when the leaf primordium is only a few millimetres high the individual leaf segments are produced in a unique manner. This process has been well-described recently by Eames (1953) and since it would be inappropriate to go into its details, the reader is referred to Professor Eames' article for exact information. The essential mechanism is that within the solid marginal tissue which ultimately produces the whole of the blade, minute splits appear, at first unconnected with the exterior of the leaf but later breaking through to the leaf surface. These splits separate the strips of tissue which ultimately become the leaflets. The subsequent growth and enormous expansion of the leaf is merely concerned with the extension of these primordial splits. When almost mature the leaf blade protrudes as a lance-like structure from the apex of the leafy crown, the leaflets being tightly folded together. As the leaf unfolds evidence that the leaflets were originally united is found in the presence of a narrow band of tissue (the reins or lorae) which connects their apices. This is torn apart as the leaflets expand and usually shrivels but sometimes it is remarkably persistent as a green band hanging from the lowest leaflets. The reins are conspicuous in such palms as *Corypha, Dictyosperma, Dypsis* and *Neodypsis*. This method of leaf development in which the parts of a compound leaf are cut out of an originally solid tissue is not found in other plants. The usual course of development of compound leaves involves the formation of a separate primordium for each segment. An obvious example is provided by the cycads in which the leaflets can be seen to be distinct at all stages of development.

The above account of morphological variation has been written without comment on the biological advantages of each modification. If there is an advantage in a particular leaf form it is not usually obvious, but the climbing palms (rattans) make a striking exception. In such liane-like palms the rachis of each adult leaf is prolonged into a long whip-like organ called a cirrus. This is armed either with numerous backwardly directed claws, as in *Daemonorops* and allied genera, or with distant pairs of leaflets modified as backwardly directed spines, as in *Desmoncus*, a few *Chamaedorea* species and in most of the African rattans. These cirri, because of their hooks, are little more than grapnels which catch in the foliage and limbs of tall forest trees and so anchor the rattan as it hauls its slender stems into the forest canopy. No doubt other structural modifications have their direct usefulness but no example is more obvious than this.

The purpose of this essay has been merely to serve as a brief outline which will guide the beginner in understanding the complexity of the palm leaf. In spite of this complexity and of the great diversity in size and form, I have tried to show that palm leaves are fundamentally all alike. There is much that remains untold. If a short essay introducing the subject can reach the length of this present article, then a proper survey would produce a whole volume.

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Palms in the Royal Botanic Gardens, Peradeniya, Ceylon

D. M. A. Jayaweera

The Royal Botanic Gardens at Peradeniya, Ceylon, were founded in 1821 at the request of Sir Edward Barnes, the Lieutenant-Governor of Ceylon at the time, by his desire to see the cultivation of coffee in the colony. The site was earlier inspected and reported on favourably by Mr. Alexander Moon who was Superintendent of Calutara Garden near Colombo.

The Gardens occupy a horseshoe-shaped peninsula round which flows the chief river of Ceylon, the Mahaweli. The Gardens are situated 68 miles from Colombo, the chief port of Ceylon, along the Colombo-Kandy road; and 4 miles from Kandy, famous for its Temple of the Tooth wherein a tooth relic of Buddha is housed. The total area is 147 acres of beautifully undulating grounds 1550 feet above sea-level. The climate is hot, moist, and very equable. The mean temperature is about 76° F., and the rainfall averages 90 inches per year spread over about 170 days. January to April is the driest season of the year. The mornings are cool (the temperature in the early mornings in January and February is sometimes as low as 56°-58° F.). April is the hottest month though the mornings are fairly cool.

Mr. Alexander Moon was appointed the first Superintendent of Botanic Gardens in 1821, and he was responsible for moving the plants from the Calutara Garden to the present site. The first official plan of the Gardens appears to

Ed. Note. Additional photographs of palms at Peradeniya are to be seen in "Cultivated Palms," in *The American Horticultural Magazine* 40: pp. 52 (*Borassus flabellifer*), 69 (*Corypha umbraculifera*), 76 (*Hyphaene thebaica*), 83, 84 (*Lodoicea maldivica*), 108 (*Roystonea oleracea*).