
Evolution of leaf forms among palms

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Among the three basic types of palm leaves—the palmate, costapalmate and the pinnate—the palmate form is considered to be the most primitive, the pinnate most advanced and the costapalmate intermediate. Ontogenetic leaf sequences in seedlings indicate that the pinnate form could have been derived from the costapalmate or directly from the palmate type. Persistent, broad and green veins are primitive while the ephemeral and colourless ones are advanced. The hastula of the palmate leaves could be an excrescence as Eames considered it or the remnant of the ventral lobe of an ancestral peltate lamina. The shedding of a large part of the laminal tissue as *haut* in *Phoenix* is interpreted as a trend towards specialisation of the intercostal lamina as the sole photosynthetic area of the leaf.

Key-words—Evolution, Palm, Leaf forms, Morphology.

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सारांश

ताड़ की पत्ती-प्ररूपों का विकास

डी० पद्मनाभन

ताड़ की पत्तियों के तीन मूल प्ररूपों—पामेट, कोस्टापामेट एवं पिच्छाकार, में पामेट प्ररूप सबसे प्राचीन है, पिच्छाकार अत्याधिक समुन्नत तथा कोस्टापामेट का स्थान इन दोनों के बीच में है। नवोद्भिदों के अध्ययन से प्रेक्षित किया गया है कि पिच्छाकार प्ररूप का विकास सीधे कोस्टापामेट प्ररूप से हुआ है अथवा पामेट प्ररूप से हुआ है। स्थायी, चौड़ी एवं हरी शिरायें आद्य हैं जबकि रंगहीन समुन्नत हैं। पामेट पत्तियों की जीभिका ऐम्स के अनुसार एक अपवृद्धि भी हो सकती है अथवा पूर्वजी छत्रिकाकार पटल की अधर पाली का अवशेष। फोइनिक्स में पटली ऊतक के अधिकतर भाग का गिर जाना एक विशेष लक्षण है।

DURING the period 1845-1925 the palm leaf was the subject of frequent research and discussion. From 1925-1953 there was no activity. The widely quoted paper of Eames entitled, "Neglected morphology of the Palm leaf" was published in 1953. This paper revived interest in the subject and Periasamy (1962) described leaf development in *Cocos*, *Borassus*, *Phoenix* and *Caryota*. However, he did not discuss the evolutionary biology of the palm leaf. The papers by Padmanabhan (1963, 1967, 1984, 1990) supported the views of Eames (1953) regarding the initiation of plications, even though with minor deviations regarding the mode of schizogenous splits but contained no information on the evolutionary aspects. The recent papers by Kaplan *et al.* (1982a, b) and Dengler *et al.* (1982) deal with the controversy over tissue splitting but evolution is totally neglected. The present paper is an attempt at

reviving the interest in evolution of leaf forms in palms.

GENERAL MORPHOLOGY OF THE PALM LEAF

Palm leaves exhibit enormous diversity in form. They may be simple, pinnately compound, palmate, costapalmate or pinnately decomposed. Despite these variations, all the types are developed basically from simple leaves by varied patterns of laminal segmentations. During development, the lamina originates as a simple uniplicate primordium and turns plicate. The plicate lamina then breaks up into segments. Plications persist in the adult leaves. Palmate leaves do not have a rachis while the

pinnate ones have well-developed rachis. In costapalmate leaves, a median rachis is present but is not long enough to cause breaking of the lamina into pinnae. Plications do not affect the marginal part of the lamina which forms what has been named by Eames (1953) as 'reins and hook'. The reins are bands of marginal tissue that connect the tips of pinnae or laminal segments after the lamina breaks up. The hook is a special thickened terminal part of the reins seen in some palms (Figure 1A, C). The reins in costapalmate leaves are slender and wiry (Figure 1B).

The rachis has three surfaces—the adaxial, abaxial and the lateral (Padmanabhan, 1984). The lateral surface originates with the inception of plications, and not only affects the lamina but also its insertion. Thus, this accounts for the plicate insertion of the lamina on the lateral surface. The adaxial surface develops further and forms an elevation which progressively narrows at the terminal zone and results in a sharp median ridge as in the leaf of *Cocos* (Figure 2D, E; Text-figure 2). The tip of the rachis may bear a single leaflet or a pair of segments formed by the median tearing of a single leaflet.

Palmate leaves develop a 'crest' or 'hastula' at the base of the rachis. According to Eames (1953), the crest is an excrescence from the rachis. An abaxial hastula also may develop in some species, for example, *Rhapis excelsa*. The hastula is a prominent, triangular growth in costapalmate leaves as in *Pritchardia* (Figure 1C). In *Arenga* and *Calamus*, the 'ligule' forms a tubular covering over the younger leaves, and the term 'ocrea' is used for these structures (Dransfield, 1979) which are morphologically the upper extensions of the sheaths.

ORIGIN AND EVOLUTION OF PALMATE AND PINNATE TYPES

According to Goebel (1926, 1932) both pinnate and palmate leaves originated from a common prototype with vertically oriented plications. The palmate condition was thought to have evolved by the lack of rachis elongation. Kaplan *et al.* (1982a) criticised this view on the ground that the model was based on mature specimens and not on developmental data. They further argued that the primordia of palmate and pinnate leaves are basically different and that there is no common character justifying a common prototype for both the kinds of leaves. These workers argued principally from a developmental standpoint without regard for evolutionary significance. Their description of the

relationship between rachis length and the number of plications may be of interest in developmental dynamics but not useful in understanding the evolutionary status of a particular leaf type. Kaplan *et al.* (1982b) stated that regression analysis of plots of plication number versus leaf length gave evidence that the leaf of *Chamaedorea* could be viewed as an arrested form of the leaves of *Chrysalidocarpus*. Because the leaves of both the species are pinnate, this information is not useful in understanding the evolution of pinnate types in palms in general.

Eames (1953) expressed the opinion that the palmate type was more advanced than the pinnate one. The palmate condition was supposed to have evolved by telescoping of the rachis of a pinnate prototype. By this process all the pinnae would be brought to the tip of the petiole. This view was stoutly opposed by Kaplan *et al.* (1982a) on developmental evidence. Eames also claimed developmental evidence as one of the reasons for his view. Current work on juvenile leaves of several palms has enabled the writer to collect developmental information which could throw some light on the problem of origin of palmate and pinnate types.

The linear, petiolate leaf with a median nerve and a few prominent laterals is the simplest leaf type among the palm seedlings. All the nerves originate from the tip of the petiole and run parallel up to the leaf apex. In the succeeding leaves, the shape remains unaltered but the number of major veins increases. A small median 'rachis' appears at the tip of the petiole as a result of fusion of the bases of the two terminal veins. In the next order of leaves, the lamina becomes cleft terminally resulting in a bifid condition (Figure 2A-C). The basal rachis has grown longer by fusion of more veins. The leaves that follow show a clear rachis and more veins are added basally. The rachis ultimately becomes a long median structure bearing numerous costae on either side. Development of fenestrations between costae (Figure 2B) leads to the separation of pinna segments. Further, the leaves become partly pinnate with free segments below and unseparated lamina above (Figure 2C). The totally pinnate leaves called 'adult leaves' follow this kind of leaves. This sequence is readily seen in young plants of coconut. The most notable aspect is the origin of rachis by partial fusion of costae.

A different kind of succession occurs in *Calamus rotang* (Text-figure 1A-E). In this species, the first leaves are palmately bifid or trifid with segments clearly separated up to the rachis. All subsequent juvenile leaves are palmately compound. In higher order leaves, more segments are added

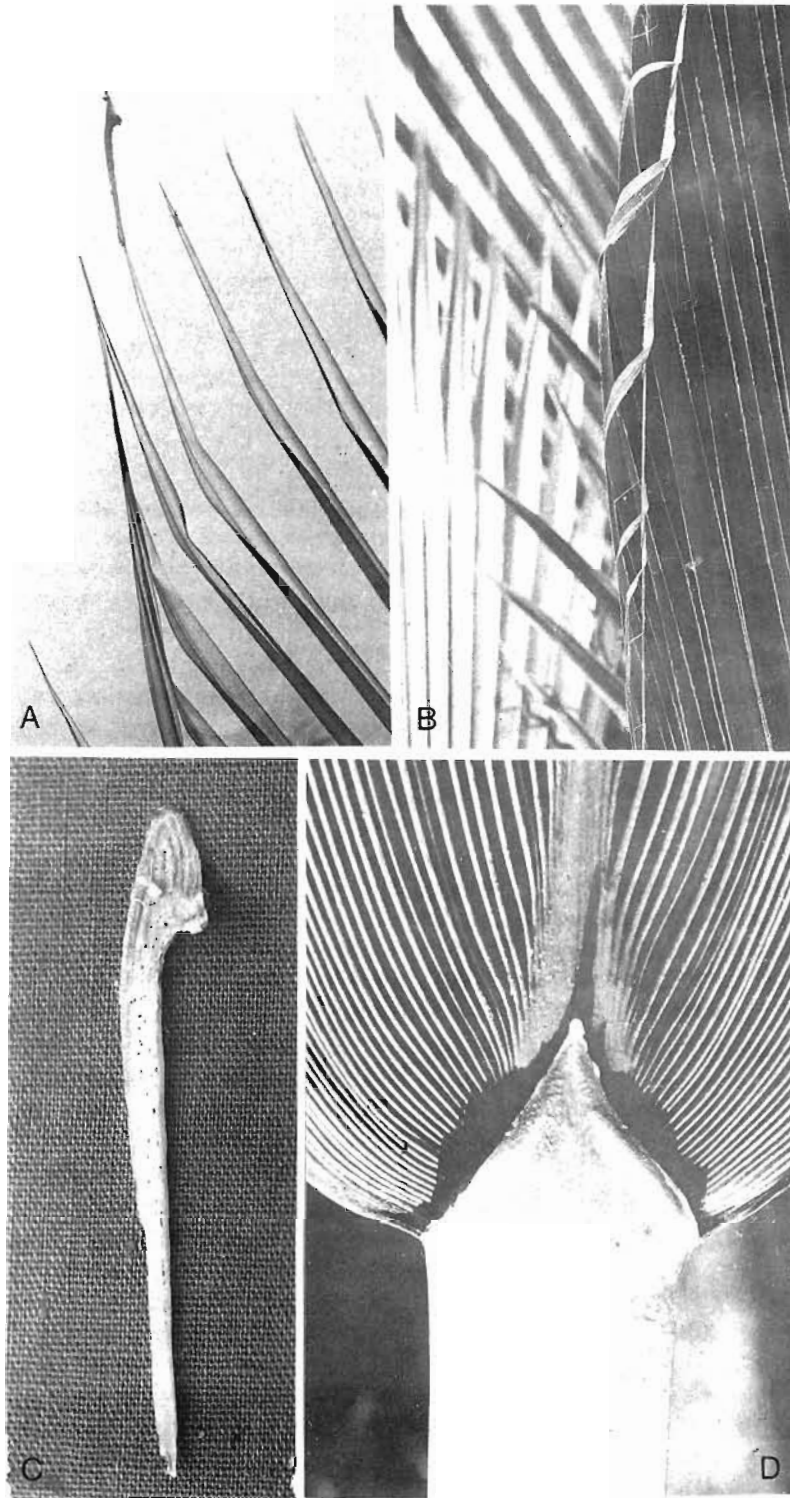


Figure 1—A-D. Photographs illustrating some aspects of palm leaf morphology. **A, C.** *Chrysalidocarpus lutescens*. **A.** Terminal leaflets of an unfolding leaf showing the reins and hook attached to tips of pinnae. **C.** A close view of reins and hook shown in **A, B, D.** *Pritchardia pacifica*. **B.** Margin of an unfolding leaf showing the wiry reins attached to the tips of laminal segments of the costapalmate leaf. **D.** Lower part of the rachis showing the large, triangular hastula covering the laminal plications on either side. (A, $\times 0.3$; B, $\times 0.3$; C, $\times 2.5$; D, $\times 0.75$).

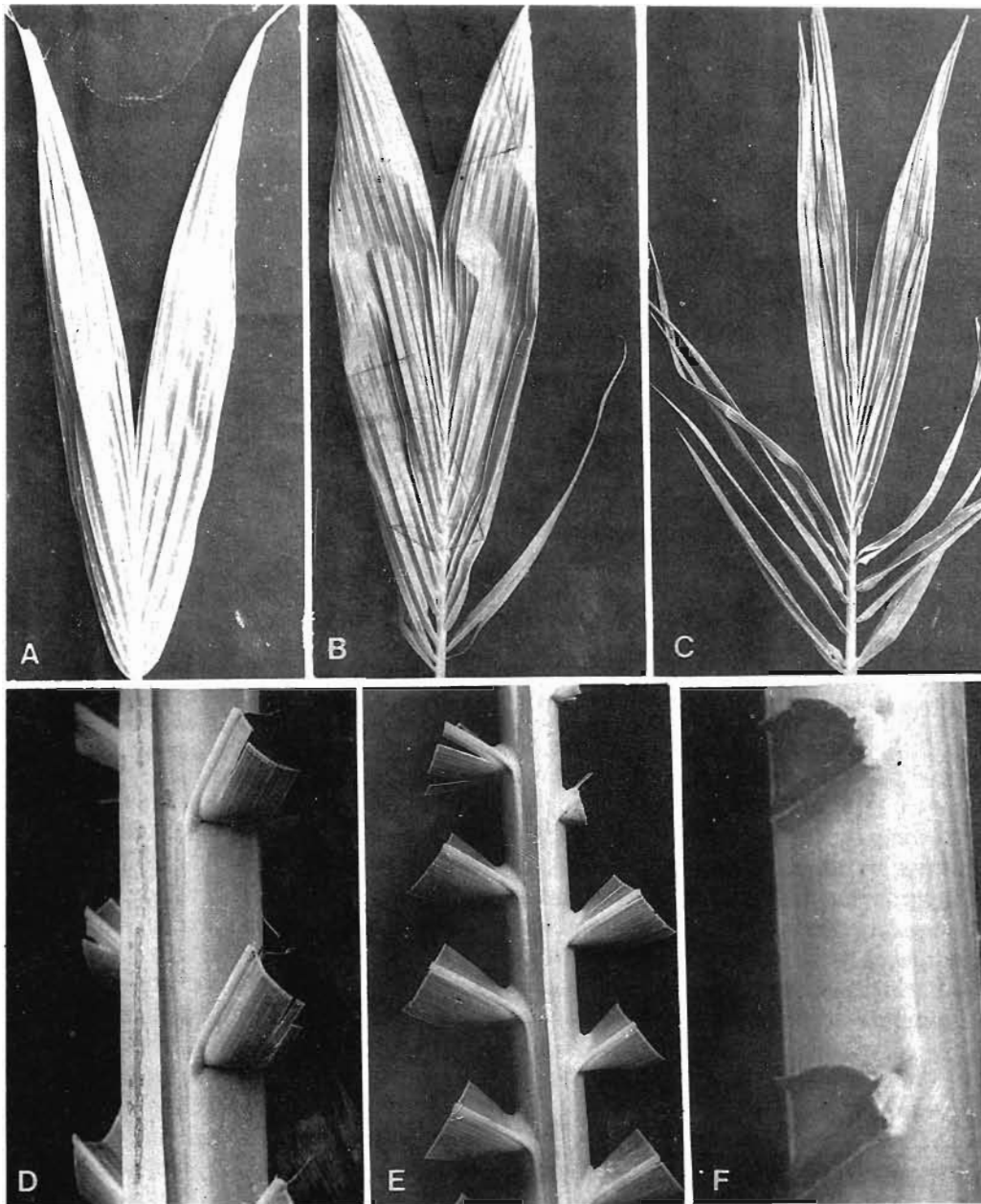
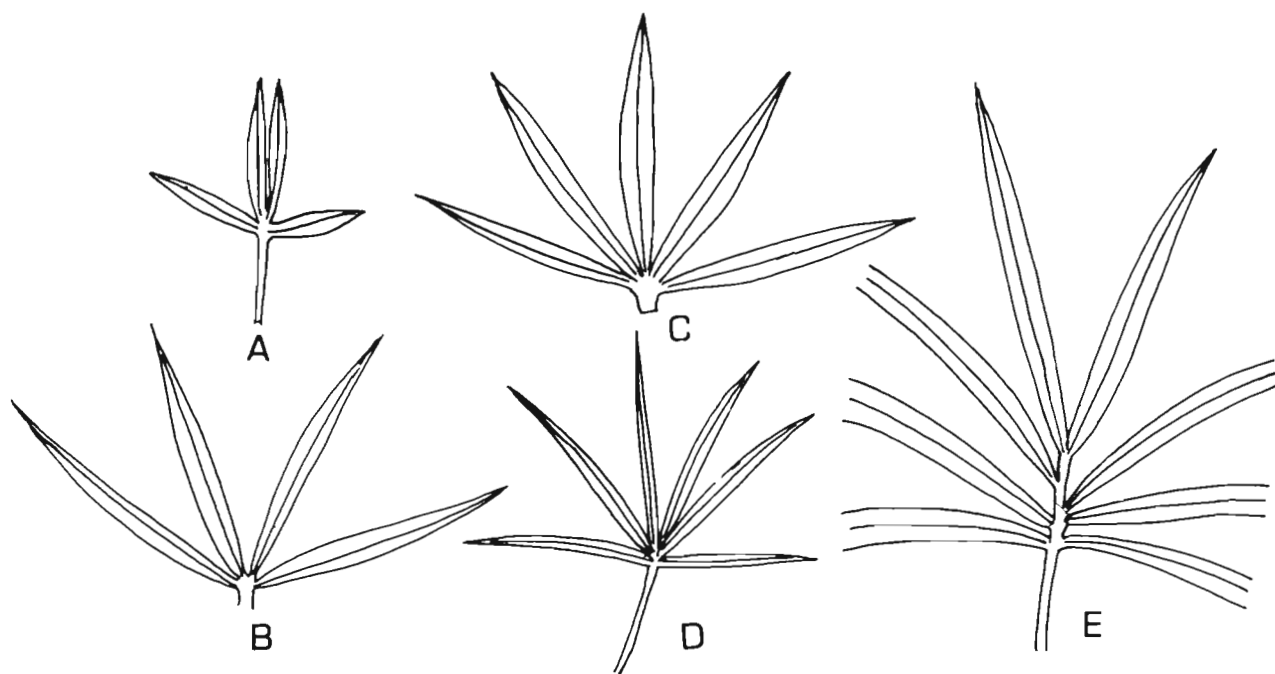


Figure 2—A-F. *Cocos nucifera*. **A-C.** Stages in juvenile leaf succession. **A,** A terminally split, 'bifid' leaf. **B,** A juvenile leaf terminal bifid condition, basal fenestrations (openings between major veins) and the separation of one leaf segment as pinna on the right. **C,** A juvenile leaf at transition stage showing terminal bifid lamina and free pinnae at the base. **D-F,** Photographs of rachis showing rachis morphology and laminal disposition (insertion) on the lateral facet of the rachis. **D,** Middle rachis; lateral view, showing insertion of lamina across the rachis. Note the median ridge of adaxial tissue and the adaxial groove between the lateral facet and the median ridge. **E,** Terminal part of rachis, ventral view, note the adaxial ridge narrowed down to a knife-edge. **F,** Close view of rachis showing inverted V-shaped insertions of the pinnae on the lateral facet. Before the elongation of the rachis the adjacent pinnae are continuous, being parts of a plicately inserted lamina.

basipetally and the median ones fuse at the base to form an incipient rachis. The rachis increases in length resulting in a pinnate leaf. This developmental sequence illustrates a second method of deriving the pinnate leaf from a palmate ancestor.

The examples cited above indicate the possibility of two different routes of evolution of the pinnate leaf form. The palmate ancestors may be primitive compared to the pinnate derivatives. The costapalmate condition could be an intermediate form in the evolution of the pinnate type. It is most



Text-figure 1A-E—*Calamus rotang*. Juvenile and transition leaf forms. **A**, A three-lobed juvenile leaf with the terminal segments splitting. All segments arise at the tip of the petiole; **B**, A 4-lobed juvenile leaf; a palmately 'compound' condition; **C**, A 5-lobed juvenile leaf; **D**, A 6-lobed juvenile leaf. Note the short 'rachis' formed in the centre; **E**, A transition leaf with a short rachis formed by fusion of leaflet bases. There are 8 lobes. The series illustrates the development of a pinnate condition from the palmate condition by the gradual inception of the rachis (all figs. $\times 2.5$).

probable that costapalmate types developed from palmate ancestors. The decomposed leaves of *Caryota* represents a separate line of specialisation within the pinnate forms. The developmental evidence (Periasamy, 1966) definitely indicates that the pinnae of *Caryota* undergo one additional plication resulting in decomposed condition.

MORPHOLOGY OF THE HASTULA

The shape and size of the hastula varies in different kinds of palmate leaves. In *Pritchardia* (Figure 1D) the hastula grows adnate to the rachis. Lamina-like extensions cover the plication bases on both sides of the leaf. The extensions have vascular bundles and green tissues simulating a lamina. These characters suggest that the hastula could be a remanant of the ventral lobes of an ancestral peltate lamina (Padmanabhan & Ilangovan, 1992). According to Eames (1953) the hastula is an excrescence of the rachis. If this view is adopted, the sharp edges of the adaxial elevation on the rachis of *Cocos* leaf could be homologous with the hastula. However, further developmental studies are needed for a better understanding of these features.

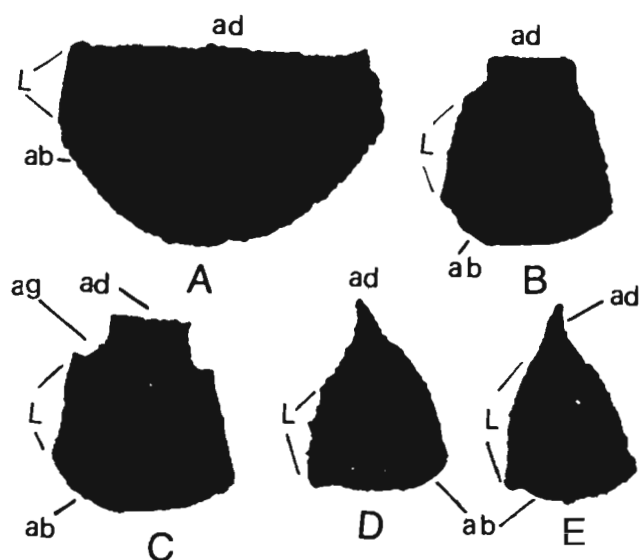
RACHIS MORPHOLOGY

Pinnate and costapalmate leaves have rachises

with special morphological features. In the leaf of the coconut palm, the rachis has a rounded abaxial surface, a flat adaxial surface and flat lateral facets (between adaxial and abaxial surfaces) on which the lamina is inserted in a plicate manner (Padmanabhan, 1984). Current studies on plication initiation have not revealed how a lamina that originates in a normal linear fashion becomes plicately inserted on the lateral facet of the rachis. The lateral facets develop concurrently with the laminal plications and at any given point the width of the facet equals the width of the laminal segments. In coconut leaves, the growing adaxial tissue forms a plateau above the lateral facet (Text-figure 2 A-E). This plateau narrows apically and forms a sharp-edged ridge. Cross sections through this region of the rachis have a vertebra-like outline (Text-figure 2 D, E). The margin of this elevated ridge overhangs the laminal insertion and forms an adaxial groove (Text-figure 2C) as mentioned by Periasamy (1962).

THE REINS AND HOOK

Even though early workers of the nineteenth century recognised the curious 'reins' hanging like ribbons on both sides of the lamina soon after the unfolding of the leaf, there was no discussion on the



Text-figure 2A-E—*Cocos nucifera*. Cross sectional impressions taken at representative levels of the rachis of an adult leaf 5 m long. The rachis was first cleared of pinnae and cut transversely at different levels with a hacksaw. The cut surface was smeared fully with black ink and the impression taken on an absorbent paper. **A.** Cross sectional impression at the lowermost levels near the petiole. Note the broad, flat adaxial surface and the rounded abaxial surface. The lateral surface is narrow. **B.** Impression at middle region of rachis. Note reduced adaxial and abaxial surfaces and the prominent lateral surface. **C.** Adaxial groove clearly marked at higher levels. **D, E.** Impressions towards terminal region. Adaxial surface reduced to a 'knife edge'. Lateral facet very prominent (**ad**—adaxial surface; **ab**—abaxial surface; **L**—lateral surface; **ag**—adaxial groove—all figs $\times 1$).

status of these structures so characteristic of palms. In some species the reins end in a terminal 'hook'. Eames (1953) illustrated the 'reins and hook' and described them to some extent. However, the subject was totally neglected by subsequent workers.

A recent study of the reins and hook in *Chrysalidocarpus lutescens* (Padmanabhan, 1992) provides more information on these structures. In this species, the terminal part of the reins is fleshy, swollen and yellowish-green in colour. It is fused with the precursor tip (vorlauferspitze) and forms the hook. In the sword leaf, the hook and the associated fleshy part of the rein appear flattened in the shape of a scalpel. This kind of scalpelliform tip is found in other palm species also. Eames (1953) has illustrated this kind of reins and hook in his paper. When the sword leaf unfolds, the pinnae are detached from the hook and reins. The detached hook (Text-figure 2C) shows the scars left by abscised tips of pinnae.

Eames (1953) did not comment on the evolutionary status of the hook even though he defined the characters of primitive reins. According

to his account, the primitive rein is broad, green and persistent throughout the life of the leaf as in *Dictyospermum album* var. *aureus* (see photograph in Eames, 1953). The thin, brown or translucent and ephemeral reins of palmate and costapalmate leaves were considered to be advanced. However, such reins may be found in 'primitive' pinnate leaves, e.g., *Chrysalidocarpus lutescens*. At present, we have very little information on the nature of reins and hook in different groups of palms and it is premature to speculate on their evolutionary significance.

THE HAUT

Early workers discovered the curious whitish tissue covering the young leaves of *Phoenix*. This was known by various names: haut, coiffe, pellicule, etc. It was later found that the haut covers only the adaxial side of the leaf and does not wrap around. More recent workers identified the haut as a part of the lamina. The haut is shed as the leaf unfolds. A large number of vascular bundles supplying the haut are also shed along with it. The tissues hang from the unfolding lamina like white shreds of tissue paper. Periasamy (1966) interpreted the haut as a product of fusion of adaxial ridges of the young leaf primordium. Current studies by the writer indicate that the haut is an extension of the marginal tissues called 'reins' by Eames (1953). In *Phoenix*, the marginal uniplicate lamina grows in an obliquely sliding fashion against the submarginal plicating part of the lamina resulting in what is called as haut. The short adaxial ridges remain free and hidden in the adaxial groove. Haut-like tissues are found in the unfolding leaves of *Arenga wightii* (Regupathy, 1980). In this species the leaflets are induplicate as in *Phoenix*. The adaxial ridges are abscised off and the marginal tissues form haut-like structures. The shedding of the haut and the marginal tissues of the lamina indicates a trend towards the specialisation of the submarginal plicate lamina as the sole photosynthetic area of the leaf.

INDUPLICATE AND REDUPLICATE LEAVES

In pinnately compound leaves the leaflets may originate by cleaving at either the adaxial or abaxial fold of the lamina. If cleaving occurs along the adaxial fold the pinnae have a V-shaped insertion on the rachis. This kind of leaflet is described as 'induplicate'. In the other type, the pinnae are inserted in an inverted V-shaped fashion and they are described as 'reduplicate'. The reduplicate condition may be considered as more advanced than the induplicate one. In the palmate leaves of

Borassus the plicate lamina cleaves only up to the middle from the margin. The cleaved portions look like induplicate leaflets. In *Caryota* the plications are 'erased' by growth (Periasamy, 1966) and the leaflets may be neither induplicate nor reduplicate.

LEAF SIZE

Even though all palms are considered as giant herbs, the amount of primary thickening that occurs in the plant body leads to very significant variations in leaf size. Giant forms like *Corypha* and *Caryota* take many years to grow and their leaves are among the largest and the heaviest in the Plant Kingdom. Leaves as long as 15 m have been recorded in some species of *Caryota*. Dransfield (1979) mentions rattan palms with very small leaves, probably the smallest among the palms. Very slow dispersal and diversification of the giant-leaved palms probably account for their rarity. In the state of Tamil Nadu, the huge trees of *Corypha* are preserved as holy trees in small village temples. The plastochronic development of the giant leaves of *Caryota* and *Corypha* is worth studying. Giant leaves and monocarpic habit appear to be associated in the species of *Corypha*. It may be recalled that the palmyra palm, *Borassus flabellifer*, with moderate leaf size, faster growth and polycarpic nature has spread wider and faster than the monocarpic *Corypha*. Fossil evidence may not support the thesis that giant leaves are primitive. However, they are not conducive to rapid evolution and spreading of the species.

CONCLUSIONS

Our present knowledge of leaf variations within the Arecaceae (the palm family), a large and diversified group of monocots, is too meagre to warrant a final decision on the lines of evolution of leaf forms in this family. Whatever beginnings have been made by Eames (1953) would, no doubt, stimulate further research. At present, leaf succession studies in young palms and seedlings point to the possibility of the palmate forms having evolved from peltate prototypes. The pinnate leaves appear to have been derived from palmate ancestors via the costapalmate forms by the inception of

rachis. However, we need to gather much more information on the range of variations in different groups of palms before a comprehensive picture of the evolution of leaf forms among palms could be drawn.

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