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## ON CERTAIN ASPECTS OF THE DEVELOPMENT OF THE LEAF OF *COCOS NUCIFERA* L.

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### Introduction

The development of the palm leaf has been drawing the attention of several eminent botanists for the last one hundred years. However, there is no unanimity of opinion on the origin and formation of the characteristic plications of the palm leaf. The coconut tree (*Cocos nucifera* L.) is a common feather palm in South India. No detailed study of its leaf development has been made so far. The present paper which deals with some aspects of the development of the leaf in the coconut palm was started at the Agricultural College and Research Institute, Coimbatore, in 1934 and continued at the Coconut Research Stations, Kasargod and Nileshwar, South India.

### Materials and Methods

The material was obtained from well developed coconut palms of about 25 years old. The growing points and the leaves of various stages were fixed in formalin-acetic-alcohol. These were dehydrated in the customary manner and finally imbedded in paraffin. Microtome sections were cut at 12 to 15 $\mu$  and stained with Delafields haematoxylin. Growing points of still older trees and of seedlings two to three years old were also examined. In addition, growing points of *Phoenix farinifera*, *P. sylvestris*, *Elaeis guineensis* (feather palms) and *Borassus flabellifer* (fan palm) were also examined for comparison.

### Observations

**EXTERNAL MORPHOLOGY** — The leaves in the crown of the coconut palm can be broadly grouped into (i) the unopened leaves in the bud (cabbage), and (ii) the

fully opened leaves. In the centre of the crown is an erect sword-leaf (Fig. 1), consisting of several leaflets tapering towards the tip. The leaf is of the feather type and attains an overall length of 17 to 20 ft. when fully developed. It consists of (a) a leaf base claspings the stem, (b) a stalk, four to five feet long, and (c) the 'Leaf-limb' with a central rachis bearing on either side numerous narrow leaflets each about five feet long. Each leaflet consists of a strong midrib with half of lamina on each side. The middle leaflets are longer, and the end ones are shorter.

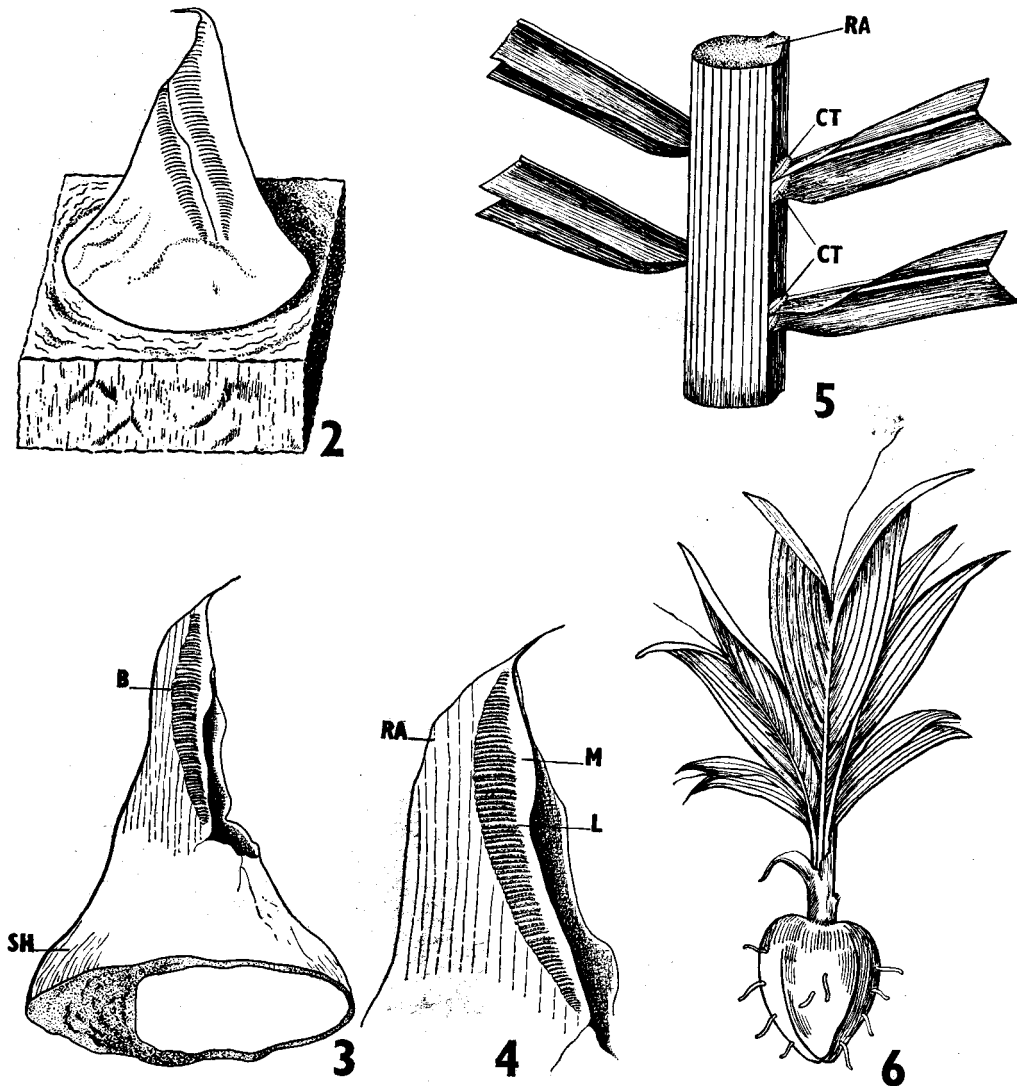


FIG. 1. Crown of a young palm with the sword leaf in the centre.

Usually, one leaf is formed in a month, and similarly a leaf is shed about the same period.

**DEVELOPMENT OF THE LEAFLET**—A longitudinal section of the growing point shows the stem apex consisting of actively dividing cells. Below the apex are leaf primordia in various stages of develop-

ment. They arise as small knob-like lateral protrusions (Figs. 8, 14) which extend laterally around the growing point in the form of an inverted cone (Figs. 2, 3, 8). About seven months after the leaf primordium becomes distinguishable, the tip of the inverted cone begins to develop into the blade and the basal portion



FIGS. 2-6.— (*B*, leaf blade; *CT*, cushion of tissue; *L*, developing leaflets; *M*, margin of the blade; *RA*, rachis; *SH*, sheath). Fig. 2. Growing point with the inverted cone-shaped young leaf.  $\times 3$ . Fig. 3. Single cone-shaped leaf with sheath and blade.  $\times 4$ . Fig. 4. Blade enlarged.  $\times 8$ . Fig. 5. A part of the dorsal view of the leaf showing the cushion of tissue. Fig. 6. A seedling with simple leaves and terminal whip.



FIG. 7. (*L*, leaflets; *R*, rein; *T*, terminal whip; *UL*, united leaflets). Upper portion of the leaf with marginal rein and whip-like terminal structure, and a few leaflets not separated.

remains as the sheath encircling the growing point. The blade further differentiates into a thick middle region, the rachis, and the two sides. The leaf blade at this stage consists of actively dividing cells full of deeply staining contents, excepting the extreme margin of the blade which remains as a distinct layer (Figs. 2-4).

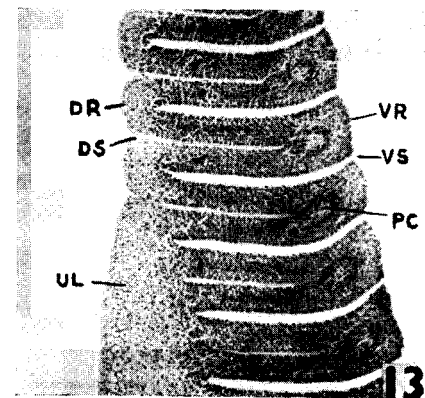
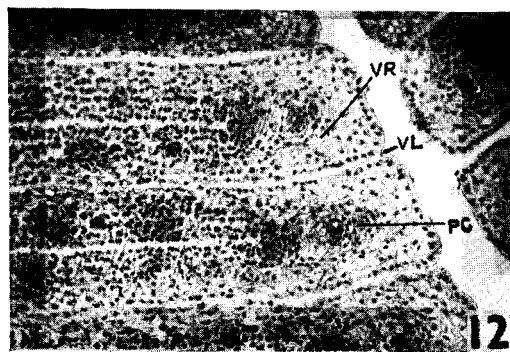
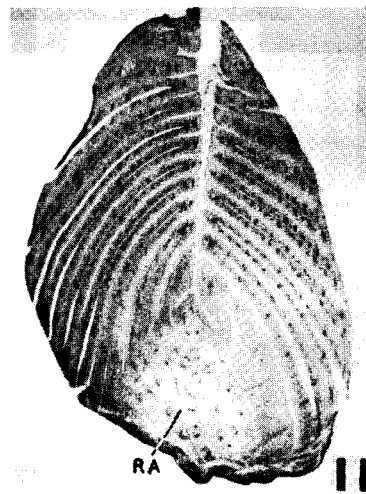
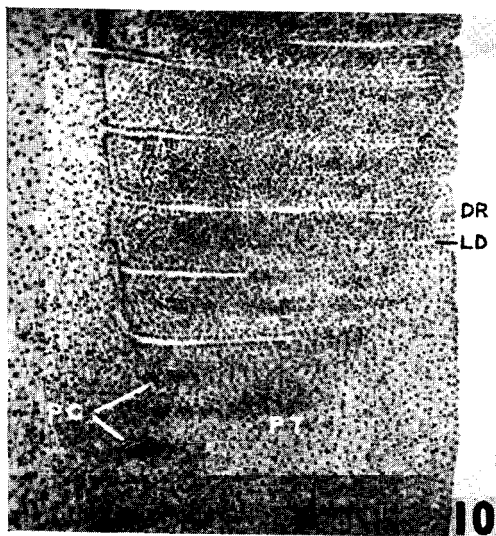
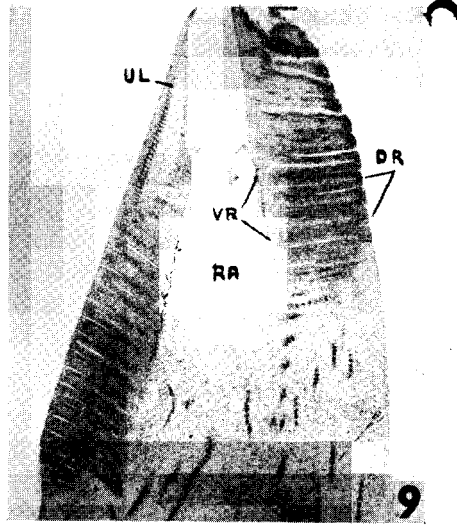
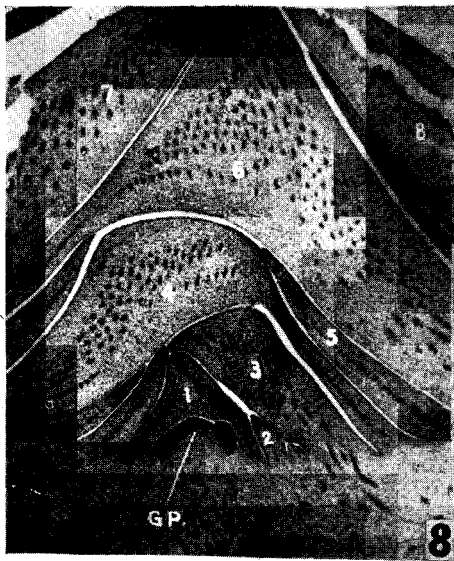
In the early stages the rudimentary blade exhibits, on both the surfaces, shallow furrows and ridges formed by differential growth. The furrows of one side are opposite the ridges on the other side (Figs. 9-11). The leaflets are formed by schizogenous splitting (Figs. 15, 16, 17). Even before the commencement of the actual splitting the line along which the splitting is to occur is discernible. The splits may occur anywhere in the line

and extend on either side (Figs. 10, 12, 15). The dorsal (abaxial) splits extend up to the ventral (adaxial) ridges in which the initials of the midribs of the leaflets are being laid down. The ventral splits extend up the ventral surface and into the dorsal ridges but not to the very surface. This undivided dorsal ridge or fold connects the two halves of the adjacent leaflets (Fig. 13). Prior to the unfolding of the leaflets, the dorsal folds split up, and the adjacent leaflets are separated completely. It is only at this stage that the leaflets are completely free from one another. Thus, the ventral splits separate the individual pinnae, and the dorsal splits separate the halves of each pinna. The splitting of the dorsal ridge takes place about a year after the commencement of the first splitting of the leaf primordium.

In the seedlings the dorsal folds persist normally without splitting; therefore, the leaf blade remains simple (Fig. 6). This non-splitting occurs towards the tips of the leaves of young palms also (Fig. 7).

When the development of the leaflets is completed, they remain in an appressed or folded condition. The leaflets which in very early stages were transverse to the rachis become almost parallel to it presumably owing to the development of the leaf under pressure exerted by the surrounding outer leaf bases. Thus the leaf emerges out like a stick or sword (Fig. 1) from the centre of the crown, and thereafter the leaf begins to unfold its leaflets.

The leaflet first separates itself from the rachis, and then the two halves of the blade unfold. The separation of the leaflets is brought about by a cushion of tissue situated at the base of the leaflet and in the upper angle made by each of the two halves of the leaflet with the rachis (Fig. 5). This tissue consists of a group of large, elongated hypodermal cells (Figs. 18, 19). These are arranged along the base of the leaflet. At the time of unfolding, these cells enlarge and as a result the leaflet is pushed away from the rachis. The two halves of the blade unfold by means of a tissue of motor-like cells situated in the inner angle made by the two halves of the blade with the midrib. This tissue extends throughout the length of the midrib. The portion of the blade



FIGS. 8-13.

which is nearer to the midrib is thinner and much constricted (Fig. 20). The epidermal and hypodermal cells enlarge, the two halves of the leaflets move apart along the constricted region which acts like a hinge. In a fully opened leaflet the enlarged hypodermal cells look like the motor cells of grass leaves, become lignified, and apparently prevent the folding back of the leaflets (Fig. 21).

On the dorsal side of the leaf, the margins of the leaflets are folded one over the other. The unfolding of these is effected about the same time by a similar mechanism of motor-like cells in the grooves of the dorsal folds (Figs. 22, 23).

The formation of leaflets in palms like *Phoenix farinifera*, *Phoenix sylvestris*, *Elaeis guineensis* and *Borassus flabellifer* was also found to be mainly by splitting. The mechanism of unfolding of leaflets in these palms is also similar to that of the coconut palm.

**THE TERMINAL STRUCTURE** — From the tip of the rachis there extends a free thin whip or chord-like structure, pale yellow in colour about a foot in length (Fig. 7). It is flattened at the base, but more cylindrical towards the tip and slightly furrowed on the ventral side. The tip is swollen and bearded with groups of long branched multicellular hairs containing tannin. This structure is a continuation of the rachis; as such it cannot be considered as separate secondary organ, a view which agrees with the findings of Arber (1922). As the leaf grows, the whip-like structure soon dries up and drops off.

**THE MARGINAL STRUCTURE** — Along the margins of the blade there is a thread-like pale yellow structure connecting the tips of all the leaflets (Fig. 7), which is either flat or somewhat cylindrical. This struc-

ture is the undifferentiated margin of the blade into which the splits do not extend and which has been referred to by Eames (1954) as rein. The two marginal reins meet at the dilated tip of the whip already mentioned above, which is named by Eames (1954) as the hook. The rein persists for some time as a narrow strip connecting the leaflets. As the leaf advances in age the structure dries up and drops off completely freeing the tips of leaflets. Arber (1922) has not mentioned this structure while discussing the morphology of the palm leaves.

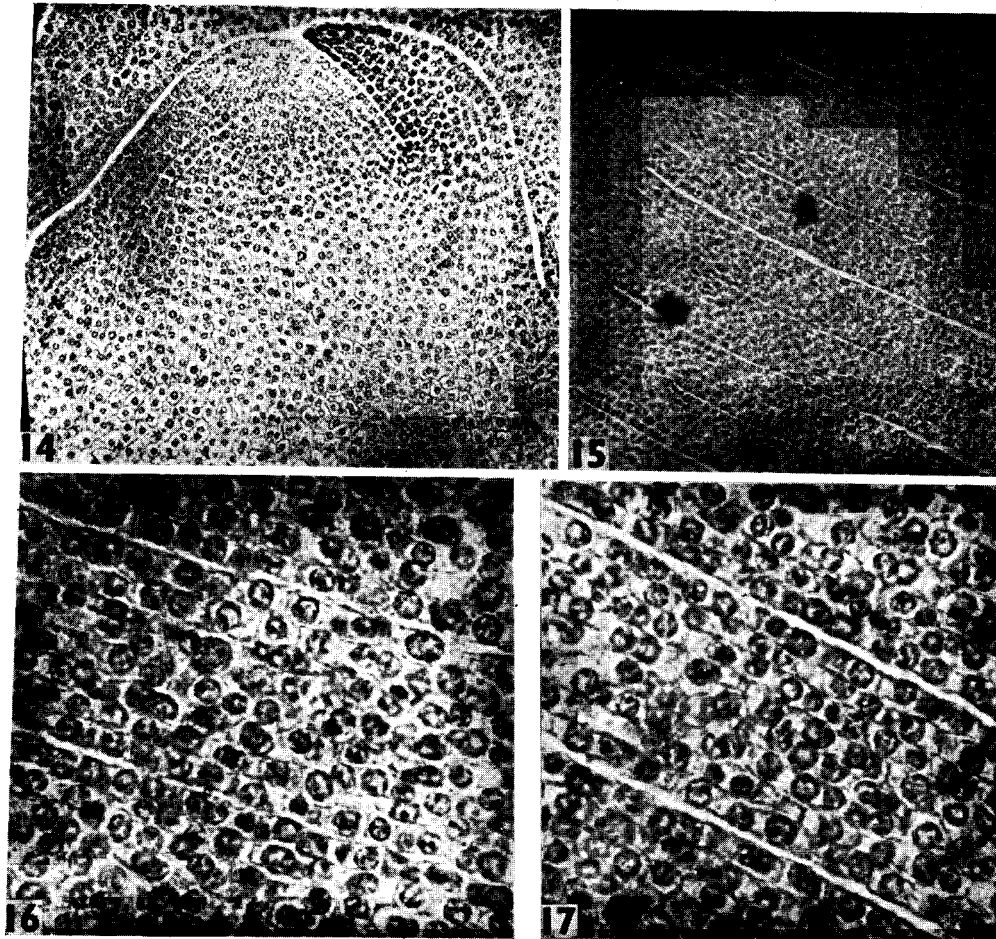
**THE "MEMBRANE" OR "COIFFE"** — The sword leaf in the centre of the crown is covered by a tomentum which is designated by some of the earlier workers as the "membrane" or "Coiffe". The "Coiffe" develops from the epidermis of the leaf, four months before its unfolding and is not really a continuous membrane but consists of isolated groups of three to six multicellular trichomes developed from the epidermal cells. The terminal cells of the trichomes develop rapidly into long radiating branched thin walled cells which overlap each other giving rise to a thick tomentum covering the exposed surface of the sword leaf. The tender and unexposed parts of the leaf are practically free from the hairs. The basal cells of the hairs contain tannin which imparts a brown colour. As the leaflets spread out the tomentum is shed. In *Phoenix farinifera*, *P. sylvestris* and *Borassus flabellifer*, the epidermal hairs are more dense and form a thick tomentum.

### Discussion

The mode of formation of the leaflets in palms has long been a matter of controversy. Some botanists (Karsten, 1847;

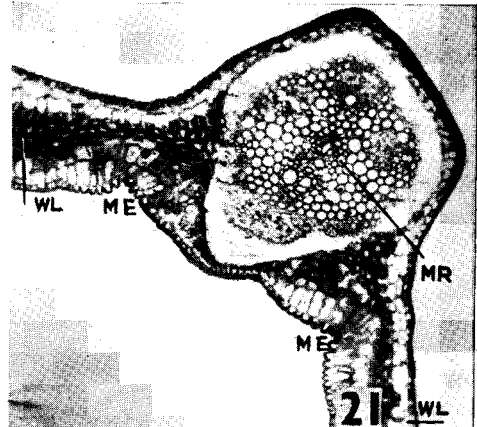
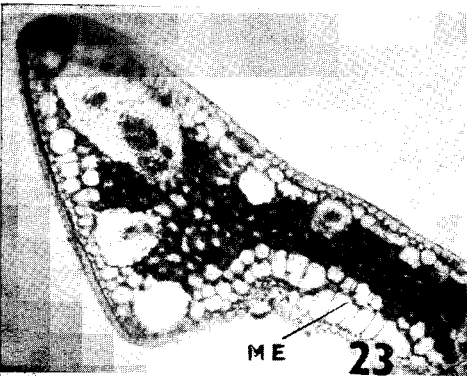
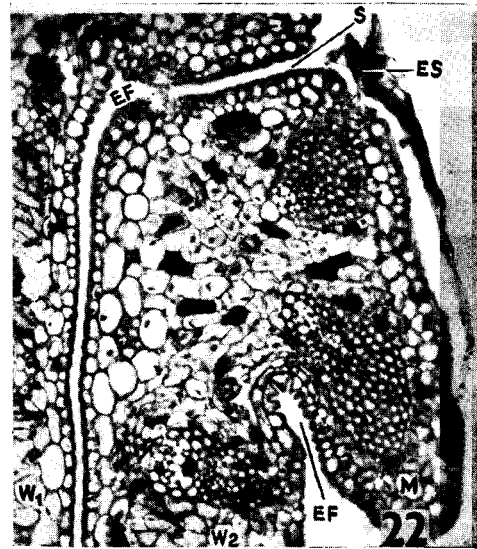
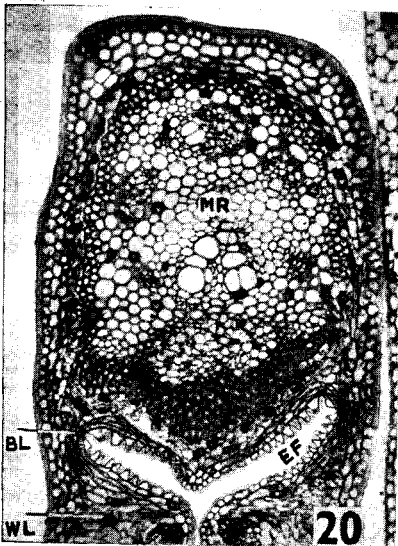
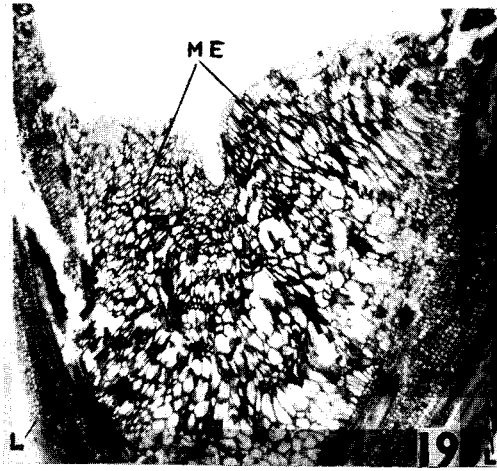
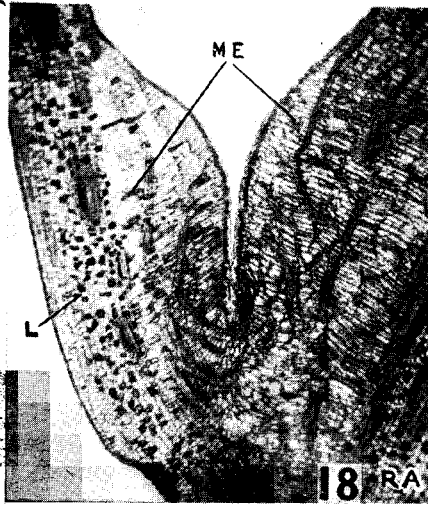
Figs. 8-13 — (DR, dorsal ridge; DS, dorsal furrow; GP, growing point; LD, dorsal split; LV, ventral split; PC, procambial strands of the midrib; PT, primordial tissue differentiating; RA, rachis; UL, undifferentiated margin of the blade; VL, line through which ventral splits occur; VR, ventral ridge; VS, ventral furrow.) Fig. 8. Median longitudinal section of the stem apex of 25 years old palm. 1, fully developed cone shaped leaf; 2-8, leaves in different stages of development. × 22. Fig. 9. L.s. of the blade showing ridges and furrows. × 24. Fig. 10. L.s. of a portion of the blade magnified showing furrows and ridges. × 97. Figs. 11, 12. T.s. of the blade showing lines along which splits occur. Fig. 11. × 15; Fig. 12. × 105. Fig. 13. L.s. of the blade showing ridges and furrows. × 65.

Deinaga, 1898; Eichler, 1885; Goebel, 1883, 1884, 1926; Hirmer, 1919) held the view that the plications of the palm leaf were formed by folding; while others (Von Yampolsky, 1922) maintained that splitting was involved. Arber (1922) was of the opinion "that the plications originate



FIGS. 14-17 — Fig. 14. Median longitudinal section of the stem apex with leaf primordia.  $\times 148$ . Fig. 15. Formation of splits during the development of leaflets.  $\times 148$ . Fig. 16. Magnified view of a portion of Fig. 15 showing the commencement of the split.  $\times 640$ . Fig. 17. Magnified view showing completion of splits.  $\times 640$ .

FIGS. 18-23 — (*BL*, constricted portion of the blade with compressed motor-like cells; *EF*, compressed epidermal cells; *ES*, epidermal scales; *L*, leaflets; *M*, dorsal margin of the leaflets; *ME*, expanded motor-like cells; *RA*, rachis; *S*, split separating the dorsal fold; *WL*, half of the blade; *W<sub>1</sub>* and *W<sub>2</sub>*, adjoining blades of the adjacent leaflets.) Figs. 18, 19. L.s. of rachis and leaflet showing cushion of tissue. Fig. 18.  $\times 25$ ; Fig. 19.  $\times 25$ . Fig. 20. T.s. of the unopened leaflet showing the constricted bases of the blade of the leaflet.  $\times 72$ . Fig. 21. T.s. of the opened leaflet.  $\times 73$ . Fig. 22. T.s. of the dorsal fold showing motor-like cells in the groove.  $\times 126$ . Fig. 23. T.s. of the opened dorsal fold of the leaflet.  $\times 94$ .



FIGS. 18-23.

by invaginations or in other words by differential growth in the course of which the outer cell layers develop more rapidly than the inner tissues and consequently become wrinkled or folded in along certain lines", and that splitting was not involved. Arber states that she found it impossible to accept the splitting theory on account of "the arrangement of the vascular elements in the neighbourhood of the grooves". She did not, however, explain exactly how the invaginations are formed and how they penetrated the leaf tissue. Among the genera she studied, the genus *Cocos* is represented by *Cocos ramanzoffiana*. Patel (1938) described certain aspects of leaf development in coconut but has not explained how the leaflets are formed exactly. Eames (1954) explains that the formation of the characteristic plications is partly by differential growth and mainly by splitting.

The observations of the author are in agreement with the view held by Eames. The early furrows and ridges on the lamina of the rudimentary leaf blade are formed by differential growth or invagination as defined by Arber (1922). The subsequent stages of pinnae-formation are by splitting. Arber's statement that the grooves penetrated in between the vascular bundles is unacceptable for the simple reason that splitting precedes the differentiation of the vascular bundles. In fact, the bundles differentiate only some months after the commencement of splitting. The ventral and dorsal ridges are the fore-runners of the midribs and dorsal loops of the leaflets respectively. The invagination hypothesis of Arber implied that the invaginations should necessarily start at the surface and penetrate deep into the tissue displacing or dissolving it. But there is no such evidence whatsoever in any of the material examined by the author at any stage. On the other hand the splitting of the leaf tissue along predetermined lines is found to commence in any part of the line — a fact that lends much support to the splitting theory.

The marginal strip or the rein, the name suggested by Eames (1954), represents morphologically the undifferentiated leaf margin that is not involved in the actual formation of the leaflets. In the coconut

palm the reins are not only seen hanging from the tip of the basal pinnae but may also break at places and hang in bits from the tip of any leaflet. The rein of this palm is of specialized type (as mentioned by Eames) being non-green, delicate and ephemeral.

The terminal whip-like structure in continuation of the rachis represents the undifferentiated leaf apex. In the coconut at the tip of the whip there is a minute dilated structure which falls off very early along with the whip. This dilated structure partly corresponds to the hook mentioned by Eames (1954). But he has not mentioned any structure corresponding to the whip in the coconut.

Regarding the nature of the "Coiffe" two views were expressed. Von Mohl (1845), Trécul (1853) and Naumann (1887) described the membrane as a primary constituent of the leaf and represent the survival of the superficial tissues which were not involved in splitting. The second view as expressed by Deinaga (1898), Hirmer (1919), Eichler (1885) and Arber (1922) is that the membrane is a secondary product and is the result of epidermal proliferations, and it does not penetrate the grooves. The first view implies the existence of superficial cell layers on the leaf-rudiment without the splits extending into them. In other words the splits should be confined within the leaf-tissue without opening on the surface. But the actual observations show that the splits open on the surface thereby indicating that no surface layers are left out without partaking in the actual formation of leaflets. In fact there is no such "membrane" in the coconut enclosing the young unopened leaf. There is only a tomentum on the exposed surface, formed by the proliferation of the epidermal cells. These findings, that it is a secondary product, are in agreement with those of Arber (1922) and others.

The mechanism of the unfolding of leaf has not been described by earlier workers.

### Summary

The mode of formation of the leaflets in the coconut palm has been described. Here the leaflets are formed mainly by splitting.

The splits occur along predetermined lines at a very early stage of the blade long before the vascular bundles are formed.

The unfolding of the leaflets from the rachis is effected mainly by the enlargement of a cushion of tissue located in the inner angle made by the leaflet with the rachis. The halves of the leaflets open out by a row of motor-like cells located along the length of the blade near the midrib and in the grooves of the dorsal folds of the leaflets.

The reins and the terminal whip are the remnants of undifferentiated leaf tissue.

The 'Coiffe' is only a secondary tissue developed from epidermal cells.

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\*Taken from Arber (1922) and Eames (1954).