Formation of Plications in the Pinnate Leaves of Chrysalidocarpus lutescens and the Palmate Leaves of Rhapis excelsa

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For over 100 years plant morphologists have known that the large, dissected leaves of palms exhibit a developmental pathway which is distinctly different from that of the compound leaves of all other flowering plants. In those dicotyledons and monocotyledons having dissected leaf blades, leaflets arise as free lobes on the margin of the primordial leaf. In contrast, leaflet inception in the palms occurs by folding of the submarginal part of the lamina, followed in most groups by the secondary splitting of the blade into individual leaflets. Since this mode of leaflet origin seems to have no counterpart in other flowering plant species and is markedly complex in character, it has received a considerable amount of attention from morphologists in the last century (von Mohl 1845, Hofmeister 1868, Goebel 1884, 1926, Naumann 1887, Deinega 1898) and more recently (Yampolsky 1922, Eames 1953, Venkatanarayana 1957, Periasamy 1962, Padmanabhan 1963, 1967, Corner 1966, Padmanabhan and Veerasamy 1973). Despite the length of time that the problem has been studied and the large number of papers devoted to this subject, controversies on the mechanism of the original folding or plication remain unresolved and misinterpretations persist.

In the past there has been general agreement amongst these investigators on the general pattern of palm leaf morphogenesis. Both pinnately compound and palmately compound leaves first appear as hood-shaped protuberances which encircle the shoot apical meristem. A series of transverse to oblique folds or plications develop near the margins of the primordium (Fig. 1A); these indicate the position of the future leaf blade. A distinctive feature of these plications is that they do not extend to the leaf margin, leaving an unplicate marginal strip of tissue. During the growth of most palm leaves a localized separation of tissue results in the splitting of the lamina into individual leaflets. In some groups of palms the splitting occurs in the ridges nearest the shoot apex (Fig. 1B,C). This is the adaxial side of the leaf and because the leaf bends away from the shoot tip as it expands from the crown, the mature leaflets are trough-shaped in cross section or induplicate. In other groups of palms, the splitting occurs in the ridges farthest from the shoot apex (abaxial ridges); this results in leaflets that are ridge-shaped in cross section or reduplicate (Fig. 1D). In some palms, the location of the zones of separation does not correspond to adjacent ridges so that individual leaflets consist of a number of the original plications (Fig. 1E). The tips of the leaflets also separate from the unplicate marginal strip of tissue which is ephemeral in many groups, but which may form a pair of conspicuous reins attached to the two basal leaflets (Eames 1953).

The source of controversy in the liter-
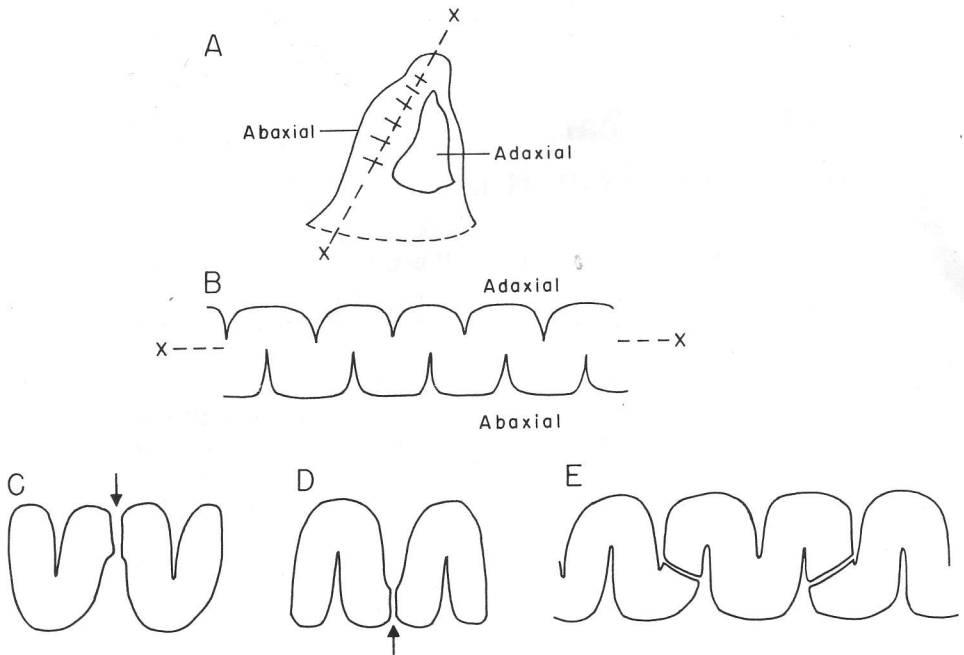
1. Diagrams illustrating an adaxial view of a hood-shaped palm leaf primordium (A) and the appearance of a section (B) made through the submarginal plications in the plane indicated by the line (X—X). Abscission through the adaxial ridges (arrow) will result in induplicate leaflets (C); abscission through the abaxial ridges (arrow) will result in reduplicate leaflets (D); or zones of abscission in the intercostal regions may result in leaflets consisting of more than one plication (E).

ature has been over the mechanism of inception of the original folds or plications in a previously smooth lamina. The point of disagreement is whether tissue separation is involved in the initiation of the plications themselves. For example, Hofmeister (1868), Goebel (1884, 1926), Deinega (1898) and more recently Periasamy (1962) and Corner (1966) conclude that the plications are formed by a process of differential growth followed by a folding of the meristematic lamina as shown in Figure 2A–C. On the other hand, von Mohl (1845), Naumann (1887), Yampolsky (1922), Eames (1953) and Padmanabhan (1963, 1967) argue that the process of pleat formation involves not only differential growth, but also the inter-

nal separation of cells in such a way that internal schizogenous slits break through the epidermal surface on alternate sides of the leaf giving the pleated appearance (Fig. 2A,D,E). At first the differences between these alternatives might appear trivial; however, each involves quite different morphogenetic processes. If tissue separation did occur, internal cells of the ground tissue lining the schizogenous spaces and normally destined to become photosynthetic mesophyll cells would now be on the external surface of the leaf and would differentiate as the protective cells of the epidermis. In contrast, the process of differential growth only involves localized zones of growth to give rise to the adaxial and abaxial ridges of tissue with-

A   Adaxial

Abaxial

B

D

C

E
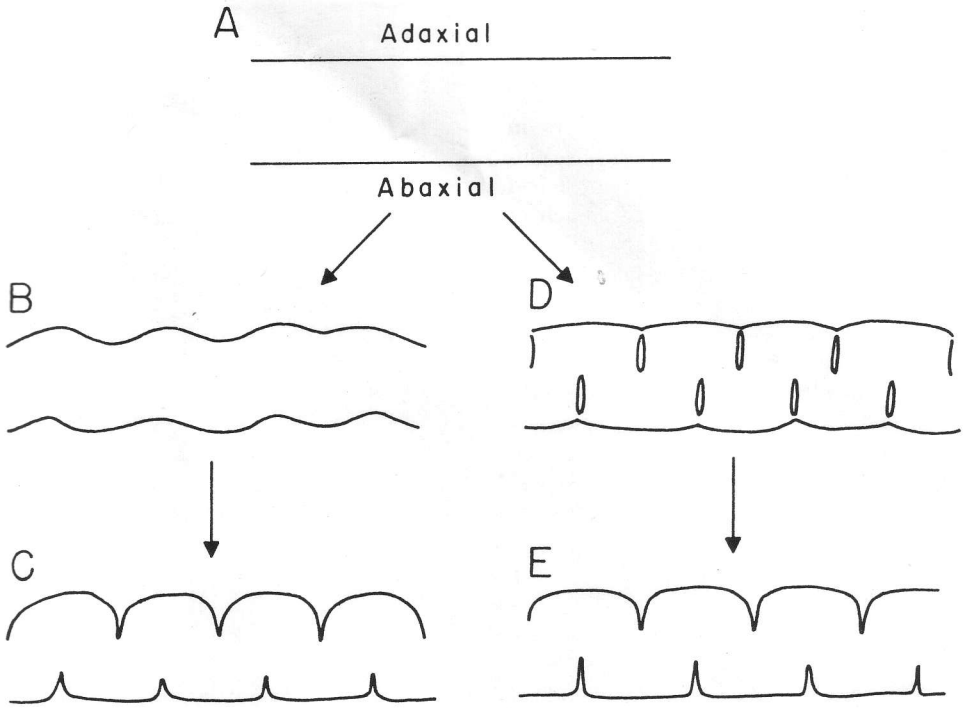
2. Diagrams illustrating the formation of alternating adaxial and abaxial ridges through differential growth (A,B,C) or through the extension of internal schizogenous slits to the surface (A,D,E).

out the complicated redifferentiation of cells.

The purpose of this study is to resolve this long standing controversy over the mechanism of plication inception and, particularly, to test the hypothesis of the schizogenous origin of the plications and subsequent redifferentiation of tissue. Since this mechanism has not been reported to occur in any other flowering plant groups, this would be a further unique feature of palm leaf development that might be of potential significance in evaluating the systematic relationships of palms, particularly with other monocotyledons having plicate leaves.

Species having the two basic types of palm leaf morphology were selected for this investigation: *Chrysalidocarpus* *lutescens* H. A. Wendl. (arecoid major group, Moore 1973) having pinnate reduplicate leaves and *Rhapis excelsa* (Thunb.) Henry (coryphoid major group, Moore 1973) having palmate induplicate leaves. Shoots of both species were collected at Fairchild Tropical Garden, Coral Gables, Florida and were shipped to the University of California, Berkeley. This investigation was carried out in conjunction with Dr. D. R. Kaplan, University of California, Berkeley, and the observations which are summarized below were reported in greater detail in three papers in the *Canadian Journal of Botany* (Kaplan *et al.* 1982a, b, Dengler *et al.* 1982). The specific methods used to study the problem of plication inception are also described in these papers.

Results

Morphogenesis in Chrysalidocarpus lu-
tescens. The mature leaf of *Chrysali-
docarpus* measures about 2 meters in
length and is differentiated into a pin-
nately compound blade, a short petiole and
a smooth, tubular base (Fig. 3). Each of
the approximately 80 leaflets has a single
major vein or rib and is reduplicate. The
leaves are arranged in either a clockwise
or counterclockwise phyllotaxis (Kaplan *et
al.* 1982*a*). The developing leaves are
tightly packed together within the apical
bud and their appearance in scanning
electron micrographs and in sectioned
material viewed in the light microscope
suggest that considerable mutual pressure
is exerted between adjacent leaves (e.g.,
Fig. 6).

Figure 4 shows a young leaf about 0.5
mm in length in which there is no external
indication of plication inception but which
clearly shows the hood-shaped lamina, and
a sheathing leaf base which encircles the
shoot apex and younger leaf primordia.
The upper limit of the sheath of the next
oldest leaf can be determined by the loca-
tion of the constriction near the base of
the leaf lamina (Fig. 4, arrow). Developing
leaves of *Chrysalidocarpus* are charac-
teristically asymmetrical. One margin of
the lamina protrudes through the sheath
of the next oldest leaf; this is the anodic
(+) margin. The other margin is appressed
against the rachis; this is the cathodic (−)
margin. The leaf illustrated in Figure 4 is
from a shoot with counterclockwise phyl-
lotaxis and therefore the right hand mar-
gin as viewed from the adaxial side is
anodic (+). Leaves from shoots with
clockwise phyllotaxis have the anodic (+)
margin on the left.

Plications first appear in leaves 0.6 to
1.0 mm in length as a series of slight
ridges and furrows having a vertical ori-
entation in the distal part of the lamina
(Fig. 5A). Formation of the ridges on the
adaxial side of the leaf is seen to precede
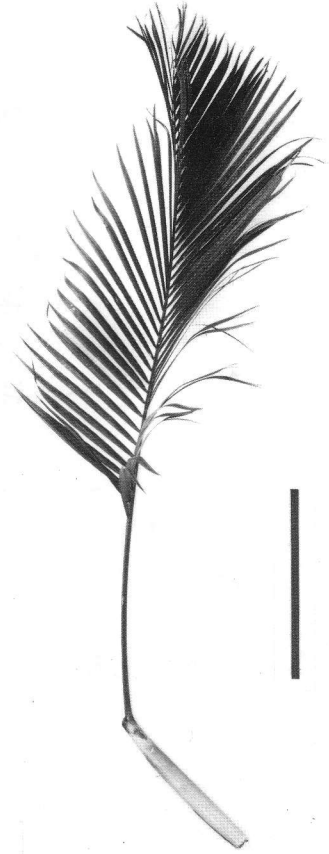
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3. Mature leaf of *Chrysalidocarpus lutescens*
showing the pinnate lamina, petiole and tubular
sheathing base. Scale line equals 50 cm.

ridge formation on the abaxial side of the
anodic margin; the folding of the cathodic
margin against the rachis obscures the
ridges (Fig. 5A,B). As the leaf develops,
the abaxial surface appears flat in surface
view and the furrows between the abaxial
ridges resemble slits incised in the surface
of the lamina (Fig. 6). Plications do not
extend to the margin or apex of the leaf,
leaving an unplicate margin and a hood-
shaped leaf apex (Fig. 6). While the first
formed apical plications have a vertical
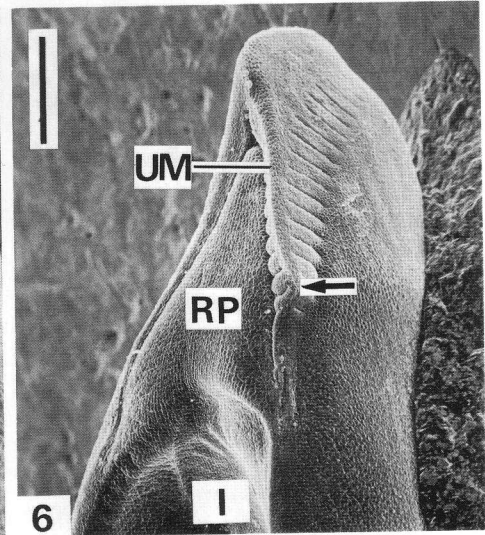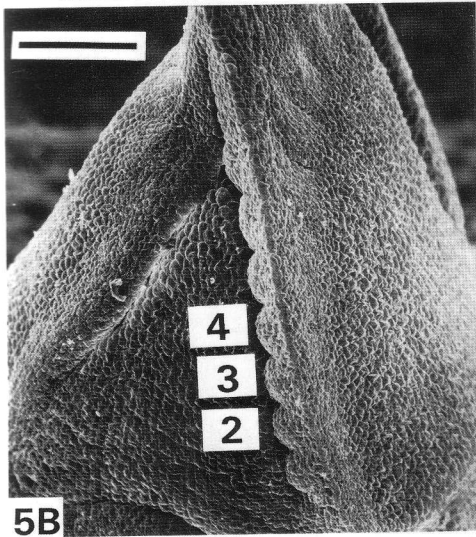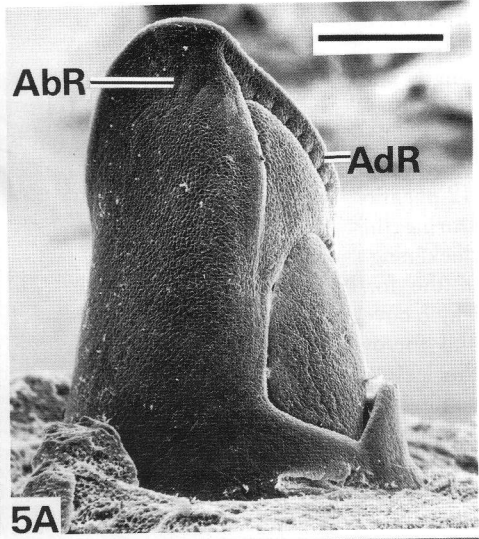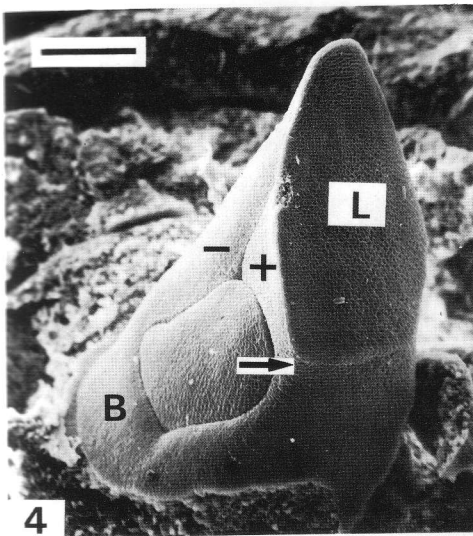
4–6.   Scanning electron micrographs of developing leaves of *Chrysalidocarpus lutescens*. Fig. 4. Leaf primordium 0.5 mm in length. Note the sheathing leaf base (B), hood shaped lamina (L) with anodic (+) and cathodic (−) margins. The arrow indicates the constriction formed by the sheath of the next oldest leaf. Scale line equals 200 μm. Fig. 5A. Leaf primordium about 1 mm in length. Note the vertical orientation of abaxial ridges (AbR) on the cathodic leaf margin and the adaxial ridges (AdR) of the anodic margin. Scale line equals 200 μm. Fig. 5B. The anodic margin of the same leaf as shown in Fig. 5A and with the plications used for histological analysis, 2, 3, 4 above the constriction, labelled. Scale line equals 100 μm. Fig. 6. Leaf 2 mm in length in which new plications are being formed basipetally below the constriction (arrow). Note the unplicate margin (UM), rachis protusion (RP) and impression of younger leaf on adaxial surface of sheath (I). Scale line equals 200 μm.

orientation, later formed plications are oriented in the horizontal plane. Based on length and surface appearance, new plications appear to be added both acropetally and basipetally until the leaf reaches a length of about 5.5 mm with about 40–42 plications on each lamina half (Fig. 7). During the period of plication initiation, thickening growth of the rachis axis results in the formation of a rachis protrusion which covers the base of the adaxial ridges and furrows (Figs. 5A,6). Elongation of the leaf, particularly above the point of confluence of the margins, marked by an arrow in Figure 7, results in a gradual reorientation of the apical plications to the horizontal plane. Later in development, elongating plications come to lie in the vertical plane. This vertical packing of leaflets against the rachis can be seen in a new sword leaf as it emerges from the crown. Prior to emergence, splitting of the blade into leaflets occurs. When the leaf is fully elongated, expansion of the pulvinus at the base of each leaflet causes it to open and bend away from the rachis (Corner 1966).

Histogenesis in Chrysalidocarpus lutescens. Documentation of the early stages of leaf development using scanning electron microscopy allowed us to understand the complex three dimensional relationships of parts of the leaf during the critical stages of plication formation and to orient young leaf primordia for sectioning. Serial sections of the anodic half of the lamina just above the point of constriction (ridges 2, 3, 4 in Fig. 5B) were made from the unplicate margin through the plications to the rachis in a plane perpendicular to the axis of plication extension. These series of sections were analyzed to determine the pattern of cell growth described below; outline drawings of sections from the midregion of the plications only are illustrated in Figures 8–12.

Prior to the formation of plications the lamina of the leaf is five to seven cell layers thick and has a smooth surface (Fig. 8). The appearance of slight ridges on the adaxial side of the lamina is associated with localized areas of periclinal (parallel to the surface) and oblique divisions in middle layers of the lamina in addition to slight cell enlargement in the adaxial protodermal and subprotodermal layers (Fig. 9). Further growth of the adaxial ridges is accompanied by the development of zones of mostly anticlinal (perpendicular to the surface) divisions alternating with the ridges (Fig. 10). This pattern of growth results in an increase in surface area of the portion of the lamina undergoing plication. Since the plicated part of the lamina is bordered by the unplicate leaf margin, the leaf apex, the rachis, and the petiole (Fig. 6), and since the enlargement of these parts of the leaf does not keep pace with the plicate lamina, the comparatively rapid extension of the confined lamina is accommodated by buckling of the lamina between adaxial ridges (Fig. 10). This growth pattern brings about the appearance of abaxial ridges and furrows, and further growth in surface area results in the compression of adjacent ridges on both sides of the leaf, giving the slit-like appearance of the adaxial and abaxial furrows (Fig. 11). The plications deepen in the radial plane by further intercalary growth in the intercostal sector, causing the adaxial and abaxial ridges to be displaced from one another (Fig. 12).

All developmental stages examined in this study lacked any indication of internal slits opening to the surface to form alternating ridges and furrows, although slightly oblique sections taken near the rachis occasionally (and incorrectly) gave the impression of internal schizogenous spaces (Dengler *et al.* 1982). Analysis of serial sections also showed that the protoderm appears as a continuous layer of cells on both the adaxial and abaxial surfaces of the leaf throughout the developmental stages observed. Both of these observations support the alternative of differential
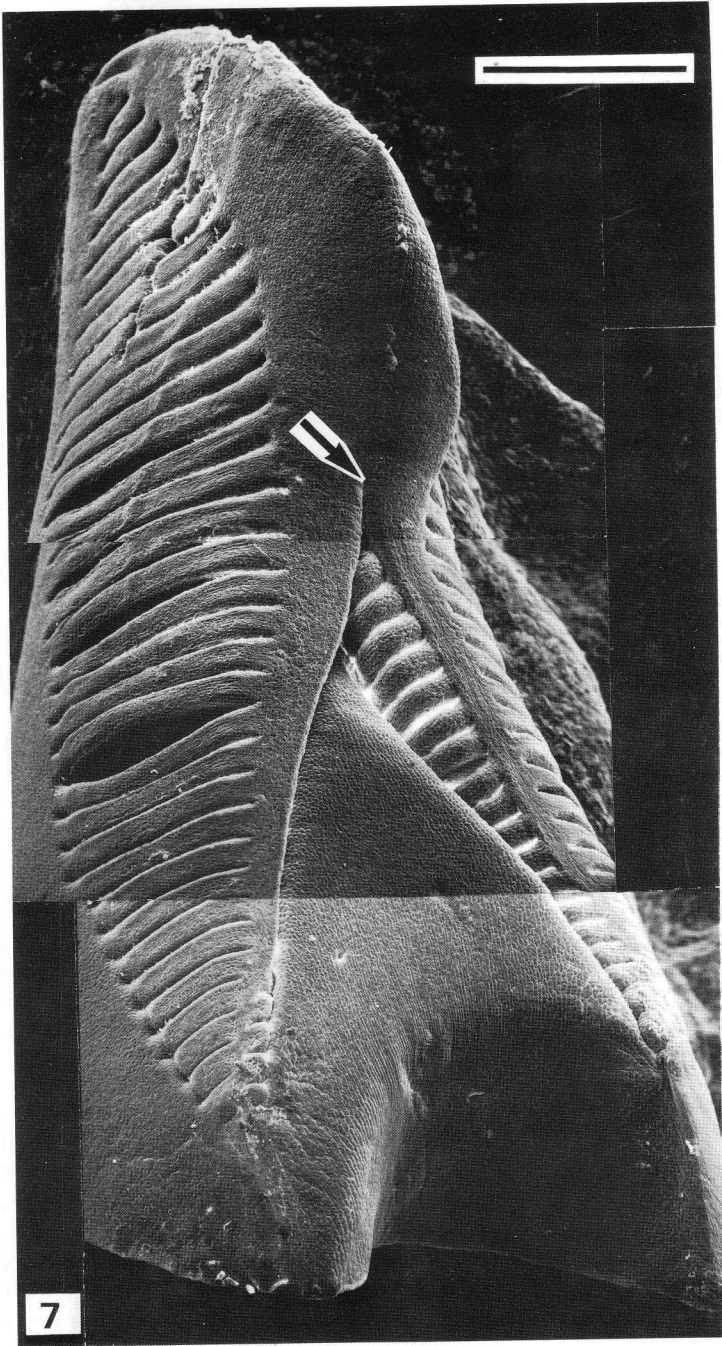
7. Scanning electron micrograph of a leaf of *Chrysalidocarpus lutescens* 7 mm in length. Arrow indicates the point of confluence of the unplicate margins with the hood-like apex. Scale line equals 500 μm.

0.5mm

1.5mm

8

AdR 0.75mm

11

9

2.5mm

AdR 1.0mm

IS

10 **12**
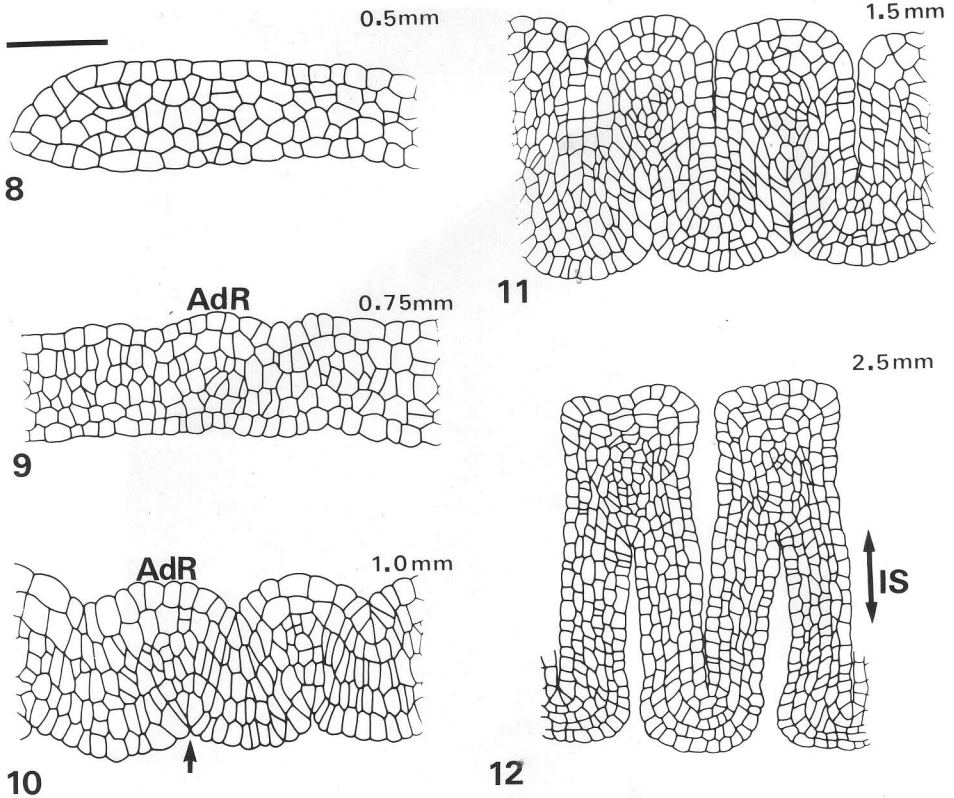
8–12. Outline drawings illustrating the midregion of plications of successively older leaves of *Chrysalidocarpus lutescens*. Sections are oriented with the adaxial surface uppermost. Scale line equals 50 μm. Fig. 8. Section of the unplicate lamina of a leaf 0.5 mm in length taken 50 μm from the margin. Fig. 9. Section of the plicate lamina of a leaf 0.75 mm in length taken 78 μm from the margin. The adaxial ridge of plication 2 above the constriction is labelled. Fig. 10. Section of a plicate lamina of a leaf about 1.0 mm in length taken 64 μm from the margin. The adaxial ridge of plication 2 is labelled. The arrow marks the position of the abaxial furrow of this plication. Fig. 11. Section of plicate lamina from a leaf 1.5 mm in length taken 84 μm from the margin. Fig. 12. Section from the plicate lamina of a leaf 2.5 mm in length taken 182 μm from the margin. Arrow shows direction of growth in intercostal sector (IS).

growth, but it can be argued that the most rigorous test of the mode of plication formation would be an analysis of the number of cell layers across the lamina. If the formation of internal schizogenous slits results in ridge and furrow inception, a decrease in the number of cell layers across the lamina at the locus of the furrows would be expected; conversely, if differential growth alone accounts for plication formation, one would expect only an increase in number of cell layers.

Counts of the number of cell layers were made at the position of the adaxial ridge (abaxial furrow); the abaxial ridge (adaxial furrow) and the intercostal sector in leaves of increasing ages as shown in Figure 13. A decrease in the number of cell layers is not observed at any stage. These comparisons clearly demonstrate a dramatic increase in the number of cell layers (from 5 to 16) in the position of the adaxial ridge (Fig. 13A); many of these cells are associated with the differentiation of the pro-
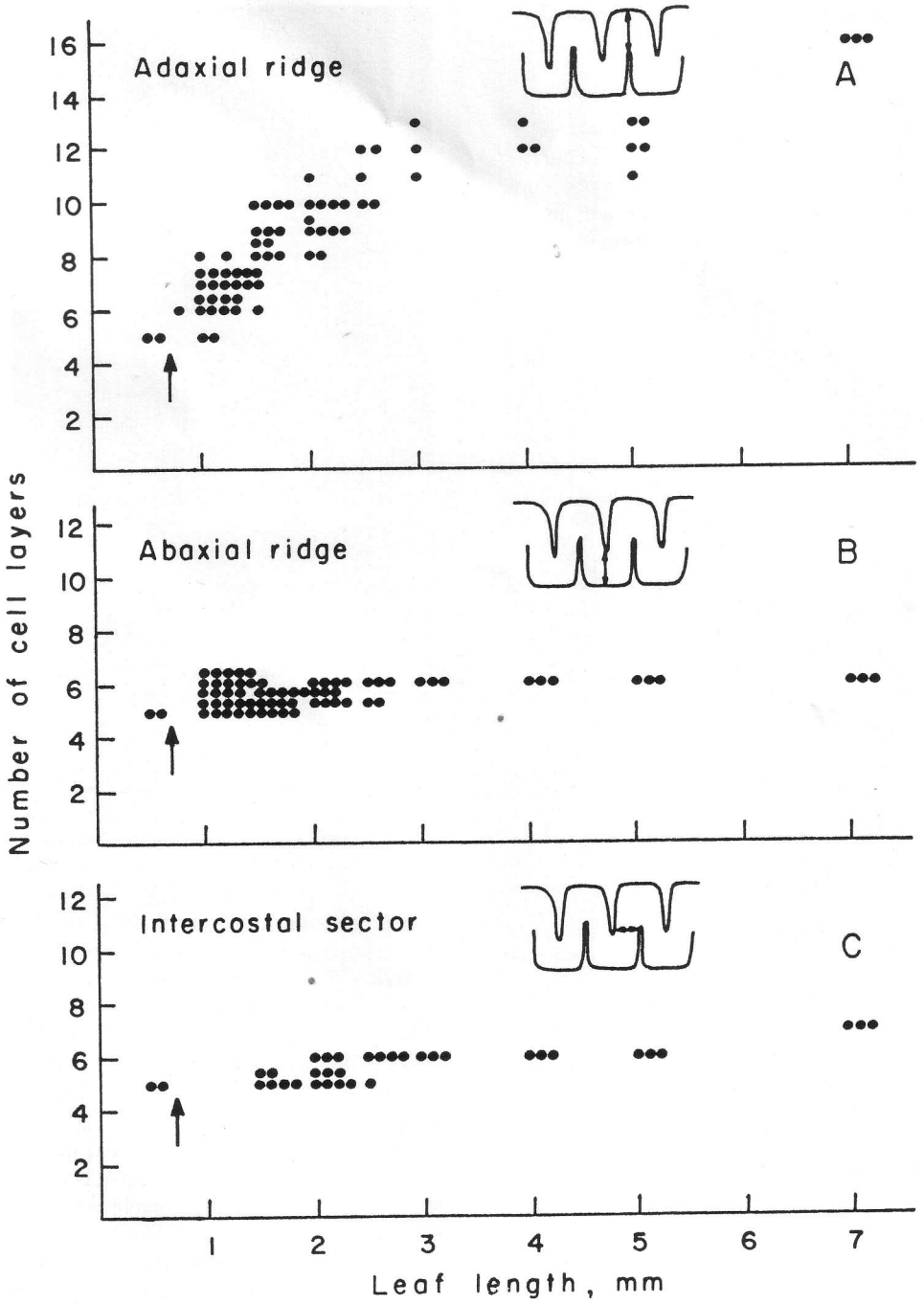
13. Scatter plots illustrating the changes in the number of cell layers in the adaxial ridge (A), abaxial ridge (B) and intercostal section (C) in the leaves of *Chrysalidocarpus lutescens* 0.5 mm to 7.0 mm in length. Arrows indicate the stage of plication inception.

cambial strand of the future leaflet mid-vein. An increase in the number of cell layers also occurs in the abaxial ridge (Fig. 13B) and the intercostal sector (Fig. 13C) although the increase is less dramatic (from 5 to 7 layers). If splitting were occurring during furrow formation and were compensated for by localized growth in the associated ridge so that the number of cell layers was not altered, one would expect to see cell wall patterns in the ridges indicative of this localized compensatory growth. Since this was not observed we conclude that all of our qualitative and quantitative histological observations are consistent with the concept of differential growth—alternating zones of the leaf lamina undergoing different growth rates resulting in plication formation.

Morphogenesis in Rhapis excelsa. The mature foliage leaf of *Rhapis* is about 0.8 meters in length and is differentiated into a palmately compound blade, a long petiole and a fibrous tubular leaf base (Fig. 14). Although the blade is divided into 10 to 12 segments, segment number does not correspond to plication number and each segment has two or more ribs along its length. A pair of small crestlike appendages called hastulae are attached at the junction of the blade and the petiole on the adaxial and abaxial sides of the leaf (Fig. 15). As in *Chrysalidocarpus*, the leaves are arranged in either a clockwise or counterclockwise spiral in the bud which imposes an asymmetry on the tightly packed developing leaf primordia (Kaplan *et al.* 1982b).

Prior to the inception of plications, the young leaf primordium of *Rhapis* consists of a tubular leaf base and a hood-shaped lamina in which an anodic and a cathodic side can be distinguished (Fig. 15). The lamina differs from that of *Chrysalidocarpus* in that the apex is prolonged into a conical protuberance or "Vorläufer-spitze" characteristic of the leaves of a
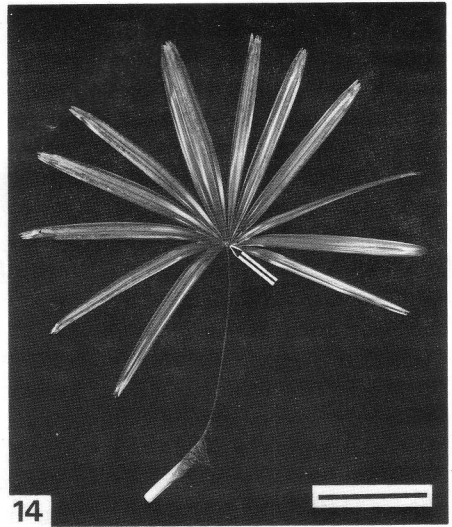
14.   Leaf of *Rhapis excelsa* showing differentiation into a palmate lamina, petiole and tubular sheathing base. Arrow indicates adaxial hastula. Scale line equals 50 cm.

number of monocotyledous species (Kaplan 1973). The concave adaxial surface of the lamina is covered by the adaxial hastula and the convex abaxial side bears the abaxial hastula. Plications are not externally visible on the abaxial side of the lamina until leaves are about 1 mm in length (Fig. 16). The first abaxial ridges appear as subtle mounds on the narrow horizontal ledge of tissue that represents the free margin of the leaf (Fig. 16). The adaxial ridges and furrows are obscured by the adaxial hastula at this stage, although sectioned leaf material reveals that the development of the adaxial ridges is actually advanced over the abaxial ridges (Kaplan *et al.* 1982b). As the leaf expands, the lamina becomes more vertical in orientation and the abaxial ridges become sharply demarcated from each other by slit-like grooves (Fig. 17). The first plications to be initiated are at the apex of the leaf and subsequent plication initiation occurs in a basipetal direction along both the anodic and cathodic margins. The
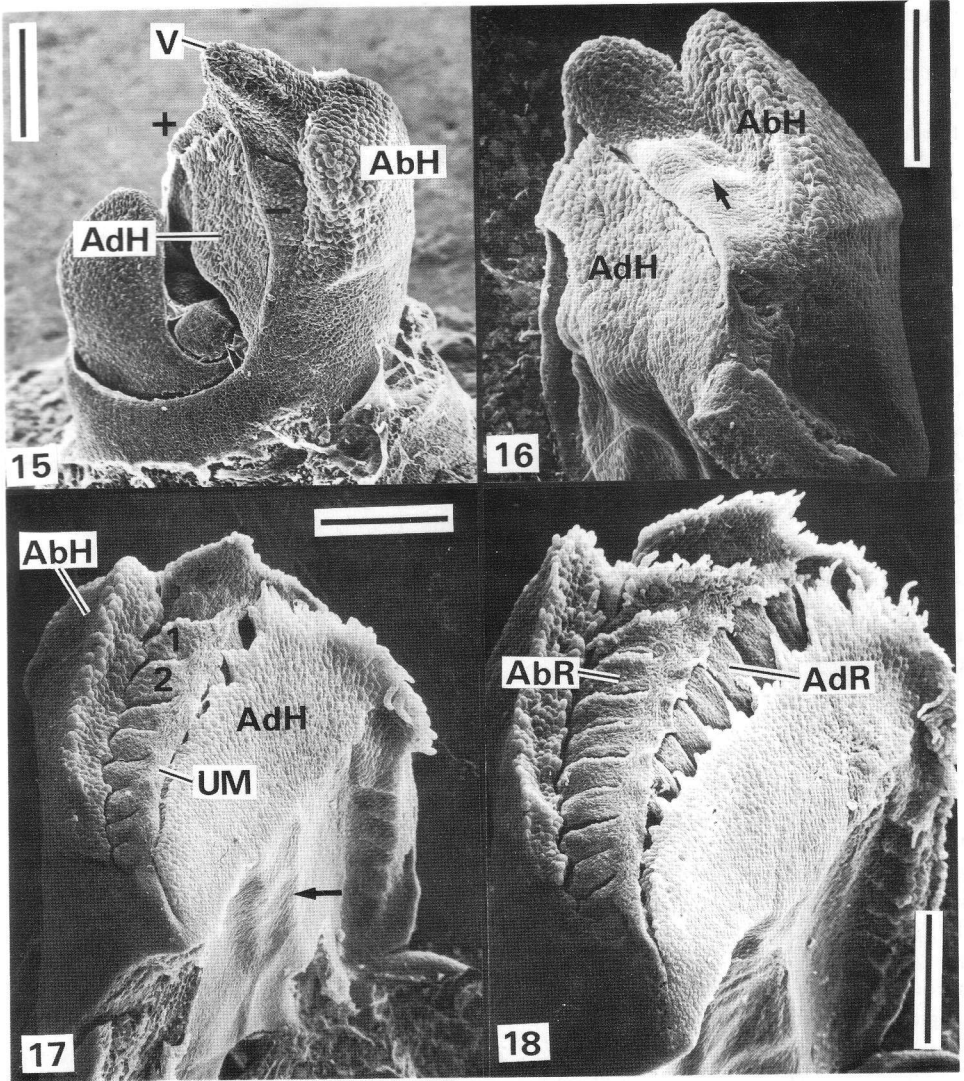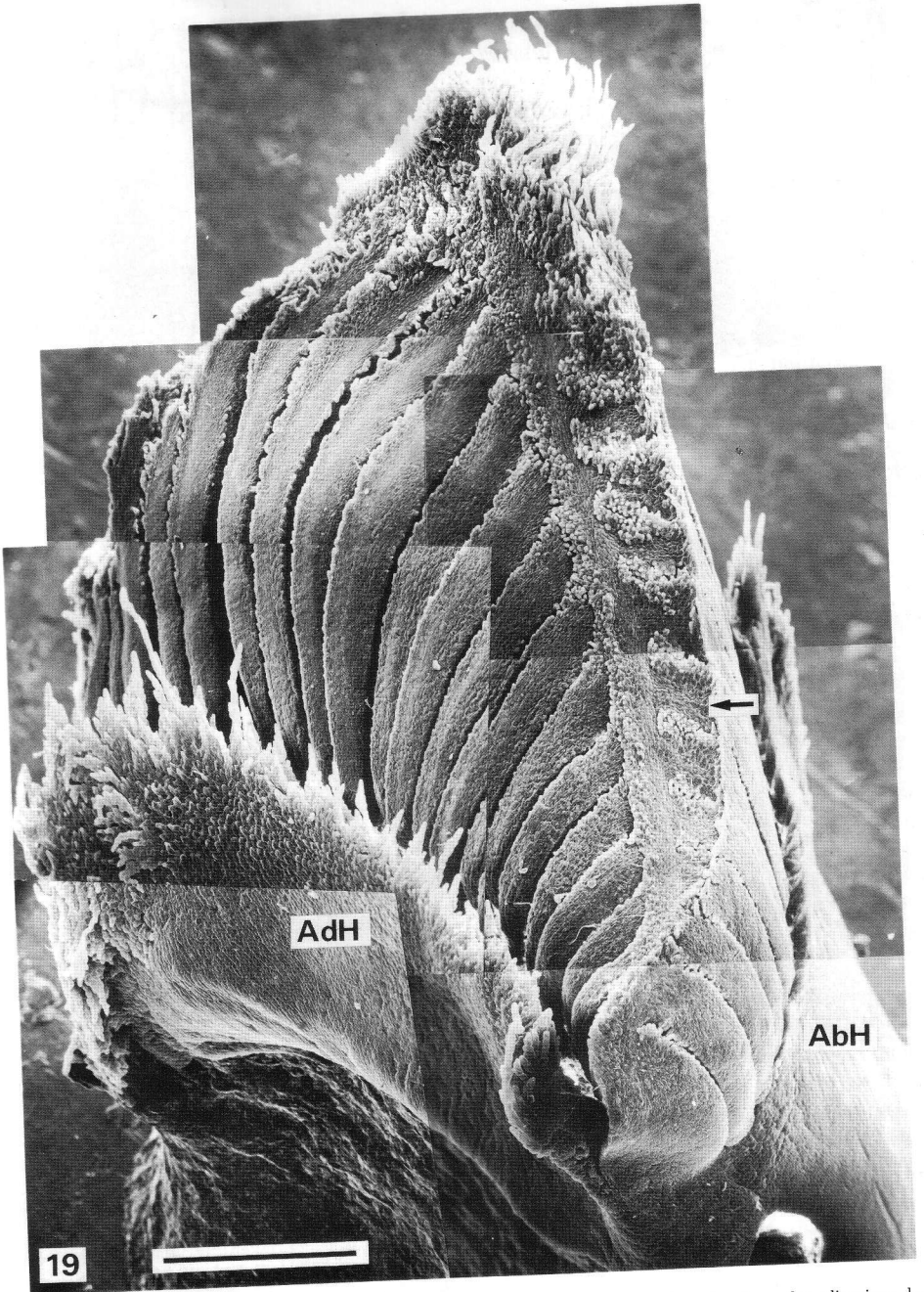
15–18.   Scanning electron micrographs of developing leaves of *Rhapis excelsa*. Fig. 15. Terminal bud showing leaves 150 μm, 400 μm and 650 μm in length. The oldest leaf exhibits an adaxial hastula (AdH), abaxial hastula (AbH), anodic (+) and cathodic (−) margins and a prominent "Vorläuferspitze" (V). Scale line equals 200 μm. Fig. 16. Leaf 1 mm in length. Slight abaxial ridges (arrow) are evident between the leaf margin and the abaxial hastula (AbH). Adaxial ridges are covered by the adaxial hastula (AdH). Scale line equals 200 μm. Fig. 17. Leaf 2 mm in length. Abaxial ridges are numbered. Note unplicate margin (UM), adaxial hastula (AdH) and abaxial hastula (AbH). Arrow indicates impression of next youngest leaf. Scale line equals 500 μm. Fig. 18. Leaf 3 mm in length. Both adaxial ridges (AdR) and abaxial ridges (AbR) are evident. Scale line equals 500 μm.

ridges and furrows of each plication clearly do not extend to the lamina margin and the crescent shaped zone of attachment of the plications to the rachis is obscured by the hastulae.

As the leaf elongates, the adaxial ridges and furrows begin to extend beyond the adaxial hastula margin (Fig. 18). The abaxial hastula elongates along with the lamina; so that while the horizontal part of the plications adjacent to the margin is exposed, the elongate, vertical portion of the abaxial ridges is protected by the hastula. The leaf illustrated in Figure 17 also shows how mutual pressures within the apical bud leave the impression of the next youngest leaf on the adaxial side of the leaf sheath (arrow). The final number of 20–24 plications is reached in leaves that are about 4.5 mm in length. Trichomes develop on the edges of the plication ridges beginning with the unplicate margin and proceeding basipetally; growth of the trichomes and margin eventually obscures the "Vorläuferspitze." Trichomes also develop on the margins of both hastulae in alignment with the plication furrows (Fig. 18). Eventually, expansion of the hastulae does not keep pace with the elongation of the plications so that both adaxial and abaxial ridges are exposed (Fig. 19). In the 6 mm leaf shown in Figure 19 the line of demarcation indicated by an arrow on the abaxial ridges delimits the original horizontal portion of the plication from the more vertically oriented part which was appressed to and covered by the abaxial hastula through much of early development. Separation of the lamina into 10 to 12 segments occurs within the intercostal zone of tissue lying between adjacent adaxial and abaxial ridges as indicated in Figure 1E. Elongation of the leaf and its segments continues until the new leaf emerges from the crown as a sword leaf. As in *Chrysalidocarpus*, expansion of the pulvinar region at the base of each segment brings about the opening of the folded segments.

Histogenesis in Rhapis excelsa. Since the orientation of the developing plications is vertical in the leaves of *Rhapis excelsa*, a histological analysis of plication inception in the leaves was based on cross sections of developing leaves. Also because of the differences in stage of development of plications of one leaf and differences along the length of each individual plication, the histological description given here will be based on cross sections from the midregion of plication 2 (Fig. 17). As in *Chrysalidocarpus*, the anodic margin of the leaf protrudes from the sheath of the next oldest leaf (Fig. 15) while the cathodic margin is somewhat compressed inside the sheath. Although this results in differences in the degrees of compression of the developing margin at early stages, plications 2 from both the anodic and cathodic margins will be used to describe histological development.

Figure 20 is a section through the anodic margin of a leaf at the stage when plication 2 first appears as a slightly convex mound which is located between the adaxially curved free margin and the adaxial ridge of plication 1. The formation of these ridges is associated with periclinal and oblique divisions in the internal cell layers (Fig. 20). At this stage the adaxial furrow between the ridges of plications 1 and 2 appears as a broad depression rather than a narrow furrow. As the leaf grows, compression of the lamina brings the ridges of adjacent plications into closer proximity, narrowing the adaxial furrow (Fig. 21). This occurs at earlier stages in plications of the cathodic margin as compared with those of the less compressed anodic margin. Internal divisions result in an increase in tissue layers at the locus of the adaxial ridge while anticlinal divisions and associated cell growth in the intercostal sector between the ridges extends the surface area of the lamina. Although extension of the plications in this palmate leaf does not occur in such a confined space as observed in *Chrysalidocarpus*, buckling of the

19.   Scanning electron micrograph of a leaf of *Rhapis excelsa* 6 mm in length when the plications have elongated well beyond the adaxial hastula (AdH) and abaxial hastula (AbH). Arrow indicates the horizontal portion of the abaxial plication ridges which are uncovered by the abaxial hastula at all stages of development. Note trichome development on leaf margin, plication ridges and margins of hastulae. Scale line equals 500 μm.
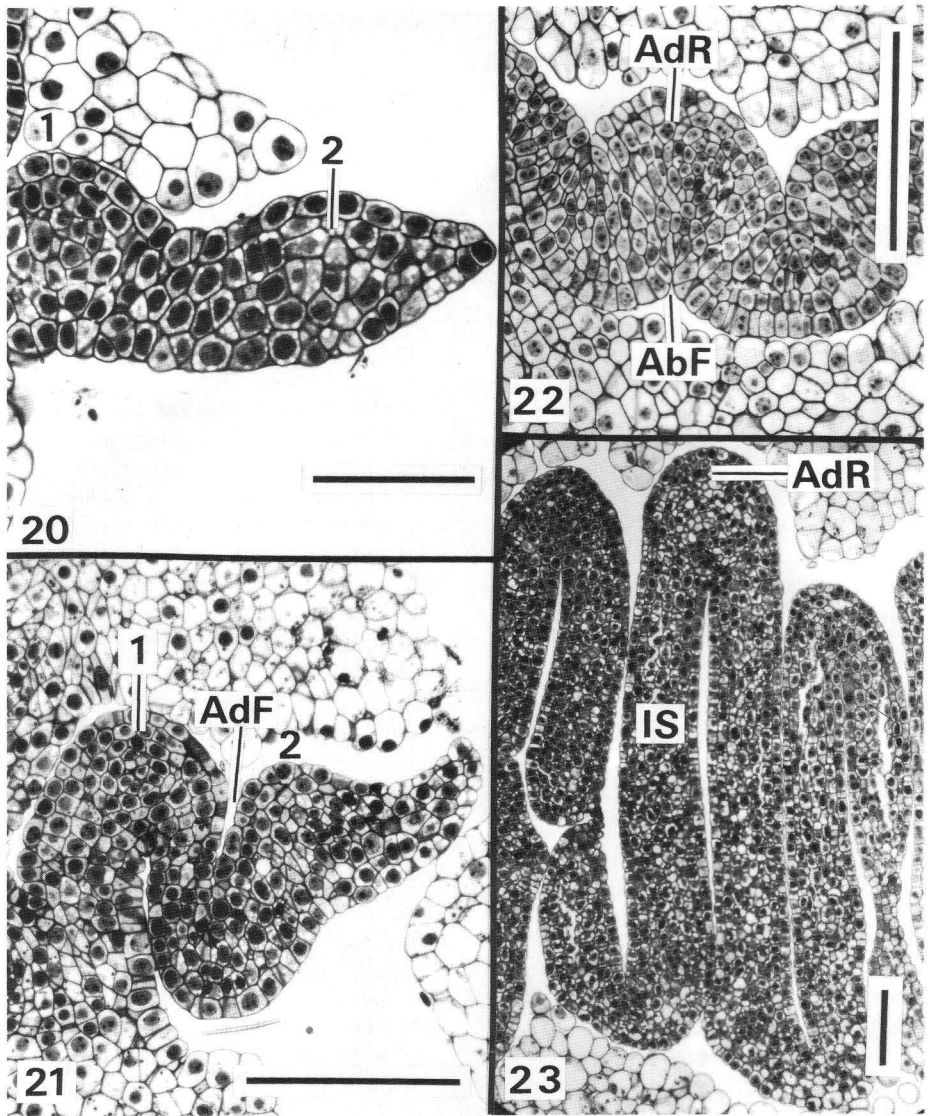
20–23.   Cross sections of developing leaves of *Rhapis excelsa* showing the midregion of plication 2. Fig. 20. Section from the anodic side of a leaf 0.8 mm in length taken 187 μm from the leaf margin. The adaxial ridges of plications 1 and 2 are associated with localized periclinal and oblique divisions. Scale line equals 50 μm. Fig. 21. Section from the cathodic side of a leaf 1.0 mm in length taken 265 μm from the leaf tip. Adaxial ridges 1 and 2 are compressed so that the adaxial furrow (AdF) between them appears slit-like. Scale line equals 100 μm. Fig. 22. Section from the cathodic side of a leaf about 1.2 mm in length taken 266 μm from the tip. The adaxial ridge (AdR) and associated abaxial furrow (AbF) of plication 2 are labelled. Scale line equals 100 μm. Fig. 23. Section from the cathodic side of a leaf 2 mm in length taken 619 μm from the leaf tip. Adaxial ridge (AdR) and intercostal sector (IS) of plication 2 are labelled. Scale line equals 100 μm.

lamina also occurs and results in the formation of broadly rounded abaxial ridges and narrow abaxial furrows (Fig. 22). Intercalary growth of the intercostal sector results in the displacement of the adaxial and abaxial ridges away from each other (Fig. 23). All of these sections show a complete continuity of the protodermal layer at all stages of development.

Although this histological analysis of plication origin in *Rhapis* gave no suggestion of splitting, the same quantitative analysis of plication growth used in *Chrysalidocarpus* was carried out as an additional test of the mechanism of morphogenesis. This analysis showed that the greatest increase in number of cell layers (from 5 to 26) occurred in the adaxial ridge (Fig. 24A); as in *Chrysalidocarpus*, this is associated with the differentiation of the procambial stand of a major vascular bundle. Although the increase in the number of cell layers in the abaxial ridges (Fig. 24B) and the intercostal sectors (Fig. 24C) was less (from about 4 to about 8 cell layers), no evidence of a decrease in the number of cell layers was observed at any developmental stage.

Discussion and Conclusions

We conclude that the process of differential growth at the locus of the adaxial ridges followed by intercalary growth between ridges accounts for the original formation of plications in a submarginal position (Dengler *et al.* 1982, Kaplan *et al.* 1982b). This conclusion is based on observations of oriented serial sections through developing plications in a closely graded series of leaf lengths; our observations of sections of over 140 leaves of *Chrysalidocarpus* and 63 of *Rhapis* were consistent with this interpretation. No sections revealed the presence of internal slits developing toward the surface or any breaks in protodermal continuity which would support the hypothesis of schizogenous origin of the plications. In addition, careful counts of the numbers of cell layers across the lamina, made along the length of the plications in leaves of a range of ages, only showed an increase in the number of cell layers. One would expect a decrease in number of cell layers if splitting were occurring; the observed increase in number of cell layers supports the concept of differential growth. Perhaps the most convincing argument for our conclusion is the similarity in the histology of developing plications in a palm with pinnately compound leaves, *Chrysalidocarpus lutescens*, and a palm with palmately compound leaves, *Rhapis excelsa*. Despite the differences in the morphology of the young leaves, the orientation of the plications and the physical contraints on the developing lamina, our cross sections of developing plications of both *Rhapis* and *Chrysalidocarpus* are strikingly similar (cf., Figs. 10,22).

Our assertion that tissue separation does not play a role in the initial formation of the plications is based on an understanding of the gross morphology of the young leaves, careful control of the plane of sectioning, use of serial sections so that position within a particular plication is known, recognition of the age of the leaf under observation and examination of a large number of individual leaves. Although the earliest investigators were handicapped by the limited techniques available to them, the fact that the mechanism of this aspect of palm leaf morphogenesis has remained unresolved for over a century is largely the result of misunderstanding one or more of the factors listed above (Kaplan *et al.* 1982a).

For instance, despite Naumann's (1887) early clear statement of the problem in interpreting plication initiation, his own anatomical observations of *Phoenix* were based on cross sections of the whole leaf, an angle which would be oblique to the developing plications. Not surprisingly, he
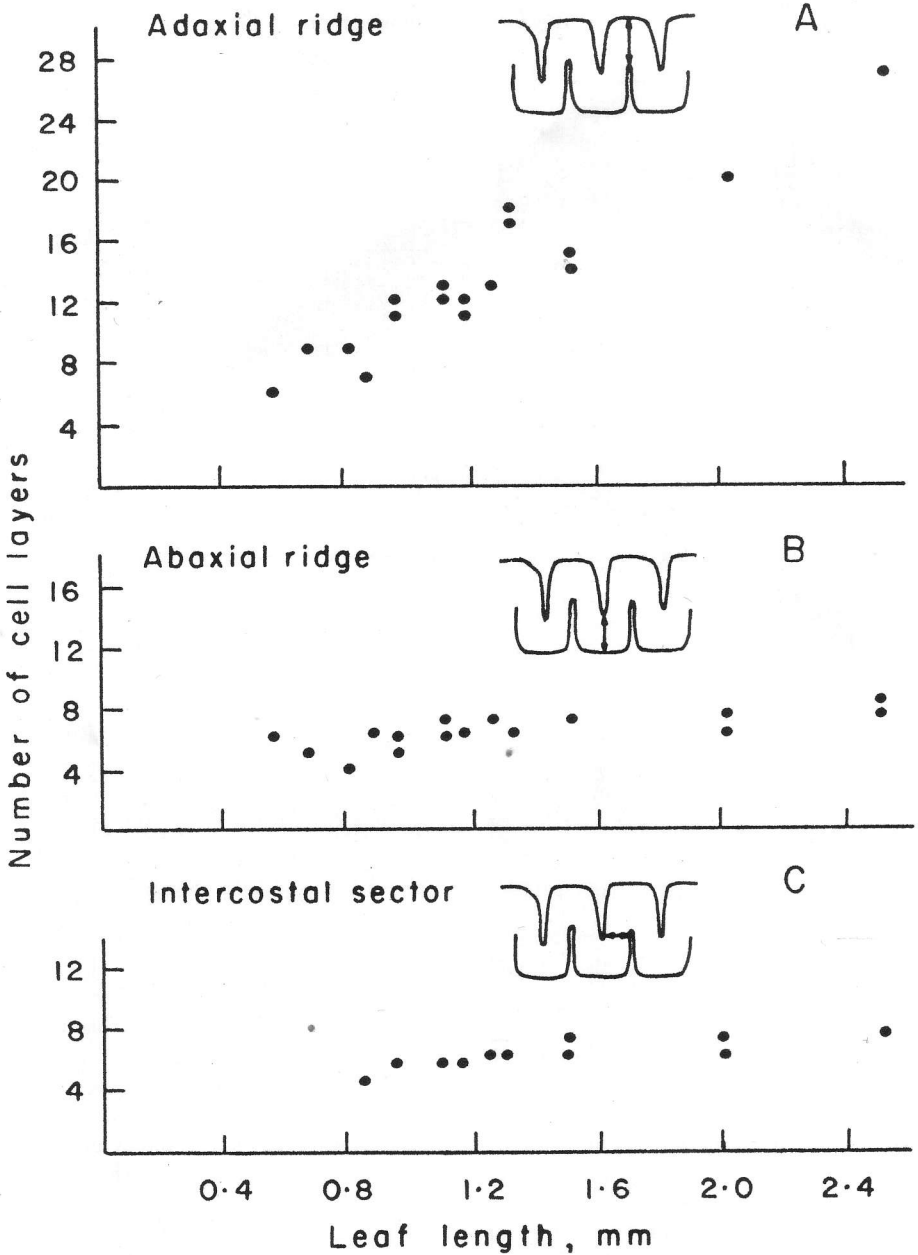
24.   Scatter plots illustrating the changes in the number of cell layers in the adaxial ridge (A), abaxial ridge
       (B) and intercostal sector (C) in leaves of *Rhapis excelsa* from 0.5 to 2.5 mm in length.

described young plications as pouches having internal slits and deduced that they were the result of tissue separation. As another example, although Goebel (1926) took care in orienting the leaves of *Elaeis* so that sections were made tangential to the margin, some of his critical stages appear to be oblique sections made too close to the unplicate strip of marginal tissue. While he concluded that differential growth was the process resulting in the formation of plications, he failed to provide convincing evidence for the mechanism. Our own observations indicate that plication inception occurs at a relatively early state which is easily missed (by a leaf length of 5.5 mm in *Chrysalidocarpus* and a length of 4.5 mm in *Rhapis*). Venkatanarayana (1957), who attributed plication development in *Cocos* to schizogenous splitting, appears to have oriented his sections properly but to have missed the actual stage of plication inception. His figures are of a relatively late stage of plication growth and most likely represent a zone of appression of two adjacent plications similar to that shown in Figure 11 of this paper.

The major lines of evidence cited in support of the process of tissue separation are: 1) the slit-like appearance of the furrows in surface views of whole leaves and in sectional views of growing plications, and 2) the occurrence of internal slits in some sections. A primary reason that *Chrysalidocarpus* was selected to test the hypothesis of tissue separation is the narrow slit-like appearance of the furrows shortly after inception (Fig. 6). However, sections through younger plications demonstrate that the plication ridges are at first rounded with the furrows only secondarily assuming a slit-like appearance as the plications expand within a confined space (Figs. 9–11). This is more dramatically illustrated in *Rhapis*. When two adjacent plications are first initiated, they are separated by a broad shallow depression (Fig. 20); only as additional plications are initiated basipetally and all the plications extend in depth do the furrows become narrow and slit-like (Fig. 22). Some investigators have missed the stages with rounded ridges and have based interpretations on the more compressed advanced stages of plication growth. For instance Padmanabhan (1963, 1967) and Padmanabhan and Veerasamy (1973) have argued that the V-shaped grooves observed in sections of the leaves of *Cocos*, *Borassus* and *Phoenix*, as well as the zigzag appearance of the walls of the furrows, is the result of separation between the internal ground meristem cells which have an irregular alignment. Again, comparison of their illustrations with our sections indicates that the early stages of plication formation were probably missed and that the irregular appearance of some furrow surfaces may be the result of distortion of susceptible meristematic tissues caused by fixation and dehydration, a problem that also plagued many of our sections.

The appearance of internal slits in some sectional views has also provided a major source of evidence in support of tissue separation (Naumann 1887, Yampolsky 1922, Eames 1953, Padmanabhan 1963, 1967). In our material of *Rhapis* and *Chrysalidocarpus* any indication of internal slits could be shown to be the result of a somewhat oblique section taken adjacent to the rachis and the apparent internal pockets could always be shown to be continuous with the external surface of the leaf by following serial sections (Dengler *et al.* 1982, Kaplan *et al.* 1980*b*).

Our observations indicate that the mechanism of differential growth alone can account for the original formation of plications in the leaves of palms. In this respect palm leaf development is similar to development of compound leaves of other flowering plants in which differential growth (in the sense of localized areas of

meristematic activity) also results in the formation of leaflets from free marginal lobes. The unique aspect of palm leaf morphogenesis is the location of this localized growth in a submarginal position and the subsequent secondary separation of the plications to form individual leaflets. While our investigation led to a rejection of the hypothesis of splitting as the mechanism of plication inception, it is clear that some sort of tissue separation must occur in the abscission of leaflets from one another and from the unplicate strip of marginal tissue. Future research on palm leaf morphogenesis must test our conclusions in a wider range of palm taxa and must also examine these more complicated aspects of leaflet separation which are among the most distinctive features of morphogenesis in this unique plant group.

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