NOTES ON *CYCAS* PLANTS GROWING AT ALLAHABAD

By Divya Darshan Pant

Department of Botany, Allahabad University

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Cycas revoluta is a common ornamental plant in the gardens at Allahabad and plants of *C. circinalis* and *C. rumphii* are also seen growing at some places. Although no species of the genus is native of the region, the plants of the above named species, being fairly hardy, are grown as a rule in the open and are thus fully exposed to the local extremely humid rainy season, cool and almost rainless winter and desiccating hot summer, sometimes without even being watered. But in spite of these somewhat exacting conditions, the plants are in general quite healthy and some of them have developed branched or unbranched trunks about eight or nine feet or more in height. Their age calculated roughly from the leaf scar sequence may be fifty or more years. Apparently these exotics feel quite at home in the local environment and the following observations, although they cannot be claimed to be based on individuals growing in their natural environment, may still be expected to hold true for a large part of Northern India.

PRODUCTION OF CROWNS

Coulter and Chamberlain (1921), and McLean and Ivimey-Cook (1951) have mentioned that a crown of leaves is produced " every other year" by plants of *C. revoluta* while Kashyap (1921) reporting his observations on Lahore plants of *C. revoluta* and *C. circinalis* says that "in young plants more than one cluster is usually produced each year while older plants produce only one cluster every year and still older ones produce clusters every other year or even at longer intervals". But in plants of *C. revoluta, C. circinalis,* and *C. rumphii* growing in Allahabad the author has repeatedly observed during the last five years that two crowns of foliage leaves are produced every year—one in or about the spring and the other during or immediately after the monsoon. The production of leaves thus coincides with the two favourable seasons of growth for most plants of this region. The production of leaves in young plants and bulbils is, however, irregular and in these leaves may be produced from time to time and more than twice during an year (very often they are produced soon after copious manuring and watering). Crowns of foliage leaves are followed by alternating crowns of megasporophylls usually only once during the year with scale leaves intervening every time between any two crowns. Before the sudden growth of fronds or megasporophylls the apices of the preceding young scale leaves are spirally twisted like the cords of a rope, securely protecting and completely hiding the underlying apex and other growing structures.

DURATION OF CROWNS

Again, according to Coulter and Chamberlain (*loc. cit.*) the "information in regard to the duration of the crowns (in *Cycas revoluta*) is scanty and uncertain". However, in the locally growing plants of *C. rumphii* and *C. circinalis* two or three earlier crowns may be seen below the latest leaves while *C. revoluta* plants may not uncommonly exhibit unabscissed leaves of four or five successive generations (see Fig. 1). In a plant of the last mentioned species, below a freshly developing light green crown of erect soft young leaves, can be seen the

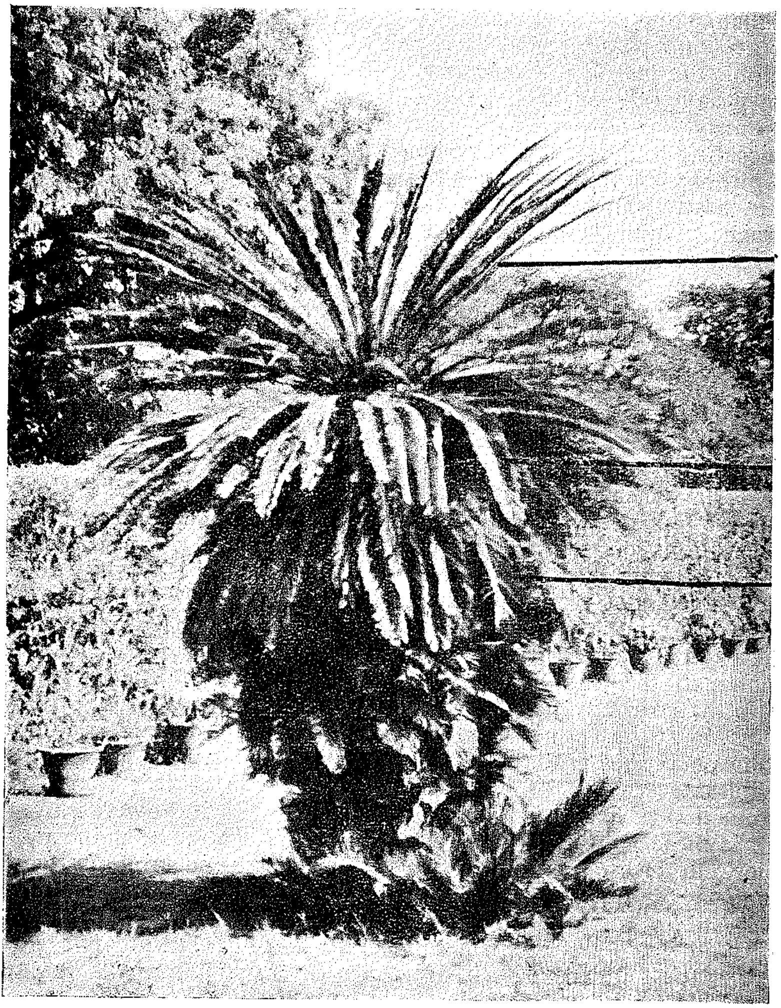


FIG. 1. A tree of *Cycas revoluta* just before the emergence of a new crown. Three crowns can be easily recognised in the Photo (I, II and III), a fourth and still older crown is completely hidden from view by the third (III) crown, ×ca. 1/20.

obliquely standing tough and leathery dark green leaves of the preceding crown followed by an earlier generation whose leaves become horizontal. Under them may be seen a still older crown of downwardly bent leaves whose apices become upcurved and sometimes even below this may be present the completely reversed and more or less dried up and withered fronds and rachises of a fifth generation, lying almost parallel and appressed to the tree trunk—these leaves are almost completely hidden from view by the obliquely reflexed fronds of the subsequent crowns.

VERNATION OF THE RACHIS OF YOUNG LEAVES

Although there is complete unanimity among various authors regarding the obvious circinate vernation of the young leaflets, there are conflicting reports about the vernation of the young rachises. Rendle (1904), Wieland (1906), Seward (1917) and Pilger (1926) mention that the developing rachis in the genus is straight while Coulter and Chamberlain (1921) and Chamberlain (1935) and others have stated that the "vernation is circinate in the midrib and the pinnules of *Cycas*". The author has, however, constantly observed that although the entire proximal part of the rachis is straight, its apex is distinctly incurved (Fig. 2) in all the three species of the genus growing at Allahabad.

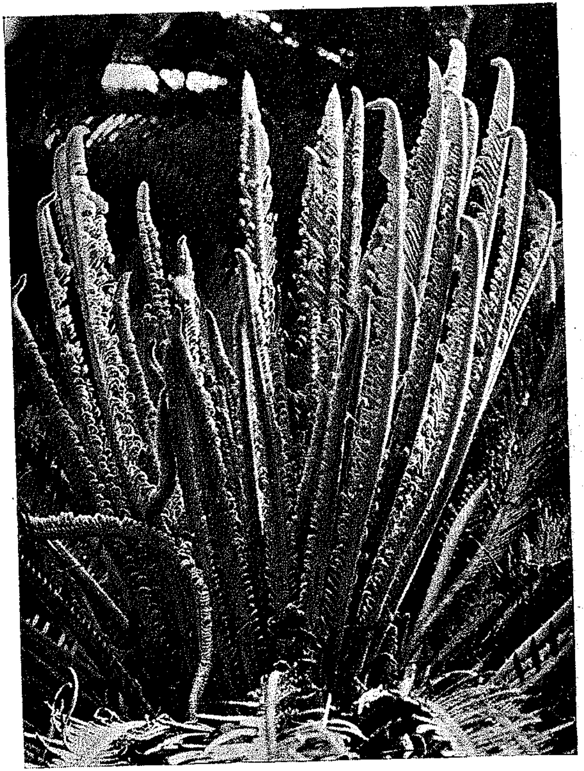


FIG. 2. A newly developed crown of leaves of *C. revoluta*. The pinnæ are circinately coiled and the rachises are incurved at the tip, ×ca. 1/3.

PITS IN OUTER WALLS OF EPIDERMAL CELLS

A unique anatomical feature noticed while examining some sections of the leaflets of *C. revoluta* is the presence of rows of pits on the outer walls of the epidermal cells. It is, of course, well known that simple pits occur in the cell walls of mesophyll and in the radial and inner walls of epidermal cells of *Cycas* pinnæ (Haberlandt, 1914, p. 264) but in the epidermal cells of the pinnæ and rachis of *C. revoluta* there are abundant simple pits (which may appear to be narrowly bordered) on all the walls. These pits are generally oval in outline and arranged in longitudinal rows on the outer walls of the ordinary epidermal cells and the numerous encircling cells of the stomata (Fig. 3). All these pits, however, appear to be occluded by the thick cuticle and their function is therefore difficult to understand.

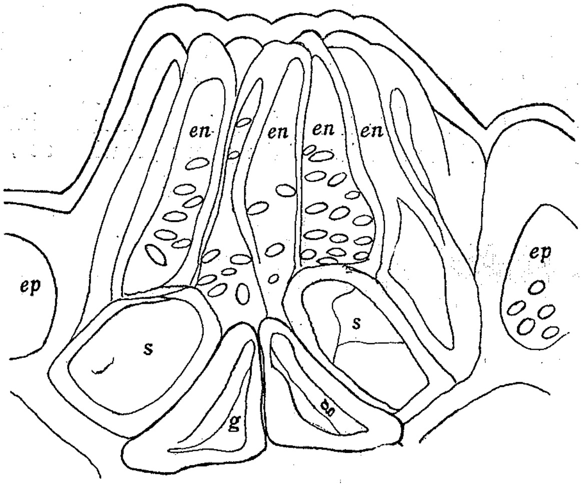


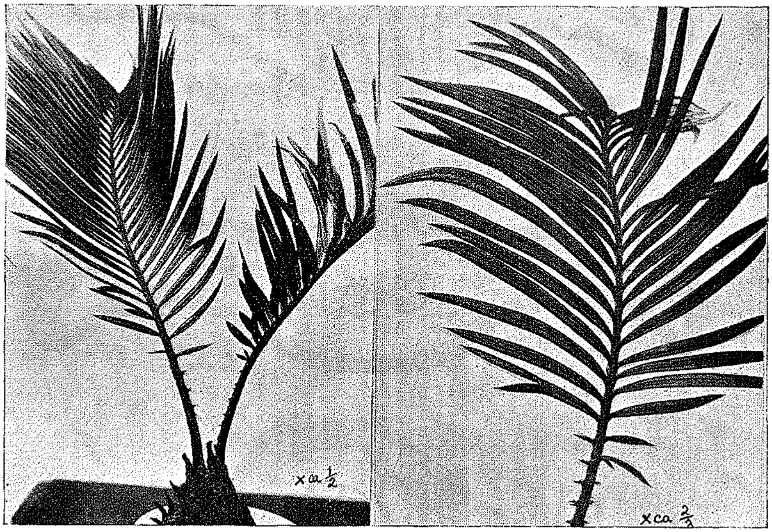
FIG. 3. A stoma of *C. revoluta* showing pits on the walls of the encircling cells (*en*) and epidermal cells (*ep*). *g*—guard cell, *s*—subsidiary cell, ×1,700.

Pits are also present in the outer walls of the epidermal cells of *C. rumphii* and *C. circinalis* pinnæ, but in these species they are neither so frequent nor so clearly marked.

ABNORMAL "V" OR "Y"-SHAPED PINNÆ

Two types of abnormal pinnæ are commonly seen in the leaves of local plants of *C. revoluta*. One of these consists of pairs of adjacent pinnæ which are often seen arising very close to each other usually towards the basal side (*i.e.*, immediately above the region of the spines on the rachis) of the first few leaves in young bulbils of *C. revoluta*. Some of these pairs are V-shaped (Fig. 4) having a common lamina at the base, but often their two veins are distinct from the very beginning. Sometimes, a preceding spine may seem to imitate the process and appear to be double (perhaps like the spines in leaves of

Encephalartos villosus (see Schuster, 1932, p. 26, Fig.6, B), a fact which obviously confirms their homologous nature with that of the pinnæ. Besides these, occasionally there may also occur some dichotomously branched Y-shaped pinnæ in which a single midrib enters the base of the leaflet and thereafter forks into two (Figs. 5 and 6). But whether they are V-shaped or Y-shaped the two forks of such pinnæ are always unequal, the basal branch being more or less smaller. In some pinnæ it seems that the basal branch is so small that it is represented only by a small spinous serration on the lower margin, and a vein terminates therein. Similar unequally forked pinnæ also occur in *Encephalartos Lehmanni* and "*E. caffer* (?)" (Wieland, 1906, p. 212 and Fig. 123, C and D), although the pinnæ of *E. horridus* (Wieland, *loc. cit.*) are simple with only laminiform spines on the lower margin of the lamina.* According to Wieland (*loc. cit*) the forked pinnæ of the former species are due "to the development of a lower basal spine into a broad lamina thus forming an unequal dichotomy of the blade". On the other hand if the theory of recapitulation be applied here the occurrence of forked Y-shaped pinnæ in the first few leaves of young bulbils and their usual absence in later leaves of *C. revoluta* would suggest that forked leaflets may be ancestral and it is quite possible that simple spinous pinnæ like those of *E. horridus* are reduced structures, their spines representing suppressed lobes of a dichotomously branched



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FIGS. 4 AND 5. The earliest vegetative leaves in bulbils of *C. revoluta* showing V and Y-shaped pinnæ and pinnæ with "laminiform spines". The petiolar spines also appear to imitate the feature.

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* Schuster (1932) on the other hand has figured forked pinnae in *E. horridus* (p. 30, fig. 8, B) and simple pinnæ with laminiform spines on both sides in *E. septentrionalis* (p. 32, fig. 9, O).

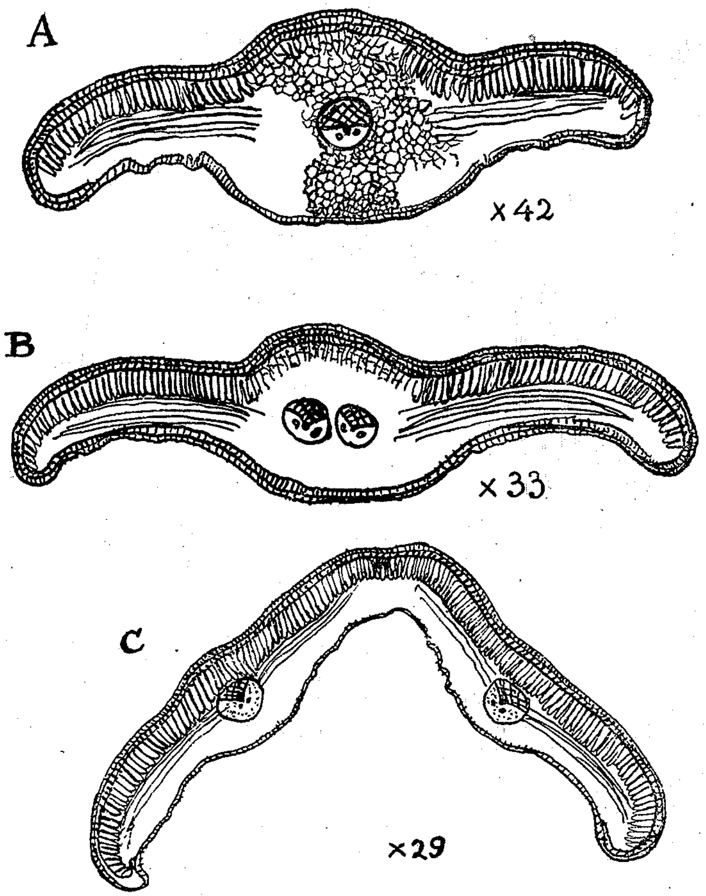

FIG. 6. Transverse sections of a Y-shaped leaflet. Section A shows a single "mid rib" bundle. In B the "mid rib" has two bundles while D passes through the region where the lamina is about to fork forming the two arms of the Y (Semidiagrammatic).

leaflet. Similarly forked or closely arising pinnate lobes are also very often found in the sterile apical part of the megasporophylls of *C. revoluta* (see Fig. 7).

ADDITIONAL PINNÆ IN ABNORMAL LEAVES OF *C. revoluta*

Another interesting and hitherto unaccounted abnormality is so frequently seen in the older horizontal or downwardly reflexed fronds of some of the local adult trees of the same species (*C. revoluta*) that it could almost be regarded as a normal feature. On their adaxial side near or some distance behind the apex of their rachises, usually at the bend of the upcurved apical portion, can be seen some much smaller accessory pinnæ which are arranged in two additional adaxial rows, each row having at the most six, but usually less than six, leaflets

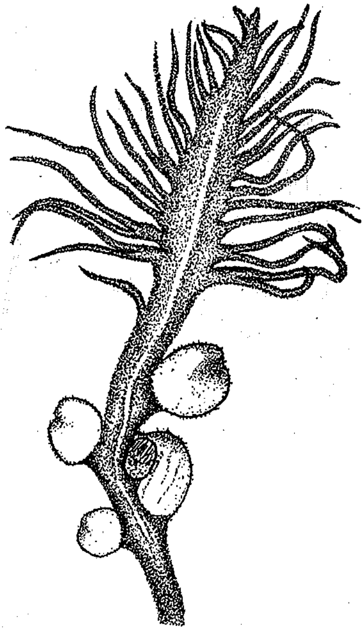

FIG. 7. Megasporophyll of *C. revoluta* showing closely arising and forked pinnate lobes in the sterile end part, ×1.

on either side of the rachis just above the normal rows (see Fig. 8). These additional pinnæ are at first absent but develop later in the mature leaves. Their growth and formation are under observation and will be reported in due course.

The form and the internal structure of these additional pinnæ are the same as those of the normal ones and each one of them receives a single vein ("mid-rib") which arises as a branch from one of the bundles of the rachis in the region of their insertion. Often, like the apical structure at the end of the two normal rows, a terminal leaflet or spine-like process is placed almost medianly at the end of these two additional rows also.

When viewed from above these additional pinnæ appear to have a peculiar inverted insertion, with their dorsal or lower sides adaxial and their ventral sides facing those of the normal leaflets. On the other hand, if we compare the four ranked arrangement of the normal and the abnormal pinnæ and their orientation in this part of the rachis with that of leaves on a dorsiventral stem like that of *Selaginella*, the rachis manifests a strange resemblance with such a stem. In fact the "dorsiventral, frond-like, anisophyllous," unbranched fossil stems of *Tingia* (see Browne, 1933 and *cf.* Fig. 9), a genus of uncertain affinities which was at one time actually referred to the cycads, form a much closer parallel. In the present case the ventral or upper sides of all pinnæ will appear to be all turned towards the apex of the rachis (like

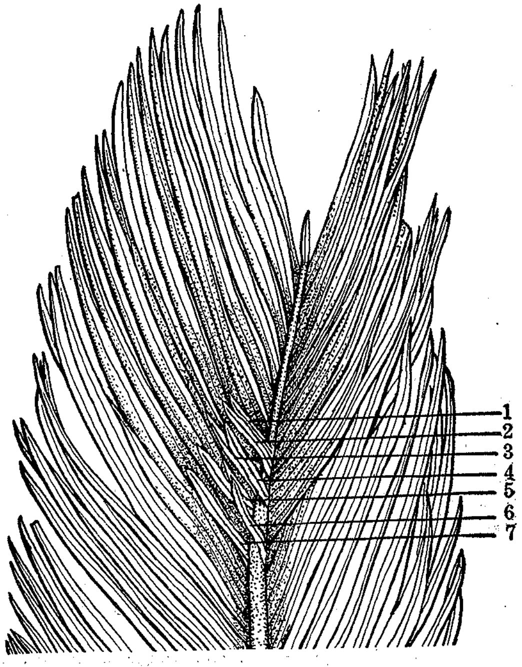

FIG. 8. Apical part of a leaf of *C. revoluta* showing adaxial accessory pinnæ. No. 1 is the median terminal pinna while Nos. 2 to 7 are arranged in two additional rows, ×ca. 2/3.

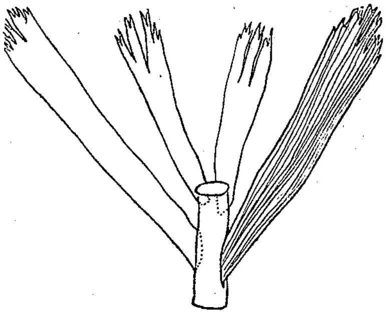

FIG. 9. Reconstruction of a part of the frond-like axis of *Tingia* (*after Lady Isabel Browne*).

the apex facing upper sides of the leaves on a stem), although in the case of *Cycas* the dorsiventrality of the frond has more or less deflected them from their normal posture.

The fronds of *Cycas* simulate stems in other ways also. It is a well-known fact that in other species of the genus (especially in *C. rumphii* and *C. circinalis*) the strong midribs of the pinnæ in the terminal part of the leaves, when seen from the lower side, actually look like a series of monopodial branches from the rachis which tend to be truly dichotomous towards its apex. The fronds of *C. micholitzii* (Schuster, 1932, p. 28, Fig. 7, B) or *Macrozamia heteromera* (Schuster, *loc. cit.*, p. 32, Fig. 9, N) go a step further—even their pinnæ are repeatedly and deeply forked. Similarly dichotomised "concrescent" pinnæ sometimes occur in *C. circinalis* (Seward, 1917, pp. 13 and 14 and Schuster, 1932, p. 28, Fig. 7, A) and as reported in these notes quite frequently in the bulbils of *C. revoluta.* These dichotomies of the exterior, in fact, appear to be seated deeper; according to Matte (1904, Pl. I, Figs. 1–4 and 8–11) the rachis of *Cycas* contains within it a dichotomously branching system of bundles, the ultimate free ends of which enter the pinnæ.

ABNORMAL MEGASPOROPHYLLS

The megasporophylls of *Cycas* are, as ordinarily described, leaf-like structures with lateral pinnately arranged sterile lobes and ovules but in the megasporophylls of *C. rumphii*, I have very often noticed ovules which are instead of being inserted in two lateral rows, attached in two rows on each side or otherwise arranged side by side dorsiventrally on either side of the megasporophyll (Fig. 10).

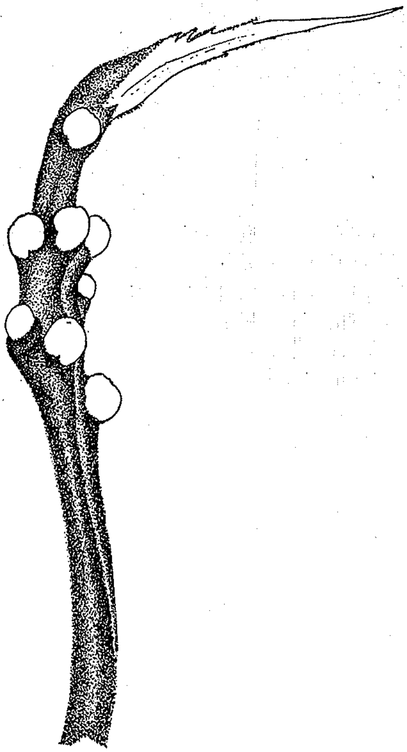

FIG. 10. Megasporophyll of *C. rumphii* showing the lower ovules arranged in two rows on either side, ×1.

The homologous nature of the fronds and the megasporophylls of *Cycas* is thus supported even by the occurrence of similar aberrations in the two types of structures (paired and forked pinnæ and dorsiventrally arranged pinnæ and ovules) but besides this the abnormalities and other facts enumerated above support their fundamentally axial nature also.

The leaf of the Pteropsida (Megaphyllous Trachæophyta) has been interpreted as a modified branch system (Prantl, 1875, Potonie, 1899 and Tansley, 1908—see Bower, 1935, p. 550). The *Cladode Megaphyll Theory* of Bower (*loc. cit.*, pp. 550–52) and the *Telome Theory* of Zimmermann (1930) suggest essentially the same thing; the latter even including the microphyll in the same generalisation. Recently Arber (1950, pp. 70–123) has suggested that the leaf should be regarded as a "partial shoot" with an "urge towards the attainment of whole-shoot-hood". Arber's *Partial Shoot Theory* is in fact not in any way contradictory but complementary to these earlier theories. Amongst other arguments in support of her hypothesis, she has quoted instances of *Brassica oleracea* and *Platanus acerifolia* leaves (Arber, *loc. cit*, pp.110 and 111, Fig. 15, A 1, A 2, B 1 and B 3) where the midribs show a "genuinely shoot-like divelopment". In addition, the author has very frequently observed similar shoot-like development in the leaves of young vigorous female plants of *Carica papaya* (the abnormality is much less frequently seen in male plants)—see Fig. 11. The present leaves of *C. revoluta* may be regarded as further examples of the same tendency of the leaf towards the attainment of whole-shoot-hood. Interpreted on this basis, at least a female tree of *Cycas* with its monopodial columnar trunk and a crown of determinate partial shoots (fronds) assumes an aspect somewhat similar to that of an *Araucaria* tree with its indefinitely growing leader surrounded by whorls of pinnately branched secondary axes.

On the other hand, there could be other ways in which these additional pinnæ could be interpreted. For instance, they could be regarded as arranged on a branch of the rachis which may be assumed to have arisen by an unequal dichotomy but which was either unable to separate or which became fused with the other. The occurrence of bipinnate fronds in *Bowenia spectabilis* and of forked rachises in the leaves of some ferns and pteridosperms, *e.g.*, *Diplopteridium teilianum* (Walton, 1931) lends colour to these ideas.

It seems, however, that whatever be the ultimate nature of the various parts involved, the *Telome Theory* can best explain all the points in a very fundamental way. Both the external dichotomies and the usually forked vascular bundles of the rachis suggest an organ which has undergone overtopping, planation, webbing and fusion like what has been pointed out for the axes of *Medullosa heterostelica* by Stewart and Delevoryas (1952). The "Foliar" ovules of *Cycas*, in particular, could be regarded as terminal megasporangia on lateral branches of an axis system which has undergone overtopping and planation. The interpretation will also bring the fertile structures of the Cycadales in line with those of other gymnosperms, *e.g.*, the Coniferales and the

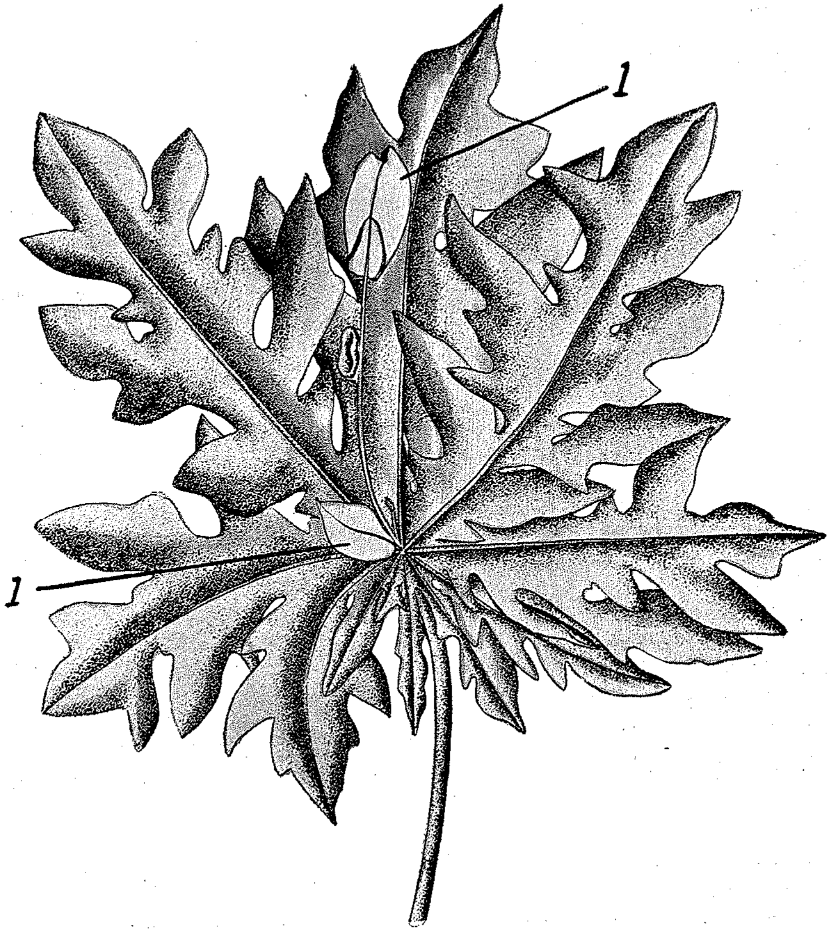

FIG. 11. Leaf of *Carica papaya* showing "tendency towards the attainment of whole shoot-hood" by forming leaf-like structures on the upper side (*l*), ×ca. 1/6.

Ginkgoales (see Wilson, 1953, p. 428–32). In the peltate megasporophylls of Cycadales other than *Cycas*, the megasporangia appear to have undergone recurvation in addition while the terminal megasporangia of *Cycas* are erect and orthotropous.

SUMMARY

In adult plants of three species of *Cycas* growing at Allahabad foliage leaf crowns are usually formed twice a year (the production of crowns in young plants is irregular). The crowns frequently last for more than an year. The raches of young leaves in all the three species are incurved at the apex. Simple pits occur in the outer walls of epidermal cells of the pinnæ. In *C. revoluta* V-and Y- shaped pinnæ are

frequently found in the first few leaves of young bulbils and megasporophylls and additional abnormal pinnæ are formed in the adult leaves of fully grown plants. The structure of these abnormal pinnæ and their theoretical significance are briefly discussed. In *C. rumphii* ovules are found attached in more than two rows.

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