

# EVOLUTIONARY TRENDS IN THE PALMAE WITH SPECIAL REFERENCE TO FOSSIL PALMS

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## ABSTRACT

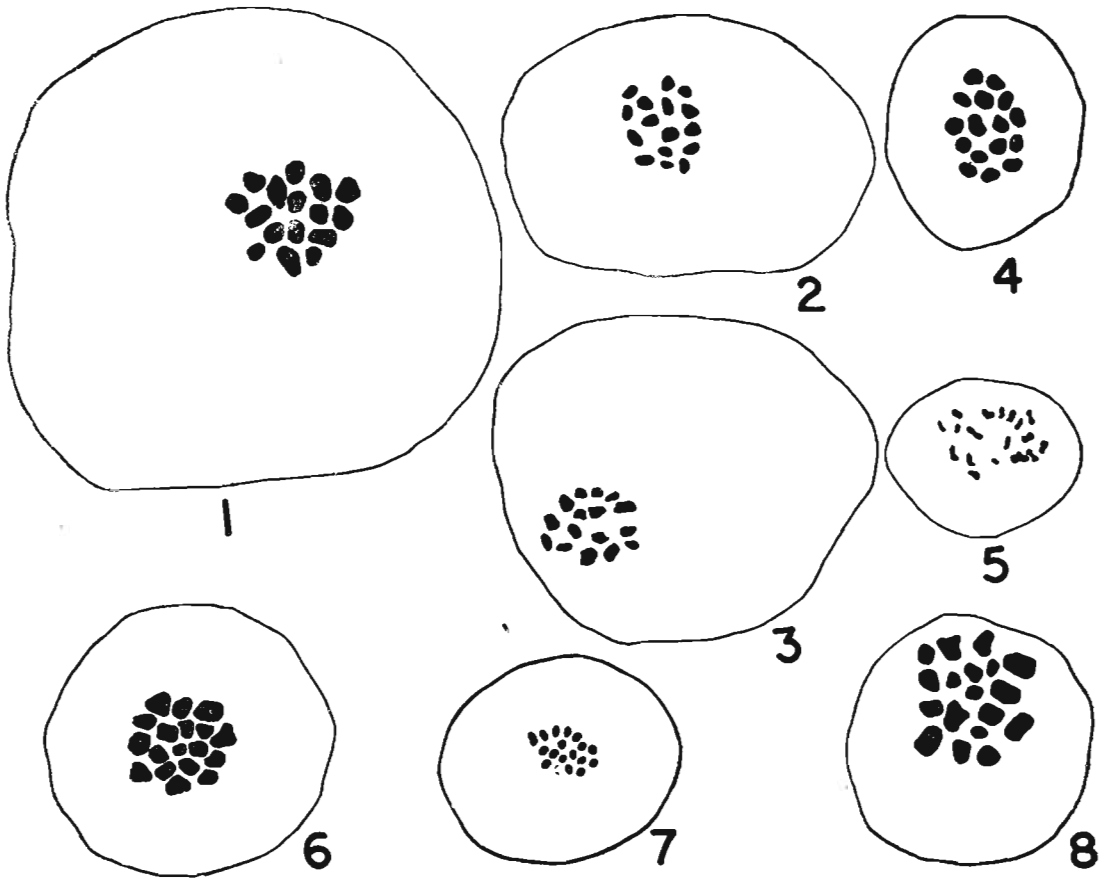
The paper gives an account of the characters generally used in determining the relationships of living palms and their classification. It tries to evaluate the utility of such characters in the identification and phylogeny of fossil palms by citing suitable examples. Many morphological characters of palms are conservative and are helpful within a limited range; others are unhelpful, especially anatomical features of isolated parts of unknown identity. Therefore, in building up any classificatory system of fossil palms, all available characters of as many parts as are available should be utilized within the range of their variability. To achieve this purpose they have to be studied in detail in the same or related genera of living palms and then correlate them with those in the fossil palms. Such a comprehensive method alone would be helpful in determining the phylogeny of fossil palms.

## INTRODUCTION

THE family Palmae consists of 210 genera and about 1200 species. The number of species is probably much larger and varieties still greater, as several species under garden conditions yield varying cultivars. The family is considered to be very ancient on account of its tree habit, and dichopodial branching of stem in some members like *Hyphaene*. Most of the genera are woody. They lack cambium and yet their tree trunk is capable of increase in girth. The inflorescence is highly complex and bears characteristic bracts in certain genera such as *Borassus*, *Hyphaene*, *Caryota*, *Elaeis*, etc. The trimerous flowers are generally borne on highly specialized scapes within leafy spathes. In some genera they are hermaphrodite and in others dioecious. In the latter case they contain either staminodes or pistillodes. They are animophilous but are reported to be entomophilous in some genera like *Sabal* or *Chamaedorea*. In this respect they resemble Cycads which by and large are animophilous but reported to be entomophilous in *Encephalartos*, *Dioon* and *Macrozamia*. The pollen grains are characteristically boat-shaped as in Cycads, monocolpate and

single-germ-pored. Still they do show slight variation in their structure and as a rule are one-celled at the time of shedding. This makes it difficult to account for several varieties noticeable in different palms under cultivation. For example, in the genus *Cocos*, *C. nucifera* alone has as many as 72 varieties having variable characters differing in habit, height, size of the tree trunk, size of fruits etc. (PL. 3, FIGS. 25-28). The same thing is true of cultivated genera such as *Areca*, *Elaeis*, *Arenga* or *Phoenix*. Yet there is great conservatism on the part of this group as is evinced by more or less uniform nature of leaves, stem anatomy and the chromosomal constitution. The leaves in palms, as is wellknown, are either pinnate or palmate despite the extraordinary range of their species (PL. 1, FIGS. 1-9). A third variation in the leaf shape is shown by fan-shaped, multicostate divergent leaves in genera such as *Caryota*, *Bactris*, *Martinezia*, *Wallichia* or *Didymosperma*.

The genomic complex also does not show much variation. It has two broad patterns. The great majority of the pinnately leaved palms have 18 chromosomes and the palmately leaved palms 16 (TEXT-FIGS. 1-8) as was earlier shown by Mahabalé and Chennaveeraiah (1953, 1957). Within the range of genus also the number of chromosomes seems to be fixed. For example in all the species of *Cocos* the chromosome number is 16, in *Caryota* 18, in *Borassus* and *Licuala* 16, in *Phoenix* 18, *Hyphaene* 18, *Sabal* 18. Apparently the causes of variation in palms are to be found not so much in their genomic structure, as in the structure of their chromosomes yet to be investigated in many species. In a few palms such as *Phoenix* even sex chromosomes have been reported (SHARMA & SARKAR, 1957), but not in many others. The cytology, therefore, does not help us much in determining the phylogeny of this large group. Several systematists, therefore, have classified palms mainly on the basis of their flower and leaf characters which provide reliable basis



TEXT-FIGS. 1-8 — Chromosomal complex in palms showing  $n$ -number of chromosomes. 1. *Cocos nucifera* ( $n=16$ )  $\times 600$ ; 2. *C. coronata* ( $n=16$ )  $\times 750$ ; 3. *C. plumosa* ( $n=16$ )  $\times 1000$ ; 4. *Licuala peltata* ( $n=16$ )  $\times 1000$ ; 5. *Sabal palmetto* ( $n=18$ )  $\times 1125$ ; 6. *Hyphaene indica* ( $n=18$ )  $\times 1500$ ; 7. *Phoenix sylvestris* ( $n=18$ )  $\times 1125$ ; 8. *Caryota urens* ( $n=18$ )  $\times 1500$ .

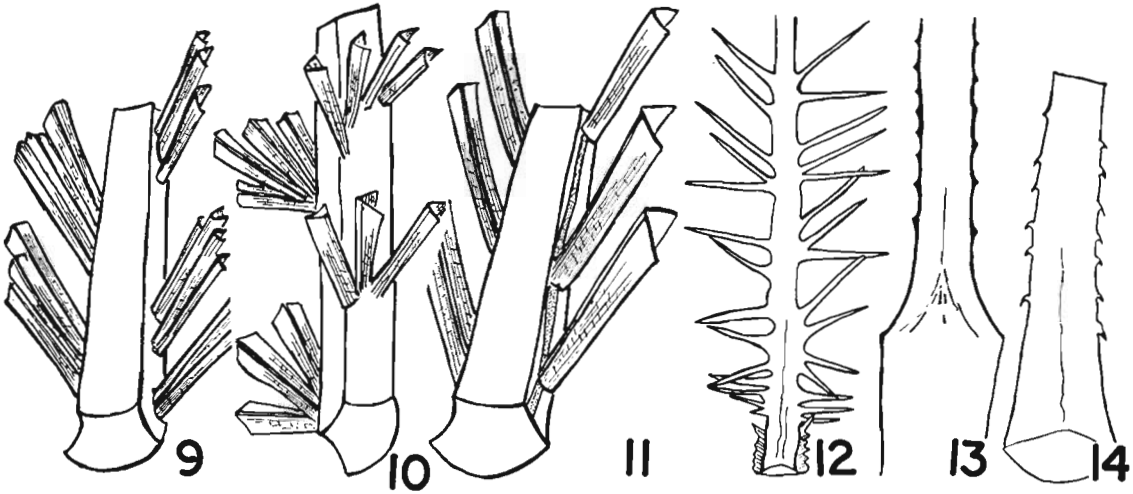
for their classification. This is further strengthened by the detail of anatomy which also is more or less conservative. The earliest classification of palms has been by Linnaeus (1737) who based it on endosperm and other characters. It was modified by Martius (1829-1850), Drude (1887), Beccari (1911), Hutchinson (1934), Beccari and Pichi Serimolli (1956) and recently by Moore (1960).

A reference to the past history of palms clearly indicates that the family is quite ancient in its origin, having been found from the Liassic to modern period, if not from Triassic. In the Tertiary floras in many parts of the world one gets a large number of fossil palms, and therefore, I thought it worthwhile seeing how far that would help

us in finding the evolutionary tendencies in the Palmae as a whole taxon.

#### FOSSIL PALM MATERIAL

The largest number of specimens available as fossil palms are (1) leaves and (2) stems; (3) a few are fruits and seeds. The leaves are obtained mostly as impressions, there being both pinnate as well as palmate types described under the name *Palmacites* or *Palmites* or more appropriately as *Palmophyllum* (PL. 1, FIGS. 4-6). But as remarked above, even in the living palms, the gross shape of leaves does not show much variation in its nature, and therefore, is not of significant help in this matter. Eames (1953) and Tomlinson (1960) have shown that more than gross



TEXT-FIGS. 9-11 — Varied attachment of pinnae in the genus *Cocos*.  $\times 1/4$  N.S.; 9. *C. coronata*; 10. *C. plumosa*; 11. *C. nicipera*.; 12-14 — Spines on palm leaves and petiole; 12. *Phoenix sylvestris*.  $\times 1/8$  N.S.; 13. *Borassus flabellifer*.  $\times 1/12$  N.S.; 14. *Livistona chinensis*.  $\times 1/8$  N.S.

characters of leaves, minute characters such as reins and hooks, hairs, stomata are of greater significance as differentials in their taxonomy. The same should be true of leaves in the fossil palms also. But in the impressions available such minute characters are seldom available. However, whenever present, they do help us that way. For example, the lower pinnae on the leaf in the genus *Phoenix* (PL. 1, FIG. 9; TEXT-FIG. 12) are converted into spines which are characteristic in different species (see MAHABALÉ & PARTHASARATHY, 1963). In the Deccan Intertrappean Series at Mohgaon (M.P.) I got a specimen in which it was possible to observe that the lower pinnae were converted into spines as in the modern *Phoenix* leaves (PL. 1, FIG. 6). This helped to confirm the identification of that specimen as *Phoenix*. In several palms the shape, size, position and kind of the leaves or spines are highly characteristic (TEXT-FIGS. 9-14 and PL. 1, FIGS. 1-6 and 8-9), and if they could be had, they would prove useful in the identification of species and genera of fossil palms.

Two other important characters of leaves that would be useful are venation and stomata. In large palm leaves described as *Sabalites* from the Tertiaries of America, Italy and other parts of Europe it is possible to compare the details of veinlets with the details of veins in different living species of *Sabal*. These clearly show that their resem-

blance is both with the dwarf *Sabal*, *S. adansonii* as well as with the tall *Sabal*, *S. palmetto* (PL. 1, FIGS. 1, 2, 4, 5). Evidently both the types of species were present in the past and hence one notices the differences in the leaves of fossil *Sabalites* obtained from different areas. Similarly when the bits of leaves of *Chamaerhops humilis* (now growing as a coastal palm from Mediterranean to Black sea, and further eastwards to the mouth of Indus in delta near Hyderabad in Sind in Pakistan) are obtained in lignitic beds, hairs on the two are easily comparable.

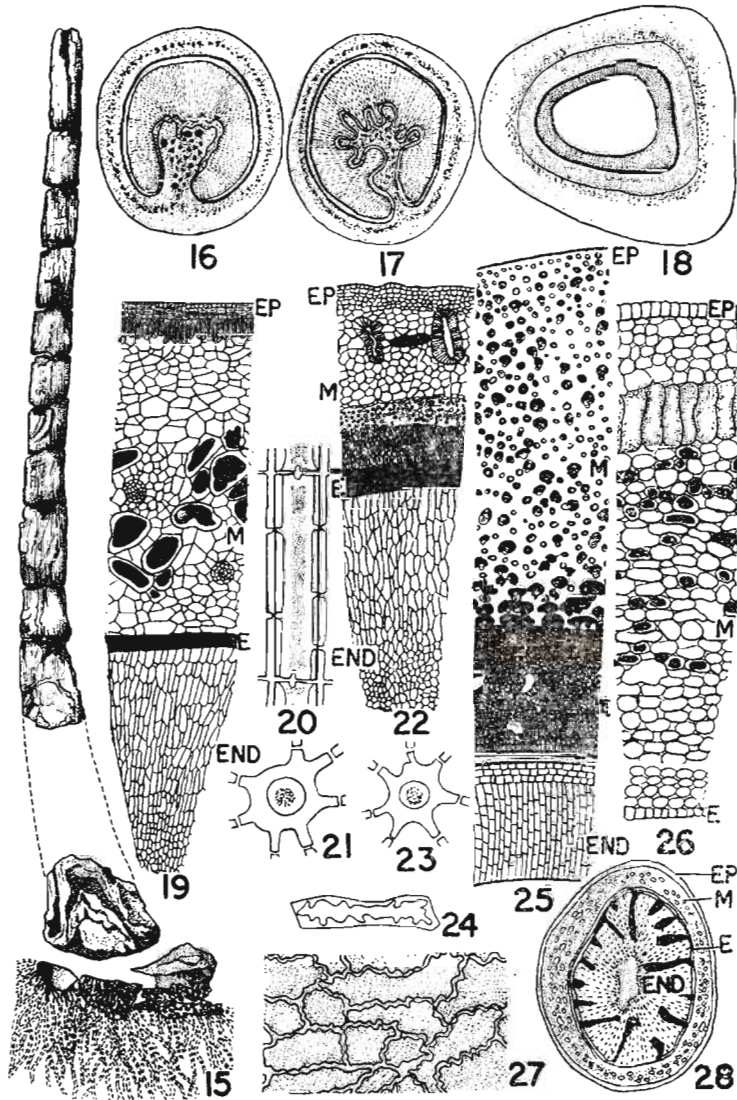
The stomatal structure in palms is of the *Graminaceous* type. Their lie and distribution per unit area, size and shape, epidermal cells, all provide another set of interesting characters for comparison. But unless they are available in fossils and show some characteristic features they are not of much significance from the paleobotanist's point of view. For example, the stomata in members of the Caryotoideae have ridges on the guard cells (PL. 1, FIG. 7) like those on the guard cells of *Equisetum*. Should they be available in fossils, one can make use of them both for generic and specific identification, as they are an exclusive feature of the leaves of the Caryotoideae.

Unfortunately, however, the great majority of fossil palms are obtained only as bits of stem or similar parts, all named as *Palmoxylon*. Various approaches have been

made to decipher them with the help of the shape of fibro-vascular bundles, their distribution, fibre bundles — their presence or absence in the pith, etc. by Stenzel (1904), ground parenchyma pattern by Kaul (1943), xylem elements by Mahabale (1958). But the more reliable method is to use the combination of all such anatomical characters of equivalent parts, as was suggested by me (MAHABALÉ, 1958). But this comparative method largely depends for its success on the details of anatomical features in different organs, and the variation shown by them in different genera and species. It is only now being realized that this anatomical method has its own limitations. For example, the ground parenchyma in the basal region of several palms shows laterally extended bands of cortical parenchyma (PL. 2, FIG. 11, *l,b*) which may or may not be present in the middle part of the tree trunk and they are generally absent in the apical parts (PL. 2, FIG. 18). Similarly such laterally extended parenchyma bands are restricted to abaxial side of wings in the petiole and are absent in the peduncle (PL. 2, FIGS. 14, 18). In the petiole cortical parenchyma is often lopsided or nearly absent on abaxial curved side, whereas in peduncles it is crushed or suppressed. The vascular bundles in peduncles have a progressive tendency towards condensation of vascular elements till they fuse with each other, and with the thick-walled conjunctive tissue (PL. 1, FIG. 18). This is not there in stem or petiole. Therefore, in deciphering material of fossil palms, all lumped together under the form genus *Palmoxylon*, one has to know the limitation of the special anatomical features of different parts in their members and variations shown by parts such as petiole, stem or peduncles. Then only one is able to draw phylogenetic conclusions. If this is true of living members, where one gets floral parts to ascertain one's conclusions, it is much more difficult to use them in fossil members where the sole guide for their identification is fragments of stem or petiole lumped together as *Palmoxyla*, and incomplete knowledge of their anatomy. Even then sometimes the anatomical method yields wonderful results on account of the relative stability of anatomical as well as morphological characters in certain genera and sub-families. For example, on the basis of stem anatomy Sahni (1946) was able to determine that a

fossil palm from Sagar, M.P. (TEXT-FIG. 15 & PL. 2, FIGS. 12, 13) having a tree trunk 6½ m. in height and 35 cm. in girth was a species of *Cocos* which he named as *Cocos sundaram* (= *Palmoxylon sundaram*). We were able to confirm this identity further by a more detailed study of the stem anatomy in the rooting region of this fossil palm with the help of pieces in which the roots and stem were found in organic connection and it became possible to compare the details of their anatomy with the anatomy of stem and root in the rooting region of the living species of *Cocos* (PL. 2, FIG. 16). It was found that anatomy of stem and roots in *Cocos sundaram* (*Palmoxylon sundaram*) compares well with that in *Cocos plumosa* which is a tree having a tall tree trunk and large rooting region like that in *C. nucifera*, but has small fruits 1.3 cm. in diameter (PL. 2, FIGS. 10 and 15-17 and TEXT-FIG. 15). It is well known that in the genus *Cocos* only *C. nucifera* has very large fruits. The rest of the species of this genus are mostly confined to South America and have small fruits (PL. 3, FIGS. 25-28) like *Licuala* (PL. 3, FIGS. 21, 22).

Many years ago I described a palm fruit under the name *Palmocarpon insigne* (MAHABALÉ, 1950) (PL. 3, FIGS. 29-33). The detailed anatomical study of the fruit in small fruited species of *Cocos* and other genera (TEXT-FIGS. 16-28) showed that this fruit resembles much with the fruits of small seeded *Cocos* like *C. plumosa* or *C. coronata* (PL. 3, FIGS. 25, 27, 28 & 34). A fruit of intermediate size is available in some varieties of *Cocos nucifera* from South India. Even then the fruit therein is at least 5 times larger than that in *C. plumosa*. Kaul (1951) has described under the name *Cocos sahnii* a coconut fruit from the Tertiary of Barmer in Rajasthan which resembles the small-sized fruits of the modern *Cocos*. However, not in all fossil palms can one get fruits and seeds like this for re-establishing relationship based primarily on anatomical characters and that too of one organ only, may be stem, petiole or root; and even then, in certain palms, one such character alone is good enough to do that. For example, Stenzel (1904) found that in one of the fossil palm roots he studied the stele was disintegrated in a way almost identical with that in the roots of living genus *Iriartia*, and hence he named the fossil root as *Iriartes*. In another root I



TEXT-FIGS. 15-28. 15. Reconstruction of *Palmoxylon sundavam* (= *Cocos sundavam*) — partly after Sahni, 1946; 16. *Phoenix sylvestris*. T.S. of fruit.  $\times 2$ ; 17. *Licuala grandis*. T.S. of fruit.  $\times 2$ ; 18. *Cocos nucifera* T.S. of fruit.  $\times 1/6$  N.S.; 19. *Phoenix sylvestris*. T.S. of pericarp.  $\times 47$ ; EP-epicarp, M-mesocarp, E-endocarp, END-endosperm; 20 and 21. Endosperm cells from the peripheral and central regions respectively of the same.  $\times 47$ ; 22. *Licuala grandis*. T.S. of pericarp and seed.  $\times 250$ ; EP-epicarp, M-mesocarp, E-endocarp, END-endosperm; 23 and 24. Endosperm cells from the periphery and central region of albumen in *Licuala grandis*.  $\times 47$ , 25. *Cocos nucifera*. T.S. of pericarp and seed.  $\times 25$ ; EP-epicarp, M-mesocarp, E-endocarp, END-endosperm. 26. *Caryota urens*. T.S. of pericarp.  $\times 25$ ; 27. Endosperm cells of the same as seen in T.S.  $\times 300$ ; 28. *Caryota urens*. T.S. of fruit.  $\times 2$ ; EP-epicarp, E-endocarp, M-mesocarp and END-endosperm.

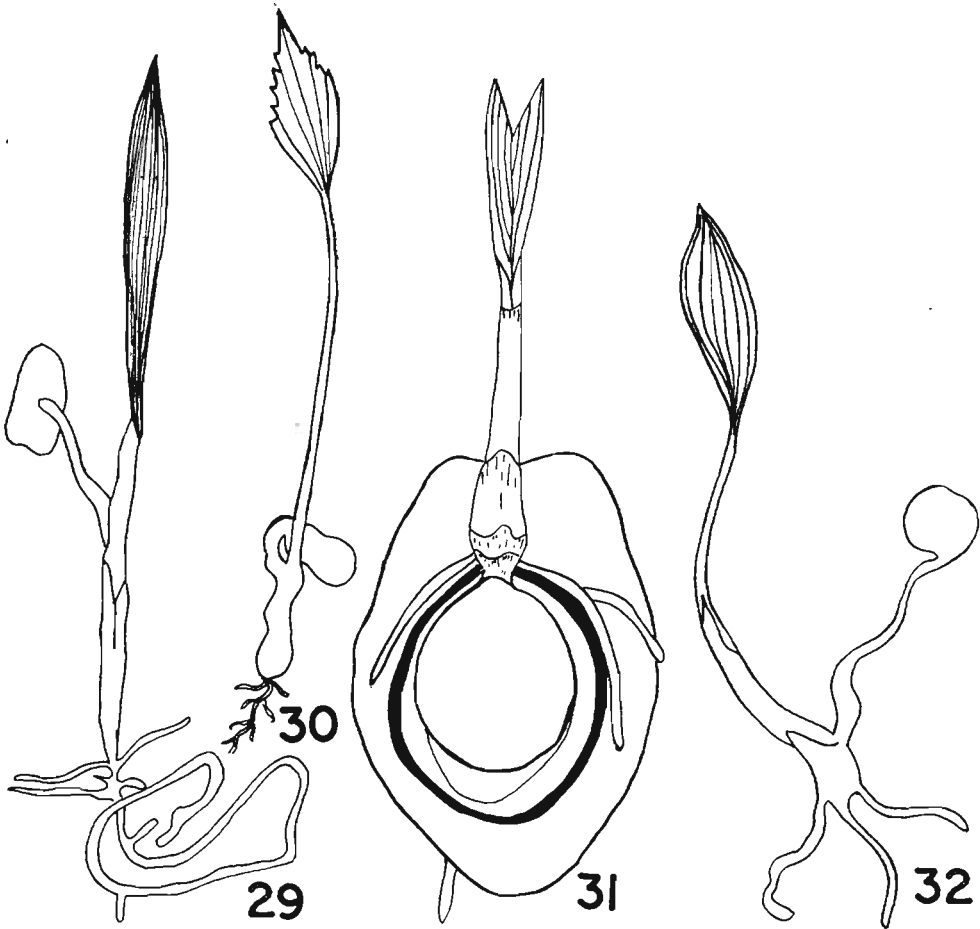
could study from the British Museum collection, it was possible to show that it belonged to some member of the Arecineae on account of the breaking of stele into segments

resulting into the so-called polystelic condition as is noticeable in some members of the living Arecineae (PL. 2, FIGS. 19, 20). Similarly the anatomy of *Palmoxylon rutoti*

described by Stockmans and Williere (1943) strongly suggests that it may be a species of fossil *Sabal*.

It seems to me, that in all sub-families of the Palmae all characters are not evolving at the same rate, and therefore, they cannot be used with equal facility in the phylogenetic discussion on fossil palms. Of course, this is true of living palms also, or as a matter for that of all living taxa. On the other hand, some plants have some conservative characters, which afford valuable clues for comparison. The genus *Nipa* would illustrate this point very effectively. Seward and Arber (1903), Stockmans (1936) who studied this genus known to paleobotanists under the name *Nipadites*, found that the anatomy of stem in fossil

*Nipa* shows slight differences from that in the living member. But their fruits even when varying in size are very much similar to those of the living *Nipa*, *N. fruticans* which is a mangrove. Thus, the fruit of *Nipa burtini* from the London Clay Flora as well as from several other localities recently enlisted by Tialau (1964), or *Nipa hindi* described by Rode (1933), Sahní and Rode (1937) and by me (MAHABALÉ, 1965 unpublished) from the Deccan Inter-trappean beds, or *Nipa sahnii* from Assam described by Lakhanpal (1952), all have the same characteristic umbo on the top of fruit, a large loose seed enclosed in the fibrous mantle of the pericarp and vertical ridges converging into umbo (PL. 3, FIGS. 35-39). This clearly indicates that the fruit is more



TEXT-FIGS. 29-32 — Germination types in palm seeds. 29, 30, 32. Remotive germination of seed in *Phoenix sylvestris*, *Caryota urens* and *Cocos coronata* respectively.  $\times 1/3$  N.S.; 31. Admotive type of germination in *Cocos nucifera*.  $\times 1/6$  N.S.



conservative than other parts and because of this, it proves more helpful in the identification of the genus. But it is not available in every case of fossil palms, mostly known from fragments. Another good example of this is afforded by the fruit of fossil *Manicaria* described by Kaul (1946) which is very much similar to that of the living member (PL. 3, FIGS. 23, 24).

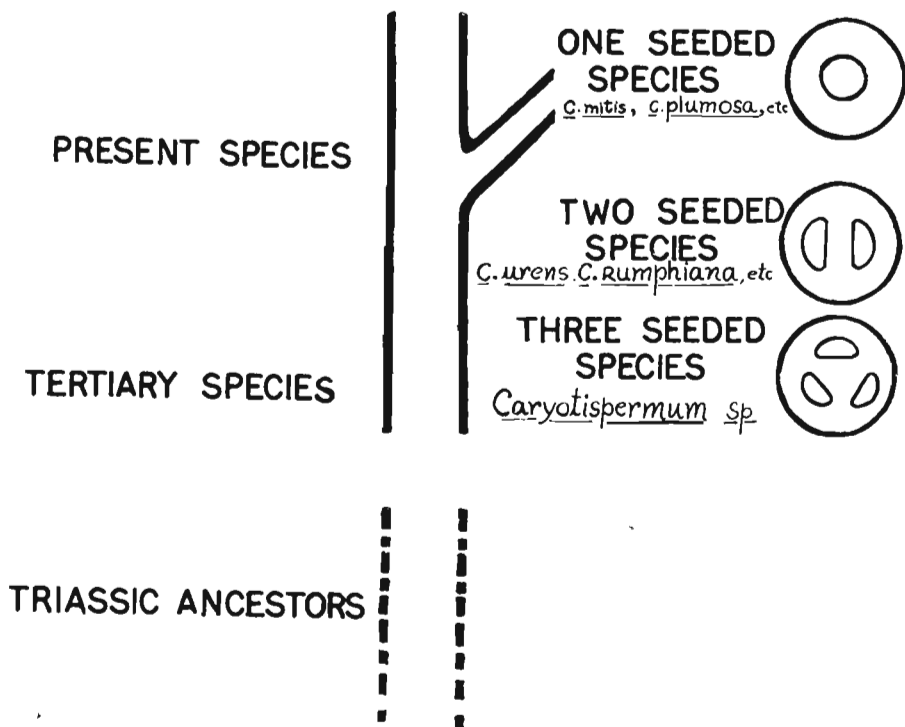
Seed germination in palms also shows differences in the developmental pattern. Saakov (1954), the Russian worker on palms, Tomlinson (1960) and others have shown that there are two types of seed germination in palms: admotive and remotive (TEXT-FIGS. 29-32). This too helps in fixing the phylogeny of species in living palms. But this is hardly possible in fossil palms. But the structure of fruit, seed, pericarp or endosperm in *Cocos*, *Phoenix*, *Licuala*, *Caryota* and other palms have a wide range of variation and that is helpful for this

purpose (TEXT-FIGS. 16-28 & PL. 3, FIGS. 21-22 & 26-34). The seed structure can also be useful in tracing the evolutionary trends as shown below in *Caryota* (TEXT-FIG. 33). In this connection Text-figs 16-18 and 28 and Pl. 3, figs. 25-34 are worthy of note.

**EVOLUTION OF SEEDS IN THE GENERA *COCOS* AND *CARYOTA***

Text-fig. 34

- A. *Seeds with fluid endosperm leaving a central cavity at maturity*
  - a. Seeds large 6-8 cm. in diameter *C. nucifera*
  - b. Seeds small, 1 cm. in diameter *C. coronata*, etc.
- B. *Seeds with cellular endosperm leaving no central cavity at maturity*
  - C. plumosa*
  - C. nucifera* var. *mekapuno*.
  - C. yatay*



**THE PHYLOGENY OF CARYOTA L**

a. Seeds ruminated

- C. schizophylla*
- C. amara*
- C. barbosa*

b. Seeds not ruminated

- C. yatai*
- C. plumosa*

- b, *Fruits trilocular at the base becoming unilocular towards apex. Seed one, irregularly trilobed.*
- b *Fruits regularly unilocular containing a single oval seed*

- C. plumosa*
- C. yatai*

CONCLUSION

Therefore, the problem of using vegetative, anatomical or reproductive characters of palms for identification of taxa, or their phylogeny in fossil palms needs detailed investigation of these characters in living members and their cautious application to the parts available as fossils. This, of course, is an ideal which is far from being near.

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## EXPLANATION OF PLATES

## PLATE 1

*Types of leaves in palms — pinnate and palmate.*

- 1-2. *Sabal palmetto*-palmate leaf.  $\times 1/6$  N.S.
3. *Phoenix sylvestris*-pinnate leaf.  $1/4 \times$  N.S.
- 4-5. *Sabalites* from the Tertiary of Italy  $\times 27$  showing close resemblance with the leaf of *S. palmetto*.  $\times 27$ .
6. *Palmophyllum mohgaonense* Mahab. showing a pinnate leaf resembling that of *Phoenix robusta* and *Phoenix zeylanica*.  $\times 1/6$  N.S.
7. Stoma with bands on the guard cells in *Caryota urens* leaf.  $\times 400$ .
8. Pinnate leaf of *Cocos nucifera* showing lateral attachment of induplicate pinnae.  $\times 1/15$  N.S.
9. *Phoenix sylvestris* leaf showing spines at the base.  $\times 1/9$  N.S.

## PLATE 2

*Anatomy of stem, root, petiole and peduncle in palms.*

10. *Cocos nucifera*. Median L.S. of the stem in the rooting region.  $\times 1/6$  N.S.
11. *C. nucifera*. T.S. of stem immediately above the rooting region.  $\times 3/8$  N.S.
12. *Palmoxylon sundaram* (*Cocos sundaram*). T.S. of stem in the peripheral vascular region.  $\times 7$ .
13. The same, passing through the central region.  $\times 7$  (figs. 12 and 13 after Sahni, 1946).
14. *Cocos nucifera*. T.S. of petiole in the basal region.  $\times 3/8$  N.S.
15. *Palmoxylon sundaram*. T.S. of stem and roots passing through the rootbearing region.  $\times 6$ .
- 16-17. *Cocos plumosa*. T.S. of root showing variable medullary bundles.  $\times 6$ .

18. *Cocos nucifera*. T.S. of peduncle in the basal region.  $\times 1/3$  N.S.

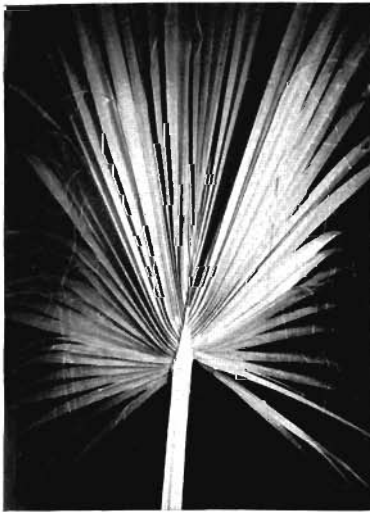
19. Root of a fossil palm from Antigua from the British Museum Collection showing anatomical resemblance with the root of *Areca* shown in fig. 20.  $\times 4$ . Note the broken stele.

20. *Areca catechu*. T.S. of root showing broken stele.  $\times 5.5$

## PLATE 3

*Fruits in fossil and living palms.*

21. Fruit of *Licuala peltata*.  $\times$  N.S.
22. Fruit of *Licuala spinosa*.  $\times$  N.S.
23. Fruit of fossil *Manicaria*, *M. Edwardsii*.
24. Fruits of living *Manicaria*, *M. saccifera*.  $\times 1$  (figs. 23, 24 after Kaul, 1946).
25. Fruit of *Cocos schizophylla*.  $\times$  N.S.
26. Fruit of *Cocos nucifera*.  $\times$  N.S.
27. Fruit of *Cocos plumosa*.  $\times$  N.S.
28. Fruit of *Cocos coronata*.  $\times$  N.S.
29. *Palmocarpon insigne* Mahab. surface view of the fruit showing hollow central cavity in the endosperm.  $\times 1.75$  N.S.
30. The same in T.S.  $\times 2$ .
31. The same, a part of pericarp enlarged (T.S.)  $\times 5.5$
32. *Pamocarpon insigne* Mahab. Entire seed seen from outside.  $\times 2$ .
33. The same.  $\times 2$ .
34. *Cocos plumosa* — T.S. of fruit showing hollow cavity of the endosperm in the centre.  $\times$  N.S.
- 35-36. *Nipa sahnii*.  $\times 1/2$ . (After Lakhnapal, 1952).
37. *Nipadites hindi*.  $\times 1/2$  N.S. (from a specimen in author's collection).
38. *Nipadites hindi*.  $\times 1/2$  (after Rode, 1933).
39. *Nipa fruiticans*.  $\times 3/8$  N.S.



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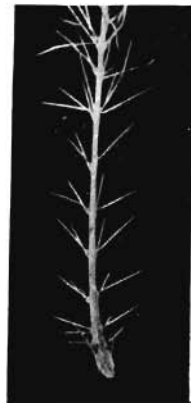
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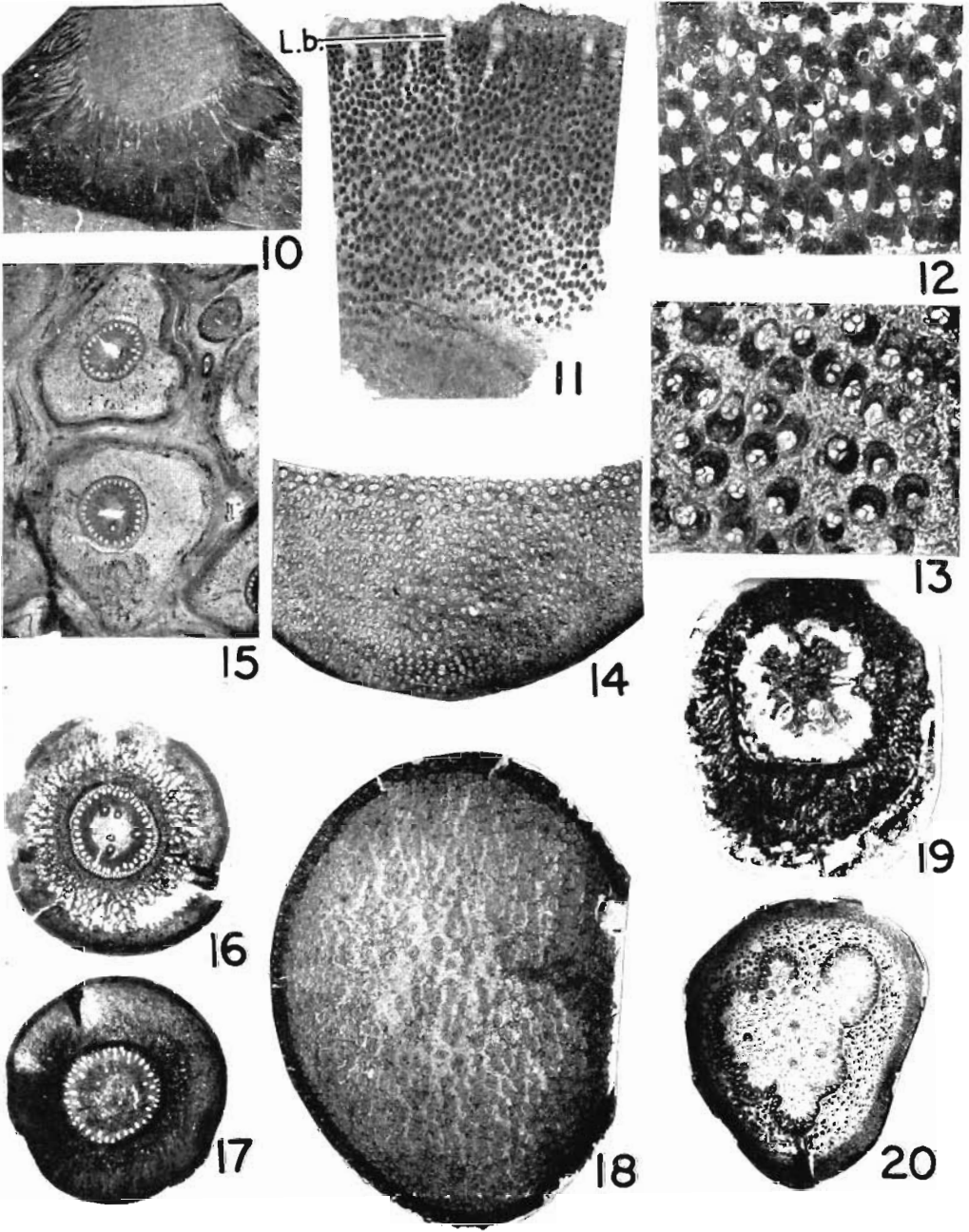
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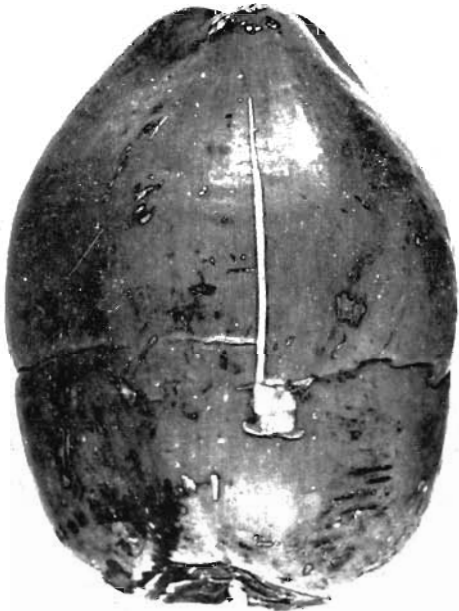


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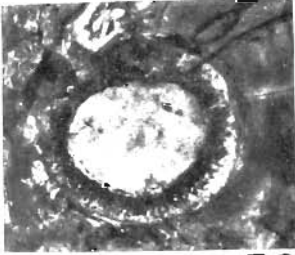
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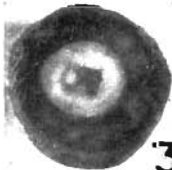
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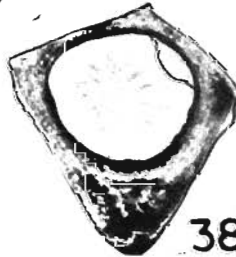
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