RESOLUTION OF THE ARTIFICIAL PALM GENUS, *PALMOXYLON*: A NEW APPROACH

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PIECES of fossil palms have been known to palaeobotanists for quite a long time, the earliest of them dating as far back as 1784, when Burtin (1784) probably for the first time described some pieces of fossil palm wood discovered accidentally in a village near Brugge and Gend in Belgium. This discovery was followed by aquisition of palm stems from different parts of the world by several workers such as De Beunie (1788), Stenzel (1850), Unger (1851, 1853), Ettingshausen (1854), Heer (1855), Schenk (1882, 1891), Delvaux (1885), Staub (1887), Knowlton (1889), Crié (1892), Rutot (1898), Sterzel (1900), Seward & Arber (1903), Lignier (1907) and others. These palm stems occurring in different parts of the world dated from Cretaceous to Pliocene periods, the only authentic record of palms belonging to earlier period being that of palm-like plants from Dolores formation (Triassic) in South Western Colorado (BROWN, 1956) and of a palm leaf described by Lignier (1907) under the name *Propalmophyllum liasinum* from the Liassic of Normandie in France. Some of the early fossil material consisting of pieces of stem, root and few leaves was described by Unger (1823-1851), Stenzel (1850), Massalongo (1854), Schimper (1872), Schenk (1882) and others and a comprehensive account of this varied material was given by Stenzel (1904) in his later monumental work "*Fossile Palmenhölzer*" published in 1904. This extraordinary piece of life's work of this great German savant, based on a rich variety of specimens, is so replete with observations, that it is rightly said to have laid the foundations of studies on fossil palms. Judging from the mere vastness of materials drawn from all over the world and the lack of modern equipment at the disposal of Stenzel (1850, 1904), one is simply struck by the tremendous industry of this untiring investigator of fossil palm stems, working for more than half a century. Naturally he developed a keen insight in palm anatomy. Many of his ideas regarding the anatomical features in palms were quite sound, which enabled him to formulate his well-known system of classification of fossil palms, but a few of them were undoubtedly such as could not have stood the scrutiny of later work, particularly those concerning the mechanism of increase in the girth of a palm tree trunk. With the publication of his work "*Fossile Palmenhölzer*" in 1904, the first phase in the history of studies on fossil palms may be considered to have come to an end.

Simultaneously with him in the same century another equally distinguished German worker Hugo von Mohl (1845) was working on the living palms and their anatomy, and in the light of his studies, he devised a readymade classification of palms based mainly on the external characters of stem. Strangely enough, both these workers had realized the importance of ground tissue in the study of palm stems and had noticed it to be quite distinct in several species. But the main interest of von Mohl was concentrated in the secondary increase in the tree trunk of palms, which, according to him, was due to stretching of some undifferentiated cells lying in between various fibro-vascular bundles and in the axils of leaves, and not due to the presence of any definite tissue-like cambium, characteristic of dicotyledons and arborescent lilies like *Dracaena* or *Cordyline*.

In the next phase of work on palms a large amount of fossil material consisting of fruits, seeds, leaves, etc., was brought to light in the Tertiary strata of various parts of the world such as the lignite beds and brown coal in Rhineland, fossil remains of stems and roots carbonized, silicified or calcified in the London Clay flora (REID & CHANDLER in 1933), Tertiary beds of Paris Basin, strata around Brussels, in the Upper Pièrre Cretaceous of South Dakota, Cretaceous of North America, Denver formations of Eocene period in the United States, in Colorado and Washington beds, in Antigua in West Indies, in Italy and Sardinia, in Central Europe, in Libya in North Africa, in Egypt, India, Korea, Japan, etc. At the same time De Candolle

(1855), Mirbel (1839), Martius (1823-1850), Griffith (1850), Hooker (1854, 1854-55), Drude (1877 , 1889), Baillon (1895), Bobisut (1904) and others were actively busy with the morphology, floristic, taxonomy and geographical distribution of living palms, while Wendland (1875), Cormack (1896), Gillain (1900), Drabble (1904), Schoute (1912), Stevens (1912) with their anatomy. A more extensive series of works on living palms appeared later by Beccari (1911-1918), Gatin (1912), Blatter (1926) Solereder & Meyer (1928), Jenkins, Glaassen & Markley (1949), Mahabalé (1954), and others who worked on their morphology, ecology, economic uses or anatomy. The total number of workers working on different aspects of palms, their morphology, systematics and economic uses has been more than 200, although only a few of them were attracted to the study of their anatomy either as representatives of monocotyledons or as an aid to our understanding of the rich fossil material of palms now known nearly from all over the world. Work of the abovementioned anatomists, however, brought out two significant facts, namely, that the secondary growth in the arborescent trunks of palms is not due to cambial activity, but to an entirely different mode of increase in the dimensions of cells located in between the young fibro-vascular bundles and the dormant parenchyma located in the axils of leaves and in the lower part of a tree trunk from where the roots arise; and that the shape and distribution of vascular bundles, in dermal, subdermal and central zones of stem, their kinds, arrangement, grouping in different organs in a palm tree, the nature of ground tissue and distribution of fibrovascular bundles are highly characteristic in different palms. In this connection the work of Cormack (1896) and Drabble (1904) on anatomy of palm roots and that of Schoute (1912) on the anatomy of stems, his application of statistical methods to the study of ground parenchyma and variation in it, and the general summary of work on palm anatomy by Solereder & Meyer (1928) deserve special mention.

A third phase in the studies on fossil palm woods began when Chiarugi (1929) found them in North Africa, Sahni (1931) and Rode (1933 a, b) found them in India and Kaul (1935-38) started attempting to resolve them into natural genera on the basis of ground tissue. On the advice of Professor Sahni (1938), Kaul (1935,1938) was able to apply quite successfully the data on the anatomy of ground tissue in living palms to the analysis of fossil palms and showed that *Palmoxylon sundaram* of Sahni was a species of coconut, *Palmoxylon mathuri* a species of *Bactris*, *Palmoxylon coronatum* a species of *Borassus* and an undescribed palm from Antigua in the collection of British Museum a species of *Phytelephas*. Their work naturally focussed the attention of workers on the importance of ground tissue in palms and on the aid it offers to workers on fossil palms in resolving the artificial genus *Palmoxylon* of Schenk.

Simultaneously with these workers, a number of other workers in India and abroad brought out many more fossil palm stems, particularly Kryshtofovich (1927), Rode (1933), Kirchheimer (1933), Gothan (1936, 1942), Jongmans (1935), Dubois (1936), Shukla (1939), Ogura (1952), Lakhanpal (1955) and others, and a new period of more intensive and critical studies based on comparative anatomy of living and fossil palms was ushered in. In this connection work on the anatomy of Cyclanthaceae by Surange (1950), reinterpretation of *Palmoxylon sahnii* Rode by Sahni & Surange (1953) need to be specially mentioned. It clearly indicated, that all the members previously included under the fossil genus "*Palmoxylon*" may not all be palms ! Some of them could as well be other monocots, such as members of the Cyclanthaceae, Sparganiaceae, Pandanaceae, Gramineae, Cyperaceae, etc., like the well-known genus *Rhizocaulon* of de Saporta (1881-1885) from Auvergne belonging to Gramineae. A very important monograph of this period, dealing with anatomy of fossil palms of Belgium was brought out by two distinguished co-partners in life and work, Francois Stockmans and Yvonne Williere (1943) who have described in detail the anatomy of nearly 12 fossil palms, several of which were quite new to science. They also made a critical estimate of the systems of classification of fossil genus *Palmoxylon* proposed by Unger, Stenzel, Sahni, Schoute and Kaul. In their concluding remarks they said:

" L'étude des *Palmoxylons* est encore dans l'enfance, dans la période de simple description, dirons-nous. Des matériaux tels que ceux de Loppem et de Beaufaux font entrevoir cependant la possibilité d'établir à quelle partie de la plante on a affaire, base ou sommet du tronc, noeud ou entre-noeud,

(1) VON MOHL'S CLASSIFICATION OF PALMS

A — *Geonoma*-like

B — *Calamus*-like

C — *Mauritia*-like

D — *Cocos*-like

E — So-called stemless

(2) STENZEL'S CLASSIFICATION OF *PALMOXYLON*

A — *Mauritia*-like:

(i) *Antiguensia*

B — *Corypha*-like:

(ii) *Cordata*

(iii) *Sagittata*

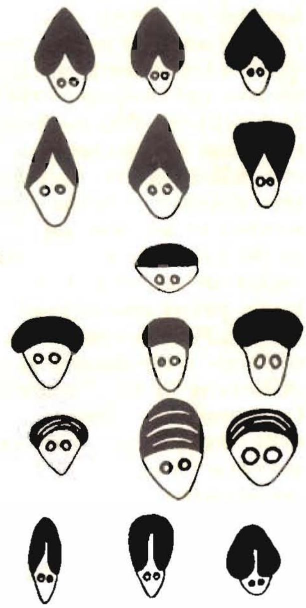
(iv) *Complanata*

C — *Cocos*-like:

(v) *Reniformia*

(vi) *Lunaria*

(vii) *Vaginata*



D — *Radices*:

(viii) Roots

TEXT-FIGS. 1, 2 — *Von Mohl's and Stenzel's Classification of Palms.*

pédoncule fructiferè, pétiole foliaire. Peut-être pourra-t-on établir dans quel groupe ils doivent se classer. Mais tant qu'on n'a pas à sa disposition une étude complète et récente des palmiers actuels faite en vue de recherches paléobotaniques, ce point de vue ne peut être envisagé. Aussi attendons-nous avec impatience les travaux pleins d'intérêt que nous ont promis le Prof. Sahni et ses élèves."

Professor Sahni (1938) also had made somewhat similar observations in 1938 regarding the resolution of the fossil genus *Palmoxylon* in his presidential address to the Botany section of the 25th Indian Science Congress at Calcutta and also in a later paper by him on *Palmoxylon sclerodermum* (SAHNI, 1943).

By about 1942 at the suggestion of Professor Sahni I took up the work on palms and worked out in detail the structure in about 30 palms embracing several aspects such as embryology, structure of seeds, cytology, anatomy of different parts such as roots, peduncles, etc. A number of my students collaborated with me in working out the details, but still much of this work is yet to be published. Very recently Eames (1953) has studied the morphology of palm leaf and has emphasized the importance of morphological studies on palm leaf. At present there is a great upsurge for studying the anatomy of monocotyledons such as grasses, palms and rushes, and references here and there are found in the works of Frost (1930 a, b), Cheadle (1941, 1943), Bailey (1944), d'Almeida and Ramaswamy (1948), d'Almeida & Correa (1949), Eames & Mac Danniels (1951), Metcalfe (1953), etc. Cheadle (1953) especially has made a comprehensive study of the vessel members in the monocotyledons.

Bailey (1944) had long ago emphasized the importance of the study of vessel specialization in dicots and monocots. Metcalfe (1950) and his school have also been doing quite a lot of work on the anatomy of angiosperms and Greguss (1955) on gymnosperms. Naturally all this work should have had its reflection on the anatomy of palms. I and my collaborators, therefore, after studying the detailed anatomy of several species wanted to see how far these modern trends in the anatomy of vascular plants would be useful in understanding the phylogeny of living palms and in resolving the fossil palm genus *Palmoxylon*. New techniques and methods were developed in the Department of Botany at the University of Poona and a large number of genera and species have been fully investigated tribewise, genuswise and partwise; and some of them are still being investigated. The results obtained so far are quite interesting and in the next few paragraphs it is proposed to show how some of these are helpful in having a new approach to the old problems of phylogeny, relationships and anatomy of fossil and living palms.

Text-fig. 1 shows von Mohl's classification of palms, based as it is, mainly on the external morphology of stem. Now by citing work on a single genus like *Phoenix* investigated in very great detail by a student of this department, Mr. M. V. Parthasarathy, it can easily be shown that von Mohl's classification breaks down in a number of cases. For example, as per Mohl's classification the species, *Phoenix acaulis* would belong to stemless type (PL. 1, FIG. 1), *Phoenix paludosa* to reedy *Geonoma-Calamus* type (PL. 1, FIG. 3), and *Phoenix sylvestris* to normal arborescent *Cocos* type (PL. 1, FIG. 2).

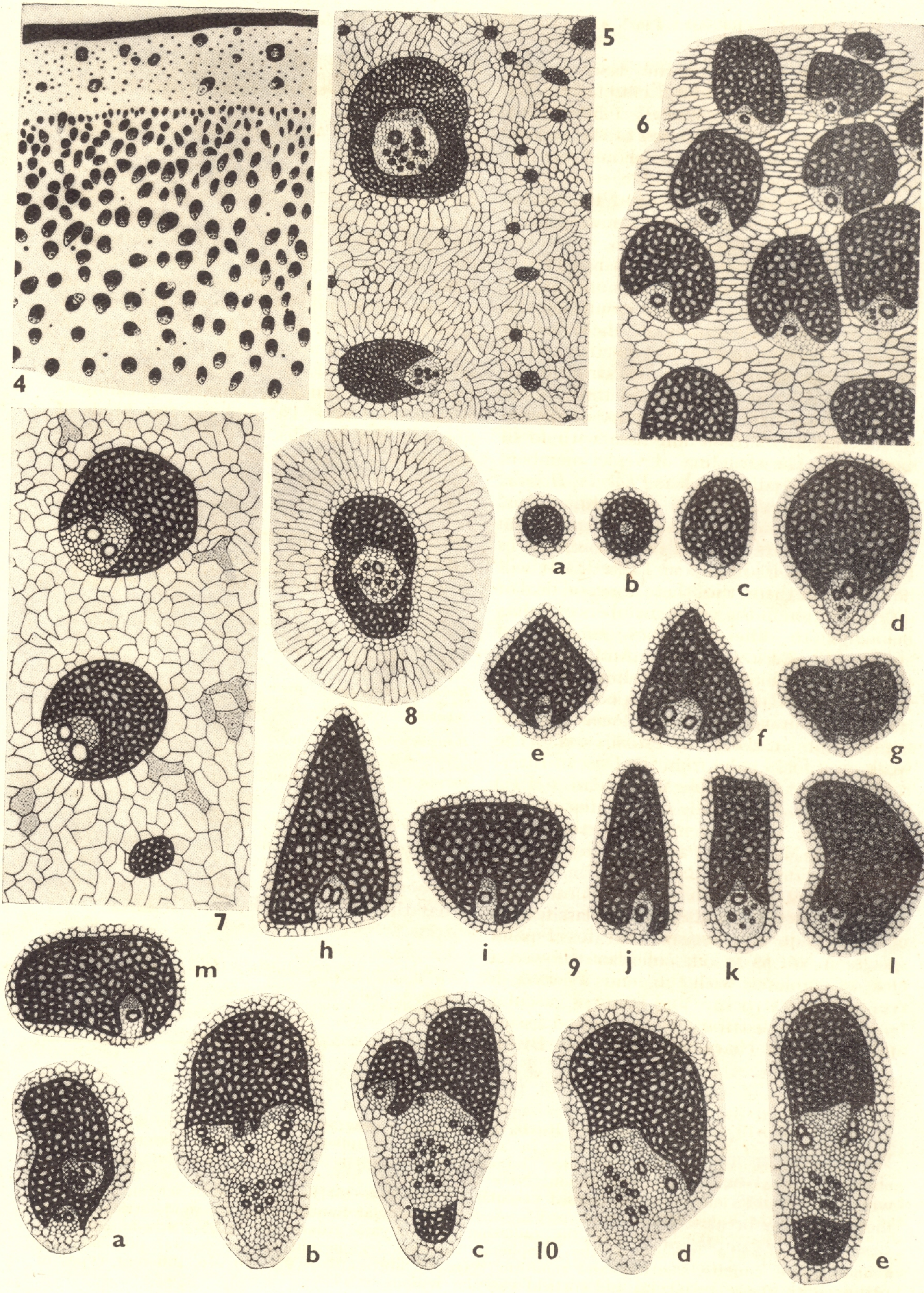
An outline of the classification of fossil palms followed by Stenzel (1904) is shown in Text-fig. 2 and its combination with Mohl's system made by Sahni (1943) is shown in Text-fig. 3. It will be seen that whereas Stenzel's classification has a greater merit, it also breaks down in a number of cases. For example, in a single species of *Phoenix* like *P. paludosa* we get all kinds of fibrovascular bundles having lunate, sagittate cordate and complanate caps of sclerenchyma (TEXT-FIG. 4), and, therefore, unless one investigates in detail, the changes that take place in the shape and distribution of vascular bundles, variability of the ground tissue in different parts of the same palm, and in different palms, it would be hazardous to rely on them while dealing with the specimens of fossil palms; because very often one cannot recognize with certainty whether a given specimen of fossil palm wood represents a stem piece, or a piece of petiole, a peduncle or the midrib of a large leaf. In the absence of this knowledge one merely goes on creating a large number of artificial species of *Palmoxylon* for every piece of fossil palm wood he gets, perhaps inevitably, little realizing that they may as well be parts of the same palm or perhaps parts of the same organ. An improvement upon this arbitrary system of classification was made by Schoute (1912) and Kaul (1935), using the nature of the ground tissue for this purpose; but as stated above, unless one is familiar with, and takes into account, the variability of ground tissue in different species of palms and in different parts of the same palm and tests it statistically, the applicability of this method also to fossil palms has a limited scope. It has, however, the merit of bringing out sometimes striking cases of similarity between living and fossil members already cited, provided one is sure that he is dealing with the corresponding parts of a non-variable species. And since this cannot always be granted,

TEXT-FIG. 3 — MOHL-STENZEL'S CLASSIFICATION OF PALMS AS COMBINED BY SAHNI (1943).

A. *Mauritia*-like palms, with the outer bundles crowded, their fibrous parts being many times greater than the vascular; and with the inner bundles far apart, their fibrous parts being smaller than the vascular.
   (i) *Antiguensia*

B. *Corypha*-like palms, with the outer bundles more or less densely crowded, the fibrous part being much larger than the vascular. The inner bundles somewhat further apart than the outer, their fibrous part being larger than the vascular.
   (ii) *Cordata*
   (iii) *Sagittata*
   (iv) *Complanata*

C. *Cocos*-like palms, with the outer and inner bundles uniformly distributed, near each other of similar size and similar structure.
   (v) *Reniformia*
   (vi) *Lunaria*
   (vii) *Vaginata*



TEXT-FIGS. 4-10.

its successful use in all the cases is not possible. It was, therefore, emphasized by me (MAHABALÉ & UDWADIA, 1950, 1951) while working on the anatomy of the peduncles in living palms, that we should use the data from all sources available collectively for arriving at decisions regarding the phylogeny of living species and for knowing their affinities with the fossil ones.

It is well known that Frost (1930), Cheadle (1941), Bailey (1944) and others have arrived at some striking results on the basis of vessel structures in dicotyledons and monocotyledons. Following this line of work, it was thought, that the structure of vessel members in palms would throw some additional light on the phylogeny of species of a genus or on their affinities with fossil members. The structure of vessel members in a number of palms such as *Phoenix, Howea, Arenga, Areca, Borassus, Corypha, Cocos, Caryota*, etc., was investigated and some important points brought out are shown in Plate 2, Figs. 16-30 and in Table 1. It will be seen from them, that there is a good deal of differentiation in the vessel members of palms belonging to different tribes, genera and species (PL. 2, FIGS. 23-30). And, therefore, this study is likely to be helpful in interpreting the relationships of species *inter se* and in resolving the fossil forms lumped together under the name *Palmoxylon*. The work on a fossil palm from the Deccan Intertrappean series of Mohgaon Kalan (M.P.) by Mr. S. R. Deshpande of this department and on the living members of the genus *Phoenix* by Mr. M. V. Parthasarathy may be cited as examples to the point.

After a detailed study of the ground tissue and fibrovascular bundles in different species of *Phoenix* it was noticed that fossil palm specimen No. 61 in our collection showed a clear resemblance with the genus *Phoenix* in regard to the structure and kinds of vascular bundles, their distribution, the ground tissue, and such other characters (Compare PL. 1, FIGS. 4, 7, 8 with PL. 1, FIGS. 13, 14, 15, and PL. 1, FIGS. 7, 8 with PL. 1, FIGS. 11, 12). Particularly it compared very favourably with those in *Phoenix robusta* and *Phoenix rupicola*. These two living species are anatomically and taxonomically closely related. The former is an endemic in a village, called Bhorkas, in Poona district, in Nandagaon Ghats in Nasik district, and in Parasnath Hills in Bihar. *Phoenix rupicola*, on the other hand, is an ornamental palm found wild in Assam and other places in the Eastern Himalayas. The ground tissue in these two species (PL. 1, FIGS. 13, 14) and in the fossil specimen No. 61 in our collection (PL. 1, FIG. 15) has similar appearance and dimensions (*see* TABLE 1); and the two kinds of fibrovascular bundles in them are similarly distributed. Comparing the structure of late metaxylem vessels in longitudinal section

TABLE 1 — SHOWING SPECIALIZATION IN THE LATE METAXYLEM VESSEL MEMBERS IN THE CENTRAL REGION OF THE STEM IN PALMS

SPECIES	VESSEL MEMBER		KIND OF BARS	NO. OF BARS IN THE PERFORATION PLATE
	Length *mm.*	Breadth *μ*		
Howea belmoreana Becc.	0·826	122	Straight	4-5
Arenga saccharifera Labill.	1·397	156	,,	3-6
Areca catechu L.	1·524	186	,,	30-35
Borassus flabellifer L.	0·953	263	,,	0-0
Corypha umbricalifera L.	1·058	202	,,	0-2
Cocos nucifera L.	1·132	198	,,	1-3
Caryota urens L.	1·205	176	,,	0-1
Phoenix sylvestris Roxb.	1·200	150	,,	2-5
Phoenix zeylanica Trim.	0·600	156	,,	0-1
Phoenix rupicola And.	0·350	152	,,	2-5
Phoenix humilis Royl.	0·380	150	,,	0-2
Phoenix paludosa Roxb.	2·750	104	,,	4-6
Phoenix robusta Hook.	1·300	200	,,	3-6
Phoenix dactylifera L.	3·700	207	Bifurcated at places	8-10
Phoenix reclinata Jacq.	3·600	125	,,	12-20
Fossil No. 61, a species of *Palmoxylon* from Mohgaon Kalan (Dist. Chhindwara). Horizon: Eocene	1·700	182	Straight	2-6

←

TEXT-FIGS. 4-10 — *Phoenix paludosa* Roxb. T.S. of stem (Diagrammatic). 4, T.S. of stem showing the distribution of fibrovascular bundles in the cortical, peripheral and central vascular regions. × 9. 5, fibrovascular bundles and fibre bundles in the cortical region. × 95. 6, fibrovascular bundles in the peripheral vascular region: Note the reniform fibre-caps. × 95. 7, two fibrovascular bundles and a fibre bundle in the central vascular region: Note the lunate shape of sclerenchyma and the pattern of the fundamental tissue. × 95. 8, a fibrovascular bundle from the mid-cortical region showing engulfing sclerenchyma and the radiating parenchyma around it. × 95. 9 a-m, different types of fibrovascular bundles in the peripheral vascular region and in the central pith showing circular, lunate, cordate, sagittate and reniform types of fibre-caps. × 95. 10 a-e, different types of fused bundles in the peripheral and cortical vascular region. × 95.

in all these three (PL. 1, FIGS. 5, 6, 9, 10), it was noticed that the end part of metaxylem vessels in the fibrovascular bundles in the central pith region of a stem, the perforation plate, possessed a similar pattern. The shape of vessel member and thickening on it were also similar; and the transverse bars were present in all the three (*cf.* PL. 1, FIGS. 6, 10, 5, 9). Obviously the fossil palm specimen No. 61 in our collection is a species of *Phoenix* and perhaps a close ally of *P. robusta* and *P. rupicola*. The real confirmation of the identification of this fossil, however, came from the structure of the secondary metaxylem vessel members in fibrovascular bundles as studied in longitudinal sections as seen in Pl. 1, Figs. 9, 10, 5 and 6.

Evidently study of vessel speicalization in palms does provide a new approach to the analysis of the fossil palms. We have reasons to believe that in due course this may enable us to understand better, affinities of different palms whether living or fossil. At any rate, it may safely be said for the present, that it will give more certainty to our conclusions based on other characters such as shape of fibrovascular bundles and the ground tissue. It should, however, be remembered that since we are dealing with extremely fine structures such as vessel characters, our conclusions arrived at on their basis alone, have to be confirmed, wherever possible, with the help of other characters anatomical and or floristic. One has, therefore, to be cautious in applying this method to the resolution of Palmoxyla which are quite a heterogeneous group. Because, Cheadle (1943, 1953) and others have shown that in monocotyledons the vessel specialization starts in roots, then in stems and lastly in leaves. We have no information whatsoever regarding the peduncles, and unless it is available, it will be rash to give an opinion merely on the similarity of vessel structure in two living or fossil palms. One has also to remember that Bailey (1944) and others believe that vessel characters have arisen independently in monocotyledons and dicotyledons polyphyletically, and, therefore, one need not be surprised if one finds a similar vessel or any other character in two different palms quite unrelated to each other. On the other hand, a group of similar characters in two or more palms is very likely to be indicative of their real affinities.

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EXPLANATION OF PLATES

PLATE 1

1-15. Morphology of the stem of some *Phoenix* species and anatomy of some living and fossil species of *Phoenix*.

1. *Phoenix acaulis* Buch. A stemless type.
2. *Phoenix sylvestris* Roxb. Arborescent, *Cocos*-type.
3. *Phoenix paludosa* Roxb. Reedy, *Geonoma-Calamus* type.

4-8. Fossil No. 61, *Palmoxylon* species from Mohgaon Kalan (Dist. Chhindwara, M.P.): Horizon Eocene.

4. T.S. of the above showing 3 vascular bundles and the ground tissue. × 48.
5. L.S. of the same showing 2 large vessels at the two extremes. × 30.
6. Perforation plate of a late metaxylem vessel showing transverse bars. × 300.
7. A single vascular bundle from the same. × 75.
8. T.S. of the same showing two types of fibrovascular bundles in the pith. × 48.
9. Perforation plate of the late metaxylem vessel in the stem of *Phoenix robusta*. × 300.
10. The perforation plate in the same in *P. rupicola*. × 300. Compare Fig. 6 with Figs. 9 and 10.
11. A single fibrovascular bundle in *Phoenix robusta* stem. × 75.
12. The same in *P. rupicola* stem. × 75. Compare Figs. 7 and 8b with Fig. 11 and Fig. 8a with Fig. 12.
13. T.S. of stem of *P. rupicola*, central vascular region, showing fibrovascular bundles. × 48.
14. The same in *P. robusta*. × 48.
15. Fossil specimen No. 61, *Palmoxylon* sp. showing the ground tissue. × 71. Compare the ground tissue here with that in *P. robusta* shown in Fig. 14.

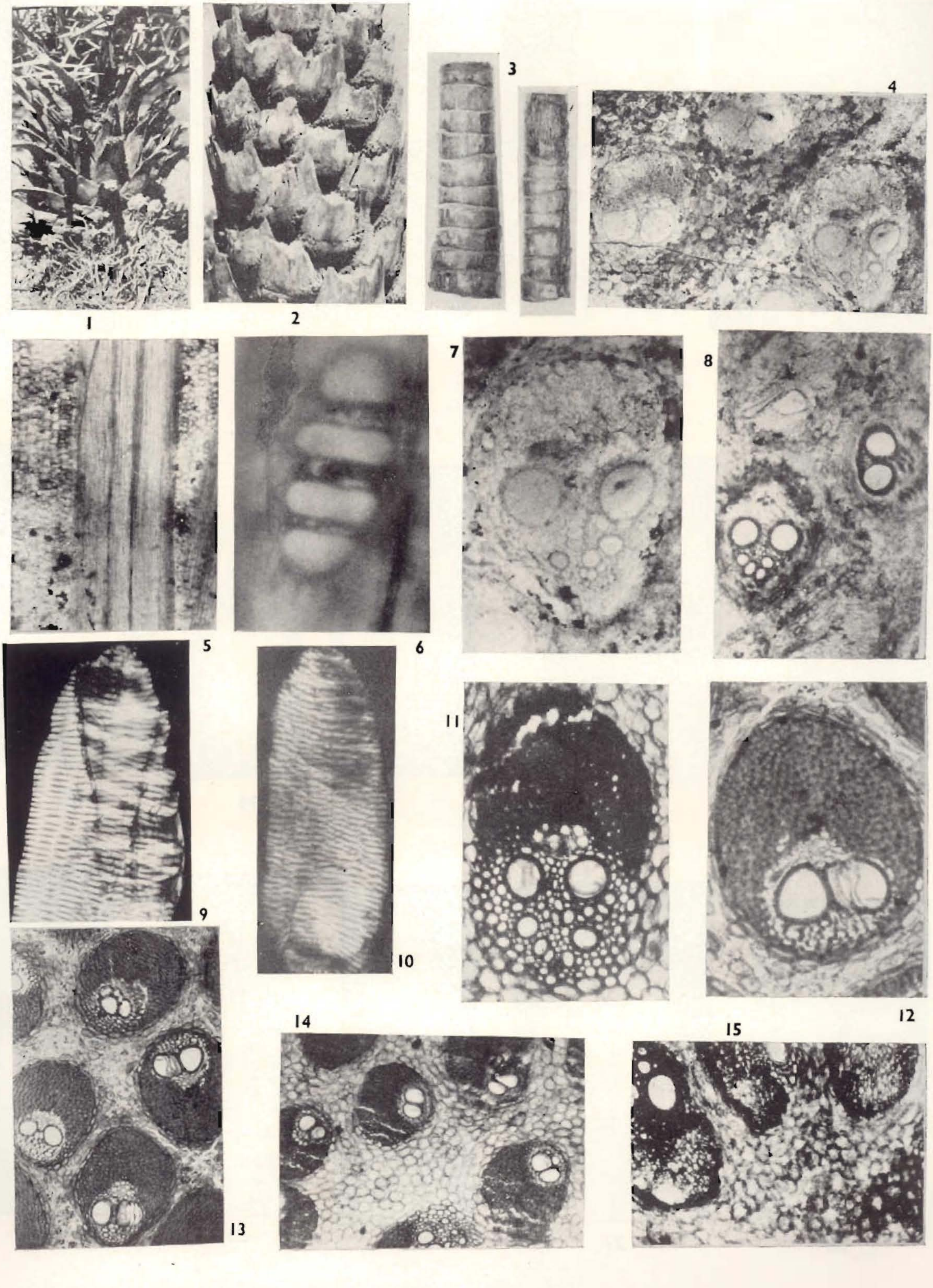
PLATE 2

16-30. Vessel specialization in the late metaxylem in palm stem. (Photographed under polarized light.)

16. *Cocos nucifera* L. × 233.
17. *Arenga saccharifera* Labill. × 273.
18. *Corypha umbraculifera* L. × 265.
19. *Howea belmoreana* Becc. × 265.
20. *Areca catechu* L. × 183.
21. *Caryota urens* L. × 266.
22. *Borassus flabellifer* L. × 217.

23-30. Vessel specialization in species of *Phoenix*.

23. *P. zeylanica* Trim. × 265.
24. *P. humilis* Royl. × 265.
25. *P. sylvestris* Roxb. × 265.
26. *P. rupicola* And. × 265.
27. *P. robusta* Hook. × 265.
28. *P. paludosa* Roxb. × 265.
29. *P. dactylifera* L. × 265.
30. *P. reclinata* Jacq. × 183.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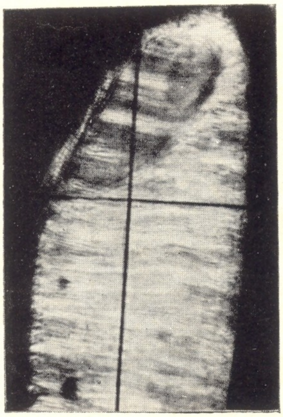

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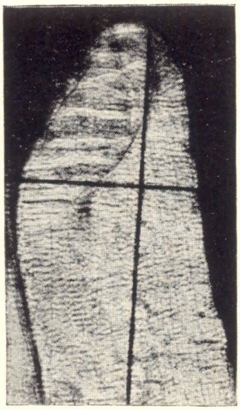

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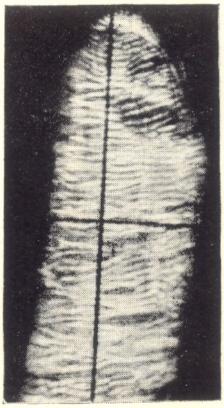

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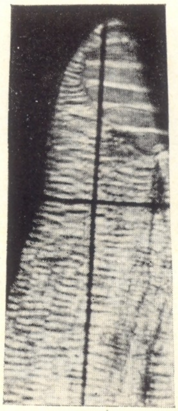

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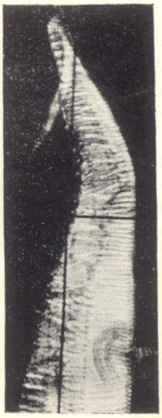

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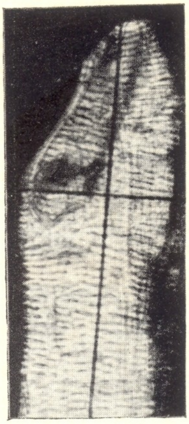

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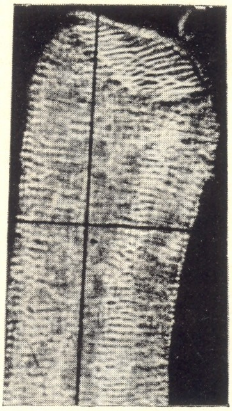

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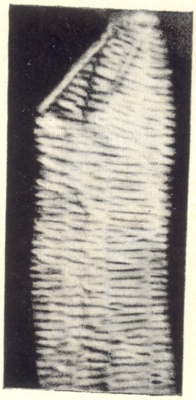

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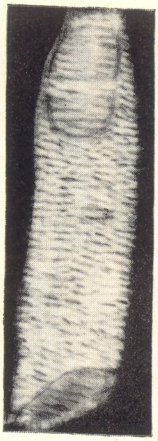

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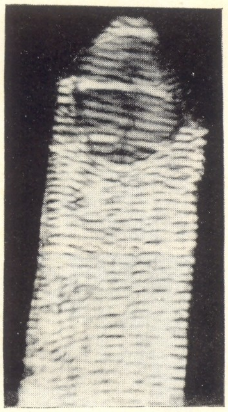

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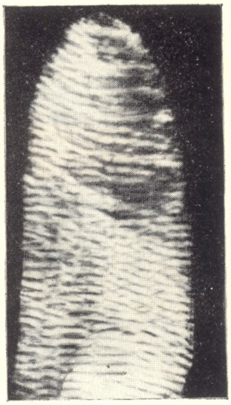

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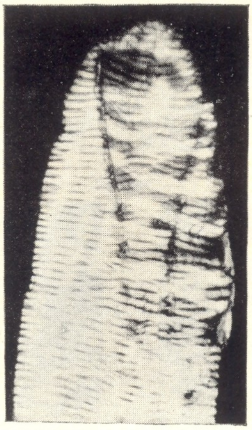

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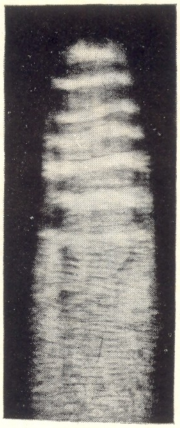

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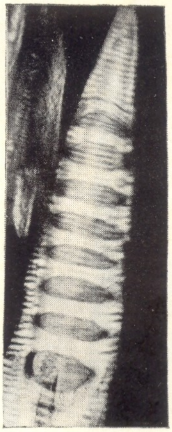

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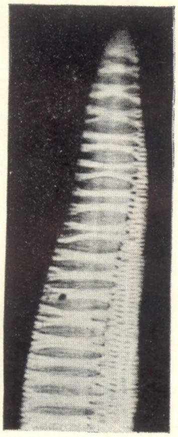

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