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TENTH BIRBAL SAHNI MEMORIAL LECTURE

THE PALMS

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CHAIRMAN, Shrimati Savitri Sahni, Members of the Governing Body, Director and Faculty members of the Institute, learned members of the gathering, ladies and gentlemen, at the outset I wish to express my deep sense of gratitude and sincere thanks for the rare privilege given to me to deliver the 10th Birbal Sahni Memorial Lecture. On this occasion, we cannot forget to pay our homage to the illustrious son and great scientist of India, who was mainly and solely responsible for the establishment of this Institute which was his life's ambition. It is our duty to stand by and put greater efforts to the cause for which he dedicated his life. We remember him always and more particularly on his birth day which falls on 14th November.

I have chosen to speak on " Palms " today, partly because of Prof. Sahni's one of the interests was in ' Deccan Traps ' where he described some palms for the first time and partly because of my initial work on living palms with Professor T. S. Mahabale.

The Tertiary flora of several lands contains numerous angiosperms many of which are impressions. Besides impressions, petrified stems, flowers and fruits are also available. These when critically identified provide very valuable information and reliable clues for phylogenetic and other considerations. To make such identification certain, one very often has to investigate quite a number of genera and species of living plants. The palms are one of those such groups. Professor Sahni who realised this very much assigned this task to Prof. K. N. Kaul and Prof. T. S. Mahabale, who have made significant contribution in the study of living palms in the course of several years.

INTRODUCTION

The palms form a characteristic feature of tropical vegetation with their familiar vegetative habit with a crown of leaves at the end of an unbranched stem. Griffith (1850) said, "Palms, although so diversified in structure form one of the most marked Natural Families of plants; they are therefore distinguishable at first sight, in all stages of their growth ". Linnaeus and later Endlicher styled them as " Principes " — the Nobles of their class. Von Martius said, " they are distinguished as the splendid offspring of Terra and Phaebus ".

Historically palms are an ancient family ranging from Cretaceous to modern period and according to some even earlier (Lignier, 1907). It is reported that the oldest fossil of flowering plant with palm-like imprints (*Sanmiguella lewsii* R. W. Brown — Triassic — Dolores Fm., near Placerville, Colorado) was found in 1953 and dated about 65,000, 000 years old. However, doubts exist with respect to its identity whether a palm or other monocot and its age. The largest leaves seem to be in ' raffia palm ' (*Raphia ruffia*) of Mascarene islands in Indian Ocean and in ' Amazonian bamboo palm ' (*Raphia toedigera*) of South America in which the leaves measure 65 feet base to apex and with petioles up to 13 feet. The largest seed is that of the double coconut (*Lodoicea seychellarum*); the single seeded fruit may weigh about 18 kg. It grows only in the Seychelles islands in the Indian Ocean.

The natural order Palmae consists of about 2779 species distributed in 212 genera (Moore, 1973). Most of them are localised in various floral regions with the exception of 3 genera *Cocos*, *Elaeis* and *Raphia*. The coconut (*Cocos nucifera*) has a wide distribution on the coasts of tropical America, in India and south seas, but all its allies are American. The oil palm (*Elaeis guinensis*) is indigenous in western tropical Africa and widely distributed. One species of *Raphia* is American, whereas several other species are widely distributed more especially in Africa and Madagascar.

The adult palm has generally a tall, woody unbranched stem bearing a crown of leaves. *Hyphaene*, however, is a branched one. The stem in palms varies greatly in form. *Nypa*, *Phytelephas* and *Geonoma* have short rhizome or stock bearing radical leaves, often branching below ground. Genera like *Calamus*, *Desmoncus* are climbers with a thin reed-like stem and long internodes. Others have a tall stem overtopped by a crown of leaves. The trunks of some are almost perfectly smooth, others are rough with concentric rings, the scars of the fallen leaves. Many are clothed with a woven or hairy fibrous covering or beset with cylindrical or flat spines.

The foliage generally forms a magnificient crown at the end of the trunk. The leaves are large, often gigantic. We can easily distinguish two main types of leaves, the palmate or pinnate, which give the popular names Fan-palm and Feather-palm respectively. Often they are with characteristic foldings or tearings, palmatisect or pinnatisect. Occasionally the segments are divided again (bipinnatisect) as in *Caryota*. The primary root soon perishes after germination and is replaced by adventitious roots arising from the base of the stem. Sometimes the development takes place above ground, the stem being supported by prop-like adventitious roots. The flowers of a palm are never solitary. They always form usually a large and much branched inflorescence, either as a simple or compound spike or a much branched panicle. The branching is racemose and the flowers are often embedded in the fleshy surface of the branches, often called the spadix. A single spathe of the "Date Palm" contains about 12,000 male flowers. In *Metroxylon rumphii* about 208,000 flowers are produced in one spathe and about 624,000 in a single tree. The inflorescence is usually axillary, arising in the axil of the current leaf or a lower one on the stem as in *Caryota*. In *Corypha* it is terminal and the life of the plant ends once it is produced.

Our knowledge of Indian palms became better due to the untiring efforts and enormous study made by Griffith (1850). As Assistant Surgeon he accompanied Wallich to Assam, explored tracts of Mishmi mountains, down the Irravadi to Rangoon, traversed 400 miles of Bhutan country, went from Kabul to Khurasan and succumbed finally to fatigue and sickness in 1845. The book "Palms of British East India" was published posthumously in 1850. Later Blatter (1926) enriched the literature on palms with the publication of "The Palms of British India and Ceylon". The literature on living palms in India is fast accumulating and hope a big monograph will be produced soon.

FOSSIL PALMS

Prof. Sahni (1940) in his Presidential Address "The Deccan Traps an episode of the Tertiary Era" to the Indian Science Congress held at Madras said, "From what we know of the geological history of stoneworts, the fungi, the water ferns and particularly of the palms, which formed such a vast proportion of the flora, everything seems to point to a Tertiary age". Fossil palms had attracted his attention and he described a palm wood *Palmoxylon sclerodermum* from Nawargaon, Wardha District, which was redescribed by Shukla (1946). As quoted by Sahni (Rao & Vimala Achuthan, 1971) Colonel W. H. Sleeman (1830) was the first to discover some palm stems near Sagar in Central India. Fossil palms have been described from time to time not only from Deccan Intertrappean beds but also from other parts of India. A full and a very useful review dealing with the fossil palms is given by Rao and Vimala Achuthan (1971). Many have been added later. My attempt to deal further, not being trained as a palaeobotanist, would be a futile one. But what seems to be certain is that the palms among all other angiosperms have a long history in fossil records.

ANATOMY

Kaul (1960) has made it amply clear how the anatomy of stem of the palms can help in deciphering the artificial genus, *Palmoxylon*. Vegetative anatomy has been dealt at great length by Tomlinson (1961). Prof. Mahabale and a band of workers in his school have worked on many of the Indian palms dealing with various parts like stem, root, petiole, leaf, peduncle, etc. These are useful works in referring the fossil genera to modern ones and in finding the relationships. For example, an attempt is made just based on the nature of vascular bundles and the number of metaxylem elements in each bundle (taking of course other factors into consideration) to refer a petrified palm petiole *Palmocaulon hyphaeneiodes* sp. nov. to *Hyphaene indica* (Shete & Kulkarni 1980). Likewise, Kulkarni and Mahabale (1971) have referred *Palmoxylon kamalam* Rode to *Roystonia regia.*

Cytoanalysis

It was hypothesized by Mahabale and Chennaveeraiah (1953) that in palms two basic series exist which correspond to the leaf types. Majority of the species with n = 16 chromosomes have pinnate or pinnatisect leaves and the species with n = 18 chromosomes have palmate or palmatisect leaves with a few exceptions in each series. At that time the chromosome numbers were known in about 60 species distributed in 32 genera. To-day the chromosome number is known in about 253 species distributed in 96 genera of palms. It is, therefore, necessary to re-examine the hypothesis earlier proposed.

The chromosome numbers known uptil now are given generawise in Table 1. The genera are arranged in major groups according to Moore (1973). The source of chromosome number is from Fedorov (1974) and from other publications (Chennaveeraiah, 1955; Mahabale, 1966; Read, 1966; Read & Moore, 1967; Murin & Chaudhri, 1970; Sarkar *et al.*, 1977, 1978a, b). Only the gametic (n) number is given irrespective of the fact whether the number was determined from somatic tissue or pollen mother cells or pollen grains. Broadly two classes of leaves (pinnate or palmate) are taken into consideration and the *n* numbers with respect to leaf types are given in Table 2.

TABLE 1 — CHROMOSOME NUMBERS IN PALMS — GENERA-WISE

I. Coryphoid Palms

1. *Trithrinax* Mart. *n* = 18 sp. 1	2. *Rhapidophyllum* H. Wendl. et Drude n = 18 sp. 1
3. *Trachycarpus* H. Wendl. n = 18 sp. 2	4. *Chamaerops* L. n = 18 sp. 2
5. *Chelyocarpus* Dammer n = 18 sp. 1	6. *Cryosophila* Blume n = 18 sp. 1
7. *Schippia* Burret n = 18 sp. 1	8. *Rhapis* L.f. n = 18 sp. 2 n = 16, 18 sp. 1
9. *Thrinax* L.F. n = 18 sp. 7	10. *Cocothrinax* Sargent n = 18 sp. 7
11. *Zombia* Bailey n = 18 sp. 1	12. *Livistonia* R.Br. n = 18 sp. 1
13. *Licuala* Thunb. n = 8 sp. 2 n = 14 sp. 1 n = 14, 16 sp. 1	14. *Pritchardia* Seem, et H. Wendl. n = 8 sp. 1 n = 18 sp. 4
15. *Acoelorrhaphe* H. Wendl. n = 18 sp. 1	16. *Serenova* Hook. f. n = 18 sp. 1
17. *Brahea Martius* n = 18 sp. 2	18. *Coperniccia* Martius n = 18 sp. 4
19. *Washingtonia* H. Wendl. n = 18 sp. 2 n = 12, 18 sp. 1	20. *Nannorrhops* H. Wendl. n = 18 sp. 1
21. *Corypha* L. n = 18 sp. 4	22. *Sabal* Adans. n = 18 sp. 13

Contd.

TABLE 1 — CHROMOSOME NUMBERS IN PALMS — GENERA-WISE — *Contd.*

II. PHOENICOID PALMS

23. *Phoenix* L.
  n = 14 sp. 2
  n = 18 sp. 10
  n = 14, 18 sp. 1

III. BORASSOID PALMS

24. *Latania* Comm. ex Juss
  n = 14 sp. 2
  n = 16 sp. 2
  n = 18 sp. 1

25. *Borassus* L.
  n = 18 sp. 1

26. *Lodoicea* Comm. ex A.P. Decand.
  n = 17 sp. 1

27. *Hyphaene* Gaertn.
  n = 18 sp. 4

IV. LEPIDOCARYOID PALMS

28. *Raphia* P. Beauv.
  n = 14 sp. 1
  n = 16 sp. 1

29. *Salacca* Reinwardt
  n = 14 sp. 1

30. *Daemonorops* Blume ex Schult
  n = 14 sp. 1

31. *Calamus* L.
  n = 13 sp. 2
  n = 14 sp. 4
  n = 12, 14 sp. 1
  n = 13, 14 sp. 1

V. NYPOID PALMS

32. *Nypa* Steck
  n = 8, 17 sp. 1

VI. CARYOTOID PALMS

33. *Arenga* Labill
  n = 14 sp. 1
  n = 16 sp. 6
  n = 32 sp. 1
  n = 13, 16 sp. 1

34. *Caryota* L.
  n = 17 sp. 2
  n = 18 sp. 1
  n = 14, 16, 17, 18 sp. 1
  n = 16, 18 sp. 1

35. *Wallichia* Roxb.
  n = 16 sp. 1

VII. PSEUDOPHOENICOID PALMS

36. *Pseudophoenix* H. Wendl. ex Sargent
  n = 17 sp. 2

VIII. CEROXYLOID PALMS

Nil

IX. CHAMAEDOREOID PALMS

37. *Synechanthus* H. Wendl.
  n = 16 sp. 1

38. *Gaussia* H. Wendl.
  n = 14 sp. 1

39. *Opisandra* O. F. Cook
  n = 14 sp. 1

40. *Hyophorbe* Gaertn.
  n = 16 sp. 2

41. *Chamaedorea* Willd.
  n = 12 sp. 1
  n – 13 sp. 15
  n = 16 sp. 4
  n = 12, 13 sp. 1
  n = 6-7, 13 sp. 1

Contd.

TABLE 1 — CHROMOSOME NUMBERS IN PALMS — GENERA-WISE — *Contd.*

X. Iriateoid Palms

Nil

XI. Podococcoid Palms

Nil

XII. Arecoid Palms

42. *Orania* Zippel
    $n = 16$ sp. 2
43. *Euterpe* Martius
    $n = 18$ sp. 1
44. *Prestoea* J. D. Hooker
    $n = 16$ sp. 1
    $n = 18$ sp. 3
    $n = 16, 18$ sp. 1
    $n = 18, 19$ sp. 1
45. *Neonicholsonia* Dammer
    $n = 16$ sp. 1
46. *Roystonia* O. F. Cook
    $n = 18$ sp. 6
47. *Chrysalidocarpus* H. Wendl.
    $n = 16$ sp. 1
    $n = 14, 16$ sp. 1
48. *Neodypsis* Baill.
    $n = 16$ sp. 1
49. *Dypsis* Norohna ex Thou
    $n = 18$ sp. 1
50. *Archontophoenix* H. Wendl. et Drude
    $n = 14$ sp. 1
    $n = 14, 16$ Sp. 1
51. *Cyrtostachys* Blume
    $n = 16$ sp. 1
52. *Calytrocalyx* Blume
    $n = 16$ sp. 1
53. *Laccospadix* H. Wendl. et Drude
    $n = 16$ sp. 1
54. *Howea* Becc.
    $n = 16$ sp. 1
    $n = 18$ sp. 1
55. *Drymophloeus* Zippel.
    $n = 16$ sp. 1
56. *Carpentaria* Becc.
    $n = 10$ sp. 1
    $n = 16$ sp. 1
57. *Veitchia* H. Wendl.
    $n = 16$ sp. 5
58. *Ptychosperma* Labill.
    $n = 16$ sp. 4
59. *Ptychococcus* Becc.
    $n = 16$ sp. 1
60. *Brassiophoenix* Burret
    $n = 16$ sp. 1
61. *Gronophyllum* Scheffer
    $n = 16$ sp. 2
62. *Siphokentia* Burret
    $n = 16$ sp. 1
63. *Hydriastele* H. Wendl. et Drude
    $n = 16$ sp. 1
64. *Gulubia* Becc.
    $n = 16$ sp. 2
65. *Pinanga* Blume
    $n = 14$ sp. 2
    $n = 14, 16$ sp. 1
66. *Areca* L.
    $n = 16$ sp. 4
67. *Pelagodoxa* Becc.
    $n = 16$ sp. 1
68. *Heterospathe* Scheff.
    $n = 16$ sp. 2
69. *Bentinckia* Berry
    $n = 16$ sp. 1
70. *Clinostigma* H. Wendl.
    $n = 16$ sp. 1
71. *Rhopaloblaste* Scheff.
    $n = 16$ sp. 1
72. *Dictyosperma* H. Wendl. et Drude
    $n = 16$ sp. 2
73. *Tavounia* Burret
    $n = 16$ sp. 1
74. *Oncosperma* Blume
    $n = 16$ sp. 1
75. *Phoenicophorium* H. Wendl.
    $n = 16$ sp. 2
76. *Nephrosperma* Balf. f.
    $n = 16$ sp. 1

XIII. Cocosoid Palms

77. *Cocos* L.
    $n = 16$ sp. 6
78. *Butia* Becc.
    $n = 16$ sp. 2
79. *Jubaea* H. B. et K.
    $n = 16$ sp. 2
80. *Syagrus* Martius
    $n = 15$ sp. 1
    $n = 16$ sp. 5
81. *Arecastrum* (Drude) Becc.
    $n = 16$ sp. 1
82. *Rhyticocos* Becc.
    $n = 16$ sp. 1

Contd.

TABLE 1 — CHROMOSOME NUMBERS IN PALMS — GENERA-WISE — *Contd.*

83. *Arikuryroba* B. Rodrigues
 n = 15 sp. 1

84. *Allagoptera* C. G. Nees
 n = 16 sp. 1

85. *Polyandrococos* B. Rodrigues
 n = 16 sp. 1

86. *Attalea* H. B. et K.
 n = 16 sp. 3

87. *Scheela* H. Karsten
 n = 16 sp. 1

88. *Orbignya* Mart. ex Endl.
 n = 16 sp. 2

89. *Elaeis* Jacq.
 n = 16 sp. 1
 n = 16, 18 sp. 1

90. *Aiphaenes* Willd.
 n = 15 sp. 2

91. *Acrocomia* Martius
 n = 15 sp. 3

92. *Bactris* N. J. Jacquin et Scopoli
 n = 15 sp. 2

93. *Astrocaryon* G. F. W. Meyet
 n = 15 sp. 1

XIV. Geonomoid Palms

94. *Calyptronoma* Grisebach
 n = 14 sp. 1

95. *Geonoma* Willd.
 n = 14 sp. 1

XV. Phytelephantoid Palms

96. *Phytelephas* Ruiz et Pav.
 n = 16, 18 sp. 1

TABLE 2 — CHROMOSOME NUMBER AND LEAF TYPES

Chromosome no. n =	Pinnate Leaf		Palmate Leaf	
	Genera no.	Species no.	Genera no.	Species no.
Regular				
8	—	—	2	3
10	1	1	—	—
12	1	1	—	—
13	2	17	—	—
14	12	17	2	3
15	6	10	—	—
16	48	87	1	2
17	2	4	1	1
18	7	23	24	65
Total	79	160	30	74
Exceptions				
6-7, 13	1	1	—	—
8, 17	1	1	—	—
12, 13	1	1	—	—
12, 14	1	1	—	—
12, 18	—	—	1	1
13, 14	1	1	—	—
13, 16	1	1	—	—
14, 16	3	3	—	—
14, 16, 17, 18	1	1	—	—
14, 18	1	1	—	—
16, 18	4	4	1	1
18, 19	1	1	—	—
Total	16	16	2	2
n = 32	1	1	—	—

Among 160 pinnate species for which the chromosome numbers are known, n = 16 is found in 87 species distributed in 48 genera. In only 23 species and 7 genera n = 18 chromosomes are seen. The other numbers found in pinnate forms are n = 10, 12, 13, 14, 15 and 17. All these exceptions together are found distributed in 24 genera and 40 species as against 48 genera and 87 species with n = 16.

The chromosome number has greater significance in palmate species. In them, n = 18 is found in 24 genera and 65 species out of 71 species in 30 genera. The number n = 16 which is characteristic of pinnate species is found in a single genus and two species. This is in *Latania commersonii* (Sharma & Sarkar, 1957) and in *Latania rubra* (Venkatasubban, 1945). The other numbers are n = 8 in *Licuala grandis* (Sharma & Sarkar, 1957), n = 14 in *Licuala spinosa* (Sharma & Sarkar, 1957; Sarkar *et al.*, 1978) and n = 17 in *Lodoicea maldivica* (Read, 1966). Barring these genera, *Licuala* and *Lodoicea*, all other palmate genera have n = 18 chromosomes. Therefore, with a few exceptions here and there, n = 16 and n = 18 are the numbers found in the majority of pinnate and palmate palms respectively. It is to be expected that in the course of evolution variation in chromosome number other than n = 16 and n = 18 has come into expression in both the groups, but more so in the case of pinnate ones.

The exceptions that we see are often due to different chromosome numbers reported by different workers for the same taxa as can be seen in Table 3.

One of the causes for variation in chromosome number within a species or among the species of a genus is perhaps due to hybridization, a conjecture made here. For example, if we consider the palmate genus *Latania*, there is variation of chromosome number in different species. It can be conjectured that as a result of hybridization of species with n = 14 (*L. loddigesi*, *L. lentaroides*, *L. verchaffeltii*) and n = 18 (*L. aurea*), species with n = 16 (*L. commersonii*, *L. rubra*) have resulted. At the specific level, *Caryota mitis* may serve as a good example, in which the number is reported as n = 14, 16, 17, 18). Between n = 14 and 18, the number n = 16 is resulted and between n = 16 and 18 the number 17 can result. Similarly, hybridization is to be expected in the genus *Phoenix*. This problem of hybridization needs to be closely examined in palms as generally they are cross pollinated.

What could be the original basic chromosome number in palms and what were the lines of evolution are difficult to comment upon. However, certain assumptions can be made. It is possible that the original basic chromosome numbers might be n = 8 and n = 9 from which both the series n = 16 and n = 18 have been derived. The number n = 8 is found in *Licuala*, *Pritchardia* and *Nypa*, but n = 9 so far is not known in any. The basic number n = 10 is found in *Carpentaria*. The number 6-7 reported by Suessenguth (1921a) in *Chamaedorea sartorii* is of doubtful nature as later on Read (1966) has reported the number in it as n = 13. Then, if we accept the original base numbers as n = 8 and 9, most of the palms are to be considered as of polyploid origin but having undergone diploidization in course of evolution. This assumption should be kept in reserve until more confirmatory evidences are available. However, there is a single report of polyploid number n = 32 in *Arenga caudata* (Read, 1966). Sato (1946) has reported somatic doubling in some root tip cells in *Exorrhiza savoryana* and *Prestoea caryotaefolia* (= *Martinezia caryotaefolia*). Still the chromosome numbers are not known in a great majority of the palms.

The relative primitive or advanced nature of the series n = 16 and n = 18, correspondingly pinnate-leaved and palmate-leaved condition cannot be decided on the basis of chromosome number alone. However, greater variation in chromosome number (n = 10, 12, 13, 14, 15, 17, 18) seen in n = 16 series with pinnate leaves is to be regarded as relatively more advanced than the series n = 18 in which there is lesser variation (n = 8, 14, 16, 17) found only in a few taxa. No attempt is made here to further distinguish the pinnate and palmate types and their evolution. However, according to Eames (1953) the pinnate leaf is the primitive type, the palmate advanced, with the costa-palmate as transitional. But Moore (1973) considers that palmate or costa-palmate leaves as less specialised and pinnate or bipinnate

TABLE 3 — DETAILS OF EXCEPTIONAL TAXA

Taxa	Chromosome number	References
Coryphoid Palms		
1. *Rhapis excelsa*	n = 16	Bosch, 1947
	n = 18	Read, 1966
2. *Washingtonia filifera*	n = 12	Nemec, 1910
	n = 18	Sato, 1953; Read 1966
Phoenicoid Palms		
3. *Phoenix dactylifera*	n = 14	Nemec, 1910; Dangeard, 1937, Doulat, 1944
	n = 18	Beal, 1937; Murin & Chaudhri, 1970
Lepidocaryoid Palms		
4. *Calamus caryotoides*	n = 13	Read, 1965b
	n = 14	Janaki Amal, (D. 1945)
5. *Calamus rotang*	n = 12	Chennaveeraiah, 1955
	n = 14	Sharma & Sarkar, 1957
Nypoid Palms		
6. *Nypa fruticans*	n = 8	Radermacher, 1925
	n = 17	Read, 1966
Caryotoid Palms		
7. *Arenga pinnata*	n = 13	Janaki Ammal, (D. 1945)
	n = 16	Sato, 1946; Read, 1966
8. *Caryota mitis*	n = 14	Eichhorn, 1957
	n = 16	Sharma & Sarkar, 1957; Sarkar *et al.*, 1978
	n = 17	Read, 1966
	n = 18	Chennaveeraiah, 1955
9. *Caryota urens*	n = 16	Sato, 1946; Sharma & Sarkar, 1957
	n = 18	Chennaveeraiah, 1955; Mahabale, 1966
Chamaeodoreoid Palms		
10. *Chamaedorea sartori*	n = 6-7	Suessenguth, 1921a
	n = 13	Read, 1966
11. *Chamaedorea ernstiaugusti*	n = 12	Eichhorn, 1957
	n = 13	Read, 1966
Arecoid Palms		
12. *Prestoea erosa*	n = 16	Sharma & Sarkar, 1957
(= *Martinezia erosa*)	n = 18	Gansser, 1941
13. *Roystonia regia* (= *Oreodoxa regia*)	n = 18	Venkatasubban, 1945; Eichhorn, 1957; Sharma & Sarkar, 1957
	n = 19	Sato, 1953
14. *Chrysalidocarpus lutescens*	n = 14	Gansser, 1941; Eichhorn, 1957
	n = 16	Venkatasubban, 1945; Sharma & Sarkar, 1957; Read, 1966
15. *Archontophoenix alexandrae*	n = 14	Eichhorn, 1957
	n = 16	Read, 1965b, 1966
16. *Pinanga kuehlii*	n = 14	Eichhorn, 1957
	n = 16	Read, 1966
Cocosoid Palms		
17. *Elaeis guinensis*	n = 16	Janaki Ammal (D. 1945); Venkatasubban, 1945; Sato, 1946; Sharma & Sarkar, 1957; Read, 1966
	n = 18	Delay, 1947
Phytelephantoid Palms		
18. *Phytelephas macrocarpa*	n = 16	Read, 1966
	n = 18	Eichhorn, 1957

as more specialised. The latter's view seems to have the cytological support as detailed above. Further, all the apocarpous genera of Moore (1973) have n = 18 chromosomes and they all have palmate leaves. The relative primitive or advanced nature of pinnate and palmate leaves may ultimately rest on the relative antiquity of these based on fossil record and palaeobotanical research.

EMBRYOLOGY

Our knowledge of the embryology of palms till 1931, as Schnarf (1931) remarked, is to be regarded as scanty. Even the little that was known was of controversial nature. Of late Prof. Mahabale and his school have made significant contributions.

In *Cocos nucifera*, the wall of the anther is 6-8-layered of which the subepidermal layer develops into fibrous endothecium and the innermost 2-4 layers function as tapetum (Juliano & Quisumbing, 1931). The wall of the anther is 5-6-layered in *Hyphaene indica* (Mahabale & Chennaveeraiah, 1957), 4-6-layered in *Borassus flabellifer* (Javalgekar, 1979), *Pritchardia*, *Licuala* and *Livistonia* (Rao, 1955a), 4-5-layered in species of *Phoenix* (Mahabale & Biradar, 1968; Biradar, 1968; Biradar & Mahabale, 1968), 4-5-layered in *Livistonia chinensis* (Kulkarni & Mahabale, 1974), 4-6-layered in *Borassus flabellifer* and *Latania verschaffeltii* (Javalgekar, 1979). It is evident from the above that the anther wall in many palms is thicker than what it is in other flowering plants.

The ovules in palms are anatropous, hemianatropous, campylotropous or orthotropous and attached basally, laterally or apically. The ovule is crassinucellate and both the integuments are well-developed. In *Hyphaene indica* the inner integument consists of 2 layers of cells, the outer integument 7-8 layers in the beginning and as the embryo sac matures the inner integument becomes 3-4-layered and the outer quite massive with 12-14 layers (Mahabale & Chennaveeraiah, 1957). The massive outer integument is supplied by a ring of 16-18 vascular traces which extend up to 2/3 of its length (Mahabale & Chennaveeraiah, 1957). This is to be considered as a primitive character. Such studies have not been extended to other members except in species of *Phoenix* where it is reported that the inner integument is 3-4-layered and the outer integument 5-7-layered at megaspore mother cell stage, but without vascular bundles. The funicular vascular strand extends up to the chalazal region without supplying branches to the integument (Mahabale & Biradar, 1968; Biradar, 1968; Biradar & Mahabale, 1968).

Various types of embryo sac development have been reported by different workers. *Polygonum* type of embryo sac development is described in *Actinophloeus macarthurii* (Radermacher, 1925) and *Areca catechu* (Swamy, 1942). *Polygonum* type reported in other members are *Phoenix sylvestris* (Mahabale & Biradar), *Phoenix pusilla* and *P. acaulis* (Biradar, 1968), *Phoenix robusta* (Biradar & Mahabale, 1968), *Livistonia chinensis* (Kulkarni & Mahabale, 1974), *Caryota urens*, *C. rumphiana* and *C. mitis* (Shirke, 1963), *Thrinax parviflora*, *Trachycarpus martiana* (Patel, 1979).

Bisporic embryo sacs have been reported in *Chamaedorea latifolia* (Jönsson, 1879-80) and *Nypa fruticans* (Radermacher, 1925), but Maheshwari (1955) doubts these reports. However, these have not been investigated later. Reliable bisporic *Allium* type of development of embryo sac is reported by Mahabale and Chennaveeraiah (1957) in *Hyphaene indica*. This has been confirmed later by Javalgekar (1979). *Allium* type of embryo sac is also reported in *Borassus flabellifer* (Javalgekar, 1979). In no other taxa so far this type of development is known.

Tetrasporic *Adoxa* type of embryo sac is reported in *Cocos nucifera* (Quisumbing & Juliano, 1927). However, Bauch (1911) had previously reported the presence of degenerating megaspores in it. Recently, Javalgekar (1979) has confirmed the *Polygonum* type of embryo sac development in *Cocos nucifera*. De Poerck (1950) reported that the megaspore mother cell develops directly into 8-nucleate embryo sac in *Elaeis guinensis*. However, Kajale and Ranade (1952, 1955) have made a detailed study and reported *Polygonum* type and also four kinds of tetrads. Therefore, still there is no authentic tetrasporic development of embryo sac in palms.

The account of antipodals in palms is quite varying. In *Chamaedorea concolor* the three insignificant antipodals are ephemeral (Suessenguth, 1921a). In *Hyphaene indica* they are not only ephemeral but remain only as nuclei (Mahabale & Chennaveeraiah, 1957). Ephemeral antipodals are also reported in *Borassus flabellifer* (Javalgekar, 1979), *Phoenix sylvestris* (Mahabale & Biradar, 1968), *Phoenix pusilla* and *P. acaulis* (Biradar, 1968), *Phoenix robusta* (Biradar & Mahabale, 1968), *Livistonia chinensis* (Kulkarni & Mahabale, 1974), *Caryota urens*, *C. rumphiana* and *C. mitis* (Shirke, 1963), *Thrinax parviflora*, (Patel, 1979). They are described to be persistent and sometimes becoming 2-3-nucleate in *Pinanga moluccana* (Lötscher, 1905) and *Calyptrocalyx* (Bausch, 1911). In *Areca catechu*, the antipodals are not only persistent but also aggressive and possibly haustorial (Swamy, 1942).

The endosperm formation is nuclear becoming cellular at a later stage, although in *Cocos nucifera* wall formation does not extend to the centre of the embryo sac and the peripheral endosperm cells divide actively and function as a meristematic layer (Lang, 1943; Javalgekar, 1979). Nuclear endosperm later becoming cellular is also reported in other members like *Phoenix sylvestris* (Mahabale & Biradar, 1968). *Phoenix robusta* (Biradar & Mahabale, 1968), *Livistonia chinensis* (Kulkarni & Mahabale, 1974), *Caryota urens*, *C. rumphiana* and *C. mitis* (Shirke, 1963), *Thrinax parviflora*, *Borassus flabellifer*, *Trachycarpus martiana* (Patel, 1979). The wall formation starts from the micropylar region and proceeds towards the chalazal region in *Actinophloeus* sp. (Rao, 1959a), but it takes place from periphery to the centre in species of *Phoenix* (Mahabale & Biradar, 1968; Biradar, 1968) in *Livistonia chinensis* (Kulkarni & Mahabale, 1974). Ruminated endosperm was observed by Rao (1959a) in *Caryota urens*, *Howea belmoriana* and *Areca catechu*. In species of *Phoenix*, the rumination of endosperm is confined to the placental region but does not extend deep into it (Mahabale & Biradar, 1968; Biradar, 1968). Endosperm haustoria are reported in *Chrysalidocarpus lutescens* and some members of Ceroxylineae (Rao, 1959b). There does not seem to be any report of cellular and helobial types of endosperm in the palms studied so far.

Very little is known regarding embryo development. Onagrad type of embryo development is reported in *Areca catechu* (Rao, 1955a) and *Hyphaene indica* (Javalgekar, 1979). In *Cocos nucifera* it is a variant of the Onagrad type. Asterad type is reported in *Chamaerops* (see Davis, 1966), *Livistonia chinensis* (Kulkarni & Mahabale, 1974). Geum variation of Asterad type is found in *Phoenix sylvestris* (Mahabale & Biradar, 1968), *Phoenix pusilla*, *P. acaulis* and *P. reclinata* (Biradar, 1968), *Thrinax parviflora*, *Trachycarpus martiana* and *Borassus flabellifer* (Patel, 1979). It is interesting to note that both *Polygonum* and *Geum* variations of Asterad type is found in *Phoenix robusta* (Biradar & Mahabale, 1968). Based on this and what has been suggested by Mahabale and Parthasarathy (1963), they consider that *Phoenix robusta* might have arisen as a cross between *P. sylvestris* and *P. acaulis*, both growing in Western Ghats. Further, they say that it may serve as one of the parents for crossing with *P. dactylifera* which is economically important.

In *Borassus flabellifer*, the formation of a rim and a depression is interesting, giving the appearance of two cotyledonary structures (Javalgekar, 1979).

The fruit and seed characters may be useful taxonomically and for identification of fossil forms (Lang, 1943; Ginies, 1955; Biradar & Mahabale, 1969; Mahabale & Kulkarni, 1972). Biradar and Mahabale (1969) have given a key for the identification of different species of *Phoenix* based on the fruit and seed structure and have shown how close the fossil fruit *Phoenicites occidentalis* described by Berry (1914) is to *Phoenix dactylifera* and *P. sylvestris*. Similarly, Mahabale and Kulkarni (1972) have shown that the seed structure in *Livistonia chinensis* is close to the fossil seeds of *Livistonia minima* from the Tertiary flora of London Clay described by Reid and Chandler (1933). It is highly desirable that similar studies are extended to other palms also.

Mainly there are two types of germination in palms, ' remotive ' and ' admotive ' types. It is interesting to note that the embryo is somewhat less differentiated in *Borassus*, *Latania* and *Hyphaene* where remotive type

TABLE 4 — SALIENT EMBRYOLOGICAL FEATURES

TAXA	ANTHER WALL	EMBRYO SAC	ENDOSPERM	EMBRYO
Actinophloeus macarthurii Sp.		Polygonum type (Radermacher, 1925)	Nuclear later becoming cellular (Rao, 1959a)	
Areca catechu		Polygonum type, antipodals persistent, aggressive (Swamy 1942)	Ruminate (Rao, 1959a)	Onagrad type (Rao, 1955a)
Borassus flabellifer	4-6-layered (Rao, 1955a; Javalgekar, 1979)	Allium type, antipodals ephemeral (Javalgekar, 1979)	Nuclear later becoming cellular (Patel, 1979)	Asterad, Geum variation (Patel, 1979)
Calyptrocalyx sp.		Antipodals persistent, 2-3-nucleate (Bausch, 1911)		
Caryota mitis		Polygonum type, antipodals ephemeral (Shirke, 1963)	Nuclear later becoming cellular (Shirke, 1963)	
C. rumphiana		Polygonum type, antipodals ephemeral (Shirke, 1963)	Nuclear later becoming cellular (Shirke, 1963)	
C. urens		Polygonum type, antipodals ephemeral (Shirke, 1963)	Nuclear later becoming cellular (Shirke, 1963) Ruminate (Rao, 1959a)	
Chamaedorea latifolia		Scilla type ? (Jönsson, 1879-80)		
C. concolor		Antipodal insignificant, ephemeral (Suessenguth, 1921a)		
Chamaerops sp.				Asterad type (Davis, 1966)
Cocos nucifera	6-8-layered (Juliano & Quisumbing, 1931)	Tetrasporic ? (Quisumbing & Juliano, 1927) Polygonum type (Javalgekar, 1979)	Nuclear later becoming cellular (Lang, 1943; Javalgekar, 1979)	Variant of Onagrad type (Javalgekar, 1979)
Elaeis guinensis		Tetrasporic ? (De Poerck, 1950) Polygonum type (Kajale & Ranade, 1952, 1955)		
Hyphaene indica	5-6-layered (Mahabale & Chennaveeraiah, 1957)	Allium type, antipodals ephemeral, remain as nuclei (Mahabale & Chennaveeraiah, 1957; Javalgekar, 1979)		Onagrad types (Javalgekar, 1979)
Latania verschaffeltii	4-6-layered (Javalgekar, 1979)			
Licuala sp.	4-6-layered (Rao, 1955a)			

Contd.

TABLE 4 — SALIENT EMBRYOLOGICAL FEATURES — *Contd.*

TAXA	ANTHER WALL	EMBRYO SAC	ENDOSPERM	EMBRYO
Livistonia chinensis	4-5-layered (Kulkarni & Mahabale, 1974)	Polygonum type, antipodals ephemeral (Mahabale, 1974)	Nuclear later becoming cellular (Kulkarni & Mahabale, 1974)	Asterad type (Kulkarni & Mahabale, 1974)
L. sp.	4-6-layered (Rao, 1955a)			
Nypa fruticans		Bisporic ? (Radermacher, 1925)		
Phoenix acaulis	4-5-layered (Biradar, 1968)	Polygonum type, antipodals ephemeral (Biradar, 1968)		Asterad, Geum variation (Biradar, 1968)
P. pusilla	4-5-layered (Biradar, 1968)	Polygonum type, antipodals ephemeral (Biradar, 1968)		Asterad, Geum variation (Biradar, 1968)
P. reclinata	4-5-layered (Biradar, 1968)	Polygonum type (Biradar, 1968)		Asterad, Geum variation (Biradar, 1968)
P. robusta	4-5-layered (Biradar & Mahabale, 1968)	Polygonum type, antipodals ephemeral (Biradar & Mahabale, 1968)	Nuclear later becoming cellular (Biradar & Mahabale, 1968)	Asterad, Geum & Polygonum variations (Biradar & Mahabale, 1968)
P. sylvestris	4-5-layered Mahabale & Biradar, 1968)	Polygonum type, antipodals ephemeral (Mahabale & Biradar, 1968)	Nuclear later becoming cellular (Mahabale & Biradar, 1968)	Asterad, Geum variation (Mahabale & Biradar, 1968)
Pinanga moluccana		Antipodals persistent, 2-3-nucleate (Lotscher, 1905)		
Pritchardia sp.	4-6-layered (Rao, 1955a)			
Thrinax parviflora		Polygonum type, antipodals ephemeral (Patel, 1979)	Nuclear later becoming cellular (Patel, 1979)	Asterad, Geum variation (Patel, 1979)
Trachycarpus martiana		Polygonum type (Patel, 1979)	Nuclear later becoming cellular (Patel, 1979)	Asterad, Geum variation (Patel, 1979)

of germination is present (Javalgekar, 1979). Further, the embryo culture experiments by Javalgekar (1979) in *Borassus flabellifer* and *Cocos nucifera* lend support to the conclusion on the basis of embryogeny that the so-called cotyledonary tube is homologous to the amplexicaul leaf base and the growth of the cotyledonary tube is mainly due to the activity of a nodal ring of meristematic cells.

The salient embryological features are given in Table 4.

USES AND DISTRIBUTION

The palms have great many uses. Pantropically they provide food, shelter, clothing and lesser necessities for living. In temperate regions they are sources of such products as copra, oil, dates, rattancane, ivory nuts, carnauba wax, etc. Particularly to the people of India, the coconut palm every part of which is put into use, plays an important role. It is, therefore, called as 'Kalpavruksha', and also considered to be sacred. Coconuts are offered at temples, marriages, etc., and its leaves used on auspicious occasions like palm Sunday. It is not possible to give the details of uses of different palms. However, they are listed in Table 5 giving the uses in abbreviations and their distribution in the last column. The following are the abbreviations used.

A = Alcoholic liquors produced by fermentation
D = Dyes and Tannins
F = Fruits, eaten by man
Fi = Fibres for weaving carpets, mats, baskets, ropes and cords for furniture
H = Horticultural plants
M = Medicinal
N = Nuts, eaten by man
O = Oil and wax
St = Starch extracted from stems
Su = Sugar extracted from stem or root
T = Tools
V = Vegetables
W = Wood

TABLE 5 — USES AND DISTRIBUTION OF PALMS

Taxa	Uses	Distribution
Coryphoid Palms		
Trithrinax brasilensis	H	S. Brazil, Parague
Trachycarpus fortunei (Windmill palm)	Fi H	China, Japan, Burma
Chamaerops humilis (Fan palm)	Fi H	W. Medit.
Rhapis excelsa	H T	S. China
R. humilis	H	S. China
Thrinax excelsa	H	Jamaica
T. morrisii	H	West Indies
Cocothrinax argentata	H	San Domingo
Livistonia chinensis (Chinese fan palm)	Fi H	Central China
L. oliviformis	H St	Malaya
Licuala grandis	H	New Britain
L. peltata	Fi	India, Burma
Pritchardia filifera	F H	W.N. America
P. pacifera	Fi H	Fiji
Copernicia cerifera (Carnauba wax)	F Fi M O St Su W	West Indies, Brazil
Washingtonia filifera (Skirt palm)	H	S.W. USA
Corypha umbraculifera (Talipot palm)	Fi H	India, Ceylon
Sabal bermudana (Bermuda palmetto)	Fi H	Bermuda
S. causiarum (Puerto Rico hat palm)	Fi W	Puerto Rico
S. minor (Dwarf palmetto)	H	S.E. USA
S. palmetto (Cabbage palm)	Fi H V W	S.E. USA
S. umbraculifera	H	Hispaniola
Phoenicoid Palms		
Phoenix canariensis	F Fi W	Canary Is.
P. dactylifera (Date palm)	A F Fi W	Persia cult.
P. franifera	A F Fi St Su	India, Ceylon

Contd.

TABLE 5 — USES AND DISTRIBUTION OF PALMS — *Contd.*

TAXA	USES	DISTRIBUTION
P. humilis	F Fi H	India, Burma, China
P. paludosa	Fi H	Bengal, Cochin
P. reclinata	A F Fi H	Tropical Africa
P. sylvestris	A Fi M Su	India
Borassoid Palms		
Latania aurea	H W	Mascarene Is.
L. commersonii	F Fi H	Mascarene Is.
Borassus flabellifer	A F Fi M Su V M	India, Malaya
(Palmyra palm)		
Hyphaene wildbrandi	F Fi	Tropical Africa
Lepidocaryoid Palms		
Metroxylon sagus	Fi St	India, Malaya
(Sago palm)		
Raphia ruffia	Fi H	E. Africa, Madagascar
(Ruffia palm)		
Calamus caryotoides	Fi H	Australia
C. rotang	Fi	India, Ceylon
Nypoid Palms		
Nypa fruticans	A Fi Su	Ceylon, Burma, Australia
(Nipa palm)		
Caryotoid Palms		
Arenga engleri	Fi H	Formosa
A. saccharifera	A Fi St Su V	India, Malaya
(Sugar palm)		
Caryota urens	A Fi H St Su W	Tropical Asia
(Kitul palm, Toddy or Fish tail palm)		
Chamaedoreoid Palms		
Hyophorbe verschaffeltii	H	Mascarene Is.
Chamaedorea corallina	Fi H	Venezuala
C. elegans	H	Mexico
C. glaucophylla	Fi H	Mexico
C. sartorii	Fi H	Mexico
Arecoid Palms		
Roystonia oleracea	V	West Indies
(Cabbage palm)		
R. regia	H	West Indies
(Cuba Royal palm)		
Chrysalidocarpus lutescens	H	Madagascar
C. madagascarensis	H	Madagascar
Cyrtostachys lakka	H O	Malaya, E. Indies
(Sealing wax palm)		
Howea belmoriana	H	Lord Howe Is.
H. foresteriana	H	Lord Howe Is.
Ptychosperma (Actinophloeus) macarthurii	H	New Guinea
Gronophyllum (Kentia) sanderiana	H	New Guinea
Areca catechu	D M N T W	Trop. Asia cult.
(Betel nut)		
A. lutescens	H	Madagascar
A. triandra	H V	India, Malaya
Heterospathe elata	H	Philippines
Dictyosperma album	H	Mascarene Is.
Oncosperma filamentosum	Fi V W	Malaya
(Nibung palm)		
Nephrosperma van-houtteana	H	Seychelles

Contd.

TABLE 5 — USES AND DISTRIBUTION OF PALMS — *Contd.*

TAXA	USES	DISTRIBUTION
Cocosoid Palms		
Cocos nucifera (Coconut)	A B Fi N O Su T W	Pacific, Indo-Malayan, Indo-African
C. schizophylla	H	Brazil
Butia bonneti	H	Brazil
B. capitata (Yatay palm)	H	Brazil
Jubaea spectabilis (Coquit)	Fi H N Su W	Chile
Arecastrum romanzoffianum (Queen palm)	H V	Tropical South America
Attalea cohune (Cohuna palm)	A Fi O	Honduras
Elaeis guinensis (Oil palm)	A Fi H M O V	Tropical Africa cult.
Aiphanes (*Martinezia*) *caryotifolia*	H	South America
Bactris utilis	A F O	South America

The distribution of palms is dealt at great length by Moore (1973). According to him the palms of each region are exclusive with certain exceptions. Broadly speaking as Mahabale (1974) has shown that the Arecoid palms are distributed all over the world in America, Asia and Australia, but mostly absent in Africa (with a few exceptions). The Coryphoid palms have largely developed in Central and South America extending to China. The Borassoid palms are mostly Indo-African. Extending up to 22° North of equator and up to 26° South of equator, the palms form a characteristic vegetation of the tropics.

CONCLUSIONS

The palms have a long fossil history and also form characteristic elements of tropical vegetation with their majestic appearance. Needless to say that a detailed knowledge of living palms will serve as useful information for identification of fossil forms and for phylogenetic considerations.

Comparative anatomy of stems at various levels and growth periods of petioles and peduncles is bound to be important for correctly identifying the fossil genera. No doubt it is a hard task and may have many difficulties due to inaccessibility of the material or other kinds of problems. In assigning, however, a fossil form to a modern genus based on anatomy, it is desirable that the palaeobotanist exercises great caution as anatomical features such as the type of bundles and ground tissue may vary within the same organ at different points and levels.

The chromosome numbers to which I have greatly devoted in this lecture, are known in about 1/10 of the species of palms. Even this little information is important in knowing the lines of evolution and inter-relationships among them. (1) It was earlier hypothesized (Mahabale & Chennaveeraiah, 1953) that there are mainly two basic series, $n = 16$ and $n = 18$, characteristic of pinnate and palmate leaved palms respectively. Barring a few exceptions, the earlier view still holds good for the majority of pinnate genera to have $n = 16$ chromosomes and palmate genera having $n = 18$ chromosomes. (2) The variation in chromosome number other than $n = 16$ and $n = 18$ is expected to have occurred in course of evolution. (3) There is greater variation in the pinnate genera than in the palmate ones indicating that perhaps the palmate leaf is primitive and pinnate leaf is advanced, a view held by Moore (1973), although relative antiquity or primitiveness can best be decided by fossil records. (4) Certain variations in chromosome numbers between species of a genus (*Latania*) or within a species (*Caryota mitis*) may be due to hybridization which cannot be ruled out. Hybridization between species of *Phoenix* is recorded on the basis of embryological and other characters (Mahabale & Parthasarathy, 1963; Biradar & Mahabale, 1968). (5) If we accept the original basic chromosome number as 8 and 9, most of the present day palms are polyploids in origin, having undergone diplodization in course of evolution. (6) The single record of tetraploidy in *Arenga caudata* (n = 32) by Read (1966) and somatic doubling found in the mixoploid tissue of root tips of certain taxa by Sato (1946) may suggest the role of polyploidy in palms. (7) Karyotypically, Sato (1946) has shown clear relationship of palms with *Yucca* and *Agave* supporting Hutchinson's (1934) derivation of Palmae from the Liliaceous stock, through part of Agavales (*Dracaena*, *Yucca*, *Cordyline*, *Nolina*) postulating a phylogenetic line Liliales → Agavales → Palmales → Pandanales → Cyclanthales.

Compared to cytological investigations, the embryological study is still more scanty. May be this study is beset with certain difficulties such as the presence of tannins and other substances which make microtoming and staining difficult. One may not get all the developmental stages in a single inflorescence and when the inflorescence emerges out, the stages may be advanced in nature. Also the presence of a solitary ovule in each carpel makes the study difficult, more so with respect to post-fertilization stages. But the little information available in embryology is of evolutionary significance. (1) That the wall of the anther consisting of more layers than in other angiosperms, sometimes the outer integument of the ovule receiving vascular traces up to a certain length as in *Hyphaene* may suggest primitiveness of the group. (2) Most of them having *Polygonum* type of embryo sac development with the total absence of tetrasporic types suggest that the palms have not advanced much. (3) The endosperm being nuclear but later becoming cellular suggests a type of development typical of the endosperm (female gametophyte) in Gymnosperms. In this respect the palms are primitive without any truly cellular type of endosperm development.

Thus the palms remain distinct from other monocots and all other angiosperms. They give evidence of great age and they are basically primitive.

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