STUDIES ON PALMS: EMBRYOLOGY OF *PHOENIX SYLVESTRIS* ROXB.

BY T. S. MAHABALE, F.A.Sc. AND N. V. BIRADAR

(Department of Botany, University of Poona, Poona-7, India)

Received December 4, 1967

ABSTRACT

The paper gives an account of the embryology of the genus *Phoenix* Linn. being intensively studied in this Department. *Phoenix sylvestris* Roxb. has been investigated as a type. Male and female flowers, pollen grains, development of ovule, male and female gametophytes, endosperm and embryo development were worked out.

The plants are dioeceous, 10–16 m. in height, with rough trunk due to persistent leaf bases. Both the inflorescences are spadix, each arising in the axil of a leaf in acropetal succession. There are 6–8 spadices at a time on a tree. The smooth and round pollen grains are shed in 2-celled condition. The ovules are anatropous, bitegmic and crassinucellate. The endosperm is nuclear to begin with but becomes cellular later.

The embryo develops according to the *Geum* variation of the Asterad type. It shows a definite tendency towards forming two cotyledons in early stages, but only one becomes massive later and attains maturity. The shoot apex is terminal. The micropyle shifts from terminal to lateral position. Besides this species, *P. pusilla*, *P. robusta*, *P. acaulis* and *P. reclinata* were also studied and they show the same pattern of embryo-sac and embryo development with certain variations.

INTRODUCTION

PALMS form a large family of tropical and sub-tropical woody plants, not well studied. They are particularly abundant in the Indo-Malayan region and South America. They comprise 227 genera and 2,613 species according to Corner (1966, p. 10), but we believe perhaps more. They are an ancient family believed to have existed from the Triassic period onwards (Brown, 1956), but more definitely from Liassic (Lignier, 1907). Its systematic treatment by different authors differs widely (*see* Bentham and Hooker, 1883;

Engler and Prantl, 1887–89 ; Hallier, 1912 ; Bessey, 1915 ; Rendle, 1930 ; Wettstein, 1935; Hutchinson, 1959 ; Moore, 1960), as opinion on the nature of taxa constituting "Spadiciflorae", "Principes", or "Palmales" is not identical.

As a rule, monocots are herbaceous, only a few are woody. In the woody members palms are the most important. In stem habit they greatly vary. *Nipa*, *Phytelephas*, and *Geonoma* are short-stemmed and rhizomatous. *Calamus*, *Desmoncus* are reedy climbers having long internodes. *Hyphaene*, *Nannorrhops* are branched. The rest are tall, woody, single-stemmed, soboliferous trees overtopped by a large crown of leaves, fan-like or feather-like.

The inflorescence is large, highly complex, and often much branched. The flowers are usually embedded in the spadix or free on spikes enclosed in spathes. The spadices arising in the axils of leaves are generally dioecious, rarely monoecious. The inflorescence in *Corypha*, is huge and terminal. Most palms are polycarpic, but *Corypha*, *Arenga* are monocarpic. The flowers are bracteate, trimerous, regular, dioecious, monoecious or hermaphrodite. Staminodes and pistillodes occur in flowers in dioecious species. In almost all cases, female peduncle grows faster during the development of fruits. The pollen grains are monocolpate and aporate, similar to those in Cordaitales, Bennettitales, Cycadales and Magnoliaceae. Economically palms are important next only to Gramineae and Leguminosae.

Despite these facts relatively little work has been done on them. This is perhaps due to the technical difficulties and scarcity of authentic material necessary for scientific investigation in all its aspects.

As regards the genus *Phoenix*, Mahabale and Parthasarathy (1963) have given an account of the taxonomy, morphology and geographical distribution of the species occurring in India. Anatomy of different species was also studied and is under publication (Parthasarathy, 1957, Thesis, unpublished). The present paper gives a detailed account of the embryology of *Phoenix sylvestris*, being a typical species of the genus. Apart from mere embryology, it was thought to be all the more important, as a small fossil fruit resembling that of *Phoenix* has been described by Berry (1934), and for comparing it with living members, the data on seed and embryo were necessary. It was wanting.

PREVIOUS WORK

Reference to previous literature shows, that much work needs to be done on the embryology of palms. Juliano and Quisumbing (1931) studied

the anther wall in *Cocos nucifera* and found 6–8 layers of which the sub-epidermal layer developed into fibrous endothecium : the innermost 2–4 layers function as tapetum. Süssenguth (1921) found simultaneous division of the microspore mother cells in *Chamaedorea sartorii, C. glaucophylla* and *C. karwinskiana,* and Schnarf (1931) in *Chamaedorea corollina, Areca triandra, Caryota* and *Pterigospermum* species, and Juliano and Quisumbing (1931) in *Cocos nucifera.* On the other hand, Radermacher (1924) found successive type of division of microspore mother cells in *Nipa fruticans.*

Various types of embryo-sac development have been reported in different palms. It is said to be of the normal 8-nucleated *Polygonum* type in *Actinophloeus macarthurii* (Radermacher, 1924) and *Areca catechu* (Swamy, 1942). The same has been reported by Rao (1959 *a*, 1959 *b*) in *Areca catechu, A. consinna, A. triandra* and in species of *Actinophloeus, Pritchardia, Licuala Livistona, Caryota, Trachycarpus, Washingtonia* and *Sabal.* However, bisporic embryo-sacs have been reported by Jönsson (1879/80) in *Chamaedorea latifolia* and in *Nipa fruticans* by Radermacher (1925). According to Maheshwari (1955) the embryo-sac in them is not bisporic as was supposed earlier. Quisumbing and Juliano (1927) have reported *Adoxa* type of embryo-sac in *Cocos nucifera.* According to them the archesporial cell functions directly as the megaspore mother cell. However, earlier Bauch (1911) had found degenerating megaspores in the same species. He also found that in *Phoenix sylvestris* the upper three megaspore cells degenerate at 2-nucleated embryo-sac stage. Later Gioelli (1930) reported a modified type of embryo-sac with 5 nuclei, 4 micropylar and one chalazal in *Chamaerops humilis.* In *Elaeis guineensis* De Poerck (1950) found that the megaspore mother cell develops directly into 8-nucleated embryo-sac, which means that it is of the *Adoxa* type in the oil palm. In the same species Kajale and Ranade (1952–53) found four kinds of tetrads and normal 8-nucleated *Polygonum* type of embryo-sac. On the other hand, in *Hyphaene indica* Mahabale and Chennaveeraiah (1957) found *Allium* type of embryo-sac development.

The number of antipodals in palms is also varying. In *Chamaedorea concolor* there are three insignificant ephemeral antipodal cells (Süssenguth, 1921). In *Pinanga moluccana* (Lotscher, 1905) and *Calyptrocalyx* sp. (Bauch, 1911), they are persistent and sometimes become 2–3–nucleate. The antipodals are said to be persistent and aggressive in *Areca catechu* (Swamy, 1942). According to Lang (1943), the endosperm is free-nuclear in *Phoenix dactylifera,* and also in *Areca catechu, Chrysalidocarpus lutescens,*

and in species of *Licuala*, *Livistona*, *Trachycarpus*, *Washingtonia*, and *Sabal* (Rao, 1955 *b*, 1959 *a* and 1959 *b*).

The embryo development in Palmae is imperfectly known, especially the later stages leading to the formation of embryo in mature seeds. Selvaratnam (1952) has described the mature embryo in *Cocos nucifera*. According to Rao (1955 *a* and 1959 *a*), in *Areca catechu* and *Actinophloeus macarthurii* there is Onagrad type of the embryo development.

MATERIAL AND METHODS

Material for the present investigation was collected in 1962–65 during December–May from trees on the Poona University campus, Hadapsar and Vithalwadi near Poona where plants grow in abundance. Formalin-acetic alcohol was employed as the fixative. Flower-buds, pre- and post-fertilized flowers, young and old fruits were fixed after removing the perianth leaves and trimming certain portions in order to facilitate quick penetration. Both alcohol-xylol and tertiary butyl alcohol series were used for dehydration. Pretreatment of the fruit and seeds with 5% hydrofluoric acid (HF) was found necessary to soften the hard seedcoat. Sections were cut at 4–10 μ for sporogenesis and gametogenesis, and 12–20 μ for endosperm, embryo and seedcoat development. For staining Heidenhains Iron-haematoxylin with erythrosin as counter-stain were used. The pollen grains were stained in basic Fuchsin and mounted in glycerine jelly. Their germination was carried out in artificial media of concentrated sucrose solution with an addition of IAA and Gibberellic acid. They were stained with aceto-carmine.

OBSERVATIONS

Morphology.—Commonly known as "Wild date" is a tall 8–16 m., unbranched graceful palm belonging to subfamily Phoenicoideae of the Palmae. Mahabale and Parthasarathy (1963), however, found some trees with 4–12 branches. The tree trunk is rough due to persistent leaf bases (Pl. V, Fig. 1). The leaf crown is large, made up of 16–35 leaves, each 3–6 m. long. The petioles are compressed towards the apex. At the base they have 4–6 channelled, triangular, short, spines 7–8 cm. long. Leaflets are 20–35, each 19–43 × 2 cm., densely fascicled, glaucous, rigid, ensiform, conduplicate at the base, ending in pointed spines.

The inflorescence is a spadix. 4–8 spadices arise on a tree, each in the axil of a single leaf. Male and female spadices are separate and are borne

on different trees. They are enclosed in a single spathe 0·75–1 m. long each (Pl. V, Figs. 7 and 8). The flowers are bracteate, trimerous and regular. Perianth leaves are tubular or companulate. The greenish-white perianth leaves have 3 short outer and 3 long inner ones (Text-Figs. 2 and 24). The male flowers have six stamens and three pistillodes on the receptacle (Text-Fig. 3). The female flowers have three prominent carpels with or without staminodes. The fruit is an oblong one-seeded berry with terminal stigma and greenish-orange or purple exocarp, fleshy mesocarp, papery endocarp and a stony seed. The seed is grooved on its ventral side. The plants flower from November to February and the fruits ripen from March–May or even later.

Inflorescence and Flowers.—6–8 interfoliar male spadices develop at a time acropetally. Each male spadix is 60–90 cm. long, erect, with spathe of about the same length. Spathes are coriaceous, nearly woody, scurfy, separating later into two boat-shaped valves, densely covered with tomentum. The halved spathes are reddish in colour from inside and whitish-brown outside. 60–75 spikes 5–10 cm. long, often fascicled, are borne closely towards the apex on the primary branch of flat peduncles, especially on its anterior face (Pl. V, Figs. 3 and 4). They are slender, flexuous and narrowed at the tip and have 17–30 flowers. The terminal narrow tip of spikes may or may not bear flowers (Text-Fig. 1, Pl. V, Fig.4).

In male peduncle there are 1,500 or even more, sessile, angular, oblique, whitish-brown male flowers (Text-Fig. 1, Pl. V, Figs. 3 and 4). Their outer perianth is cup-shaped, having 3 short rounded teeth. It is hard and persistent. The three inner perianth lobes are 3–4 times longer than the outer. They are concave, warty outside, deeply ridged and furrowed inside (Text-Fig. 2). There are 6 stamens in a male flower (Text-Fig. 8). The filaments are very short, if any, and are free. Anthers are linear and adnate, shorter than the petals. There are three pistillodes in male flowers (Text-Fig. 3). A number of insects are attracted to male cobs at the time when pollen is shed due to sweet smell emitted by it (Pl. V, Fig. 7). Huge mass of pollen grains is produced by the male spadices which do not grow in length after anthesis.

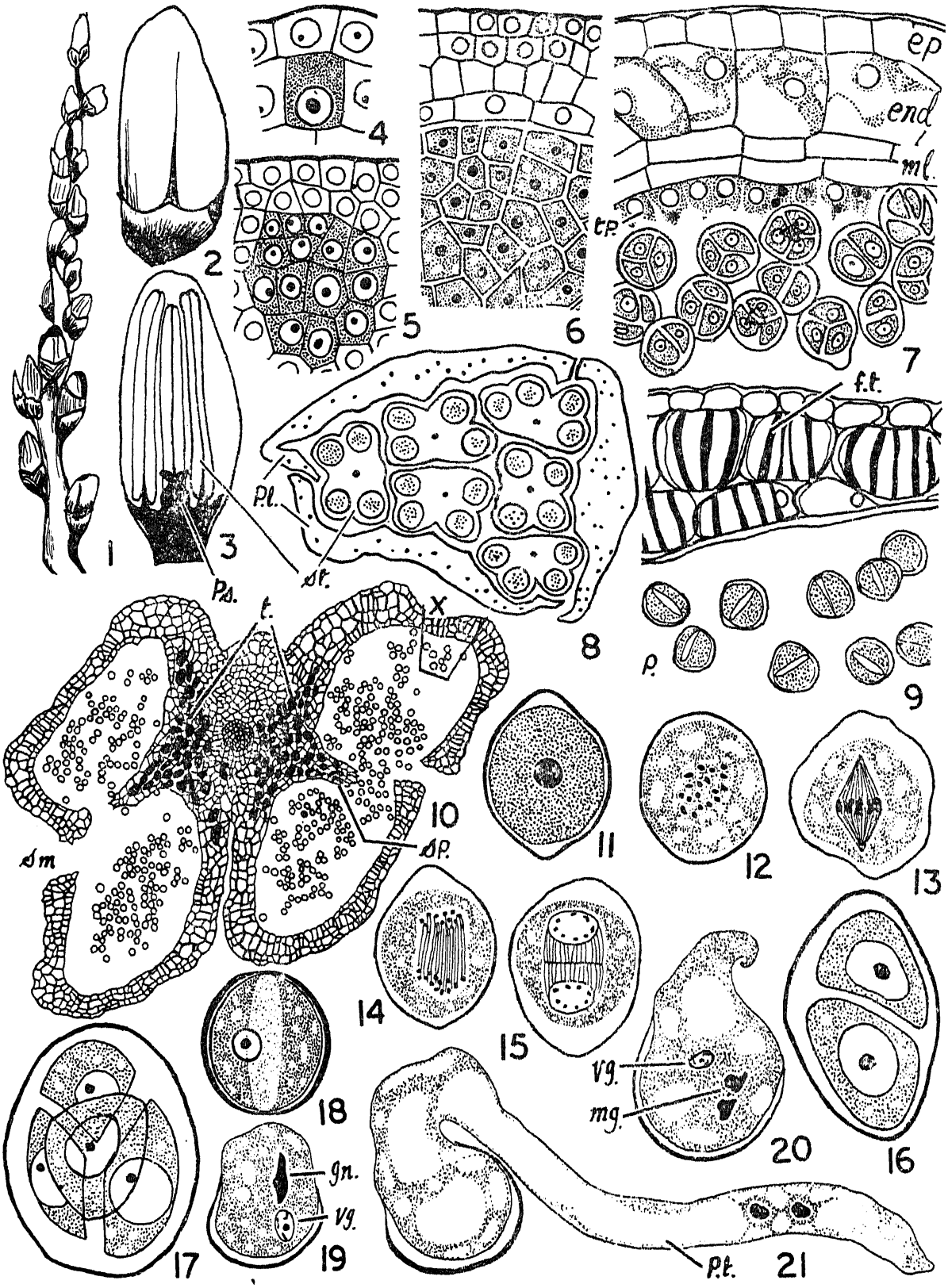
The female spadix and enclosing spathes are much the same as in male one (Pl. V, Fig. 8). Spikes are 30–45 cm. long, golden in colour, arranged in distinct groups. They are narrow at the tip, with or without flowers (Text-Fig. 22, Pl. V, Fig. 11). Flowers are sessile, distant and round (Text-Fig. 24, Pl. V, Fig. 11). Calyx is cup-shaped, 3-toothed, and persistent.

Petals are 3, broad, convolutely imbricated and have small opening at the apex. Staminodes are 4–6. Carpels as a rule are 3, rarely 4, erect and free. The style is short, recurved and open. Stigma is simple and curved (Text-Fig. 23). Fruiting spadix is 92 cm. long, golden in colour, nodding at the apex due to weight of developing fruits 2–4 cm. long. Pendulous peduncles are also golden in colour (Pl. V, Fig. 2). The fruits are oblong, ellipsoid, orange, yellow or black purple in colour and have terminal stigma surrounded by persistent perianth lobes at the base. It is interesting to note here that in a few female flowers, 4 instead of 3 carpels are seen (Text-Fig. 26, Pl. V, Fig. 6). All the carpels and ovules are equally well formed, but only one carpel develops into a fruit after fertilization.

Microsporangium.—In a young anther lobe, one of the hypodermal cells is differentiated as an archesporial cell at each of the 4 corners of the anther. The cells divide periclinally to form the primary parietal and primary sporogenous layers (Text-Fig. 4). The parietal cells divide anticlinally and periclinally forming 4–5 wall layers (Text-Figs. 6 and 7). Juliano and Quisumbing (1931) observed eight layers of cells in the anther wall of *Cocos nucifera*, Rao (1959 *b*) observed 4-5-layered anther wall in *Borassus flabellifer*, *Pritchardia*, *Licuala* and *Livistona* species, Mahabale and Chennaveeraiah (1957) found 5–6-layered anther wall in *Hyphaene indica*.

The outermost layer of the anther acts as an epidermis and becomes cutinized (Text-Fig. 7). The sub-epidermal layer develops into endothecium and the innermost functions as tapetum. The two layers next to endothecium are thin-walled and act as "middle layers" (Text-Fig. 7). Tapetal cells are uninucleate initially, but become binucleate or even more later (Text-Fig. 7). Mahabale and Chennaveeraiah (1957) had observed similar binucleate tapetal cells in *Hyphaene indica*, and Rao (1959 *a* and *b*) in members of the Arecineae, Cocoineae and Sabalae.

Microsporogenesis and Male Gametophyte.—The primary sporogenous cell divides to form a mass of sporogenous tissue (Text-Fig. 5). The cells are polygonal when young but become round later (Text-Fig. 6). The division in the pollen mother cells is of the successive type (Text-Figs. 7 and 11–17). Cytokinesis takes place by cell plate formation. Similar successive type of division was also seen in *Hyphaene indica* by Mahabale and Chennaveeraiah (1957). On the other hand, Rao (1959 *a*) observed simultaneous cell plate formation in *Chrysalidocarpus lutescens*. The spore tetrads are usually iso-bilateral, sometimes tetrahedral (Text-Fig. 7). Mahabale and Chennaveeraiah (1957) observed "*T*"-shaped and linear



TEXT-FIGS. 1–21

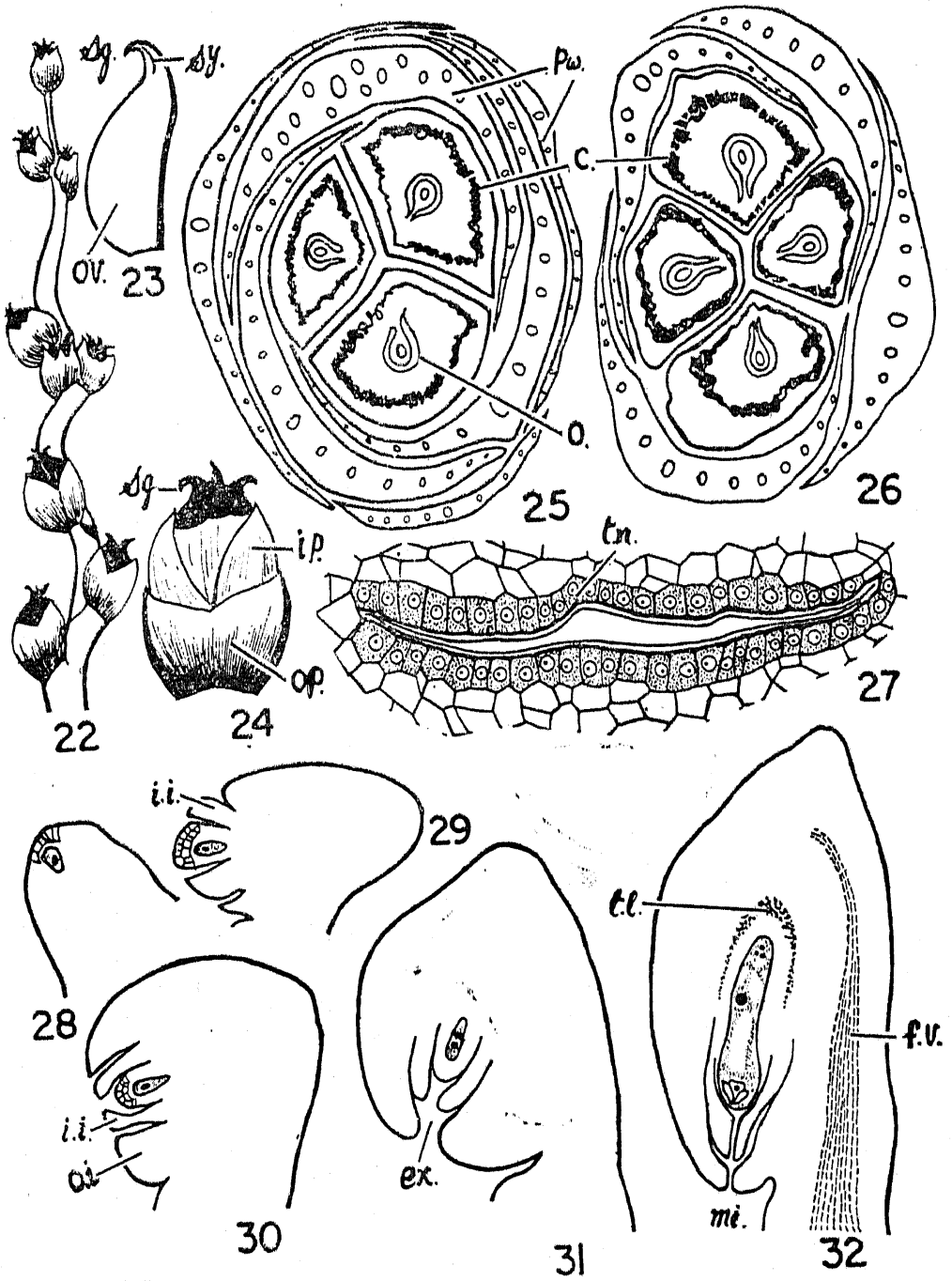
tetrads, in addition to the iso-bilateral and tetrahedral tetrads in *Hyphaene indica*. Rao (1959 *a*) had noted tetrahedral, dicussate and bilateral tetrads in *Areca catechu* and *Chrysalidocarpus lutescens*.

The microspores separate from the tetrads and grow in size 13 × 13 μ. A newly formed microspore has dense cytoplasm and centrally placed nucleus. Mature pollen grains are shed in 2-celled stage. They are almost spherical and monocolpate. The exine is smooth and thick-walled (Text-Fig. 18, Pl. V, Figs. 9 and 10). According to Mahabale and Chennaveeraiah (1957) pollen grains are warty in *Hyphaene indica* similar to those in *Borassus flabellifer* (Erdtman, 1952). Rao (1959 *a*) observed reticulate thickening on the pollen grains in *Areca* and *Caryota* species. The nucleus of microspore divides and forms a round vegetative cell and a lenticular generative cell (Text-Fig. 19, Pl. V, Fig. 10). The vegetative cell measures 2·4 × 3·7 μ and generative cell 2·52 × 6 μ. The generative cell divides to form two male gametes. They are oval or elliptical, 2 × 3 μ (Text-Figs. 20 and 21).

Ovary and Ovule.—The ovary is superior, tricarpellate, trilocular having a single ovule in each loculus (Text-Fig. 25). Ovules are bitegmic, crassinucellate and anatropous (Text-Fig. 32). Text-Figures 28–32 show stages in the growth and curvature of the anatropous ovule. In *Hyphaene indica* Mahabale and Chennaveeraiah (1957) observed orthotropous ovules, and Rao (1959 *a*, *b*) pendulous ovules in *Howea* and *Actinophloeus* species, orthotropous and transverse in *Bactris* sp., and orthotropous and erect in *Caryota* sp., hemianatropous in *Livistona rotundifolia*, and in species of *Sabal*, *Chrysalidocarpus* and *Areca*, anatropous in *Pritchardia*, *Washingtonia*, *Licuala* and *Trachycarpus*.

At the time of archesporial initial, the ovule has no integuments (Text-Fig. 28). By the time the archesporium cuts off parietal layers, the young megaspore mother cell gets differentiated and an inner integument is formed (Text-Fig. 29). At fully matured megaspore mother cell stage, the inner integument is 3–4-layered, and outer integument 5–7-layered without any vascular bundles. Micropyle is formed by both the integuments and is curved (Text-Figs. 31 and 32). In *Livistona rotundifolia*, in species of *Sabal* and *Pritchardia* the micropyle is formed at the 2-nucleated stage, and at the megaspore mother cell stage in *Washingtonia* and *Licuala* species (Rao, 1959 *b*). Funicular vascular strand ends in the chalazal region without supplying branches to the integuments (Text-Fig. 32). In *Hyphaene indica*, however, there are 16–18 vascular bundles extending to two-thirds length of the outer massive integuments (Mahabale and Chennaveeraiah, 1957).

As the embryo-sac matures, a zone of cells thickened with tannin develops below the embryo-sac in each ovule and extends to the micropylar region encircling the embryo-sac (Text-Fig. 32). But its pronounced development is in the chalazal region, which indicates a tendency to form an incipient hypostase.



TEXT-FIGS. 22–32

Integumentary tapetum is formed from the inner layer of the inner integument with radially elongated and glandular cells (Text-Fig. 48),

Similar integumentary tapetum occurs in *Cocos* sp., and *Areca concinna* (Rao, 1959 *a*).

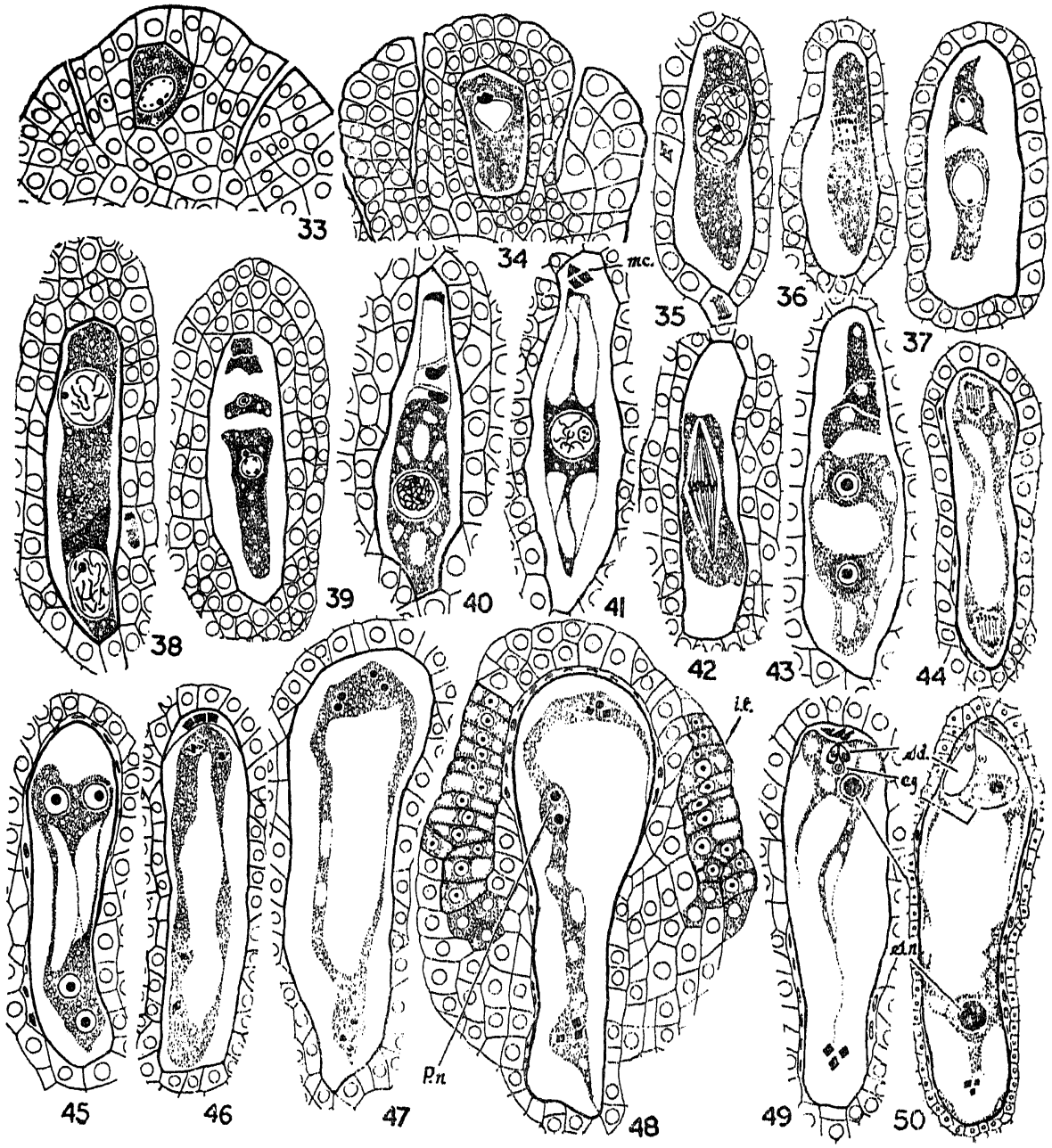
All the three ovules develop to mature embryo-sac stage, but as a rule only one ovule develops further after fertilization. The other two ovules are suppressed completely during the development of the fruit and are represented by two black dots on the fruit enclosed by persistent perianth lobes on the fruit.

Megasporogenesis and Female Gametophyte.—A single hypodermal cell differentiates as the archesporium in ovule primordium (Text-Fig. 33, Pl. VI, Fig. 12). The archesporium does not directly act as a megaspore mother cell as in *Cocos nucifera* (Quisumbing and Juliano, 1927). The archesporium divides periclinally to produce a parietal cell and a sporogenous cell which directly acts as a megaspore mother cell (Text-Fig. 34, Pl. VI, Figs. 13 and 14). The parietal tissue is 3-layered. Kajale and Ranade (1953) observed the same in *Elaeis guineensis*, but Rao (1959 *b*) noted only single-celled parietal tissue and nucellar cap in *Livistona rotundifolia*. There is a single megaspore mother cell in each ovule ; but supernumerary megaspore mother cells are often noticeable here as in *Cocos nucifera* (Bauch, 1911) and *Elaeis guineensis* (De Poerck, 1950) (Text-Fig. 38). Occurrence of twin embryo-sacs has been known in *Elaeis guineensis* (Kajale and Ranade, 1953), but has not been seen in this or other species of *Phoenix*.

A fully developed megaspore cell is tapering and elongated, its nucleus lying in the micropylar half (Text-Figs. 34–36). The nucleus of the megaspore mother cell undergoes typical synizesis resulting in the formation of a dyad, the micropylar cell being smaller than the chalazal (Text-Fig. 37, Pl. VI, Fig. 15). This is followed by a secon dtransverse division in each dyad cell, resulting in a linear tetrad of megaspores (Text-Figs. 39 and 40, Pl. VI, Fig. 16). Rao (1959 *a*) had observed both linear and "*T*"-shaped tetrads in *Caryota mitis*, *Chrysalidocarpus lutescens*, and Dr. (Miss) Shirke (1963) in *Caryota urens*. Kajale and Ranade (1953) noted four different types of megaspore tetrads in *Elaeis guineensis*.

The functional megaspore cell enlarges considerably crushing the surrounding nucellar cells (Text-Figs. 40 and 41). Text- Figure 42 shows the nuclear division of the functional cell. The resulting two nuclei get polarized and form the primary micropylar and primary chalazal nucleus (Text-Fig. 43). It is interesting to note in this connection that three degenerating megaspores are sometimes still distinctly seen at the two-nucleate embryo-sac stage (Text-Fig. 43). Bauch (1911) had also noticed this in *Cocos nucifera*

and *Phoenix sylvestris*. Text-Figure 44 shows the late anaphase at the 2-nucleated embryo-sac stage. At 4-nucleated embryo-sac, the two micropylar nuclei lie side by side and the chalazal nuclei lie one above the other (Text-Fig. 45, Pl. VI, Fig. 17). Text-Figure 46 shows metaphase in equatorial view at 4-nucleated embryo-sac stage. The resultant 8 nuclei form a group of micropylar and chalazal quartet (Text-Fig. 47). Text-Figures 48–50 show the organisation of mature embryo-sac having two synergids, an egg, secondary nucleus and three antipodal nuclei. Position of the



TEXT-FIGS. 33–50

secondary nucleus is variable, sometimes near the egg, or at the centre, or near the antipodal cells (Text-Figs. 49 and 50).

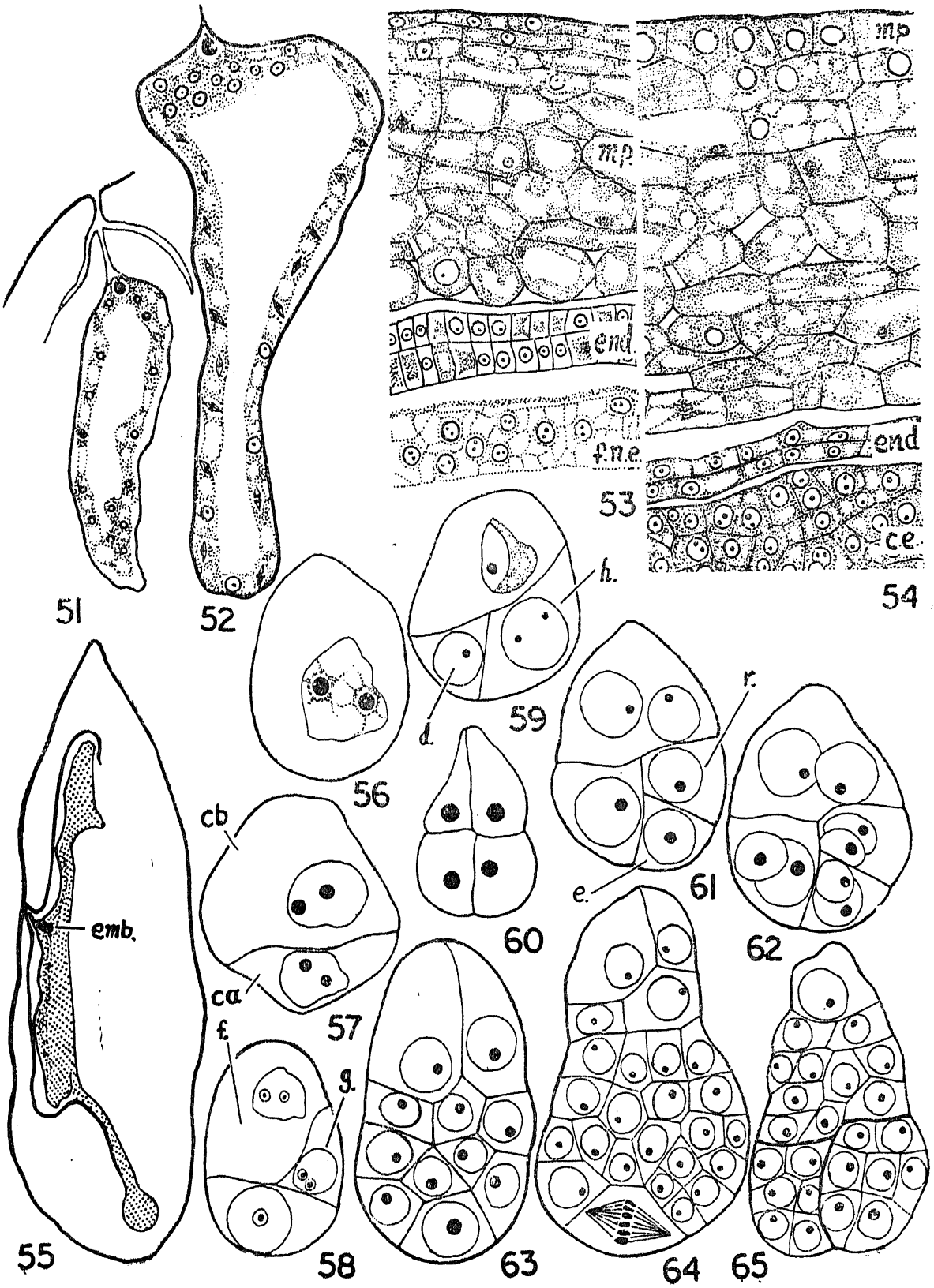
The antipodal nuclei are ephemeral not organised into cells. They degenerate before fertilization. They show variable arrangement either in "*T*" or "⊥" or linear group at the chalazal end of the embryo-sac.

The development of female gametophyte on the whole thus conforms to the monosporic 8-nucleate *Polygonum* type of Mahaeshwari (1948), as in members of the Arecoid and Sabaloid palms, as against bisporic 8-nucleated *Allium* type of female gametophyte found in *Hyphaene indica* by Mahabale and Chennaveeraiah (1957).

Fertilization and Endosperm.—The pollen tube traverses through rich protoplasmic cells of the style and enters the ovule porogamously affecting the synergids by its entry into the embryo-sac (Text-Fig. 27).

The endosperm is free-nuclear to begin with but becomes cellular later. The primary endosperm nucleus divides rapidly after fertilization into two. The resultant nuclei move to the micropylar and chalazal ends, which in their turn divide repeatedly to form a number of nuclei embedded in the cytoplasm. The cytoplasmic cord and its numerous nuclei line up at the periphery of the embryo-sac and form a central vacuole (Text-Fig. 51). Rao (1959 *a*) had observed similar type of arrangement in *Actinophloeus* and *Areca* species. The aggregation of nuclei in the micropylar region is more here than that at any other part of the embroy-sac (Text-Fig. 52). In early stages endosperm nuclei are small, 4 μ, but they become large, 11 μ or more in later stages. They vary in shape, size and number of nucleoli. Cell wall formation in them starts at the periphery of the embryo-sac when the embryo is globular and proceeds towards the central cavity. In *Actinophloeus* sp. according to Rao (1959 *a*) cell wall formation starts in the micropylar region at 8–10-celled stage of the embryo, and proceeds to the chalazal region as in members of Ceroxylineae. The endosperm cells near the placental groove are small, squarish or round, but those towards the periphery are radially elongated. They develop plasmodesmata at maturity. The rumination is placental, unbranched, not extending deep into the endosperm. Ruminate endosperm was observed by Rao (1959 *a*) in species of *Caryota*, *Howea* and *Areca*.

Embryo.—The first division of zygote is transverse forming 2-celled proembryo of which the basal cell, *cb*, is longer than the shorter terminal cell, *ca* (Text-Figs 56–57, Pl. VI, Figs. 18–19). The 3-celled proembryo is formed by a vertical division either in cell *ca* or *cb*. A vertical wall is laid



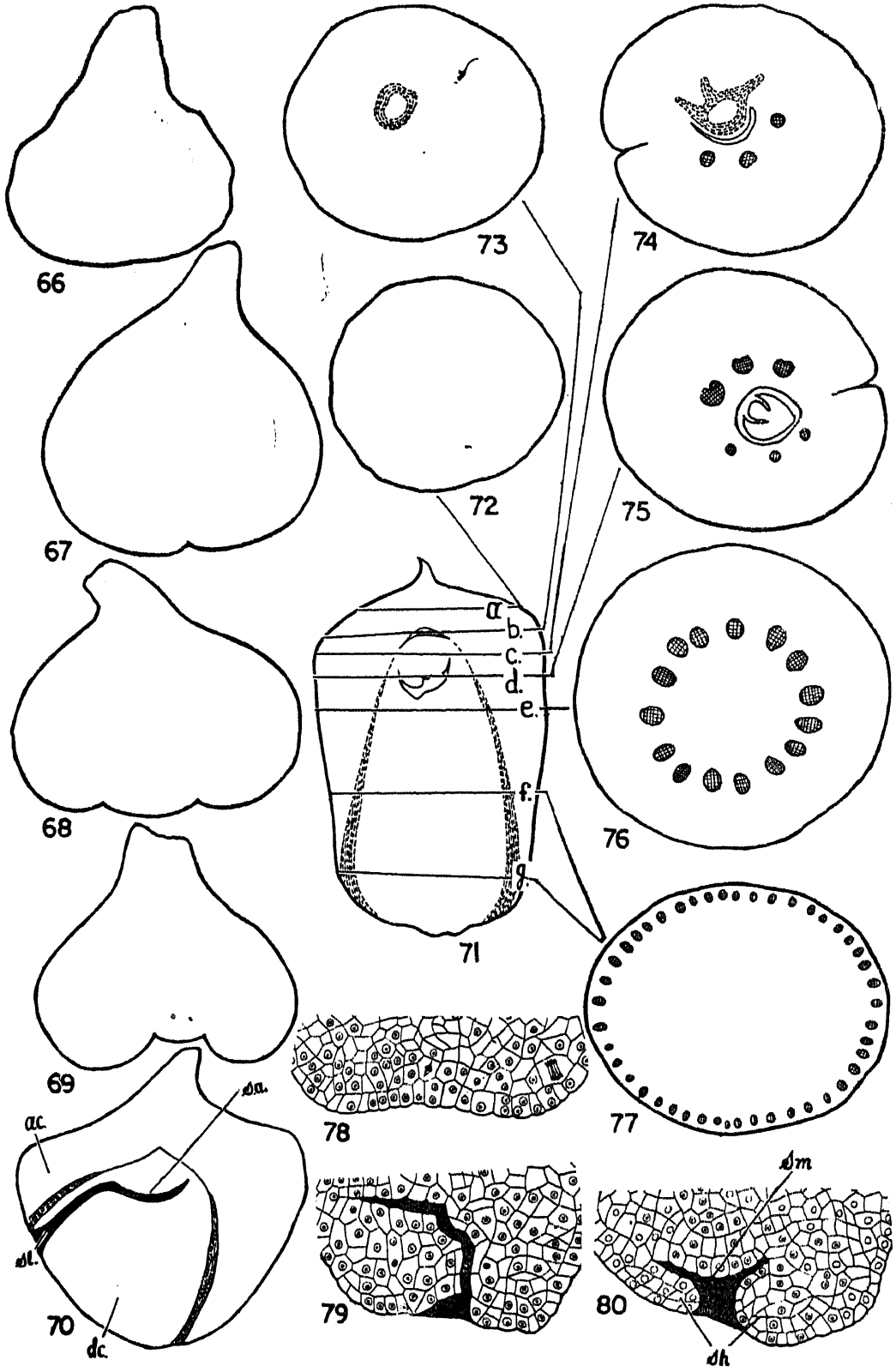
TEXT-FIGS. 51–65

in *ca* giving rise to *h* and *d* cells (Text-Fig. 59, Pl. VI, Fig. 20). By another vertical division in the cell *cb* a 4-celled proembryo is formed giving rise to cell *f* and *g* (Text-Figs. 58 and 60). An epiphysial cell *e* is formed from the cell *h* after an oblique vertical division in it (Text-Fig. 61). Next a vertical division at right angles divides the lower tier of cells formed from *ca* into an 8-celled embryo (Text-Fig. 62). Both basal and terminal cells take part in the formation of the mature embryo. The mode of cell divisions in zygote and its subsequent stages conform to the *Geum* variation of the Asterad type of embryo development of Johansen (1950). According to Rao (1955 *a*, 1959 *a*) there is *Trifolium* variation of the Onagrad type of embryo development in *Areca catechu.*

A number of divisions take place in the 8-celled embryo periclinally and anticlinally resulting in a globular mass (Text-Figs. 63–65, Pl. VI, Figs. 21–22). The globular embryonal mass differentiates into "dermatogen" later (Text-Fig. 66). The broad portion of the globular embryo further differentiates into two lateral cotyledonary lobes with apical meristem in the centre forming a heart-shaped structure like the one present in most of the dicotyledons and in a few monocotyledons such as *Commelina karwinskyi* and *Tinantia erecta* indicating thereby a tendency towards the development of two lateral cotyledons and the terminal shoot apex (Text-Figs. 67–69, Pl. VI, Figs. 22–23). On the other hand, Rao (1955 *a*, 1959 *a*) found that position of the shoot apex in *Areca catechu* and *Actinophloeus macarthurii* is lateral. In the later stages of embryo one of these two cotyledons grows more than the other and arches over the other cotyledon, the shoot apex retaining its terminal position, leaving a narrow slit on one side of the embryo, due to close approach of the margins of its two cotyledons (Text-Fig. 70, Pl. VI, Fig. 24).

The more vigorous and pronouncedly developing cotyledon elongates considerably, forming a single conspicuous cotyledon at maturity (Text-Fig. 71, Pl. VI, Figs. 25 and 28). The other cotyledon is completely arrested and becomes vestigial in the mature embryo near its shoot apex.

The radical as shown in Text-Fig. 71 and Pl. VI, Fig. 25 is formed opposite the shoot apex. The terminal end of the cotyledon which encloses the shoot apex broadens and increases in thickness. The mature embryo is cylindrical. It has a single massive well-developed cotyledon. Its shoot apex is differentiated into sheathing leaf, stem apex, nodal plate, radical and highly condensed hypocotyledonary region (Text-Figs. 71, 78–80, Pl. VI, Fig. 25). Text Figures 72–77 show a series of T.Ss. of the mature embryo,



TEXT-FIGS. 66–80.

The nodal plate is clear in them. It gives rise to six vascular strands (Text-Figs. 74 and 75, Pl. VI, Fig. 27), which divide and redivide to form a ring of

28–30 vascular strands in the basal region of the enlarged filiform cotyledon (Text-Figs. 76–77, Pl. VI, Figs. 29–30).

A very important feature noticed during the development of the embryo-sac and embryo was the gradual shifting of the micropyle from its earlier terminal position to a lateral one in the seed in later stages (Text-Figs. 51 and 55). This is rather interesting as it helps in identifying seeds of the genus *Phoenix*. On the basis of this and other characters the fossil seed of *Phoenix* described by Berry (1934) compares very favourably with that in *P. dactylifera* rather than with *P. sylvestris* and other species studied.

REFERENCES

*Bauch, K. .. "Beiträge zur entwicklungsgeschichte und physiologischen anatomie der palmenblüte," Berlin, 1911.

Bentham, G. and Hooker, J. D. *Genera Plantarum*, 1883, **3**, 1–1258.

Berry, E. W. .. "Fruits of a fossil date-palm in the Tertiary deposits of Eastern Texas," *Amer. Jour. Sci.*, 1934, **37**, 403–06.

Bassey, C. E. .. "Phylogenetic taxonomy of flowering plants," *Ann. Mo. Bot. Gard.*, 1915, **2**, 1–155.

Brown, R. W. .. "Palm-like leaves from the Dolores formation (Triassic) S. W. Colorado," *U.S. Geol. Surv. Pro. Paper*, 1956, **274** (4), 205–09.

Corner, E. J. H. .. *The Natural History of Palms*, University of California Press, Berkeley and Los Angeles, 1966, 1–393.

De Poerck, R. A. .. "Contribution a l' etude' de Palmier a huilé African (*Elaeis guineensis* Jacq.) *Ole' aegineux*," 1950, **5**, 623–28.

Hutchinson, J. .. *The Families of Flowering Plants—II, Monocotyledons*, London, 1959, 511–792.

Johansen, D. A. .. *Plant Embryology*, Waltham, Mass., U.S.A., 1950, 1–305.

*Jönsson, B. .. "Om embryosackens utveckling hos Angiospermerna," *Lunds. Univ. Årsskar.*, 1879/80, **16**, 1–86.

Juliano, J. B. and Quisumbing, E. .. "Morphology of the male flower of *Cocos nucifera* L.," *Philipp. Jour. Sci.*, 1931, **45**, 449–58.

Kajale, L. B. and Ranade, S. C. "Occurrence of four kinds of tetrads in *Elaeis guineensis* Jacq.," *Curr. Sci.*, 1952, **21**, 170.

——— .. "The embryo-sac of *Elaeis guineensis* Jacq., a reinvestigation," *Jour. Ind. Bot. Soc.*, 1953, **32**, 101–07.

Lang, E. M. .. "Developmental anatomy of the fruit of deglect noor-date," *Bot. Gaz.*, 1943, **104**, 426–36.

*Lignier, O. .. "Novelles recherches sur le *Propalmophyllum liasinum*," *Mem. Soc. Linn. Normandie*, 1907, **23**, 1–15.

Mahabale, T. S. and Chennaveeraiah, M. S. — "Studies on *Hyphaene indica* Bec. I. Morphology," *Phytomorphology*, 1957, **7**, 184–94.

———— .. "The genus *Phoenix* L. in India," *Jour. Bom. Nat. Hist. Soc.*, 1963, **60** (2), 371–87.

Mahabale, T. S. .. "Evolutionary trends in the Palmae with special reference to fossil palms," *The Palaeobotanist*, 1965, **14** (3), 214–22.

Maheshwari, P. .. *An Introduction to the Embryology of Angiosperms*, McGraw-Hill Publication, N.Y. and London, 1950, 1–453.

Maheshwari, C. .. "The occurrence of bisporic embryo-sacs in angiosperms—A critical review," *Phytomorphology*, 1955, **5**, 67–69.

Moore, H. E. .. "Botany and classification of palms," *Amer. Hort. Mag.*, 1960, **2**, 17–26.

Parthasarathy, M. V. .. "Studies on palms: Anatomy of the genus *Phoenix* L.," A thesis submitted to the University of Poona for the M.Sc. degree (Unpublished), 1957.

Quisumbing, E. and Juliano, J. B. "Development of ovule and embryo-sac of *Cocos nucifera* L.," *Bot. Gaz.*, 1927, **84**, 279–93.

Radermacher, A. .. "Die gametophyten von *Nipa fruiticans* and *Actinophloeus macarthurii*," *Ann. Jard. Bot. Buitenz.*, 1925, **35**, 1–54.

Rao, C. V. .. "Embryo development in Areca-nut," *Nature*, 1955 *a*, **175**, 432–33.

———— .. "Endosperm and seed development in *Chrysalidocarpus lutescens* H. Wendel," *Curr. Sci.*, 1955 *b*, **24**, 381–82.

———— .. "Contribution to the embryology of Palmae. Part II. *Ceroxylineae*," *Jour. Indian bot. Soc.*, 1959 *a*, **38**, 46–75.

———— .. "Contribution to the embryology of Palmae. Part I. *Sabalae*," *Proc. Nat. Inst. Sci. Ind.*, 1959 *b*, **29**, 134–64.

Schnarf, K. .. *Vergleichende Embryologie der Angiospermen*, Berlin, 1931.

Selvaratnam, E. M. .. "Embryo of coconut," *Nature*, 1952, **169**, 714.

Shirke, N. S. .. "Studies on palms: Genus *Caryota* L. in India," Ph.D. thesis submitted to the University of Poona (Unpublished), 1963.

*Süssenguth, K. .. "Beträge zur frage der systematischen ausschlusses der monokotyl," *Beih. bot. Zbl.*, 1921, **38**, 1–70.

Swamy, B. G. L. .. "Embryological studies in Palmae. A preliminary note on the megasporogenesis in *Areca catechu*," *Curr. Sci.*, 1942, **11**, 109.

* Not seen in the original.

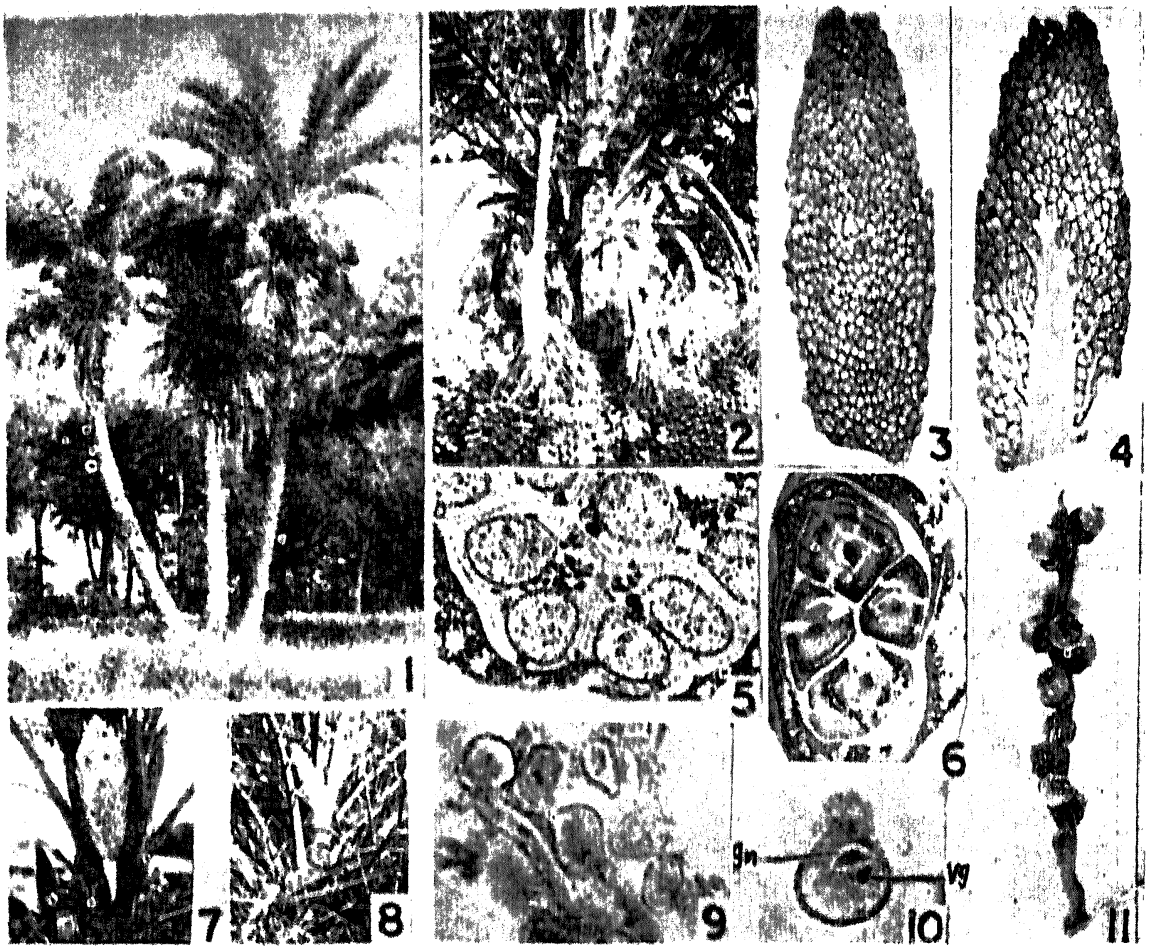
Explanation of Text-Figures

Text-Figs. 1–21. *Phoenix sylvestris* Roxb. Male flower, microsporogenesis and male gametophyte. Fig. 1. Secondary axis of a male peduncle showing arrangement of male flowers, × 2. Fig. 2. A male flower, × 4. Fig. 3. L.s. of female flower showing pistillodes—*ps* and

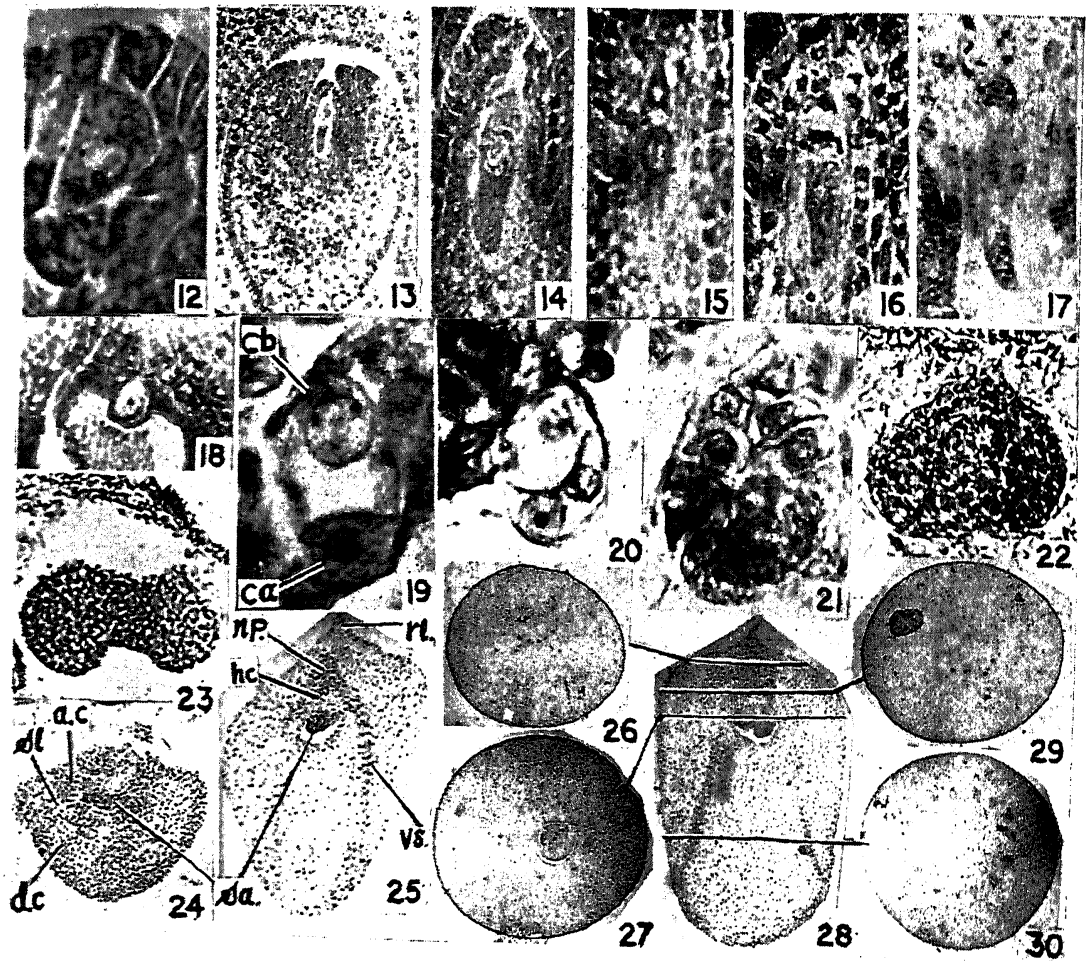
stamens—*st*, on receptacle, × 5. Fig. 4. An archesporial initial cell, × 1,125. Fig. 5. Sporogenous tissue, × 645. Fig. 6. T.s. of anther lobe showing separation of pollen mother cells, × 645. Fig. 7. T.s. of mature anther showing epidermis—*ep.*, endothecium—*end.*, middle layers—*ml.*, uni-binucleate tapetal cells—*tp*, tetrahedral and isobilateral tetrads, × 425. Fig. 8. T.s. of male flower showing inner whorl of perianth leaves—*pl.* and 6 stamens—*st.*, × 15. Fig. 9. An enlarged view of the portion marked *x* in Fig. 10, showing fibrous thickening—*ft.*, in endothecium and mature pollen grains—*p*, × 425. Fig. 10. T.s. of mature anther: Note the tannin deposition—*t*, in the connective part, septum—*sp.*, and stomium—*sm.*, × 110. Fig. 11. Microspore mother cell, × 1,125. Fig. 12. Microspore mother cell showing 18 chromosomes, × 1,125. Fig. 13. Microspore mother cell at metaphase, × 1,125. Fig. 14. Microspore mother cell at anaphase, × 1,125. Fig. 15. Microspore mother cell at telophase, × 1,125. Fig. 16. Dyad, × 1,125. Fig. 17. A tetrahedral tetrad, × 1,125. Fig. 18. A mature pollen grain with a colpus, × 1,125. Fig. 19. Early germinating pollen grain showing vegetative cell—*vg.* and generative cell—*gn*, × 1,125. Fig. 20. Pollen grain showing a short-curved pollen tube, vegetative cell—*vg.* and two male gametes—*mg.*, × 1,125. Fig. 21. Germinating pollen grain with long pollen tube—*pt.* and two male gametes, × 1,125.

TEXT-FIGS. 22–32. *Phoenix sylvestris* Roxb. Female flowers and ovule. Fig. 22. The secondary axis of a female peduncle showing arrangement of flowers, × 2. Fig. 23. A single carpel showing enlarged region of ovary—*ov.*, short curved style—*sy.* and stigma—*sg.*, × 4. Fig. 24. A female flower with inner—*ip.* and outer perianth leaves—*op.* and stigma—*sg.*, × 5. Fig. 25. T.s. of female flower showing two perianth whorls—*p w.* 3 distinct carpels—*c* and three ovules—*o.*, × 15. Fig. 26. T.s. of a tetracarpellate flower with 4 perianth leaves and 4 carpels—*c.* × 14. Fig. 27. T.s. of open style showing transmitting cells of nectary around—*tn*, × 425. Fig. 28. L.s. of young ovule showing hypodermal archesporial initial, × 150. Fig. 29. Ovule, l.s. showing early differentiation of inner integument—*ii.*, × 150. Fig. 30. Ovule, l.s. showing inner integument-*ii.*, and outer integument—*oi.*, grown to the same level: Note that the ovule is placed at 90° to the axis of ovary, × 110. Fig. 31. Ovule, l.s.: Outer integument overgrown forming exostome—*ex.*, × 110. Fig. 32. Ovule, l.s. showing anatropous condition and micropyle—*mi.*, formed by both integuments. Funicular vascular strand—*f.v.*, ending at the chalazal region and deposition of tannin layer—*tl.*, around the embryo-sac, × 110.

TEXT-FIGS. 33–50. *Phoenix sylvestris* Roxb. Megasporogenesis and female gametophyte. Fig. 33. Archesporial initial, × 475. Fig. 34. Archesporial cell divided transversely to form outer 2 layers of parietal cells and the sporogenous initial acting as megaspore mother cell, × 475. Fig. 35. L.s. of ovule: megaspore mother cell in prophase: Note nuclear divisions in the adjacent nucellar cells, × 475. Fig. 36. Megaspore mother cell in anaphase, × 475. Fig. 37. Dyad, × 475. Fig. 38. L.s. of ovule: A supernumerary cell arising below the normal megaspore mother cell, × 475. Fig. 39. Linear megaspore tetrad showing enlarged chalazal cell and 3 small micropylar cells, × 475. Fig. 40. L.s. of ovule showing degeneration of 3 micropylar megaspores and one enlarged chalazal, × 475. Fig. 41. Functional chalazal megaspore forming uninucleate embryo-sac and three degenerating micropylar megaspores—*mc.*, × 475. Fig. 42. Metaphase division in uninucleate embryo-sac, × 475. Fig. 43. 2-nucleated embryo-sac with degenerating megaspores, × 475. Fig. 44. 2-nucleated embryo-sac in anaphase, × 475. Fig. 45. 4-nucleated embryo-sac, × 475. Fig. 46. Nuclei at metaphase equatorial division in the 4-nucleated embryo-sac, × 475. Fig. 47. 8-nucleated embryo-sac showing micropylar and chalazal quartet, × 475. Fig. 48. 8-nucleated embryo-sac: micropylar and chalazal polar nuclei—*pn.*, embedded in a common cytoplasmic mass and integumentary tapetum—*i.t.*, × 415. Fig. 49. Embryo-sac showing egg apparatus, secondary nucleus—*sn.*, lying very near to egg—*eg.* and 3 antipodal nuclei, × 475. Fig. 50. Mature embryo-sac showing 2 synergids—*sd.* and egg-*eg.*, secondary nucleus—*sn.*, near the antipodal cells and 3 ephimeral antipodal nuclei, × 184.



FIGS. 1–11


12
13
14
15
16
17
18
cb
19
ca
20
21
22
23
a.c
dl
dc
24
np
rl
hc
da
25
vs
26
27
28
29
30

FIGS. 12–30

TEXT-FIGS. 51–65. *Phoenix sylvestris* Roxb. Endosperm and proembryo. Fig. 51. L.s. of ovule: Early endosperm cord with nuclei and a central cavity, × 110. Fig. 52. The endosperm nuclei dividing and getting concentrated in the micropylar region, × 70. Fig. 53. T.s. of a young fruit showing mesocarp—*mp.*, two-layered endocarp—*end.*, and free nuclear endosperm—*f.n.e.*, × 200. Fig. 54. Enlarged portion of mature seed to show the massive mesocarp—*mp.*, 2-layered papery endocarp—*end.*, and a cellular endosperm—*c.e.*, × 425. Fig. 55. L.s. of mature seed showing laterally placed embryo—*emb.*, and micropyle in the seed at the time of shedding fruits from the tree, × 15. Fig. 56. Zygote, × 1,125. Fig. 57. 2-celled proembryo, showing elongated basal cell—*cb* and short terminal cell—*ca*, × 1,125. Fig. 58. 3-celled proembryo with an oblique division in *cb* giving rise to *f* and *g* cells, × 1,125. Fig. 59. 3-celled proembryo: Note the oblique division in *ca* cell differentiating unequal cells *d* and *h*, × 1,125. Fig. 60. 4-celled proembryo, × 1,125. Fig. 61. 5-celled proembryo: Note the oblique division in cell *h* giving rise to epiphysial cell *e* and cell *r*, × 1,125. Fig. 62. 8-celled proembryo, × 1,125. Fig. 63. Early globular embryo with two elongated suspensor cells, × 1,125. Figs. 64–65. Stages showing the development of globular embryo, × 1,125.

TEXT-FIGS. 66–80. *Phoenix sylvestris* Roxb. Embryo. Fig. 66. L.s. of a globular embryo, × 285. Fig. 67. Two cotyledonary lobes differentiated, × 285. Fig. 68. Terminal shoot apex and two lateral cotyledonary lobes, × 285. Fig. 69. Heart-shaped embryo, × 133. Fig. 70. One of the cotyledons arching over the other cotyledonary lobe, the shoot apex—*sa*, retaining its terminal position: Note the arrested cotyledon—*ac.*, developing cotyledon—*dc.* and a slit—*sl.* at the left hand side, × 100. Fig. 71. Mature embryo in l.s. of which T.Ss. were taken at different levels marked *a–g*, × 45. Fig. 72. T.s. of embryo below the region of radical showing only parenchymatous tissue, × 22. Fig. 73. T.s. of mature embryo showing the ring of nodal plate, × 22. Fig. 74. Six vascular bundles in two sets of which one set has divided, × 22. Fig. 75. T.s. of embryo at the level of shoot apex, × 22. Figs. 76–77. T.s. of embryo showing multiplication of the vascular strands, × 22. Figs. 78–80. Stem apex—*sm* showing differentiation of sheathing leaf—*sh*, × 22.

EXPLANATION OF PLATES

PLATE V

FIGS. 1–11. *Phoenix sylvestris* Roxb. Morphology.

FIG. 1. *Phoenix sylvestris* entire trees.

FIG. 2. Pendulous peduncles with numerous fruits borne on secondary axes.

FIG. 3. Male peduncle showing posterior surface view with numerous male flowers, × N.S.

FIG. 4. The same—anterior view—showing secondary axes, × N.S.

FIG. 5. T.s. of anther, × 18.

FIG. 6. A tetracarpellate female flower, × 5.

FIG. 7. An opened interfoliar male spadix between two boat-shaped spathes. Black spots on it are insects, × 2.

FIG. 8. Unopened interfoliar female spadix, × ¼ N.S.

FIG. 9. Germinated pollen grains, × 185.

FIG. 10. A germinated pollen grain showing round vegetative cell—*vg* and lenticular generative cells—*gn*, × 375.

FIG. 11. A secondary axis of female peduncle showing female flowers and pointed tip, × ⅛ N.S.

PLATE VI

FIGS. 12–30. *Phoenix sylvestris* Roxb.

FIG. 12. L.s. of ovule, showing hypodermal archesporial initial, × 240.

FIG. 13. L.s. of ovule showing outer and inner integuments and megaspore mother cell, × 80.

FIG. 14. Megaspore mother cell in prophase, × 180.

FIG. 15. A dyad, × 240.

FIG. 16. A linear tetrad, × 180.

FIG. 17. 4-nucleated embryo-sac, × 145.

Fig. 18. Zygote, × 140.

Fig. 19. 2-celled proembryo: Note the transverse division and elongated basal cell *cb* and small terminal cell *ca*, × 180.

FIG. 20. 3-celled proembryo, × 240.

FIG. 21. Globular embryo, × 145.

FIG. 22. Globular embryo differentiating into lateral cotyledonary lobes, × 60.

FIG. 23. L.s. of embryo showing two lateral cotyledons and the central shoot apex between them, × 100.

FIG. 24. L.s. of embryo showing one of the cotyledons over-arching the other, the shoot apex—*sa*, still retaining its terminal position: Note the arrested cotyledon—*ac*, developing cotyledon—*dc* and a slit-*sl* to the left hand side, × 22.

FIG. 25. L.s. of embryo showing shoot apex—*sa*, hypocotyledonary region—*hc*, nodal plate—*np*, radical—*rl* and vascular strands—*vs*, × 72.

FIG. 26. T.s. of mature embryo above the nodal plate showing two kinds of cells of the cotyledon, some loose and some compact, × 8.

FIG. 27. T.s. of a mature embryo passing through the shoot apex region, × 5.

FIG. 28. L.s. of a mature embryo. T.s. was taken of it at 4 different levels as shown, × 12.

FIG. 29. T.s. of a mature embryo showing the ring of nodal plate, × 5.

FIG. 30. T.s. of cotyledon passing through the middle region showing 15 vascular strands, × 5.

38-68. Printed at The Bangalore Press, Bangalore City, by M. S. Narayanamurthy, Secretary and Published by B. S. Venkatachar, Editor, "Proceedings of the Indian Academy of Sciences," Bangalore