# STUDIES ON PALMS: EMBRYOLOGY OF *LIVISTONA CHINENSIS* R. BR.

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ABSTRACT

The paper gives an account of the embryology of a palmatel-leaved palm *Livistona chinensis* R. Br., a native of China and Japan. It is quite commonly cultivated in India. One species *L. jenkinsiana* Griff. grows wild in Assam Hills.

Various types of embryo sac and embryo development have been reported in different palms, but in the large majority of them it is of the monosporic 8-nucléate *Polygonum* type, except in *Hyphaene indica* in which it was found to be of *Allium* type (Mahabalé and Chennaveeraiah, 1957). The embryo sac in this palm is of the 8-nucleate *Polygonum* type. This type is found both in the palmate- and pinnate-leaved palms. The embryo development conforms to *Asterad* type. In early stages of embryogenesis meristem lies in between two growth centres which later develop into cotyledons. One of these, however, is suppressed very early and is over-grown by the other cotyledon. The growing point is terminal and looks to have a single over-grown cotyledon.

The development of embryo upto globular stage is as in other monocotyledons, but its later development is more like that in *Agapanthus umbellatus* or *Ranunculus ficaria*. The embryogeny thus appears to support the view of suppression of one cotyledon in monocots by the other which overgrows. It would support the contention that both the monocot and dicot embryos might have arisen from some polycotyledonous ancestors.

## I. INTRODUCTION

PALMS are divided into two broad groups—those with pinnatisect leaves and those with palmatisect leaves. A large number of them have been worked out by Dr. T. S. Mahabalé and his associates. One of the commonly cultivated palm in Indian gardens having palmate leaves is

*Livistona chinensis* R. Br. The genus comprises about 20 species of which *Livistona chinensis* is the most commonly cultivated. Another species not common, is *L. jenkinsiana* growing wild in India in Assam Hills.

These two groups of palms show a variety of differences in their leaf vernation, anatomy, etc. It was, therefore, thought worth-while investigating embryology of this species, *viz.*, *Livistona chinensis* var. *chinensis*, a species native to China and Japan. Material of it was readily available. The results obtained are described in this paper.

*Previous work.*—Reference to the previous literature on the embryology of palms shows that much work needs to be done yet. Juliano and Quisumbing (1931) studied the anther-wall in *Cocos nucifera* and found that its 6–8 subepidermal layers developed into fibrous endothecium, of which innermost 2–4 layers functioned as tapetum. Süssenguth (1921) found simultaneous division of microspore mother cells in *Chamaedorea sartorii*, *C. glaucifolia* and *C. karwinskyana*. Radermacher (1925), however, found successive type of division of microspore mother cells in *Nypa fruticans*.

Various types of embryo sacs have been reported in different palms. It is said to be normal 8-nucleate *Polygonum* type in *Actinophloeus macarthurii* (Radermacher, 1925) and in *Areca catechu* (Swamy, 1942). The same has been reported by Rao (1959 *a*, 1959 *b*) in *Areca catechu*, *A. concinna*, *A. triandra* and in species of *Actinophloeus*, *Licuala*, *Trachycarpus*, *Livistona*, *Pritchardia*, *Washingtonia* and *Sabal*. In *Livistona rotundifolia* Rao (1959 *b*) has described only two stages in embryo sac development, namely, megaspore mother cell and a linear tetrad, and in *L. chinensis* mature embryo sac. Radermacher (1925) has reported bisporic embryo sac in *Nypa fruticans*. According to Maheshwari (1955) the embryo sac in them is not bisporic as was supposed to be earlier. Quisumbing and Juliano (1927) have reported *Adoxa* type of the embryo sac in *Cocos nucifera*. According to them the archesporial initial functions directly as megaspore mother cell. A reinvestigation of embryo sac development in *Cocos nucifera* by A. R. Kulkarni (1965) has confirmed that it is of the monosporic *Polygonum* type. Bauch (1911) has also found degenerating megaspores in this species. According to him (Bauch, 1911) in *Phoenix sylvestris* the upper three megaspore cells degenerate at 2-nucleate embryo sac stage. In *Elaeis guineensis* De Poerck (1950) found that the megaspore mother cell develop directly into 8-nucleate embryo sac, which means that it is of the *Adoxa* type. Kajale and Ranade (1953), however, found four kinds of tetrads and normal 8-nucleate *Polygonum* type of embryo sac in the same species. In *Hyphaene indica* Mahabalé

and Chennaveeraiah (1957) found *Allium* type of embryo sac development. Mahabalé and Biradar (1968), and Biradar (1968) have reported 8-nucleate *Polygonum* type of embryo sac development in *Phoenix sylvestris, P. robusta, P. pusilla, P. acaulis* and *P. reclinata.*

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 become sometimes 2–3-nucleate. The antipodals are said to be persistent and aggressive in *Areca catechu* (Swamy, 1942).

According to Lang (1943) endosperm is free-nuclear in *Phoenix dactylifera.* Similar type of endosperm has also been reported in *Areca catechu, Chrysalidocarpus lutescens* and in species of *Licuala, Livistona, Trachycarpus, Washingtonia* and *Sabal* by Rao (1955 *a*, 1959 *a*, 1959 *b*). Mahabalé and Biradar (1968), and Biradar (1968) have also reported free-nuclear endosperm in all species of *Phoenix* they studied. The endosperm in it later becomes cellular.

The embryo development in Palmae is imperfectly known, especially later stages leading to the formation of embryo into mature seeds. Selvarathnam (1952) has described the mature embryo in *Cocos nucifera.* According to Rao (1955 *a*, 1959 *a*) the embryo development in *Areca catechu* and *Actinophloeus macarthuri* is of the *Onagrad* type. He has also reported a few stages of embryo development and nature embryo in *Pritchardia pacifica* (1959 *b*). Recently Mahabalé and Biradar (1968), and Biradar (1968) have made detailed investigations on the embryo development in five species of *Phoenix.* According to them the embryo development in *Phoenix* is of the *Asterad* type. They also report a definite tendency on the part of embryo towards the formation of two cotyledons in early stages of development of embryo; but out of these two only one becomes massive later and attains maturity. In the present work embryo development in *Livistona chinensis* var. *chinensis* has been described.

## II. Description

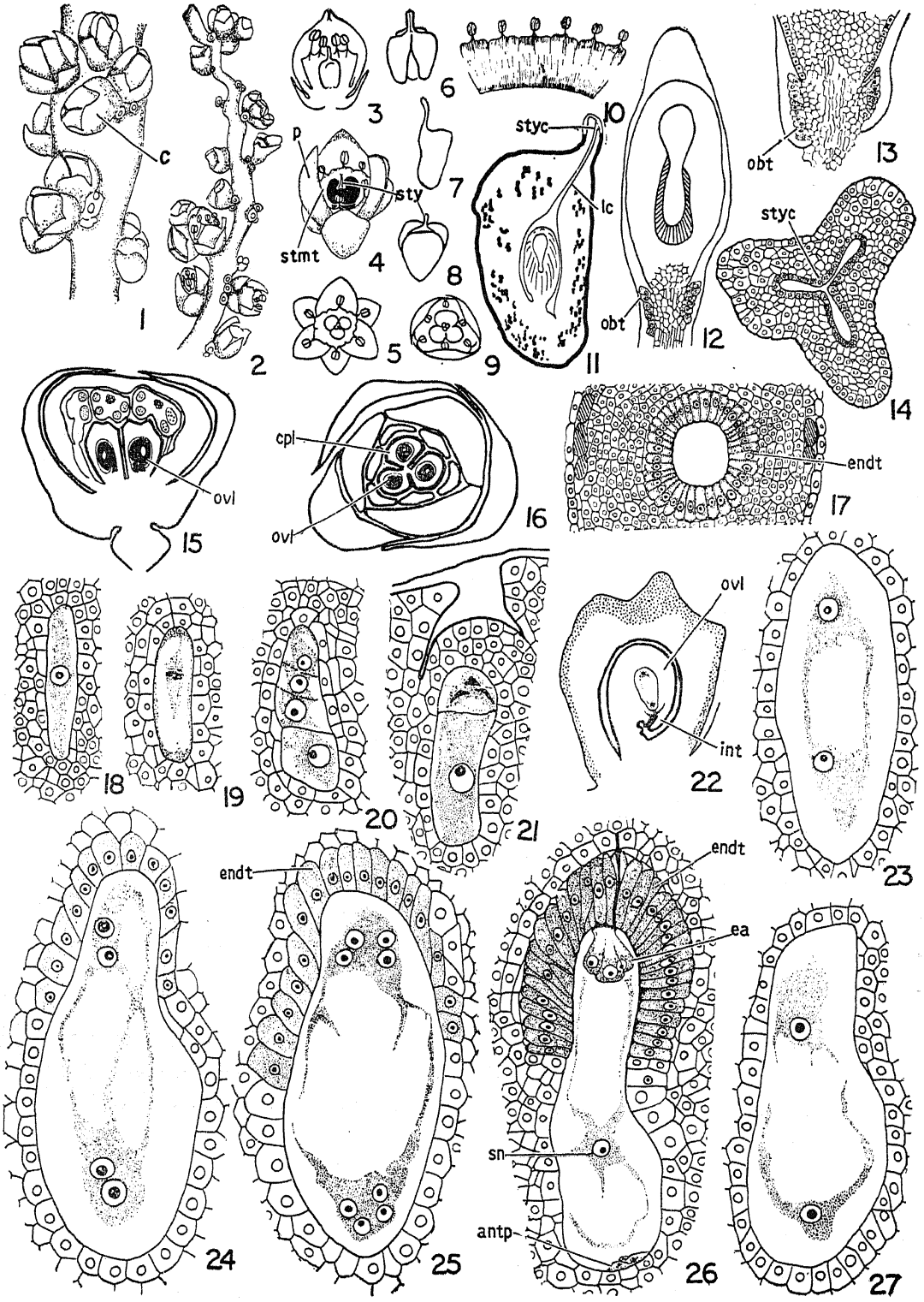
*Inflorescence and flowers.*—The inflorescence in *Livistona* is a large panicle arising from a large interfoliar spadix, bearing numerous flowers on tertiary axes surrounded by glabrous or slightly villous spathes at the base. The primary peduncle consists of a slender axis which bifurcates irregularly

in the upper part. The erect secondary branches arise a little above from the base of the primary axis and bear 10–15 tertiary branches each. They spread irregularly and bear numerous hermaphrodite, small yellowish-white flowers usually four together. They ripen and form small olive-shaped, dull purple drupes. The secondary spathes are lanceolate and open obliquely.

The flowers are trimerous, regular, hypogynous and actinomorphic. They have a pulvinate base (Text-Figs. 1, 2, Pl. Fig. 1) and measure 3–4 mm long, and about the same width. The outer perianth whorl or the calyx is formed of three sepals which are fused almost to the middle to form a cup. The inner perianth whorl consists of three petals alternating with three sepals, fused at the base only. Each petal is leathery, almost double the size of sepal (Text-Figs. 3–5). The stamens are six, included, united to form an epipetalous tube (Text-Figs. 5, 9, 10, Pl. Fig. 2). The anthers are ovate and dorsifixed. Gynoecium consists of three carpels free at the base. The style is slender. In mature pistil three separate stylar arms fuse together in the upper part (Text-Figs. 6–8). Each locule extends as a narrow locular canal and fuses with the common stylar canal. The ovules are anatropous, elliptic and bitegmic.

*Ovary and ovule.*—The gynoecium in *L. chinensis* consists of three carpels, free at the base. The three separate stylar arms fuse together in the upper part. The locules extend as narrow canals into the stylar arms upto the top of the locules (Text-Fig. 11). The locular canals fuse with the common stylar canal and extend to the top of the pistil as a triradiate canal (Text-Fig. 14). They are lined by glandular cells. Rao (1959 *b*) has described the gynoecium in *Livistona rotundifolia* as a single uniovulate carpel which is not the case in this species.

The ovules are bitegmic, crassinucellate and anatropous (Text-Figs. 15, 16, 22, Pl. Fig. 5). Two or three vascular bundles enter funicle and branch slightly in the raphe and chalaza. According to Rao (1959 *b*) in hemianatropous ovule of *L. rotundifolia* a ring of 6–7 vascular bundles enters the funicle and branches further in the body of the ovule. Eames and MacDaniels (1947) remarks " when the ovule represents the surviving member of a group in which reduction has occurred, it may have captured the trace supply of two or more ovules." It may be recalled here in this connection that in *L. chinensis* the pistil consists of three uniovulate carpels while in *L. routundifolia* it shows only a single uniovulate carpel. The funicle in *L. chinensis* develops a basal swelling, the epidermal cells of which are




TEXT-FIGS. 1–27

markedly elongated and glandular, and it functions as obturator (Text-Figs. 12, 13, Pl. Fig. 4). The locular canal and the obturator adjoin together (Text-Fig. 22). The stigmatic glandular tissue and the glandular cells of the transmitting tissue form a continuous path of richly protoplasmic cells for the passage of pollen tubes.

The integuments are free from each other only for a small distance around the micropyle of the ovule. Tannin accumulates in the cells of chalaza. The outer integument appears when the ovule is in tetrad stage. The initials of both the integuments become demarcated simultaneously with differentiation of the megaspore mother cell in the ovule. Micropyle is formed by both the integuments by the time the embryo sac is two- or four-nucleate (Text-Fig. 22). The micropyle is somewhat elongated and zigzag. In *Cocos nucifera* micropyle lies in a shallow depression at the top of the outer integument (A. R. Kulkarni, 1965). Such a micropylar depression is also a characteristic feature of *Hyphaene indica* (Mahabalé and Chennaveeraiah, 1957) and *Elaeis guineensis* (Kajale and Ranade, 1953).

The outer integument is 4–5-layered, and the inner 2–3-celled thick. The integumentary tapetum is well organised. The glandular endothelium becomes prominent by the time the embryo sac is matured (Text-Figs. 17, 26, Pl. I, Figs. 8, 11). Cells of the inner epidermis of the inner integument become elongated and rich in cytoplasm at 4–8-nucleate stage of the embryo sac. Due to prominent endothelium, inner integument equals or even excels the outer one in thickness (Text-Figs. 17, 26, Pl. Figs. 8, 11).

The ovule is crassinucellate, but the size of nucellus is small in relation to that of the ovule. A mature embryo sac is surrounded by 4–5 layers of nucellar cells, some of which persist for some time even after fertilization. Later however, the whole nucellus is crushed.

All the three ovules form mature embryo sac, but as a rule one ovule develops further after fertilization. The other two are completely supressed during the development of fruit. In some cases a second fruit develops, but only half way.

*Megasporogenesis and female gametophyte.*—The embryo sac in *L. chinensis* develops according to normal 8-nucleate *Polygonum* type. The archesporium consists of a single hypodermal cell. It divides periclinally and forms the primary parietal cell outside, and the megaspore mother cell inside. This division occurs very early in the ovule primordium. The

megaspore mother cell grows for a considerable time and 1–3-layered parietal tissue is formed by divisions in the primary parietal cell and its derivatives.

A fully developed megaspore mother cell is tapering and elongated, its nucleus lying in micropylar half (Text-Fig. 18). Nucleus of the megaspore mother cell undergoes a division and forms a dyad (Text-Fig. 19), followed by a second transverse division in each cell of the dyad resulting in a linear tetrad (Text-Fig. 20).

The functional megaspore enlarges crushing the surrounding nucellus. Its cytoplasm becomes vacuolated and nucleus shifts to the centre of the cell. Three micropylar megaspores degenerate even before first division of the functional megaspore (Text-Fig. 21). At the uninucleate embryo sac stage much of the nucellus and abortive megaspores are crushed.

Division of the nucleus in embryo sac is followed by the polarization of resultant nuclei (Text-Figs. 23, 27, Pl. Fig. 9). Further stages in the development of the embryo sac pass off quickly. At the 4-nucleate and 8-nucleate stages, the micropylar and chalazal quartets are equal in size (Text-Figs. 24, 25, Pl. Fig. 10). The antipodal part of the embryo sac becomes broader and broader from the two-nucleate stage onwards (Text-Figs. 24, 25, 27, Pl. Figs. 10, 11). The antipodals are ephemeral.

The nucleus and cytoplasm in the synergids are restricted to their lower half, upper half forming a prominent vacuole (Text-Fig. 26). The nucleus and cytoplasm of the egg cell are also restricted to the lower half of the cell. The nuclei of the egg and the synergids are of the same size (Text-Fig. 26).

The polar nuclei fuse before fertilization and secondary nucleus stands in the middle of the embryo sac. Mature embryo sac has narrow micropylar and broad antipodal end.

The development of the female gametophyte on the whole thus conforms to the monosporic 8-nucleate *Polygonum* type of Maheshwari (1950) as in other members of the Sabaloid palms (Rao, 1959 *b*), as against the bisporic *Allium* type found in *Hyphaene indica* by Mahabalé and Chennaveeraiah (1957).

*Microsporangium.*—The archesporium of anther consists of one or two rows of hypodermal cells in each of the four lobes. By a periclinal division they form primary parietal cells outside and primary sporogenous cells inside. By further divisions in the parietal cells anther wall becomes 4–5-

layered. During the wall formation sporogenous tissue remains 4–5-celled in T.S., the secondary increase being brought about after the differentiation of wall layers. Epidermal cells in the mature anther become tangentially flattened and develop thick cuticle. Cells of the hypodermal layer enlarge considerably and develop fibrous thickening (Text-Figs. 30, 31, Pl. Fig. 7). Sometimes thickenings extend to two layers of cells. Cells of the septum between two loculi of an anther are tangentially flattened and thin-walled. The cells outside the septum are small and thick-walled. They constitute the stomium (Text-Figs. 29, 30, Pl. Fig. 3). In a mature anther, septum shrinks and loculi coalesce. The shrunken septum persists for some time even after the dehiscence of anther. Cells of the connective contain tannin (Text-Fig. 30).

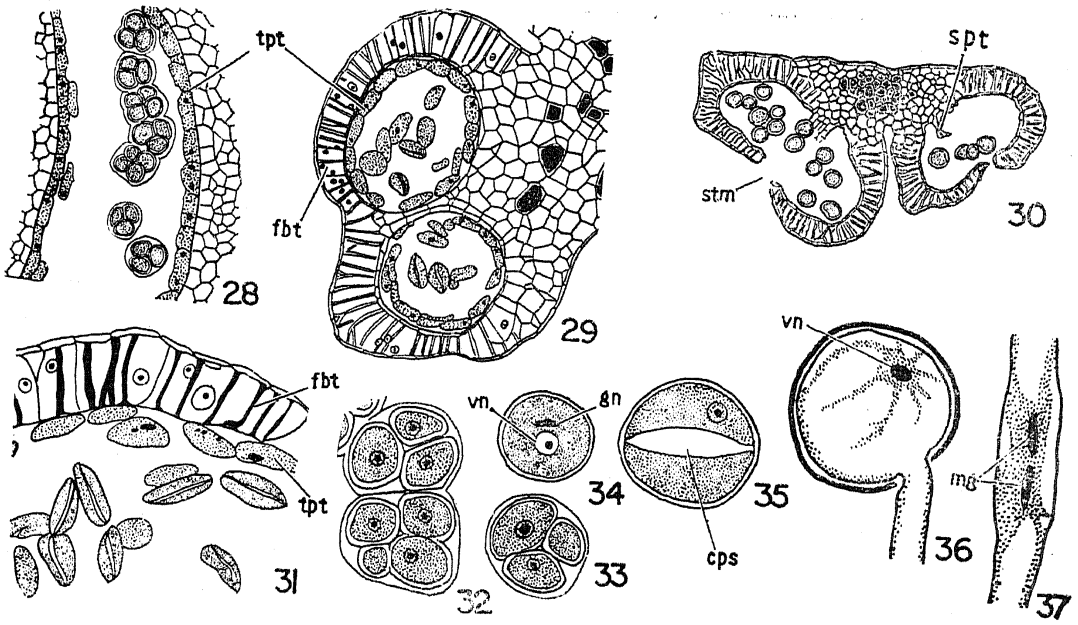
The innermost of the two layers of wall cells function as tapetum. 2–3-layers of wall are crushed towards the end of meiotic divisions. Tapetum is of the secretory type and shows 2-nucleate cells. Their walls are tangentially flattened (Text-Figs. 28, 30, 31). Such binucleate tapetal cells are common in palms. They have been reported in *Hyphaene indica* by Mahabalé and Chennaveeraiah (1957), in some members of the Sabaleae by Rao (1959 *b*), and in *Phoenix* by Mahabalé and Biradar (1968).

*Microsporogenesis and male gametophyte.*—The young sporogenous tissue is 4–5-celled in T.S. Increase in the sporogenous tissue is brought about only after the wall layers have been fully organised. Cells of the sporogenous tissue are polygonal when young but become round later. They develop a thick wall around them before they divide. The microspore tetrads are usually tetrahedral (Text-Figs. 28, 32, 33). The microspores become ellipsoidal by the time they separate out from the tetrads and show a distinct colpus as a narrow longitudinal slit (Text-Figs. 31, 35, Pl. Fig. 6). In a fully grown microspore there is a large nucelus and the rod-shaped generative cell. The pollen grains are shed in two-celled condition (Text-Fig. 34). They are monocolpate, aporate, and have smooth exine (Text-Fig. 35, Pl. Fig. 6).

*Germination of pollen.*—Pollen grains were germinated on solutions of sugar having different percentage. 4% sugar solution was found satisfactory. They germinated in 4–6 hours. It was found that pollen of slightly opened inflorescence germinated readily.

During the first few hours pollen grains swell up: their germ pore is marked out as an hyline area. Pollen tube emerges through the germ pore

and grows more or less straight for a considerable length. After reaching maximum growth its tips swells and releases the contents. The vegetative nucleus never enters the pollen tube but degenerates in the grain itself. The generative nucleus divides in the pollen tube and forms two somewhat oval nuclei (Text-Figs. 36, 37).




TEXT-FIGS. 28–37

*Fertilization and endosperm.*—The pollen tube traverses through the rich protoplasmic cells of the style and enters the ovule porogamously, affecting the synergids by its entry into the embryo sac. After the pollen tube has discharged its contents into embryosac, one of the male gametes fuses with the egg, and the other with the secondary nucleus.

The endosperm is formed as a result of the fusion of the two polar nuclei and one of the two male gametes. Since all the three fusing central nuclei are haploid the endosperm contains the triploid number of chromosomes. The endosperm is of the nuclear type, wherein the first division, and several following it, are unaccompanied by wall formation. But in the later stages the nuclei are separated by walls. As the divisions progress, nuclei are pushed more and more towards the periphery, so that the centre is occupied by a large vacuole. Due to this central vacuole, cord of cytoplasmic mass along with its numerous nuclei moves towards the periphery and the nuclei line up along the wall of embryo sac (Text-Figs. 38, 48).

The nuclei then multiply by repeated divisions and persist. Concentration of the endosperm nuclei is more around the proembryo than elsewhere. Cell wall formation starts at the periphery of the embryo sac, and proceeds towards the central cavity (Text-Figs. 39, 40). By this time, the embryo becomes globular in shape. Newly formed endosperm cells have centrally placed nucleus and peripheral lining of the cytoplasm. As the endosperm matures, these cells get filled with reserved food material in the form of oil globules.

With the development of embryo there is increasing elaboration of the chalazal region. Fertilized ovule grows rapidly first in length and then in diameter. The embryo sac including embryo widens at antipodal end. During early stages in seed development there is considerable proliferation of cells surrounding the lower part of the embryo sac (Text-Fig. 48). Cells of the chalaza and the integuments accumulate tannin. The former persists as a ridge in the seed opposite the embryo. The embryo sac expands to the sides of the chalazal protuberance. The vascular strands of the funicle extend into this protuberance and branch slightly (Text-Fig. 48). During the development of embryo micropyle gradually shifts from its terminal position to a lateral one (Text-Figs. 41, 48).

*Embryo development.*—First division of the zygote is transverse giving rise to two-celled proembryo. The basal cell *cb* of the proembryo is slightly broader than the terminal cell *ca*. *ca* in some cases is somewhat tapering. otherwise *ca* and *cb* are almost equal in size (Text-Figs. 42, 43, Pl. Fig. 12). A vertical division in *ca* forms a three-celled embryo (Text-Fig. 44). By another vertical division in the cell *cb*, an isobilateral four-celled embryo is formed (Text-Figs. 45, Pl. Fig. 13). The two terminal cells now divide by a wall at right angles to the first, giving rise to a six-celled, eight-celled and then to globular embryo. The distal cells of it by further development give rise to shoot apex and cotyledons, and the proximal ones to hypocotyl (Text-Figs. 46, 49, Pl. Figs. 14–16).

All the cells of 8–10-celled embryo enlarge considerably and divide by periclinal walls, the outer cells forming dermatogen. An epiphysial initial differentiates at the apex of this globular mass. The spherical embryo continues to enlarge with iurther divisions of its constituent cells (Text-Figs. 50–52, Pl. Fig. 17). It is evident that derivatives of both *ca* and *cb* take part in the formation of embryo. The embryo development therefore conform to the *Asterad type*.

The broad portion of the globular embryo further differentiates into two lateral cotyledonary humps or lobes with apical meristem in centre forming a heart-shaped structure similar to that present in most of the dicotyledons and 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-Fig. 53, Pl. Figs. 18, 21). On the other hand, Rao (1955 *a*, 1959 *a*) found that the position of the shoot apex in *Areca catechu* and *Actinophloeus macarthuri* is lateral. In the later stages one of the two cotyledons grows more vigourously than the other and arches over the other cotyledon, leaving a narrow slit on one side of the embryo formed by the close approach of the margins of its two cotyledons (Text-Figs. 54–56, Pl. Figs. 19, 20). There is thus a definite tendency towards the formation of two cotyledons in early stages, and towards the massive development of only one of them, as reported in species of *Phoenix* by Mahabalé and Biradar (1968), and Biradar (1968).

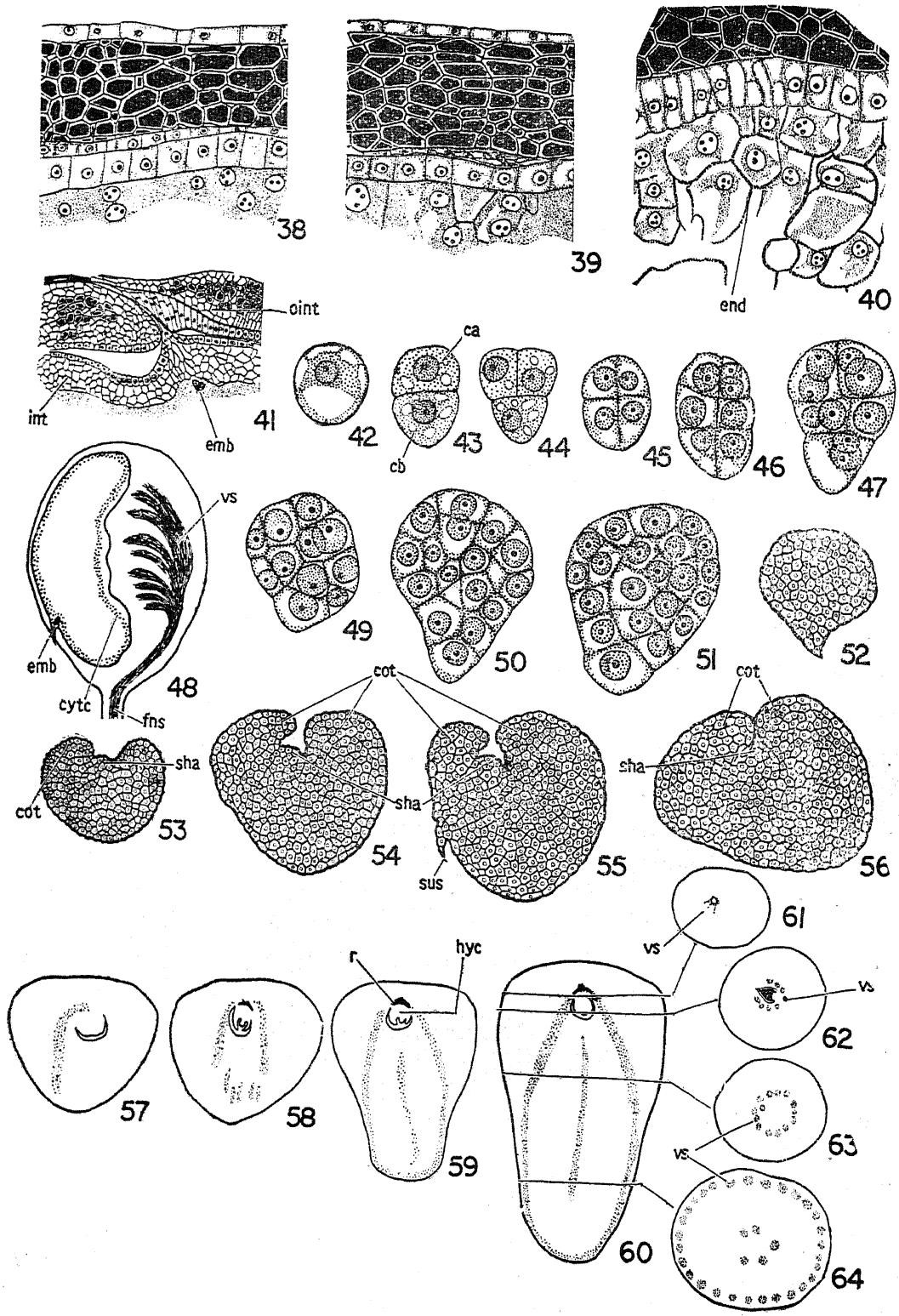
The more vigorously and pronounced developing cotyledon elongates considerably forming a single conspicuous cotyledon at maturity. The other cotyledon is completely suppressed and becomes vestigial in the mature embryo close to the shoot apex.

The mature embryo is cylindrical and is embedded in the micropylar half, with radicle pointing towards the micropyle. The shoot apex is differentiated into sheathing leaves, stem apex, nodal plate, radicle and highly condensed hypocotyledonary region (Text-Figs. 57–59, pp. Fig. 22). The embryo is supplied with a ring of vascular bundles arising at the nodal plate which traverse to periphery. They divide and redivide to form several vascular strands in the elongated cotyledon. But they unite once again at the apex of this massive cotyledon (Text-Figs. 60–64).

## Discussion

Development of the embryo in this palm upto the globular stage is normal and is as in other monocotyledons. But afterwards it is different and need much greater consideration, as palms as a group have many characters of primitive angiosperms.

The origin of monocotyledonous embryo has long attracted the attention of botanists. In dicotyledonous embryo, the plumule is typically distal and is situated symmetrically between the two equivalent cotyledons. In monocotyledons embryonic shoot apex occupies a lateral indentation in




TEXT-FIGS. 38-64

a somewhat cylindrical embryo, with the result that the single cotyledon looks terminal. Upto a certain stage during the development of embryo, the two types of embryos seem to be very closely comparable, both being cylindrical or club-shaped axial bodies. Many workers have suggested that in the monocotyledonous embryo has resulted by the fusion of two orginally separate cotyledons, or that one of the two cotyledons is suppressed. Development of embryo in *L. chinensis* seems to support the latter view.

Some other investigators have attempted in a different way to ascertain whether the single cotyledon is truly terminal organ or not and whether it is a lateral organ *ab initio* coming to occupy distal position later. In *Agapanthus umbellatus* (Fam. Liliaceae) a widening distal tubular cotyledonary zone with two primordia grows at its tip and they surround a sunken shoot apex at certain stage in the embryo development. If both the primordia would develop equally well, a dicotyledonous embryo would be formed; but as it happens more frequently, one of the two primordia soon stops growing, while the other grows rapidly and becomes conspicuous terminal organ leaving the shoot apex in a relatively lateral position.

The idea that monocotyledons are off-shoot of some relatively primitive dicotyledonous stock has long been entertained by many botanists. It receives some support from monocotyledonous embryos in a dicot like *Ranunculus ficaria* and in a monocot with two cotyledons like *Corydalis cava.* Takhtajian (1954) considers that monocots have descended from some dicotyledonous or polycotyledonous plants, as their embryo development affords evidence of their derivation from ancestral dicotyledons or polycotyledons in the early stages of evolution of angiospersm. The change from two to one cotyledon must have been very slow and might have involved the substitution of two cotyledons by one, both developing simultaneously during embryogeny for some time. Several investigators suggest that the single cotyledon is not likely to be explained in terms of abortion or suppression of one of the primordia in an initially polycotyledonous or dicotyledonous organization. If we assume that the ancestors of monocotyledons had two or more cotyledons then we have to imagine that at some stage in phylogeny a critical genetic change or series of successive adaptive changes might had had taken place, resulting finally in the monocotyledonous condition. The ultimate problem then is to know how at a certain stage in the dicotyledonous type of embryo development, the reaction system became so modified as to yield this new type of organization in which one cotyledon prevails over the other, possibly becoming suctorial and remaining within

seed as in Piperaceae. It has also been suggested that the monocotyledons might have been a polyphyletic group, and that some of them might have diverged from a very primitive dicotyledonous stock very early; and later other groups, both of dicot and monocot, formed more developed angiosperms or their ancestors.

But unfortunately, both these views defy solution at present, though the palm embryogeny makes the second view look more probable. It is hoped that experimental embryogeny of monocot embryos might throw some further light on this problem.

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## Explanation of Text-Figures

Text-Figs. 1-27. Flower, ovary, ovule and development of the female gametophyte. Fig. 1. Basal part of the tertiary branch showing the arrangement of the flowers, × 3. Note the cup-like calyx—*c*. Fig. 2. Apical part of the tertiary branch of inflorescence showing the arrangement of flowers, × 3. Note the pulvinate bases on which the flowers are lodged. Fig. 3. A L.S. of the flower, × 4. Fig. 4. Entire flower slightly tilted, showing short style—*sty* of the gynoecium staminal tube—*stmt* and petals *p*, × 4. Figs. 5 and 9. A flower (diagrammatic) showing the arrangement of different whorls. Fig. 6-8. Gynoecium showing the union of stylar portions—*sty* and free basal part, × 12. Fig. 10. Androecium showing the united base of the stamens, × 4·5. Fig. 11. L.S. of carpel showing locular canal—*lc* leading to the stylar canal—*styc* lined by glandular cells, × 168. Fig. 12. L.S. of ovule showing funicular obtuator—*obt*, × 24. Fig. 13. Funicular part of the same magnified to show obturator—*obt*, × 36. Fig. 14. T.S. of style showing triradiate stylar canal—*styc* lined by glandular cells, × 168. Fig. 15. L.S. of young flower showing two carpels and anatropous ovules—*ovl*, × 18. Fig. 16. T.S. of a young flower in the middle part showing three carpels—*cpl* and the ovules—*ovl*, × 12. Fig. 17. T.S. embryo sac showing endothelium—*endt*, × 140. Fig. 18. Megaspore mother

cell, × 225. Fig. 19. Megaspore mother cell dividing to form dyad, × 225. Fig. 20. A linear tetrad showing large chalazel megaspore, × 225. Fig. 21. A uninucleate embryo sac showing three degenerating megaspores, × 225. Fig. 22. L.S. of a carpel showing anatropous ovule—*ovl* and integuments—*int*, × 36. Fig. 23. An early two-nucleate embryo sac, × 375. Fig. 24. A four-nucleate embryo sac, × 375. Fig. 25. An eight-nucleate embryo sac, × 225. Endothelium—*endt*. Fig. 26. A mature embryo sac showing prominent endothelium—*endt*, egg-apparatus—*ea*, the secondary nucleus—*sn*, the degenerating anutpodals—*antp*, × 112. Fig. 27. Two-nucleate embryo sac showing broad chalazal part, × 375.

TEXT-FIGS. 28–37. Microsporangium and microsporogenesis. Fig. 28. L.S. of young anther showing tetrads, × 110. Note the tapetum—*tpt*. Fig. 29. L.S. of a young anther showing tapetum—*tpt* and the fibrous thickening—*fbt* on the anther wall, × 100. Fig. 30. T.S. of mature anther showing remnants of the septum—*spt* and the stomium—*stm*, × 50. Fig. 31. T.S. of anther showing pollen grains separated from the tetrads, × 200. Note the tapetal cells—*tpt* and fibrous thickening—*fbt* on the anther wall. Figs. 32 and 33. Pollen tetrads, × 334. Fig. 34. A fully grown pollen showing vegetative nucleus—*vn* and a generative nucleus—*gn*, × 334. Fig. 35. A pollen grain showing colpus—*cps*, × 366. Fig. 36. A germinated pollen grain showing a part of the pollen tube and the generating vegetative nucleus—*vn*, × 666. Fig. 37. A part of the pollen tube showing two male gametes—*mg*, × 666.

TEXT-FIGS. 38–64. Endosperm development and development of embryo. Fig. 38. Free nuclei in the cytoplasm lining the wall of the embryo sac, × 150. Figs. 39–40. Subsequent stages in the wall formation in endosperm—*end*, × 150. Fig. 41. Micropylar region of the embryo sac showing the inner integument—*int* and the outer integument—*oint*, × 150. Note the embryo—*emb*. Fig. 42. A zygote, × 400. Fig. 43. A two-celled proembryo showing the terminal cell—*ca* and the basal cell—*cb*, × 334. Fig. 44. A three-celled proembryo, × 334. Fig. 45. A four-celled proembryo, × 334. Figs. 46–47 and 49–51. Successive stages in the embryo development leading to the formation of a globular embryo, × 334. Fig. 48. L.S. of young seed showing embryo—*emb*, vascular strands—*vs*, continued from funicular strands—*fns* and the cytoplasmic cord—*cytc* lining the embryo sac, × 12. Fig. 52. A globular embryo, × 100. Fig. 53. Embryo showing differentiation of cotyledons—*cot* and shoot apex—*sha*, × 100. Figs. 54–55. Embryo showing one of the two cotyledons—*cot* overgrown, and the shoot apex—*sha*, × 50. Note the suspensor—*sus*. Fig. 56. Embryo showing two cotyledons—*cot*, and the shoot apex—*sha*, × 50. Figs. 57–59. Successive stages in further growth of the embryo showing differentiation of the radicle—*r* and the hypocotyledonary region—*hyc*, × 22. Fig. 60. A mature embryo, × 14. Figs. 61–62. T.S. of embryo through the nodal plate and the shoot apex showing vascular supply—*vs*, × 10. Fig. 63. T.S. of embryo through region below the shoot apex showing the vascular supply—*vs*, × 10. Fig. 64. T.S. of embryo through the apex of the massive cotyledon showing the vascular strands—*vs*, × 24.

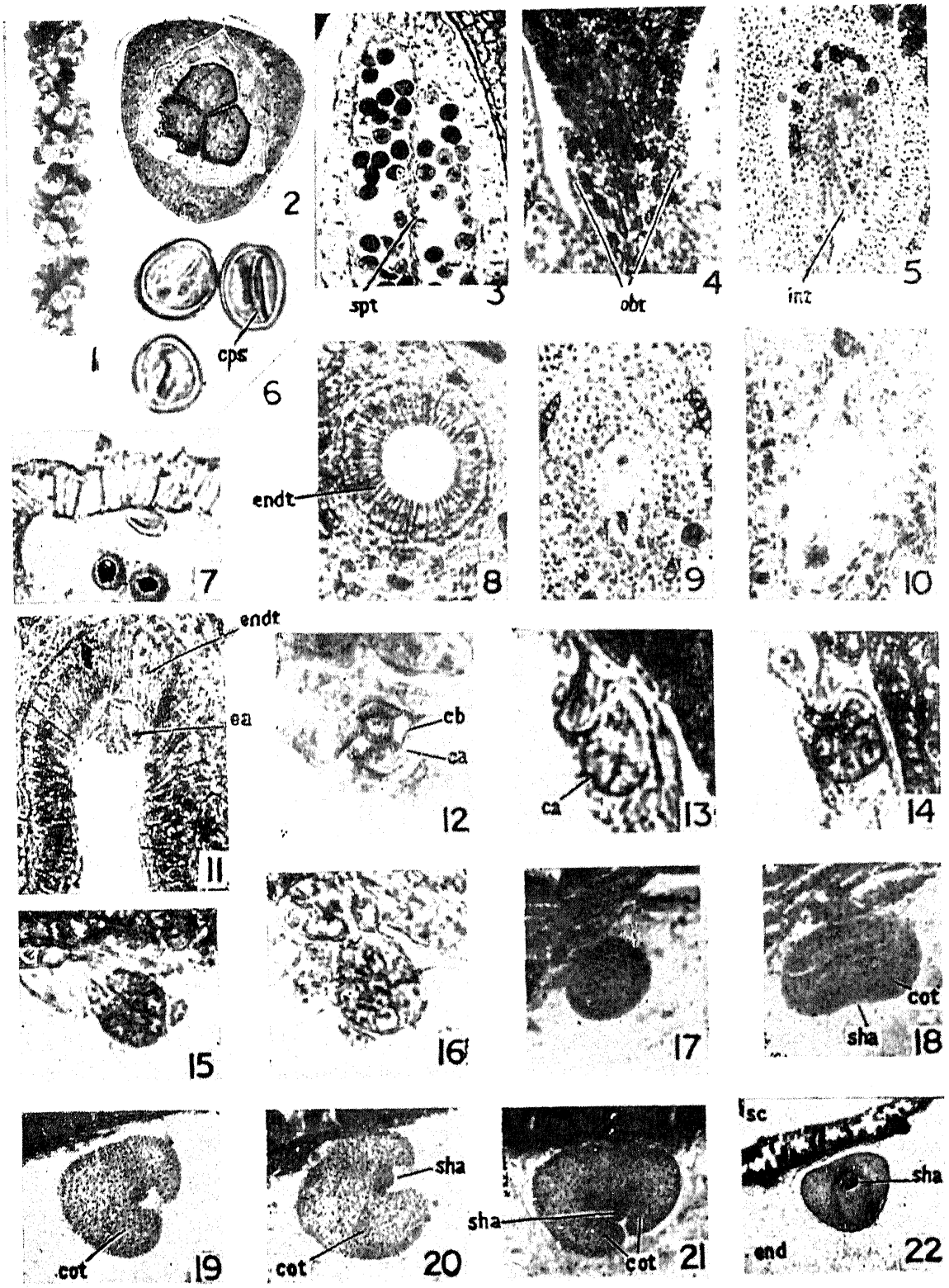
## EXPLANATION OF PLATE I

FIGS. 1–22. Ovule, development of female gametophyte, microsporangium and development of embryo.

FIG. 1. A part of the tertiary flowering branches showing the arrangement of the flowers, × 3/4.

FIG. 2. T.S. of the flower showing separation of androecium from the corolla, × 12.

FIG. 3. L.S. of an anther showing pollen and the septum—*spt*, × 60.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FIGS. 1–22

FIG. 4. L.S. at the base of the ovule showing funicular obturator—*obt.* × 64.

FIG. 5. An anatropous ovule showing the integuments—*int*, × 60.

FIG. 6. Fully grown pollen grain showing a colpus—*cps*, × 400.

FIG. 7. T.S. of anther showing fibrous thickening on the wall, × 120.

FIG. 8. T.S. of embryo sac showing endothelium—*endt*, × 160.

FIG. 9. A two-nucleate embryo sac, × 136.

FIG. 10. Four-nucleate embryo sac, × 240.

FIG. 11. Upper half of the embryo sac showing the endothelium—*endt* and the egg apparatus—*ea*, × 120.

FIG. 12. A two-celled embryo showing the basal cell—*cb* and the apical cell—*ca*, × 256.

FIG. 13. A four-celled embryo showing vertical division in *ca*, × 240.

FIGS. 14-16. Successive stages in the embryo development leading to the formation of globular embryo; Fig. 14, × 200; Fig. 15, × 160; Fig. 16, × 200.

FIG. 17. A fully grown globular embryo, × 60.

FIG. 18. Embryo differentiating to form two cotyledons—*cot* and shoot apex—*sha*, × 120.

FIGS. 19 and 20. Embryo showing the cotyledons—*cot* overgrown, and the shoot apex—*sha*, × 32.

FIG. 21. Embryo showing two cotyledons—*cot* and shoot apex—*sha*, × 32.

FIG. 22. Embryo showing shoot apex—*sha* completely surrounded by the cotyledons, × 16. Seed coat—*sc*, endosperm—*end*.