LIFE HISTORY OF *TYPHONIUM TRILOBATUM* SCHOTT.

By I. BANERJI, *D.Sc., Department of Botany, Calcutta University.*

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The genus *Typhonium* contains about 25 species, distributed over the tropical regions of the world. It occurs in Burma, Malaya, Siam, Ceylon, China, Malayasia and North Australia. It has been reported from various parts of India, such as Bengal, Bihar, Orissa, Chota-Nagpur, Madras, the Eastern and Western Ghats and Assam.

Typhonium trilobatum is one of the common aroids of Bengal. It is a perennial herb and is easily recognised by its three-lobed hastate leaves, which appear to arise directly from the ground. The plants grow in waste places and profusely flower from about the later part of May to the end of October. Rarely they form a pure community. More often they grow along with such plants as *Cynodon dactylon*, *Digitaria sanguinales*, *Paspulasm scrobiculatum*, *Ruellia tuberosa*, *Tridax procumbens*, *Boerhaavia repens* and *Colocasia antiquorum*.

T. trilobatum thrives in moist and partially shaded localities. There is, however, considerable variation in size of the leaves according to conditions of growth. At the end of the growing season the above ground portion of the plant dies down, and no trace of it is observed above the soil. With the advent of the next monsoon, leaves appear again from the underground stem.

Two varieties of *Typhonium trilobatum* have been reported to occur. Var. *genuinum* Engler, has lamina hastately trisect and the apex of the spadix red, whereas the Var. *Schotti* (Prain) Engler, has lamina hastately trilobed and the apex of the spadix white. The former variety occurs in lower Bengal.

PREVIOUS WORK.

The family Araceae has received much attention from botanists. Towards the beginning of this century Campbell (1900), Duggar (1900), Gow (1913) and others worked on the embryology of the family. Later, Engler (1920) monographed the family, while Solereder (1928) gave a comprehensive account of its anatomical features. Jussen (1928) described in detail the haploid generation of some members, while Schnarf (1931) reviewed the relevant literature on the embryology of plants. Ertl (1932) studied the nature of the venation. Since 1928 a few more important publications on the morphology and cytology of plants belonging to this family have appeared, of which mention may be made of Boodle and Hill's (1929) work on *Typhonodorum Lindleyanum*, Dudley's (1937) on *Calla palustris*, Buell's (1938) investigations on the life history of *Acorus calamus* and Goldberg's (1941) on *Peltandra virginica*.

In India, not much work has been done on this family. Blatter (1932) has revised the species occurring in the Bombay Presidency. Barnes (1934) has described the morphology and the mode of pollination in the genus *Arisaema* occurring in the Nilgiri Hills. He (1938 and 1940) has also recorded his observations on right and left handed asymmetry in South Indian Aroids, and has described a new species of *Arisaema* (*A. psittacus*). Asana and Sutaria (1935) have recorded the number and the morphology of the somatic and meiotic chromosomes of *Arisaema murrayi*. This was followed by a contribution by the present writer (Banerji, 1937) on the sterility of *Colcocasia antiquorum*. Later, Asana and Sutaria (1939) gave an

account of the morphology and the number of chromosomes of some Indian aroids. McCann (1943) has recently described the 'light windows' in the genus *Cryptocoryne*.

Material and Methods.

The material used in this investigation was mostly obtained from plants growing under natural conditions. A few plants, however, were grown in the experimental garden for the purpose of closer observation.

For anatomical work pieces of petiole, leaves, tuber, spathe, spadix and roots were fixed in Formalin-acetic-alcohol. Microtome sections were made of these parts. Free-hand sections were also cut and examined. The sections were stained either with Safranin and Fast green, or Gentian Violet and Bismarck Brown combinations.

For cytological studies, root tips were collected from corms grown in saw-dust and fixed in various modifications of Lewitsky's fluid. The morphology of the chromosomes was best seen in material fixed in 1% Chromic acid one part and 10% Formaldehyde 2 parts.

For the study of meiosis, inflorescences (the staminate portion) in all stages of development were cut into discs 5 to 8 mm. thick. These were treated with Carnoy's fluid and then fixed in Nawashin's or Belling's modified Nawashin's fluids. Other fixatives were also tried but these did not give good results.

For embryological work, Allen's modified Bouin's fluid and Licent's fluid were chiefly used. In this case also the material was cut into small discs to facilitate penetration.

Fixation was carried out at different periods of the day. It was found that meiotic stages in the sporocytes were best obtained at about 8 a.m., whereas mitosis in the root tip cells was most common at about 11 a.m. The fixation was always done in the field and an exhaust pump was used whenever it was found necessary. The materials were dehydrated and cleared in the usual way and finally embedded in paraffin. Sections were cut 8 to 20μ thick depending on the stage required for study.

Heidenhain's Iron-alum Haematoxylin and Newton's Gentian-Violet-Iodine were the stains used for cytological studies. For the determination of chromosome-nucleolus relationship, as also the number of nucleoli in telophase, Bhaduri and Semmen's (1939) Feulgen Light Green stain was used. Slides showing embryological stages were stained with Heidenhain's Haematoxylin. Orange G as a counter-stain was used for certain preparations.

I. Morphology.

The stem of *Typhonium trilobatum* is a subterranean corm of many internodes. This is evident from the presence of withered leaf bases and scars on the surface of the corm. The corm originates from an axillary or terminal bud of the previous season's corm. During the growing season a large number of axillary buds develop on the mother corm; these have their bluntly conical apices projecting upwards. Sometimes these buds give rise to foliage leaves, but generally they do not attain full development in the season. They remain in a dormant condition while attached to the mother corm. In the next season these buds develop into separate plants, while the mother corm shrivels and disintegrates. This accounts for the occurrence of a large number of plants in close aggregation.

In form, the corm is somewhat sub-globose or cylindrical and white in colour. At the lower end is attached the dark brown shrivelled residue of the previous season's corm. In size it varies from 1 to 5 cm. in diameter. The growing point is situated at the top covered by the leaf bases. Vegetative buds do not develop in the axils of the leaves of the growing season.

Adventitious roots arise in two or more layers below the terminal portion of the corm. These roots radiate more or less horizontally and are closely aggregated (Fig. 1). They pierce through the leaf-bases in many instances. The roots are white in colour except the tips, which are somewhat yellowish. The rest of the corm is distinctly free from roots. The older roots are slightly fusiform at their base and show corrugated foldings of their surface, which extend from their point of insertion to a distance of about 30 mm. or more in certain cases, suggesting thereby their contractile nature. Various stages of contraction are noted in different roots and it thus appears that there is no dimorphism in this respect and all the roots originating directly from the corm contract with age. These roots branch at some distance. The branch roots are slender and non-contractile. Where a number of daughter corms develop together, each of them develops its own root system, which agrees in all essential features with that of the mother corm.

The lamina is glabrous, characteristically hastate in form and somewhat trisect (Fig. 3). The depth of lobation is a variable feature and depends on the size of the leaf. The median lobe is slightly larger than the laterals. The margin is entire and the apices of the lobes acute. The petiole varies in length from 24 to 60 cm. It is somewhat circular in outline except at the proximal portion where it becomes markedly grooved due to the development of the basal leaf sheath. At the distal end also it shows the presence of a slender furrow on the adaxial side close to the lamina. It is green in colour with a few disjoined red streaks on its surface. The leaf base encircles the stem at its point of insertion (Fig. 2). It encases completely the next leaf and the adjoining inflorescence during the early stages of their development by overlapping of one of the margins. Ligular structures noted in some aroids are absent.

As is characteristic of aroids, the leaf is reticulately veined. The trilobed lamina is characterised by three principal veins. All the three primary veins extend up to the apex of the lobes. The primary vein (midrib) of the central lobe appears to be a direct continuation of the petiole, whereas the other two, branch at angles varying from 75° to 90° and proceed for about a centimetre or more without throwing off any lateral vein on the outer sides (Fig. 3). Thus the lamina is absent at these regions. The lateral primary veins then throw off secondary branches as shown in figure 3. The lateral lobes of the leaf being asymmetrical, the secondary and tertiary veins are greater in number and branch more profusely on the outer side. In all the three lobes, between the main veins, there are simple cross-connections, which mostly form sharp angles. The fields formed in this way are again intergraded into smaller fields by means of irregular running vascular bundles and also by cross-connections. It is in these smaller fields that nerve endings are frequently seen and they appear to be branched.

Apart from this reticulate type of venation there are two sub-marginal veins, which run parallel in the leaf, coming very close together only at the apices of the lobes. The inner sub-marginal vein is placed slightly inwards and delimits the reticulated areas formed by the secondary and tertiary veins, as a result it is somewhat wavy in contour. The other sub-marginal vein is placed very close to the edge and follows the outline of the lamina. These two veins are connected by a series of almost equidistant parallel veins, which branch slightly at the distal ends.

The leaves are arranged on the top of the corm in a pentastichous manner. The sixth leaf occurs directly above the first.

The vernation is somewhat peculiar. The leaf buds remain completely encased by the cataphylls inside the sheathing base of the petiole of the subtending leaf. Owing to the growth in length of the petiole they emerge through the cataphylls from the bases of the subtending leaves as pointed structures (Fig. 5). Close examination reveals that the inner margins of the two lateral lobes of the leaf roll respectively towards the right and left side of the petiole. This process extends as far as their midribs. The left median lobe as well as its corresponding lateral then roll

sinistrorsely, enclosing the previously rolled portion. This process, as noted before in the lateral lobes, extends only up to the midrib. The right median lobe along with its corresponding lateral lobe then rolls over in a dextrose manner and covers the previously rolled portion of the median lobe as a flap. In all these processes the inner surface of the leaf always remains inside, but the vernation cannot be said to be convolute or involute.

Figure 6 illustrates diagrammatically the nature of ptyxis as observed in serial sections. *A* and *B* represent the basal lobes which will be seen to roll in opposite directions. *C* represents the left half of the median lobe which rolls in a reverse direction to that of *B*. Whereas *D* rolls over *C* and partly encases it, this being the right half of the median lobe.

The unfolding of the leaf follows the elongation of the petiole and in this process the median lobes first uncoil in reverse directions followed by the laterals (Fig. 4).

The inflorescence is a spadix closely enclosed by the spathe. It arises as an axillary structure and during its early developmental stages lies completely encased inside the leaf base. It emerges only after the leaf has attained its full dimension. In size it is variable, generally it is about 15 cm. long. The peduncle is comparatively short, it is greenish white in colour with conspicuous red streaks on its upper end. It is somewhat oval in outline and shows the presence of a longitudinal groove on the inner surface. At the distal end, this groove demarcates the position of the lobes of the spathe.

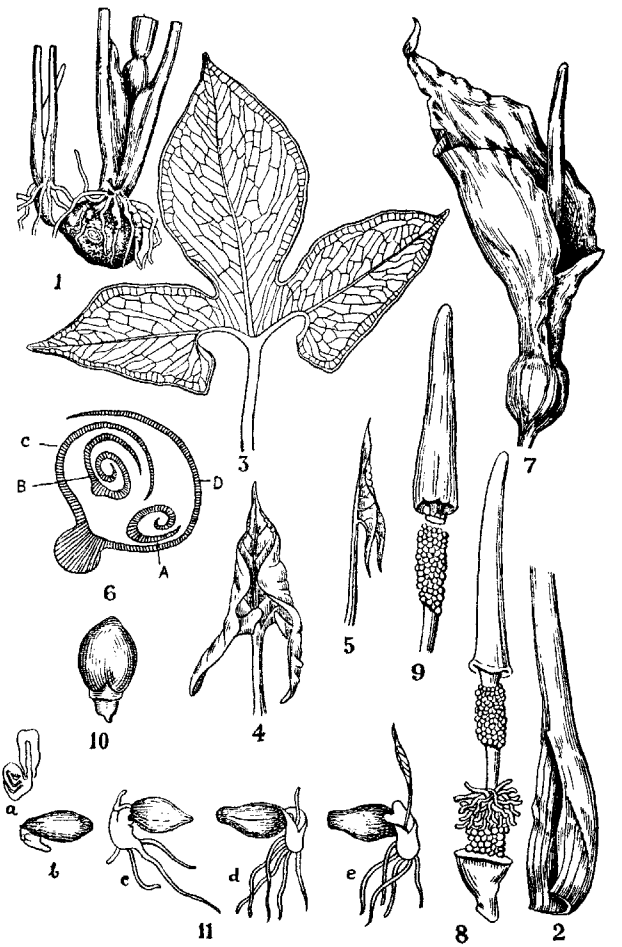
In the bud stage the spathe is convolute and encases the spadix completely. The direction of the twist of the spathe as observed previously by Barnes (1938) is both left- and right-handed. The latter, however, seems to be more frequent. The spathe is about 20 cm. long, but its size, as of all other organs, is variable. It is broadest at the central region and tapers at the apex. When fully expanded it stands out as a conical structure of which one side is greatly extended. Below the conical base a barrel-shaped chamber is formed, the top of which is constricted. The spathe is green with red streaks on the dorsal surface and scarlet on the ventral surface up to the neck of the constriction. This surface is velvety to touch. Inside the constricted area the ventral surface is green except for the presence of occasional red streaks.

The unfolding of the spathe takes place by the unwinding of the flap above the constricted region, the process being completed in the course of 3 to 4 hours. When fully opened, part of the spathe stands out at one side as a scarlet standard behind the crimson coloured appendage of the spadix. Below the constricted region the overlap is retained and the barrel-shaped chamber persists.

It is interesting to note that only the spathe shows parallel venation. This is very clearly seen on the dorsal surface, the veins converging towards the tip.

The region of the spadix above the peduncle can be separated into two regions commonly referred to as the fertile and the sterile regions. The latter occupies about $\frac{2}{5}$ the length of the axis and is situated at the top. It is a conical, somewhat swollen, crimson coloured structure, with a broadly pointed end. This is commonly known as the appendage. Below the appendage the rachis becomes very much attenuated for a very short distance (a few millimetres) and then comes the region of male flowers followed by a short white barren area (about 1 to 2 cm.). Immediately below this region lies the neuter flowers, these being represented by long white filiform processes which give a brush-like appearance. The female flowers occur immediately below this and extend up to the base of the spadix. The neuter and the female flowers lie inside the barrel-shaped chamber of the spathe; while the male flowers and the appendage lie above the constricted region. Figure 8 shows diagrammatically the nature of the spadix and the spatial distribution of the flowers. It would be noted that the area occupied by the male flowers is greater than those occupied by either the neuter or the female flowers.

The male flowers are arranged in an acyclic manner on the axis. The staminate inflorescence appears to be red with white dots on the surface. This is due to the



FIGS. 1–11. *Typhonium trilobatum.* Fig. 1. The corm; note the axillary bud and the nature and origin of the contractile roots (½ Nat. size). Fig. 2. The amplexicaul nature of the leaf base (⅛ Nat. size). Fig. 3. The leaf, illustrating its form and nature of vention (⅛ Nat. size). Figs. 4 and 5. The nature of opening of the leaves (¼ Nat. size). Fig. 6. Diagrammatic representation of a transverse section of a bud showing the nature of ptyxis. Fig. 7. The spathe with appendage; note the barrel shaped chamber below (⅜ Nat. size). Fig. 8. The spadix showing the appendage, male, neuter and the female flowers (½ Nat. size). Fig. 9. The appendage and the region of male flowers: note some stray anthers at the base of the appendage (½ Nat. size). Fig. 10. The mature fruit (×2). Fig. 11*a*. A section of a germinating seed: *b-e*.—Stages of germination (×2).

difference in colour of the anther lobes and the connective, the former being pink and the latter white. The flowers are without any perianth and consists of a single stamen, with a broad connective and bilocular anthers, the filament being extremely reduced. The connective is slightly depressed at the top and also compressed laterally. The pollen grains are spherical, rose coloured and show granulations on the surface.

The neuter flowers, as already stated, are represented by white filiform processes, which are about 40 mm. long and have rounded ends.

The female flowers are also devoid of any perianth and consist of a pitcher shaped ovary with sessile stigmas. The ovary is unilocular and contains a single basal orthotropous ovule.

A study of the mode of pollination shows that the flowers are proterogynous and the spathe unfolds itself towards the evening. The inner scarlet surface of the spathe, as also the foetid odour given out by the spadix attract insects. The barrel-shaped chamber enclosing the female and neuter flowers is not tightly closed at this stage, so that small insects can find easy access. Insects alighting on the spathe, slip down to the neck of the chamber on account of the velvety surface of the latter and get inside the chamber. Late at night, the constricted neck closes tightly so that the insects (mostly small beetles) find egress impossible and are trapped inside. The anthers dehisce late in the evening next day and one notices masses of pollen grains lying at the neck of the constriction. Later on, when the constriction opens, the insects come out, their bodies covered with pollen grains. These insects when they visit other flowers get entrapped and thus cross-pollination is effected. Laboratory experiments on pollen germination show that the pollen grains remain viable for a period of 48 to 72 hours after shedding and thus chances of cross-pollination appear to be great.

The spathe shows signs of degeneration on the second day. The degeneration of the papillate cells is particularly evident, as a result of which the colour fades and within a week everything above the constricted region degenerates, so that only female flowers remain (the neuter flowers are mostly eaten away by the insects). The mouth of the constriction remains closed. The fruit takes from 20 to 25 days to mature. When the fruits become mature the spathe unrolls backwards exposing the fruits. This facilitates their dispersal.

The fruit is an ovoid one-seeded berry, about 10 mm. long. The distal end is greenish white, while the proximal end is white and glossy. Seeds are 4–6 mm. long, about 3 mm. wide, greyish-black, ovate, broad at the base and slightly constricted at the middle (Fig. 10). The funiculus is about 1 mm. long. Endosperm is present.

The seeds germinate in moist saw dust and in ordinary tap water in the course of a week. Laboratory experiments as also observations made in the field seem to indicate that the seeds have no period of rest.

The first sign of germination is the protrusion of a part of the cotyledon through the micropyle (Fig. 11*b*). Sections of germinating seeds at this stage show that the base of the cotyledon protrudes out carrying along with it the plumule and the radicle. Part of the cotyledon which remains inside the seed serves as an absorbing organ (Fig. 11*a*). The radicle next elongates and gives rise to the primary root, while the plumule gives out the first leaf which appears in a convoluted form through the cotyledonary slit. The hypocotyledonary region above the primary root next increases in size and becomes globular. This is subsequently transformed into the corm. At this stage the primary root generally perishes and is replaced by adventitious roots which arise above the radicle. Figure 11, *b*, *c*, *d* and *e* illustrate various stages of germination.

The first leaf of the seedling is small and cordate in shape. The later leaves show an increase in the size of the lateral lobes and gradually become somewhat auriculate in form. From this by gradual stages the typically trilobed structure is reached.

The mode of propagation of the plants appears to be both sexual and vegetative. The latter method has been discussed before. The seed germinates in the soil very soon after dispersal and sends out one or more leaves, which, however, disappear very soon on account of the end of the growing season; the corm which perennates underground sends up the aerial organs next season.

II. Anatomy.

Corm.—The corm is composed of a compact mass of parenchymatous cells which do not show the presence of intercellular spaces. These cells are rich in starch contents. Vascular bundles are of the closed collateral type, but do not show the typical scattered arrangement and appear to be disposed more or less in the form of a ring. The typical scattered arrangement, however, is met with at the points of insertion of the petiole and the peduncle. The corm grows in thickness by the multiplication and enlargement of the ground parenchymatous cells.

Periderm formation takes place at a very early stage when the corm has a diameter of about 8 mm. This process continues even in mature corms. The periderm does not form a continuous cylinder but occurs in isolated patches. The phellogen is hypodermal in origin (Fig. 18). It cuts off a large number of cork cells on the outside and a few layers of phelloderm cells on the inside.

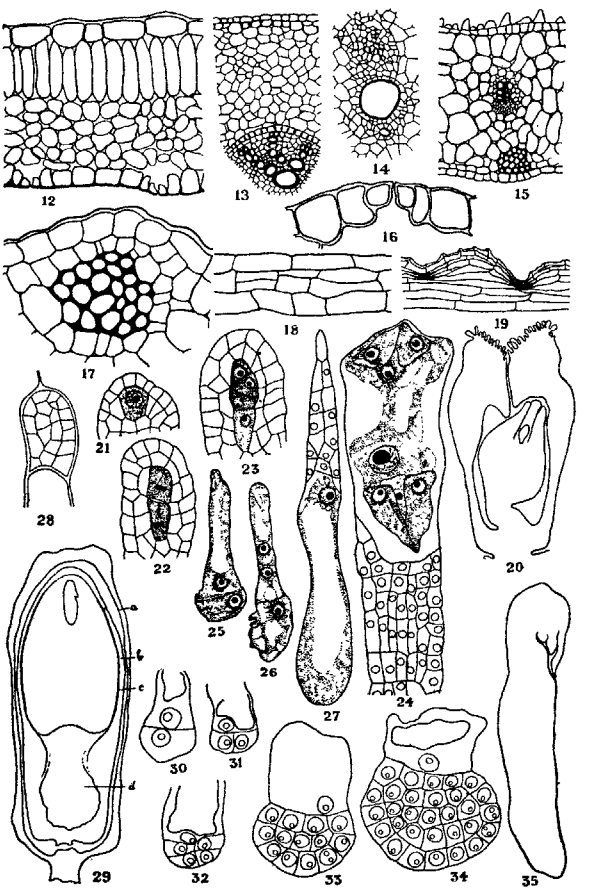
The cells composing the phellem are uniform in shape and radially elongated. They are empty, non-living and without pits. The cells of the phelloderm show the presence of cytoplasm and nucleus and are loosely arranged. The phellogen occurs as a single layer of cells and shows the usual features.

Petiole.—A cross-section of the petiole shows the presence of slightly elevated ridges and furrows. Externally it is bounded by a single layer of somewhat rectangular epidermal cells, the outer walls of which are not thickly cutinised. Stomata are few in number and these are found mostly in the furrows and lie at the same level as the epidermal cells. Ovoid bands of mechanical tissues are situated as hypodermal bands below the ridges. These are composed of a large number of collenchymatous cells (Fig. 17). The number of such bands occurring in a single petiole is variable, generally about 20 are present, but this depends mainly on the diameter of the petiole. Infrequent union of such bands is noted at the distal end of the petiole. The collenchymatous cells are of the prosenchymatous type and superficially resemble sclerenchymatous fibres. The cells show unequal thickenings and have pointed ends which are unthickened. The length of these cells is very variable. They measure from 180 to 700μ, the mean length being about 400μ. Transverse sections show that they are of the angular type. A single nucleus is present in each cell.

Chlorenchymatous cells, two to three layers in thickness, occur below the epidermis in between the bands of collenchymatous cells. Interspersed among these are present a variable number of cells containing red anthocyanin pigment. These are generally separate from one another. The ground tissue is composed of isodiametric parenchymatous cells with intercellular spaces. Vascular bundles are closed, collateral and show a scattered arrangement. The outermost vascular bundles occur in the form of a ring below the collenchymatous bands with the xylem facing inwards. They are, however, separated from these bands by two to three layers of parenchymatous cells. The xylem consists of a large annular and two or three smaller spiral and annular vessels. Reticulated or pitted elements are entirely absent. A few xylem parenchyma cells are also present. The phloem is composed of sieve tubes and companion cells, phloem parenchyma being totally absent (Fig. 14).

Leaves.—The leaves are dorsiventral. The upper epidermal cells are somewhat rectangular in shape with their outer walls thickly cutinised. The cuticle can be separated from the walls when treated with sulphuric acid. Stomata occur on both surfaces. The average number of stomata per sq. mm. was found to be 2 in the upper and 8 in the lower epidermis. Subsidiary cells are present along with the guard cells and as usual a respiratory cavity occurs below each stoma (Fig. 16). The mesophyll consists of a single layer of pallisade cells and 4 to 6 layers of spongy parenchyma (Fig. 12). The vascular bundles show the usual structure. Associated with each vascular bundle is a hypodermal band of collenchymatous cells, which occur on the dorsal side.

Spathe.—Anatomy of the spathe shows that the inner scarlet covered velvety surface is closely covered by papillose protrusions. These cells have thin walls and contain red anthocyanin pigment in the vacuoles. A few stomata (1 per sq. mm. area) occur in between these cells. Immediately below this occur rectangular cells in a single layer. These cells closely resemble the dorsal epidermal cells, but are somewhat larger. Next to this and extending up to the lower epidermal cells, are found chlorenchymatous cells. There is slight development of intercellular spaces.



FIGS. 12–35. *Typhonium trilobatum.* Fig. 12. Section of leaf (×125). Fig. 13. T.S. of part of a root (×40). Fig. 14. A vascular bundle of the petiole (×125). Fig. 15. T.S. of a spathe (×100). Fig. 16. The stoma and subsidiary cells (×420). Fig. 17. Collenchymatous band of the petiole (×400). Fig. 18. The hypodermal origin of the phellogen (×125). Fig. 19. L.S. of a contractile root to show the nature of corrugation and the disposition of the tissues (×15). Fig. 20. L.S. of the ovary showing the stylar canal and the acentric nature of the orthotropous ovule (×10). Fig. 21. The hypodermal origin of the M.M.C. (×420). Fig. 22. Homotypic division (×420). Fig. 23. Linear tetrad of megaspores (×125). Fig. 24. The mature embryo-sac: note the 'postament' like cells at the base (×420). Fig. 25. Micropylar and chalazal chamber produced by the 1st division of the endosperm nucleus (×300). Fig. 26. The enlargement of the basal chamber and the division of the micropylar nucleus (×300). Fig. 27. A later stage of endosperm formation: note the enlarged basal cell (×150). Fig. 28. The nucellar cap (×45). Fig. 29. L.S. of a mature fruit: *a*—ovarian wall; *b*—outer integument; *c*—crushed inner integument; *d*—empty basal chamber (×5). Figs. 30–34. Stages in the development of the embryo (×150). Fig. 35. A fully developed embryo (×30).

The outer walls of the lower epidermal cells are unthickened. The average stomatal frequency is 8 per sq. mm.

Vascular bundles are situated mostly in the central region. Associated with each bundle is present a strengthening band composed of collenchymatous cells. These bands occur at the abaxial side of the spathe below the epidermis. They are separated from the vascular bundles by a few layers of parenchymatous cells (Fig. 15).

A cross-section of the appendage shows it to be circular or ovoid in outline. It is bounded by a single layer of epidermal cells, which show slight variation in size. Stomata are present, but are few in number. The ground tissue is composed of starch-filled parenchymatous cells which are separated by intercellular spaces. Wide schizogenous cavities are sometimes present at this region. Vascular bundles occur below the starch-filled cells and are of the usual closed collateral type. These bundles send out traces diagonally which end at the hypodermal region. Elongated crystal sacs containing raphides are disposed radially in one or two series in the peripheral region amongst the starch containing cells. They are absent in the central region.

Root.—The growing point of the root shows the presence of a root cap. The root cap and the histogens of the root are derived from a common primordial meristem. The cells composing the root cap are larger in size and contain starch grains. These are, however, located mainly in the central region (Columella of Němec) of the root cap and the surrounding cells are free from it. The three histogenic layers become differentiated a little below the primordial meristem. The plerome appears to be wider than the periblem.

A t.s. of the mature root shows the presence of exodermis, which is two-layered at certain regions. This is followed by the cortex composed of many layers of parenchymatous cells with slight development of intercellular spaces. The endodermal cells have their radial walls suberised. Below this occurs a single layer of parenchymatous cells of the pericycle. The vascular bundles show the characteristic radial arrangement. The number of xylem strands varies from six to eight, the largest number of roots possessing six. A single large annular vessel and a few spiral vessels are the elements of the xylem, while phloem is composed of sieve tubes and companion cells; no conjunctive tissue or pith is present.

Figure 13 represents t.s. of a part of a root which is octarch. It will be noted that the central region is occupied by a large vessel. Developmental studies indicate that this is a protoxylem element, which is the first to differentiate into an annular vessel. Metaxylem elements as in the petiole are absent.

A study of the constricted region of the roots shows that the depth of constriction extends radially to about half the cortex and is not nodal in character. The folding is of the nature of ridges and furrows, which may be narrow or broad. Longitudinal sections show that the outer cortical tissue is alone concerned in the process, the epidermal cells above remain intact at most places. At the point of constriction the cells get extremely compressed laterally and give a lamellated appearance. Those lying inside the ridges as well as the cells occurring below the region of constriction appear to have increased in length (Fig. 19), the latter being longer than the former.

Calcium Oxalate Crystals.—Needle shaped crystals of calcium oxalate are present in different parts of the plant body. They are, however, absent in the mature roots and in the axis of the spadix below the appendicular region. The size of the crystal sacs occurring in the different parts of the plant is variable. The largest are found in the appendage of the spadix, where they range from 65·2 to 234·72μ, the average being 169·52μ. The disposition of the crystals inside a sac is variable, and the occurrence of more than one bundle of crystals inside a sac is not infrequent. The average length of the individual crystal is about 50μ.

The first indication of the origin of the crystal sacs is noted by the slight increase in size of the cell, followed by a corresponding increase in size of its nucleus and nucleolus. The cytoplasm is very dense at this stage. At the next stage small

vacuoles become apparent in the cytoplasm and the nucleus is pushed to the periphery. At this stage the appearance of granular matter is first noted inside the vacuoles. Along with the progressive increase in size of the cells, its nucleus and nucleolus also increase in size, and the raphides become apparent. The nucleus generally lies at one side of the cell but in a few instances it has been observed to occupy a central position surrounded by groups of crystals. When the sac attains its full dimension the nucleus disorganises, and no trace of it or the cytoplasm remains.

It is interesting to note in this connection that with the gradual increase in size of the nucleus, the chromosomes become differentiated and generally two or three of them are seen to be attached to the nucleolus. The prophasic condition of the nucleus continues till the crystals are organised, when it disappears. Thus it appears that the nucleus has a distinct rôle in the formation of the crystals.

III. Embryology.

The early indication of the development of the pistillate flowers is noted by the protrusion of the papillate processes on the axis. The growth of the primordia soon becomes arrested and from its base meristematic tissue appears in the form of a ring. This grows upwards and later curves inwards to meet at the centre. Thus the ovary is organised as a closed chamber. The centre of the primordial tissue later gives rise to the placenta from which a single orthotropous ovule develops. The growth of the ovule, as compared to that of the ovary, is comparatively rapid. In most cases on account of the absence of space inside the ovarian chamber the tip of the ovule lies eccentrically at one side due to the curvature of the funicle as illustrated in figure 20. Later, however, when the ovule becomes fully developed the funiculus straightens itself, still, in most cases the micropyle is eccentrically placed. The stigma is sessile and somewhat concave on the outer surface, from which unicellular hairs are produced. A very slender stylar canal is present, this is bounded inside the ovary by auricular processes of the ovarian wall.

The primordium from which the ovule arises grows upwards from the basal placenta as a hemispherical mass of tissue. The inner integument soon becomes differentiated and by its rapid growth encloses the nucellar tissue at an early stage of its development. The primordium of the outer integument appears soon after the inner, but its growth is comparatively slow. In the mature ovule the nucellus is completely encased by the inner integument, the tip of which becomes somewhat swollen and forms a narrow micropyle. The outer integument stands at a slightly lower level and the portion next to the funiculus is broader than the apex. The inner integument is composed of three layers of cells except at the tip where it is swollen and consists of four to six layers of cells. The cells lining the micropyle have dense cytoplasm and are radially elongated. The inner layer of the inner integument subsequently forms the tapetal layer of the megagametophyte and is composed of rectangular cells with their longer axis perpendicular to the longitudinal axis of the ovule.

Three vascular traces enter each ovule. These unite in the funicle and split in the chalazal region into two branches, which enter the outer integument and extend nearly up to the micropyle.

A single hypodermal cell at the apex of the ovule becomes differentiated as the archesporial cell and directly functions as the megaspore mother cell (Fig. 21). It enlarges during the meiotic divisions and the cytoplasm becomes finely vacuolate. During diakinesis 9 pairs of chromosomes are seen inside the nucleus. At this stage the epidermal cell overlying the megaspore mother cell divides periclinally so that it is pushed inside the nucellus. Two cells are produced following the first division of the M.M.C. Both of which divide simultaneously and the spindles lie

parallel to the longitudinal axis of the ovule (Fig. 22). The result of these divisions is the production of a linear tetrad of megaspores (Fig. 23).

The micropylar megaspore is the first to degenerate followed by the next two in succession. The chalazal megaspore by its activity gives rise to the megagametophyte. At the binucleate stage a large vacuole forms between the two nuclei which lie at each end. Further divisions of these nuclei lead to the production of a four-, and later, of an eight-nucleate megagametophyte. From the binucleate stage onwards degeneration of the surrounding cells of the nucellus is noted and the process is almost complete at the eight-nucleate stage, when the embryo sac is directly in contact with the inner integument. The cells derived from the epidermal cell above, however, have divided several times and produced a nucellar cap composed of many cells (Fig. 28).

In the eight-nucleate megagametophyte the synergids are somewhat pear-shaped and have the usual basal vacuole. The egg is somewhat inconspicuous and generally lies covered up by the synergids (Fig. 24). The polar nuclei migrate to the centre of the megagametophyte and fuse. Due to the differential growth of the embryo-sac following the fusion of these nuclei it comes to lie adjacent to the antipodals. The antipodals are three in number and appear as distinct cells. They are about twice the size of the synergids and are triangular in form, with the pointed ends projecting downwards. Fig. 24 illustrates a mature embryo-sac and its component parts.

The pollen tube enters the embryo-sac by the way of the micropyle and its remnants can be seen in many preparations showing this stage. Stages of fertilisation were, however, not observed. After syngamy the synergids and the antipodals degenerate and the egg remains suspended from the micropylar end of the sac. It appears to be somewhat elongated at this stage. The embryo-sac becomes considerably elongated after fertilisation and the primary endosperm nucleus lies close to the base of the sac. At this stage the cells of the nucellus lying in contact with the chalazal end of the embryo-sac show a typical 'postament' like appearance (Fig. 24). But it should be noted that with the gradual enlargement of the embryo-sac, which occurs during the post-fertilisation stages resorption of the nucellus at the chalazal end takes place and all trace of this strand like tissue is lost.

As in most plants the endosperm nucleus divides before the oospore. It migrates slightly towards the centre of the sac before division. Karyokinesis is followed by wall formation and the embryo-sac becomes divided into a large micropylar and a small basal chamber (Fig. 25). The latter, however, increases very much in size in later stages. The micropylar endosperm cell very soon divides transversely (Fig. 26). This is followed by divisions in similar planes of the daughter cells. At this stage the cells of the lower tiers divide longitudinally while those of the upper might divide several times transversely. Later divisions take place in various planes and a typical cellular endosperm is formed capping the large basal cell (Fig. 27). Along with the growth of the ovule the endosperm cells multiply rapidly and extend inwards in the form of an arc which, however, later becomes convex in form (Fig. 29). The lateral edges of the endosperm tissue which are one cell in thickness extend inwards and line the basal chamber for a considerable distance. In the later stages of development the endosperm increases mainly due to the activity of its outermost layers of cells, which line the basal chamber. The inner cells become conspicuously vacuolated and elongated. With the rapid development of the endosperm tissue the nucellar cap disintegrates and no trace of it is found in later stages. The cells of the endosperm show abundant starch grains.

The chalazal cell never divides but reaches an enormous size, occupying nearly one-third the space of the embryo-sac cavity; its nucleus also shows corresponding increase in size and is surrounded by dense cytoplasm. The form of the nucleolus appears to be somewhat irregular at this stage. In later stages of the development

of the seed it completely disintegrates. With the development of the endosperm in the micropylar chamber, the basal chamber gradually becomes reduced in size and in the mature seed it occupies about one-third the space of the embryo-sac. The nucellar cells lying immediately below the basal chamber show signs of disintegration as the chamber increases in size. This is very conspicuous in the later stages. Thus it appears that the basal cell is haustorial in function and brings about a disintegration of the surrounding cells by the secretion of an enzyme. In the mature seed the micropylar portion containing the endosperm and embryo are prominent, while the basal chamber with the haustorial cell along with the surrounding coat of the parent sporophyte remains as a withered protuberance at the chalazal end (Fig. 10).

The embryo develops more slowly than the endosperm. The oospore divides after a few cells have been formed in the micropylar chamber of the endosperm and the first division is periclinal (Fig. 30). The micropylar cell is larger and grows slightly in size at later stages but does not undergo any further division and remains as a one-celled suspensor. The smaller distal cell gives rise to the embryo proper. Its first division is longitudinal, i.e., perpendicular to the previous plane of division (Fig. 31). This is followed by transverse divisions in both the daughter cells (Fig. 32). The next stage observed shows the embryo to be composed of two tiers of cells. The immediately succeeding stages have not been observed and a globular embryo is next noted in which the dermatogen appears to have differentiated (Fig. 33). Cell division now takes place in various planes and the embryo becomes somewhat ovoid in form. Very soon a notch appears at one side of the embryo which separates the terminal cotyledon from the lateral plumule primordium. In later stages the terminal cotyledon enlarges rapidly with the result that the plumule is pushed close to the micropylar end of the embryo. The radicular portion of the embryo does not appear to be well differentiated even at this stage. In the mature embryo, the growing point appears to be a hemispherical projection covered up by a few rudimentary cauline leaves (Fig. 35).

A transverse section of the embryo in the region of the plumule shows the hemispherical growing point partly encased by the leaf primordia.

Figure 29 represents a longitudinal section of a mature fruit where the comparative size and position of the embryo, endosperm and basal chamber are clearly seen. Externally the fruit is covered by the pericarp. Below this occurs the outer integument, while the inner integument is seen as a disorganised layer closely adpressed to the endosperm. At the lower end, the large empty basal chamber remains surrounded by the partly disorganised cells of the nucellus.

IV. Cytology.

Mitosis.—The diploid number of chromosomes as determined from root tip cells in *Typhonium trilobatum* is 18. The complement is made up of 6 long, 6 medium and 6 short chromosomes. Of these 4 chromosomes possess trabants and two show secondary constrictions. The centromere constrictions appear to be differently located. Thus of the 6 long chromosomes 4 have sub-terminal constrictions and 2 median, the 6 short chromosomes median, and of the 6 medium chromosomes, 2 have subterminal and 4 median attachment, while the 4 SAT-chromosomes have median constrictions. The Sat-chromosomes show slight difference in length of the filament but the nature of the trabant appears to be the same (Fig. 36).

When the onset of prophase the chromosomes appear as small globular bodies which lie mostly adpressed to the nuclear membrane. From these the organisation of closely coiled threads inside the nucleus soon becomes apparent. The nucleus as also the nucleolus attain their maximum size at this stage. The latter lies somewhat eccentrically and is seen to be connected to a number of chromosomes. Careful examination of Feulgen-Light-Green preparations shows that the secondary constricted

and Sat-chromosomes are alone attached to the nucleolus. Figure 37 shows an attachment by three such chromosomes. The number of nucleoli occurring at this stage is variable. Generally a single large nucleolus is present, but two nucleoli are frequently seen, while three or more are less frequent. Where there are more than one nucleoli, an appreciable size difference is noted.

With the disappearance of the nuclear membrane the chromosomes become regularly aligned at the equatorial region of the spindle. The nucleolus as a rule disappears at this stage, but in a few instances it has been noted to lie either in the central region or move bodily to one of the poles in advance of the chromosomes. In the former case it generally divides into two unequal halves which move to the opposite poles, and are later cast out into the cytoplasm.

Polar view of metaphase shows that the chromosomes are double. The nature of the twisting of the chromatids could not, however, be made out on account of their small size.

The anaphasic movement of the chromosomes appears to be regular and no laggards have been noted. The chromosomes on reaching the poles lie free from one another and the homologue of each chromosome can be made out. The longer chromosomes do not appear to be situated at the periphery of spindle.

Examination of telophase nuclei shows that the chromosomes have undergone a certain amount of expansion and appear as elongated threads. In some of the chromosomes the split for the next division is apparent. The number of nucleoli in each nucleus appears to be variable at this stage. The maximum number of independent nucleoli observed was six (Fig. 38). Fusion of these nucleoli commonly takes place and one large or two equal sized nucleoli are generally seen at later stages.

During early telophase the protoplast assumes a phragmoplastic appearance and a hyaline cell plate appears in the central region. The phragmoplast soon increases in size and extends laterally. Along with this the spindle fibres in the central region disappears, but those at the periphery become conspicuous. As the phragmoplast touches the lateral walls of the cell, these striations also disappear and the cell plate extends both ways. Thus the phragmoplast brings about a division of the cell by its growth and lateral expansion. It is interesting to note that such a mode of cytokinesis has been observed previously by Sharp (1911) in *Physostegia virginiana* and recently by Rao (1942) in *Santalum album*.

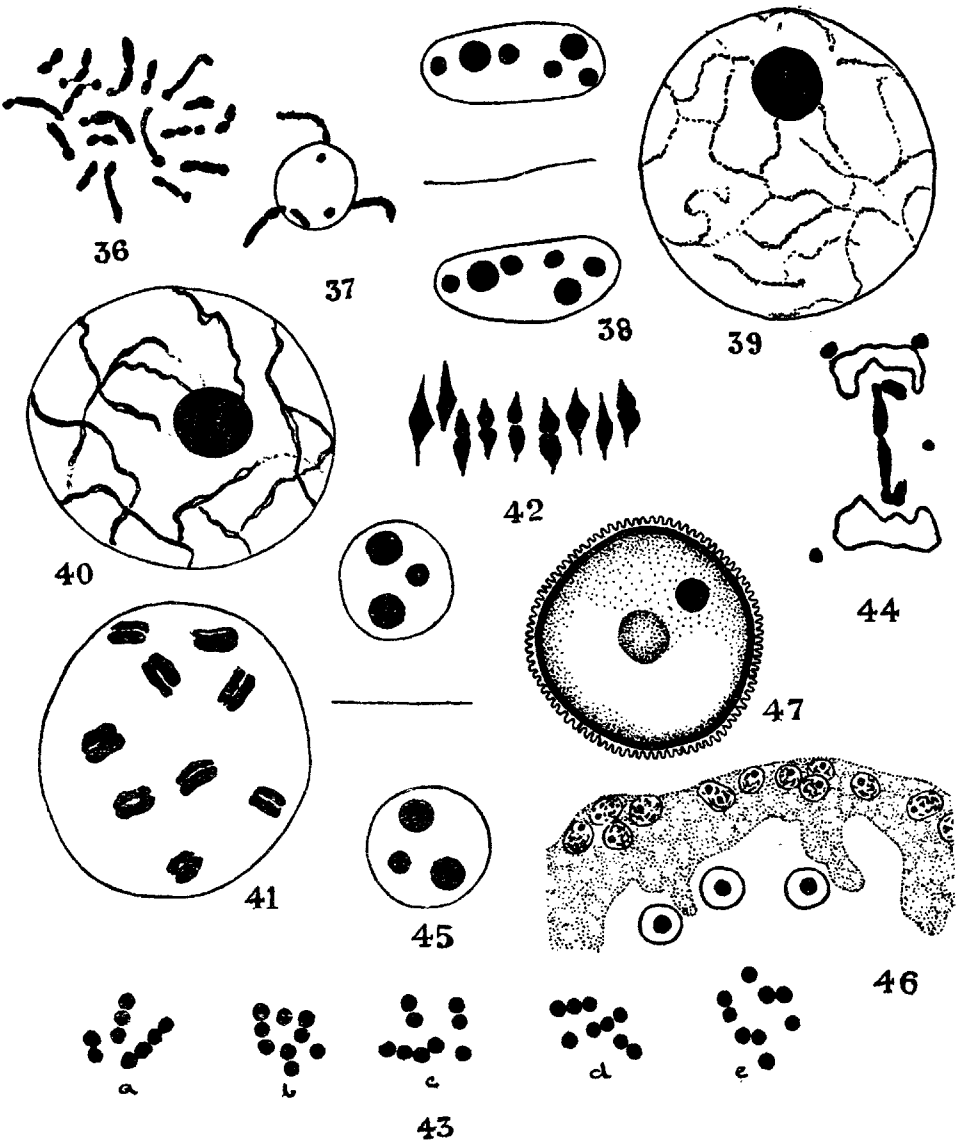
Meiosis.—The primordia of the anthers develop later than those of the ovule, while those producing the filiform processes, the so-called neuter flowers develop last.

The initiation of anther primordia is noted by the increase in length and anticlinal division of the hypodermal cells in the staminate region of the spadix. The cells in this region become demarcated in groups of actively dividing cells. Very soon the surface of the spadix becomes wavy in outline and gradually the anthers protrude out. These appear to be quadrilocular in transverse sections.

The development of the sporogenous cells could not be definitely traced, but the archesporial cells are hypodermal in origin. When the sporogenous cells are first noted they are seen to be separated from the epidermis by six layers of cells. Of these the outer four layers are somewhat elongated and form the parietal layers, while the inner two represent the tapetal layers and are somewhat polygonal in shape.

The sporogenous cells could be made out by their bigger size, greater chromaticity and dense cytoplasm. The nucleus of the mother cell is spherical in shape and has a well-defined nuclear membrane. It contains a deeply stained nucleolus and faintly stained chromatic threads, which are spread uniformly throughout the nuclear cavity. Prophase of the meiotic division is noted by the greater chromaticity of the threads which appear to be somewhat twisted. The separate threads could not be tracted at this stage. Occasionally, however, free ends are seen. Pairing of the leptotene threads is noted by the appearance of threads which are thicker at certain

regions and thinner at others. When pairing is complete the threads become thicker and shorter and contract to one side of the nuclear cavity and finally condense into a tight synizetic knot. Generally one nucleolus is present at this stage, which may



FIGS. 36–47. *Typhonium trilobatum*. Fig. 36. The somatic complement of 18 chromosomes (×3500). Fig. 37. Attachment of Sat. and Sec. constricted chromosomes to the nucleolus. (×3500). Fig. 38. Telophase nuclei (somatic)—with six nucleoli in each nucleus (×3500). Fig. 39. Prophase of meiotic nucleus (×3500). Fig. 40. Pachynema (×3500). Fig. 41. Diakinesis (×3500). Fig. 42. Configuration of bivalents at metaphase (×3500). Fig. 43*a–e*. Various types of secondary association (×2440). Fig. 44. Anaphase I. Chromosome bridge and fragment (×3500). Fig. 45. Telophase, I division: note three nucleoli in each nucleus (×3500). Fig. 46. Part of periplasmodium showing the peripheral position of nuclei (×450). Fig. 47. Binucleate pollen grain. (×3500).

or may not be enclosed in the meshes of the contracted knot. Loops are frequently thrown out from the synizetic knot and these are distinctly double in nature. Tight synizetic knots as seen in this material are now regarded as artefacts produced by fixing agents accentuating the real contraction of the chromosomes. Nevertheless, synizesis represents a very delicate condition of the nucleus. On recovery from synizesis the threads become distinctly thicker and lie freely distributed inside the nuclear cavity (Fig. 40). The double nature of the chromosomes becomes evident at places. A single nucleolus is present, to which three pairs of chromosomes are seen to be attached.

Progressive condensation of the chromosomes takes place till the diplotene stage is reached, which is noted by the separation of the paired chromosomes. The quadripartite nature of the chromosomes could not, however, be made out, but the chromosomes seem to have an irregular outline. At this stage chiasmata are seen to connect the chromatids. The chiasmata undergo terminal movement on the condensation of the chromosomes to form the bivalents.

At diakinesis terminalisation of the chiasmata is complete and the nine bivalent chromosomes which appear as rod-shaped bodies lie approximately equidistant from one another. According to Lawrence (1931) this is due to a repulsion phase which is initiated earlier and continues up to diakinesis. In most preparations showing this stage three bivalents are regularly seen to be attached to the nucleolus which is spherical in shape. The bivalents appear to be almost similar. In no case was multivalent formation noted. It is at this stage that the pollen mother cells show signs of rounding off.

Towards the close of diakinesis, the nucleolus disappears by progressive diminution in size and the bivalents move towards the centre of the nucleus forming groups or associations. This is the commencement of the secondary pairing of the chromosomes which becomes marked in metaphase. This association of chromosomes is also observed in metaphase II.

An analysis of different types of secondary association as observed in metaphase I is presented in Table I below.

TABLE I.

Types of Secondary Association.

No. of cases.	No. of bivalents in association.				Maximum association.	Basic number derived from max. association.
	1	2	3	4		
6	3	..	2	..	2(3)+3	5
3	3	3	..	..	3(2)+3	6
13	2	2	1	..	1(3)+2(2)+2	5
7	..	1	1	1	1(4)+1(3)+1(2)	3
3	1	1	2	..	2(3)+1(2)+1	4
17	4	1	1	..	1(3)+1(2)+4	6
2	9	..	..	..	9	..
5	2	..	1	1	1(4)+1(3)+2	4
3	1	4	..	..	4(2)+1	5
3	1	2	..	1	1(4)+2(2)+1	4
1	3	1	..	1	1(4)+1(2)+3	5
5	1	1	2	..	2(3)+1(2)+1	4
4	5	2	..	..	2(2)+5	7
2	6	..	1	..	1(3)+6	7

74 Total.

The maximum number of association between bivalents was found to be 1(4)+1(3)+1(2). It shows one group of four, one group of three and one group of two making three separate associations.

Side view of metaphase shows that the bivalent chromosomes group themselves regularly on the equatorial region of the spindle. They appear to be equally spaced and the two members of a pair can be easily made out in most cases (Fig. 42). Secondary association is maintained to some extent at anaphase. Different views have been expressed for the anaphasic separation of the chromosomes. Kuwada (1929) believes this is due to polar attraction, while Darlington (1932) is of opinion that it is a 'polar' repulsion, which is essential for metaphasic equilibrium. Catcheside (1934) suggests that the attachment constrictions are the regions of localised forces, which lead to a mutual repulsion of the chromosomes of a bivalent. Alam (1936) thinks that the anaphasic separation is the result of more than one force. 'Repulsion between attachment constrictions and the attraction of the poles.'

Separation at anaphase I is normal in most cases. In a very few anthers (less than 5%), however, the pollen mother cells show the presence of inversion bridges. Each of these bridges produce a dicentric chromosome and an acentric fragment (Fig. 44). The acentric fragments are very small indicating that not only the inverted segments are small but also the chiasmata are extremely terminal. The fate of these inversion bridges could not be clearly followed, but their absence during second division shows that they are not included in the gametes. The few lagging bivalents noticed during first division are due to mechanical difficulty consequent upon chiasma formation in inverted segments. All such bivalents later develop into true inversion bridges releasing the acentric fragment incidentally.

The chromosomes on reaching the poles organise a telophase nucleus. They become somewhat elongated and the split for the 2nd division is apparent in most of the chromosomes. Careful examination shows the presence of three nucleoli in each nucleus, of which two are almost equal in size and one smaller (Fig. 45). The interkinetic stage seems to be of some duration. The protoplast assumes a phragmoplastic appearance and a cell plate appears in the centre, which divides the cell into two equal halves.

The two separated daughter nuclei as a rule divide simultaneously. Anaphasic separation is normal; the two groups move simultaneously and no lagging univalents are seen. On reaching the poles, grand daughter nuclei are organised, each of which shows the presence of two to three nucleoli and slender chromosomes. As in telophase of division I, a cell plate appears in the central region at the end of telophase and pollen tetrads are produced. Various forms of arrangement of the tetrads are seen. This depends mainly on the arrangement of the spindles during II division. Tetrahedral and isobilateral modes of arrangement being very common; such diverse modes of arrangement appear to be a common feature of monocotyledonous plants. The pollen grains are at first uninucleate. The nucleus soon divides and gives rise to a generative and a vegetative nuclei. This is the condition in which the pollen grains are shed (Fig. 47). Mature pollen grains have an average diameter of 45μ, when examined in lactic acid.

Periplasmodium.—At the time of differentiation of the sporogenous cells, the tapetum is two-layered. The cells are uninucleate and contain dense cytoplasm. At an earlier stage some of the tapetal cells have been observed to divide by periclinal walls. Such divisions are generally completed before prophasic changes become apparent in the microspore mother cells. Binucleate tapetal cells have not been observed.

During synizesis the innermost tapetal cells are first noted to protrude into the anther cavity. The cytoplasm alone moving inwards. The nuclei are spherical and the walls delimiting the cells are distinct at this stage. During later stages of meiosis (I division onwards) the cytoplasm progresses further inwards and even reaches across the anther loculus at places, dividing the microsporangium into

compartments. At this stage the walls delimiting the individual tapetal cells disappear and the nuclei are seen to be situated at the periphery of the anther cavity embedded in a homogeneous cytoplasmic mass. At the pollen tetrad stage the tapetal nuclei are seen to leave their peripheral position and migrate into the microsporangium. At this stage the plasmodium fills up the anther cavity completely but is not in contact with the pollen tetrads. The nuclei of the plasmodium which are irregularly distributed aggregate at places and retain their original form. This close aggregation of nuclei very often leads to their fusion resulting in the production of nuclei of variable shape and size. When the microspores have been organised the plasmodium comes in contact with the pollen grains but the nuclei remain separate and present a conglomerated appearance. Fusion of two or more nuclei is commonly seen at this stage. In no case was amitotic division of the nuclei observed. With the development of the exine of the pollen grains the plasmodium becomes highly vacuolated and ultimately during the binucleate condition of the pollen grains it completely disappears. At this stage the parietal layers of the anther wall become crushed and obliterated, while the endothecial layer becomes radially elongated, except at the tip of the connective, where it is represented by smaller unthickened cells. Rupture of these cells brings about the dehiscence of the anthers, which is thus 'porous' in nature.

Discussion.

Morphology.—The occurrence of contractile roots seems to be a characteristic feature of *Typhonium trilobatum* as all aroids do not possess it. Anatomical studies indicate that it is mainly the outer tissue of the cortex, which shows the corrugation while the stele and the inner cortex remain unaffected. The limited observations that have been made on the nature of the contractile roots of different plants show that the zone of contraction is restricted to the outer cortex. Rimbach (1897) was the first to explain the cause of wrinkling. He states 'that the shortening is due to a change of form of the inner cortical cells, which increasing in a radial and tangential direction suffers a great decrease in length.' Woodhead (1904) supports this view, but Arber (1925) working on *Hypoxis* failed to find any evidence in this direction and pointed out the baffling nature of the problem. Evidence obtained in the course of the present study supports partially Rimbach & Woodheads' observations, as there is an increase in volume of the outer cortical cells which, however, also show an increase in length. Nevertheless, it is difficult to understand how an increase in radial and tangential directions of the outer cortical cells alone could bring about the contraction unless we assume the presence of cells at regular intervals, which retain their original dimensions. Such a mode of contraction would present a different appearance to what has been seen in the present material, which indicates that apart from an increase in volume of the cells of the outer cortex, an internal pull is exerted by certain cells at intervals, due to which the cells at these regions present a lamellated appearance. This gives rise to the so-called furrows at the constricted regions. The origin of this pull might be due to physical or chemical changes in the cell-wall.

The nature of ptyxis is also peculiar, but does not appear to be a characteristic feature as it has been noted in *Colocasia antiquorum* and *Alocasia sps.* It appears that aroids with trilobed leaves show this peculiar mode of folding of the leaves.

The appendage of the spadix has received much attention from various investigators. Arber (1925) on anatomical evidence suggested that it was composed of the fused bases of the male flowers and represented a region of the inflorescence in which sterilisation is marked. This view has been confirmed by Engler (1881–84) who has shown by a comparative study 'that the club is not a naked axis but it consists of an incompletely developed part of the inflorescence'.

In the course of the present investigation, a spadix was obtained in which a few isolated male flowers (stamens) occurred a little below the appendage and in continuation of the male inflorescence. These were comparatively large, being four to six times the size of the normal stamens and of the same colour as the appendage. The microsporangia were also larger and contained abundant pollen grains which, however, were of the same size as those found in normal anthers. At a slightly higher level and still closer to the appendage occurred other stamens, which were sterile. Figure 9 shows the region of the spadix where the sterile flowers are located, while the empty space below indicates the position of the larger fertile stamens. This gradual transition indicates that the appendage is derived by the union of such sterile flowers. Further evidence in this direction is obtained on anatomical grounds, which shows that vascular traces are given out regularly from the central strands of the appendage. The number of such separate traces are quite large and extend to the periphery. It is interesting to recall that each stamen is supplied by a single vascular trace, which character persists even in the appendage.

Anatomy.—The anatomy of the petiole shows difference in the various genera due primarily to the mode of distribution of the mechanical tissue which may be collenchymatous or sclerenchymatous. Solereder (1928) states that the mechanical tissue in the petiole may be either disposed in the form of a complete ring below the epidermis, or it may be narrower or broader at different regions and protrude into the ground tissue, or it may occur in isolated patches separated by chlorenchymatous cells. The mechanical tissue of *T. trilobatum* is composed entirely of collenchymatous cells whose structure has been already described. It occurs in isolated patches in the hypodermal region of the petiole, as has also been noted in *Philodendron*. It thus forms a sub-epidermal girder system, which is the most suitable type of arrangement for cylindrical inflexible organs. This mode of arrangement of the mechanical tissue is also found in *Colocasia antiquorum* where, however, the mechanical strands vary in size and are regularly arranged at the periphery being associated with mestome bundles.

An interesting observation made in the course of this study was the absence of metaxylem elements in the vascular bundles of the petiole and root. In the bundles of the petiole, generally a single large vessel is present, or there may be one or more smaller ones associated with it. In the roots where the exarch arrangement prevails the xylem elements (apart from the xylem parenchyma) consist of an inner bigger vessel and two or three smaller outer ones. The size of the larger vessel and its position would seem to indicate that it is a metaxylem element, but developmental studies show that it is the first to differentiate and it shows the annular thickening. Further, examination of macerated material from roots and petioles confirmed these observations.

The concept of protoxylem and metaxylem has undergone considerable change since Russow (1872) and Van Tieghem (1887) first introduced these terms. The original meaning of the words was modified later when the sculpturing of the wall was taken into account. Esau (1943) states 'eventually the tendency to ascribe to protoxylem and metaxylem a definite wall morphology became prevalent and it influenced the formulation of concepts of primary xylem by writers of modern reference works'. The International Association of wood anatomists recognise the metaxylem as the pitted tracheal elements (the scalariform elements also included). Frey-Wyssling (1940), however, favours the abandonment of delimitation of these two tissues on the basis of wall sculpture and suggests the 'reintroduction of the ontogenetic aspect into the classification'. He finds difference in the structure of metaxylem elements in different groups of plants which in certain instances have been noted with spiral secondary thickening. Esau (1943) also states that the thickening of the metaxylem elements may vary from spiral to pitted.

Popham (1941) has suggested the abandonding of the terms 'protoxylem' and 'metaxylem', because 'in the differentiation of xylem cells, location, time of enlarge-

ment, time of secondary wall lignification, time of differentiation and the pattern of the secondary wall do not always bear a specific or constant relationship to the kind of origin, whether primary or secondary'.

Embryology.—A review of the literature shows that the archesporial cell in the family Araceae may be one or many. The former condition, however, appears to be more common and the archesporial cell is hypodermal in most members of the family. In some plants such as *Anthurium crystallinum, A. violaceum, Symplocarpus foetidus,* it cuts off a parietal cell and then functions as the megaspore mother cell. In *Arum maculatum, Homalonema alba, Acorus calamus* and others it directly functions as the megaspore mother cell. This condition has been observed in *T. trilobatum,* which comes under the tribe Arineae to which *Arum maculatum* also belongs. The epidermal cell which overlies the megaspore mother cell forms a nucellar cap by repeated divisions. Such nucellar caps have also been noted in *Peltandra virginica, Arum maculatum, Calla palustris* and in other plants. In *Acorus calamus,* however, the nucellar cap is composed of a single layer of cells formed by the division and radial elongation of the epidermal cells.

More than one type of embryo-sac development has been recorded in this family. Schnarf (1931) records the occurrence of 'Lilium-type' of development in *Dieffenbachia seguine* and *Anthurium violaceum.* The 'Scilla-type' of development has been found in *Homalonema argenta* and *Nephthytis Grayenreuthii,* whereas, in the majority of plants investigated 'Normal-type' of development prevails. In the tribe Arineae, to which *T. trilobatum* belongs the development of the female gametophyte has so far been recorded in *Arum maculatum* and *Arisaema triphyllum* both of which show normal type of development. Maheshwari (1937) has noted that *Acorus calamus, Richardia africana* and *Zantedeschia aethiopica,* which have been recorded as belonging to the 'Adoxa-type' (Lilium type) by early workers, have on re-investigation been found to belong to the 'Normal-type'.

The chalazal macrospore does not always produce the embryosac. Schnarf (1931) states that in *Anthurium crystallinum* and *Spathiphyllum Patinii,* the micropylar megaspore produces the embryo-sac. But it should be noted that in most of the plants, as in *T. trilobatum* it is the chalazal megaspore that functions.

A remarkable feature one comes across in the literature on the embryology of the Araceae is the development of the basal apparatus. The nucleus of the basal chamber may remain undivided or it may divide without the formation of walls or give rise to a number of cells as a result of division. The nature of the basal apparatus in *T. trilobatum* has already been described and it needs only be pointed out in this connection that it agrees closely with Jacobson-Palay's (1920) findings in *Arum maculatum.* The 'chalazal cell' (basal apparatus in *T. trilobatum*) increases in size with the development of the seed and brings about a degeneration of the surrounding cells of the nucellus on account of its haustorial nature. But no haustorial processes radiate from this chamber as observed by Boodle and Hill (1929) in *Typhonodorum Lindleyanum.* It remains throughout as a hollow spherical chamber. Consequent on the increase in size of the basal chamber the postament like strand of tissue observed in the early stages disappears completely. In *Acorus calamus,* Buel (1938) notices the postament even in the later stages and it seems to be concerned with the nutrition of the embryo. From the nature of the postament observed in *Acorus calamus* and other plants one is inclined to believe that the strand like tissue observed at the base of the embryo-sac in *T. trilobatum* could not be strictly referred to as such.

Cytology.—A vast amount of literature has accumulated on the origin of the nucleolus and its relation to the chromosomes. Wager (1904) working on *Phaseolus* observed that the nucleolus was suspended in a nuclear net-work by numerous strands. It was Latter (1926) who first discovered the nucleolus to be connected to a loop of the spireme in the pollen mother cells of *Lathyrus.* Her observations have later been confirmed in other plants and it is now known that the 'nucleolar

bodies' of Latter with their attached chromosomes represent particular chromosomes responsible for organisation of the nucleolus at telophase. Working on *Galtonia*, Navashin (1912) observed the nucleolus to be attached to a pair of satellites. Sorokin (1924) also reported such chromosome-nucleolus relationship in *Ranunculus acris*. Heitz (1931) first showed that the nucleolus was produced either on the satellite stalk or on the secondary constriction of the chromosome. Resende (1937) working on *Aloe* confirmed Heitz's findings. McClintock (1934) found that in *Zea mays*, the nucleolus is organised around a deeply stained body on the chromosome at the base of the satellite stalk, which she called the nucleolar organising body, responsible for the organisation of nucleolus. Similar relationship has been observed in recent years by many workers. Gates (1937) has recently reviewed the relevant literature on the subject.

A critical study of chromosome-nucleolus relationship has not been made in the present investigation, but the evidences obtained during the course of study show that the four satellited and two secondary constricted chromosomes play an important rôle in the organisation of the nucleolus, as during mitosis these chromosomes have alone been seen to be attached to the nucleolus. The organisation of six nucleoli in the telophase nucleus leads one to infer that these nucleoli have been organised independently by these satellited and secondary constricted chromosomes. During meiosis also, the number of bivalents seen attached to the nucleolus at diakinesis was three, and the number of nucleoli organised at telophase of I division in each nucleus was again three. It is now generally agreed that the Sat-chromosomes and the secondary constricted chromosomes each organise a nucleolus and the number of independent nucleoli found in a nucleus corresponds with the number of such chromosomes. Thus Bhaduri (1940) found the constant presence of four nucleoli to correspond to the four secondary constricted chromosomes in species of *Oenothera*.

Chromatid bridges in the anaphase of I division has been observed in very few anthers (less than 5 per cent.). Such bridges disjoin with difficulty; fragments are seen which indicate that they are formed by the breakdown of the bridges. The presence of such dicentric chromatid bridges with acentric fragment may be expected on the basis of crossing over within an inversion. Richardson (1936) and others have discussed the processes which lead to the formation of bridges and it is not proposed to discuss it here. Upcott (1937) has correlated bridge formation with sterility in *Tulipa*. According to her, more than 10 per cent inversion bridges lead to considerable sterility. The very low percentage of bridges and the absence of sterile pollen indicate that such aberration in meiosis is not of any significance in *T. trilobatum*.

Kuwada (1910) was the first to notice the association of bivalents at metaphase I in *Oryza sativa*. Ishikawa (1911) also noticed such association of chromosomes at metaphase II of *Dahlia variabilis*. Since then the phenomenon has been observed by several investigators, but its real significance was not clearly understood until Lawrence (1931) pointed out that it is an expression of ancestral homology between the associated bivalents. Secondary association according to Lawrence is an indication of allopolyploidy. The association is best seen at prometaphase and it remains so until interkinesis when a repulsion force develops and keeps the chromosomes away from one another. It is apparent again at metaphase II. Secondary association of chromosomes has been observed in a large number of plants and it has led to the determination of the primary basic number in certain genera. Lawrence (1929) by a study of secondary association has shown that though the lowest haploid number of chromosomes of the Dahlias is 16, it must have been evolved from a species with 8 haploid chromosomes which has now become extinct. Nandi (1936) also found evidence to show that $n = 12$ number in *Oryza sativa* has been derived from the basic number five. Similarly in *Solanum tuberosum* ($2n = 24$), Muntzing (1938) found the basic number to be six.

From Table I it will be seen that excepting two cases out of seventy-four, the bivalent chromosomes during 1st metaphase of the P.M.C. as a rule showed different degrees of secondary association. Only in two cases, nine free bivalents were observed. It will be further noticed that the maximum secondary association for the present material is 1(4)+1(3)+1(2) and the basic number accordingly should be 3. Assuming the theory of secondary association to be correct, the present observation leads to the conclusion that *T. trilobatum* is a secondary polyploid and the haploid number, $n = 9$, is derived from the original basic number 3. Such a low number has, however, not been reported in any other species of *Typhonium* or in any other related genera. In *Arum* and *Theriophonum* the haploid number has been found to be $n = 8$. A thorough survey of the chromosome numbers in other related genera might show lower number than 8. The meiotic behaviour of the present species indicates the presence of a perfectly balanced chromosome set. The pairing between the homologous chromosomes is complete and the disjunction of the chromosomes is quite regular and normal. *T. trilobatum* should, therefore, be considered as a balanced secondary polyploid. Although evidence of secondary polyploidy could not be gathered from the chromosome numbers of related genera, the study of the SAT-chromosomes and the nucleoli in the present material confirms the above view. According to the present conception regarding the phylogenetic significance of the number of nucleoli present in the gametic cells of plants, a true diploid should have only a pair of identical and homologous nucleoli in the body cells corresponding to a pair of homologous and homomorphic SAT-chromosomes present in the somatic complement. Increase in the number of nucleoli is brought about by polyploidy, duplication of some chromosomes or through non-homologous segmental interchange. The presence of three distinct pairs of nucleoli of two different sizes corresponding to two pairs of SAT-chromosomes and another pair of chromosomes with a secondary constriction in each nucleus, shows that *T. trilobatum* is a secondarily balanced polyploid and not a true diploid. It is also not a structural hybrid except to a certain amount of inversion heterozygosity present in the P.M.C. Further, the complete absence of multivalent formations, absence of any chromosome present in triplicate, and two different sizes of nucleoli rule out the possibility of its being an auto-polyploid species.

Summary.

The paper gives an account of the morphology, anatomy, embryology and cytology of *Typhonium trilobatum*—a common aroid of Bengal.

1. The stem is a sub-globose corm of many internodes; axillary buds occur on the surface, these develop into separate plants next season, when the mother corm shrivels and disintegrates.
2. Adventitious roots occur in two or more whorls on the crown of the corm. The roots are contractile and are spread out almost horizontally in the soil.
3. The leaves occur at the top of the corm and enclose completely the growing point which is a dome shaped structure. The lamina is characteristically hastate in form and somewhat trisect. The petiole is long and leaf base encircles the stem at its point of insertion. During developmental stages the younger leaf and inflorescence are completely encased inside the petiole of the subtending leaf.
4. The mode of distribution of the veins of the leaf has been described. Free nerve endings are seen, which appear to be branched.
5. The phyllotaxis is pentastichous and the nature of ptyxis, which has been described in detail, is of a special type.
6. The spathe is constricted in the lower region and forms a barrel shaped chamber inside which the neuter and the female flowers are lodged. The spadix has an appendage. The male flower is reduced to a stamen, the neuter flower to a filiform process and the female flower to a pistil.
7. The flowers are entomophylous. The mode of pollination has been described in detail.
8. The fruit is an ovoid one-seeded berry. Seeds are ovate, greyish black and slightly constricted at the middle from which projects the partially shrivelled basal region.
9. The germination of the seed has been studied. Its mode being the same as observed in other plants of the tribe. The plant is propagated both sexually and vegetatively.

10. The corm consists of a mass of starch filled parenchymatous cells with the vascular bundles disposed more or less in the form of a ring. The corm grows by the multiplication and enlargement of the ground parenchymatous cells.

11. Periderm formation is noted at an early stage of the development of the corm. The periderm does not form a continuous cylinder but occurs in isolated patches. The phellogen is hypodermal in origin.

12. Internally the petiole shows the presence of hypodermal bands of collenchymatous cells placed at regular intervals. Chlorenchymatous cells occur in between these bands. Ground tissue is composed of isodiametrical parenchymatous cells with intercellular spaces.

13. The vascular bundles of the petiole are closed and collateral. They show a scattered arrangement. Xylem consists mainly of annular and spiral vessels: reticulated or pitted vessels are absent.

14. The leaves show the typical dorsiventral structure. Collenchymatous bands are present at the ribs. Stomata occur on both suraces.

15. The inner surface of the spathe is covered by papillose protrusions. The rest of the tissue (excepting the dorsal epidermis) is parenchymatous. Vascular bundles are accompanied by collenchymatous bands which occur hypodermally on the abaxial side of the spathe.

16. The root shows the normal anatomical features. The central region is occupied by one or more large vessels, which differentiate first and show annular thickening. In contractile roots the outer cortical region is alone affected. At the point of constriction the cells get compressed laterally and present a lamellated appearance.

17. The distribution of crystals of calcium oxalate in the different parts of the plant body has been recorded. The rôle of nucleus in the development of the crystals has been studied.

18. The development of the male and female flowers as also of the ovules has been studied. The ovules are orthotropous and bitegmic. A nucellar cap is present.

19. A single hypodermal archesporial cell differentiates as the megaspore mother cell. This produces a linear tetrad of megaspores. The chalazal megaspore functions and produces an eight nucleate embryo-sac. The antipodals are larger than the synergids and are triangular in shape.

20. The endosperm nucleus on division produces two chambers. The nucleus of the upper chamber produces the entire endosperm tissue, while the lower remains undivided and goes down to the lower part of the embryo-sac and functions as a haustorium.

21. The earlier stages in the development of the embryo have been studied. The embryo shows the usual monocotyledonous features and has a one-celled suspensor.

22. The diploid number of chromosomes is 18. The complement is made up of 6 long, 6 medium and 6 short chromosomes. There are two secondary constricted and four Sat-chromosomes.

23. The telophase nucleus of the somatic cells shows six nucleoli. The phragmoplast appears to play an important rôle in the formation and growth of the cell plate in mitosis.

24. During meiosis secondary association of chromosomes has been noted. The basic number based on maximum association has been found to be three.

25. Chromatid bridges and fragments have been found during the anaphase of division I. Chromosome-nucleolus attachment has been observed at different stages of meiosis and mitosis.

26. Pollen formation is of the successive type and the pollen grains are binucleate at the time of shedding. The pollen grains have a granulated exine.

27. The formation and development of the periplasmodium has been followed and the behaviour of the nuclei of the plasmodium recorded. Some of the nuclei have been observed to fuse.

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