CONTRIBUTION TO THE MORPHOLOGY AND CYTOLOGY OF *ALPINIA CALCARATA* ROSC., WITH SPECIAL REFERENCE TO THE THEORY OF ZINGIBEROUS FLOWERING

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1. *Introduction*

THE most exhaustive work of recent times on the Scitamineæ is that of Mauritzon (1936). It deals with the structure of the ovule, in some cases its development, and the embryology of representative genera of the four families comprising the Scitamineæ. In the course of this work, a brief reference is also made to the genus *Alpinia* under the Zingiberaceæ. Comparatively little is known of this family both as regards the chromosome numbers of the important genera and developmental morphology. Gregory (1936) recorded the chromosome numbers of *Elettaria cardamomum* ($2n = 48$), *Costus malarotiensis* ($2n = 18$), *Hedychium Elwesi* ($2n = 66$). He also worked out the floral anatomy in some detail especially for the elucidation of the morphology of the labellum in *Elettaria cardamomum*. While this paper was being prepared for the press, we have seen a paper on the life-history of *Costus speciosus* by Banerjee (1940) in which a short account is given of the work on the Zingiberaceæ done so far. Humphrey (1896) was one of the earliest to pay attention to the Scitamineæ. He described the development of the seed in a number of genera and incidentally described a few disconnected details regarding the organization of the embryo-sac. Some of these details have been controversial and a few have had to be revised; for instance, in the genus *Costus*, he had suggested '*Adoxa*-type' of embryo-sac development. This however was found to be incorrect by Banerjee and Venkateswarlu (1935). They found a normal type of embryo-sac formation.

From no point of view is the Zingiberaceæ more interesting than from that of the morphology of the flower. One of the most recent workers in this field is Thompson (1933). He has subjected to a critical ontogenetic study a large number of representative genera and has come to conclusions, a brief mention of which will be made further down in this paper.

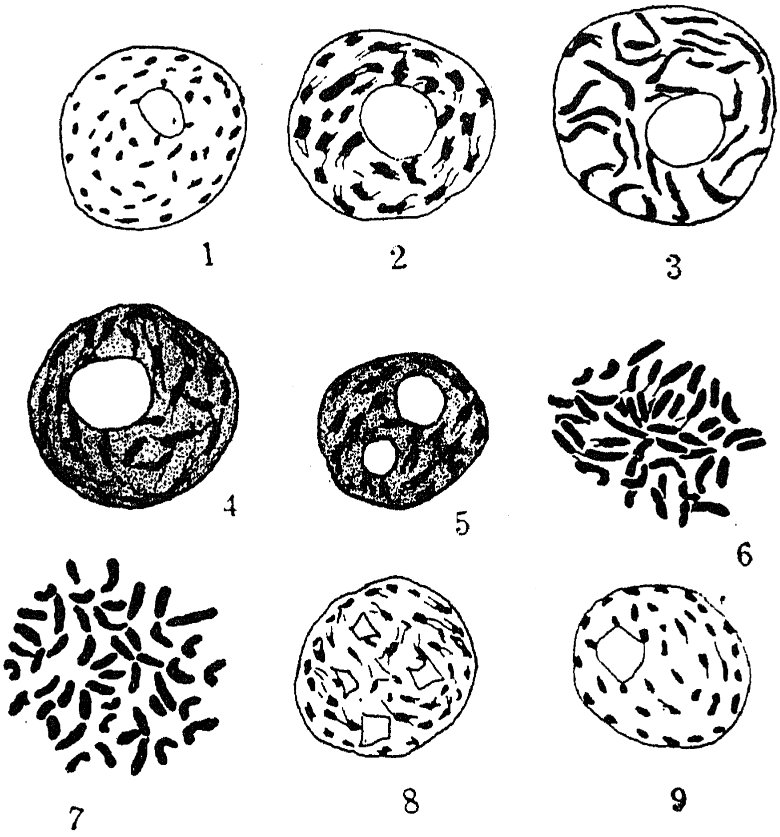
In the present paper the somatic chromosome number of *Alpinia calcarata* Rosc. has been recorded for the first time. Some cytological details as well as details of the embryo-sac development are also given. Effort has also been made to study the ontogeny of the flower and of the floral group in order to throw some light upon the morphology of the much-discussed labellum.

Alpinia calcarata is extensively grown in gardens for its showy flowers and aromatic leaves. It is a perennial herb which flowers in these parts in the months of February and March. No fruits are formed; and the reason for this will be found in the body of the paper.

The technique adopted does not call for any special mention. For the cytological work, root tips were fixed in Navashin's fluid after pre-fixation in Carnoy. Chloroform was used as the paraffin solvent. Newton's Iodine Genation violet was used for staining. Ovaries and young flower buds were fixed in F. A. A. and stained in Delafield's and Haidenhain's Iron-alum hæmatoxylin.

II. The Ovule and the Embryo-sac

The ovary is tri-carpellary with axile placentation. The ovlue at a very early stage develops the inner integument, and almost simultaneously with this, a sub-epidermal archesporial cell is differentiated (Text-Fig. 10). This cell cuts off a primary parietal cell (Text-Fig. 11), which undergoes usually an anticlinal division (Pl. XVII, Fig. 8). Usually it does not undergo any periclinal division, so that there is only one layer of wall cells between the nucellar epidermis and the embryo-sac. In *Costus* Mauritzon (1936) found that the primary parietal cell did not undergo any further division and it became radially stretched capping the embryo-sac (*cf.* Fig. 11 of Mauritzon).



TEXT-FIGS. 1–9. (× Ca 5400)

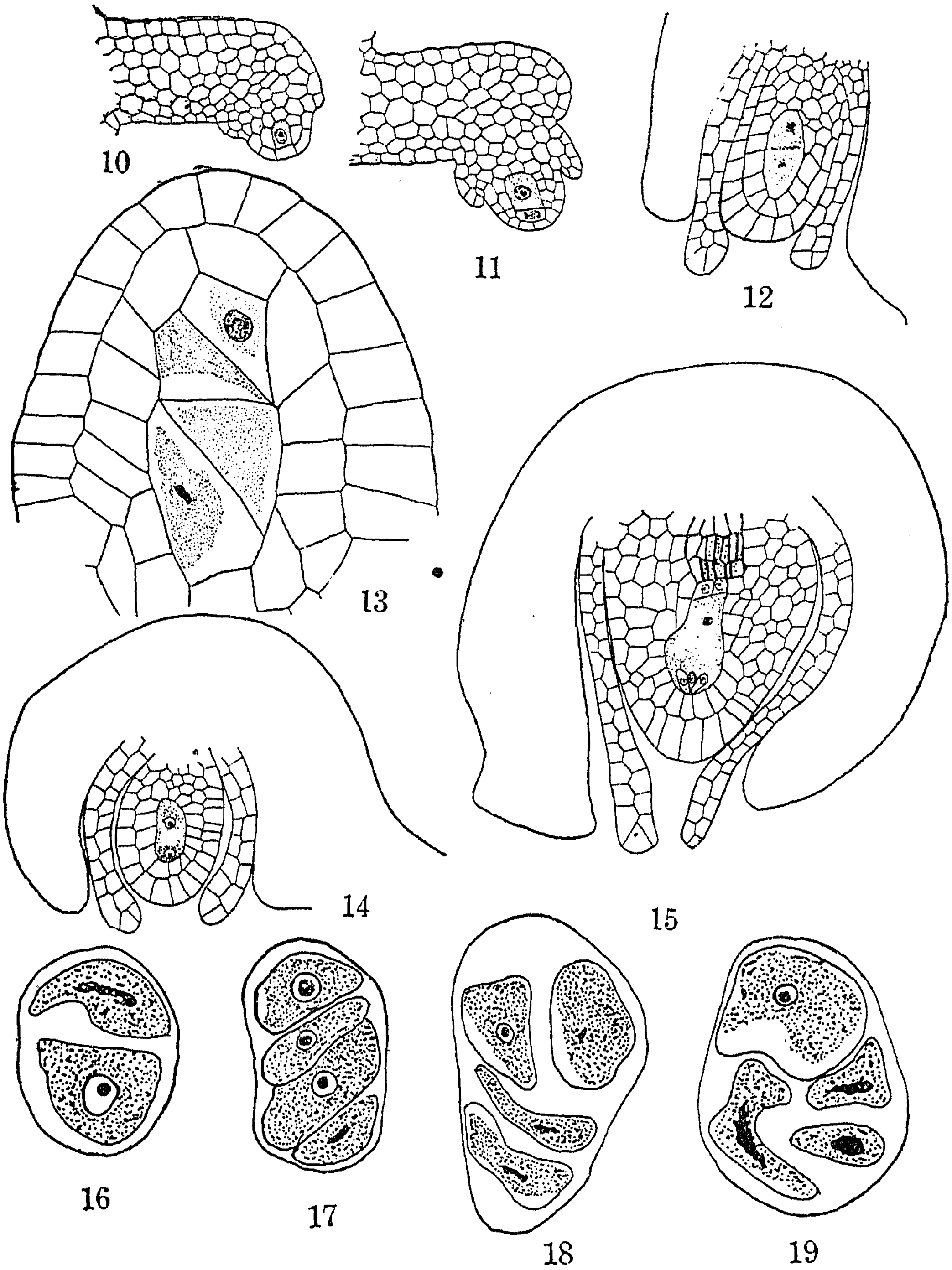
FIG. 1. 48 prochromosomes are seen distributed peripherally ; note 4 prochromosomes attached to the nucleolus. FIGS. 2–5. Prophase stages ; note the presence of the threads forming a sort of a reticulum. FIG. 6. Prometaphase. Note that the distal ends of a few chromosomes thread-like structures emanate. FIG. 7. Somatic Metaphase, $2n = 48$. FIGS. 8–9. Early and late telophases.

The inner integument is the first to be initiated and its development follows the usual lines. It remains two-layered throughout. It protrudes beyond the outer integument forming a beak-like structure (Text-Fig. 15) and frequently shows a tendency to fuse. Humphrey (1896) in describing the post-fertilization ovule of *Costus* says that " Just after fertilization the fore-end of the outer integument and the free portion of the funiculus begin to fuse and close the micropylar opening finally obliterating the inner integument ". This mass formed by the coalescence, he termed the ' arillode '. Though in this species no seed is set and as such post-fertilization stages could not be followed, the early tendency of the inner integumental halves to fuse is suggestive of the general tendency of the family towards the formation of that large and fleshy aril which caps the micropylar end of each seed.

The megaspore-mother cell undergoes the usual divisions to form the linear tetrad (Figs. 11–13). Even at this stage degenerations in the gametophyte begin. Text-Fig. 13 shows a linear tetrad that is undergoing degeneration. Text-Fig. 12 shows a dyad in metaphase. In some cases the chalazal megaspore enlarges and develops into an embryo-sac. There can thus be no question of the formation of the '*Adoxa*-type' of embryo-sac, so far as this genus is concerned. The further development is normal but extensive degeneration is met with. Fig. 14 shows a binucleate embryo-sac. The mature embryo-sac is not oval in configuration, but has a narrow antipodal region suggestive of a haustorium (Pl. XVII, Fig. 10). Colour is lent to this by the occurrence of thick-walled cells radially elongated, just around this haustorial structure. Text-Fig. 15 shows a mature embryo-sac. No further development of the embryo-sac takes place beyond the 8-nucleate stage.

III. Pollen Formation

Normally only one anther in a flower develops, but in a few cases two fertile stamens were found. Earlier stages in the micro-sporangial development are of the normal type and hence are not described in any detail. There are about 6–8 layers of parietal cells of which the innermost one is the tapetum. The tapetum is of the intrusive type such as has been described for *Elatteria* (Gregory, 1936) (Pl. XVII, Fig. 11). The tapetal cells are bi-nucleate and they do not become pluri-nucleate. By the time the tetrads are organized, the tapetal cells get completely disorganized and only traces of them could be made out. The formation of the pollen tetrads calls for some remarks. In most monocotyledons, the tetrads are arranged iso-bilaterally. Banerjee (1940) has figured such an arrangement for *Costus.* In *Alpinia calcarata,* however, such an arrangement is met with almost as an exception. Text-Fig. 16 shows a pollen dyad in which wall formation has taken place after the first division as is the case in most monocotyledons. Text-Fig. 19 shows a pollen tetrad arranged on an iso-bilateral plan. But very often the pollen tetrads are arranged in a linear fashion (Text-Fig. 17), resembling the linear tetrads of the megaspores. Frequently T-shaped configuration is also met with (Text-Fig. 18). Similar arrangements—linear tetrad, and T-shaped tetrads have also been met with in *Alœ sisilana* (Vignoli, 1937). Most of these microspore tetrads exhibit irregular outlines with their nuclei very much elongated and in a state of degeneration (Text-Fig. 19). Though normal pollen grains are formed in several cases, it is our impression that in a good many anthers, the tetrads in each locule undergo degeneration *en masse.* The non-seed-setting of the species is, therefore, to be explained both by the failure of the development of the embryo-sac, and also by pollen degenerations.



TEXT-FIGS. 10–19. (× Ca 380, except Fig. 13 which is × 900)

FIGS. 10–15. Development of the embryo-sac. FIG. 11. Same as Plate XVII, Fig. 8. FIG. 12. Same as Plate XVII, Fig. 9. FIG. 13. Linear tetrad degenerating. FIG. 14. 2-Nucleate embryo-sac. FIG. 15. Mature embryo-sac with attenuated antipodal end. Only two antipodal cells are seen. Note also the presence of thickened cells around this end. FIGS. 16–19. Pollen formation. FIG. 16. Pollen dyad. FIG. 17. Linear tetrad of microspores. FIG. 18. T-shaped tetrad of microspores. FIG. 19. Iso-bilateral arrangement 3 of the microspores degenerating.

IV. Prochromosomes

The diploid chromosome number is 48 (Text-Fig. 7). From an examination of root-tip mitosis, it is found that this species of *Alpinia* exhibits prochromosomes. The question of prochromosomes has been discussed somewhat thoroughly in a previous paper (Raghavan, 1938). It was shown in that paper that the prochromosome, also called the chromocentre by some authors, represents a part of the chromosome namely, that portion on either side of the spindle fibre attachment. The most important proof of this is the fact of the identity in number between the prochromosomes and that of the chromosomes. Since the prochromosomes are distributed peripherally over the spherical nucleus, the determination of the exact number is rendered more difficult than that of the chromosomes at metaphase, where they form a flat plate-like configuration. All the same about forty-eight bodies could be made out in Fig. 1 showing early prophase. Text-Figs. 1–9 show a number of stages in the mitotic cycle. In Text-Fig. 1 we see about 48 darkly staining oval bodies peripherally distributed around a central rounded nucleolus. Very often, we find four of these bodies attached to the nucleolus. Sometimes, there are two nucleoli, frequently differing in size, to each of which two prochromosomes are attached (Text-Fig. 5). Doutreligne (1933) raised a very important question regarding the structure of the nuclei exhibiting prochromosomes. She held that there was no reticulum such as appears in the nuclei which do not show prochromosomes. This is intimately connected with the occurrence or otherwise of chromonemata in plants with prochromosomes. Though no detailed study such as has been made on *Polanisia* (Raghavan, 1938) has been possible in the present case, the few stages that have been represented will reveal beyond doubt that a reticulum is present and that the chromosome cycle at least so far as somatic division is concerned, is essentially similar to that of plants with large chromosomes. In other words, the chromosome structure (chromonematic) as well as the chromosome cycle in plants with prochromosomes are fundamentally the same as in plants without them.

The commencement of prophase is indicated by these bodies becoming more chromatic and slightly bigger and since in this plant almost all the chromosomes are characterised by a terminal centromere, no prominent traces exist of attachment constrictions in these bodies (Text-Fig. 2). Here and there however there are a few sub-median constrictions. At a later stage, these bodies become somewhat irregular and angular and they are now more chromatic than before, and are seen to be connected by a delicate thread-system (Text-Fig. 4). The angularities are soon lost and in well differentiated preparations, it could be seen that threads emerge from the distal ends of these angular bodies (Text-Fig. 5). It can then be seen that this structure results from the intertwining of two chromonemata with the spindle fibre attachment at the proximal end. In fact, it is something like a highly condensed prophase chromosome. No satellites were visible. As prophase advances, there is a stretching of these bodies (Text-Fig. 3). Of the chromonematic make-up of these bodies, there can now be no doubt. With the passage into prometaphase, there is a further increase in the chromaticity and thin strands are occasionally present connecting one chromosome with another (Text-Fig. 6). Metaphase is characterised by still further contraction (Text-Fig. 7). Text-Fig. 8 shows telophase when the organisation of four irregular nucleoli can be recognised. These bodies have by now attained the angular shapes and fine strands are seen emanating from their ends to form a sort of a network. Very often, these nucleoli fuse together forming an irregular mass. As telophase advances, these strands disappear (Text-Fig. 9). The chromaticity of the prochromosomes is also diminished. Their angularities are lost and with the assumption of a peripheral disposition of these bodies, the passage from late telophase into the resting condition may be regarded as complete. It would thus appear that starting from anaphase, where we find the chromosomes of normal length, they assume a shortened appearance as telophase advances. This is correlated with an apparent increase in the amount of chromatin in the regions immediately adjacent to the spindle fibre constrictions. This has taken place at the expense of the other regions of the chromosomes, which consequently have almost lost their chromaticity. But fibres extending from the ends of these shortened chromosomes are visible. This portion that persists through the telophase is the prochromosome.

V. The Inflorescence

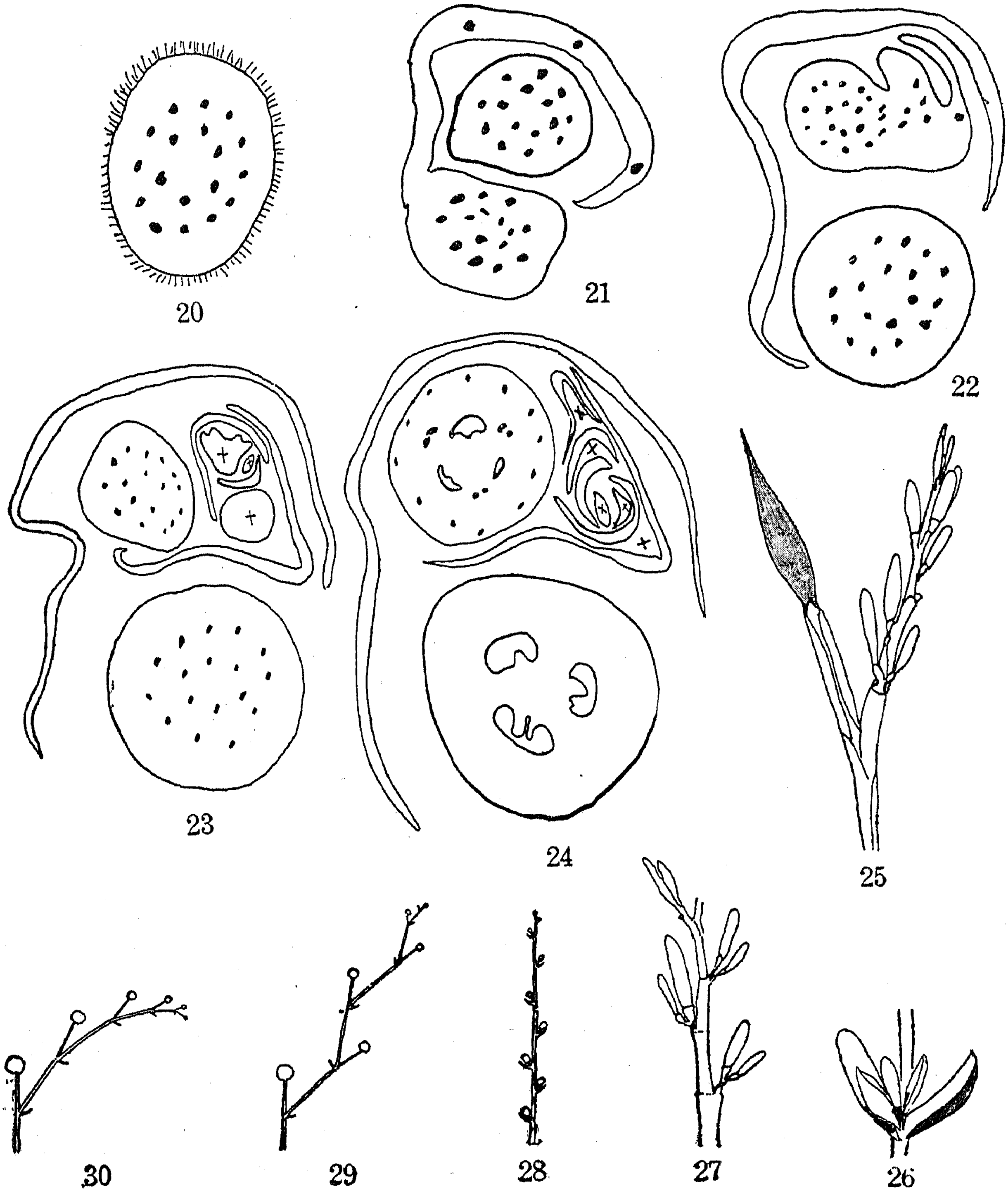
There is some amount of ambiguity in the usual description of the inflorescence of the Zingiberaceæ. An unbranched inflorescence with twin flowers in the axil of each bract, Payer (1857) described as a succession of unipaired scorpiod cymes on a common rachis. Eichler (1875) also maintained that the inflorescence was not so simple but was complicated by fertility of the floral bract. By such fertility between a flower and its bract a cymose system is initiated with sub-floral branching. Thus a cymose system is countenanced in the axil of a spathe. The view that is most commonly held is that of Weisse (1932) according to whom the several flowers in the axil of a single bract, were members of a cincinnate development. Elaborating this Rendle (1904) says that " branching may occur and a monochasial cyme (a cincinnus) is developed in each bract axil ".

Thompson (1933) after an elaborate ontogenetic study of several genera found no indication of sub-floral branching such as cymosity demands, and considered it racemose. The suggestion of cymose branching characteristic of maturity is, according to him, entirely due to later tortuous growth of the support. Thus he thinks, several species of *Alpinia* are characterised by monopodially branched inflorescence. The lateral branches are commonly monopodial systems and each major axis of the inflorescence is arrested immediately following the formation of a twin-flowered cone.

In this species on the floral axis are groups of two flowers at different intervals in conformity with the distichous phyllotaxy (Text-Fig. 27). Text-Fig. 25 is that of a floral axis younger in age. This axis is monopodial in growth. Though only two flowers mature at each node, of which the upper is always at a more advanced state of development than the lower, an ontogenetic study of the floral group shows, that usually four to seven floral primordia are initiated. Text-Figs. 20–24 are serial transverse sections of inflorescence axis taken at successively higher levels. Each cluster of flowers is enveloped by a bract and successive sections show that each flower or floral primordium is subtended by a bract. This is accomplished in the following manner. The oldest flower is subtended by a bract which embraces not only the flower in question but envelopes the entire floral group (Text-Figs. 22–24). Similarly the next bract envelops all the flowers of the group except the oldest, which comes to be just outside this bract. In a like manner the bract of flower No. 3 envelops all the flowers except flowers 1 and 2 which consequently come to lie outside this. Text-Fig. 26 is that of a floral group at a node, of which only two mature as shown in Text-Fig. 27. Each group unopened, appears single as in Text-Fig. 25.

Of the 4 to 7 floral primordia initiated the basal one is the earliest to be formed and develops into a flower. The whole floral cluster at each nodal portion presents a zig-zag appearance. In a normal monochasial cyme of the scorpiod type, suppression of the lateral flowers is effected on alternate planes (Text-Fig. 29), so that on a straightened axis, an appearance is presented of a spikate inflorescence with the flowers arranged alternately along the axis. This axis, however, is not to be regarded as the peduncle such as is found in the case of a real spike, but is composed of successive pedicels of the individual flowers. In a monochasial cyme of the helicoid type (Text-Fig. 30) such a straightening would result in the flowers occurring more or less along one plane of the axis. The axis in the previous case is compound being a sympodium.

If we imagine both these types of monochasial cyme undergoing an extreme form of compression, then the flowers which were distributed along an elongated axis become flattened out; and the position of the flowers is dependent upon whether it is a helicoid or a scorpiod cyme. If it is of the former type, all the flowers of a group will be arranged in a circular manner beginning with the oldest at the base. If a straightened cyme of the scorpiod



TEXT-FIGS. 20–30

Alpinia calcarata

FIGS. 20–24. Serial T.S. of the infloresence axis. The × marking in the Figs. 23 and 24 epresent the primordia of flowers which abort. × Ca 50. Fig. 25. Inflorescence at an early stage. IG. 26. One of the floral groups spread out. FIG. 27. Inflorescence axis at a slightly later stage ith only two flowers at each node. FIGS. 28–30. Diagrammatic represenatation respectively of pike, scorpioid cyme and helicoid cyme.

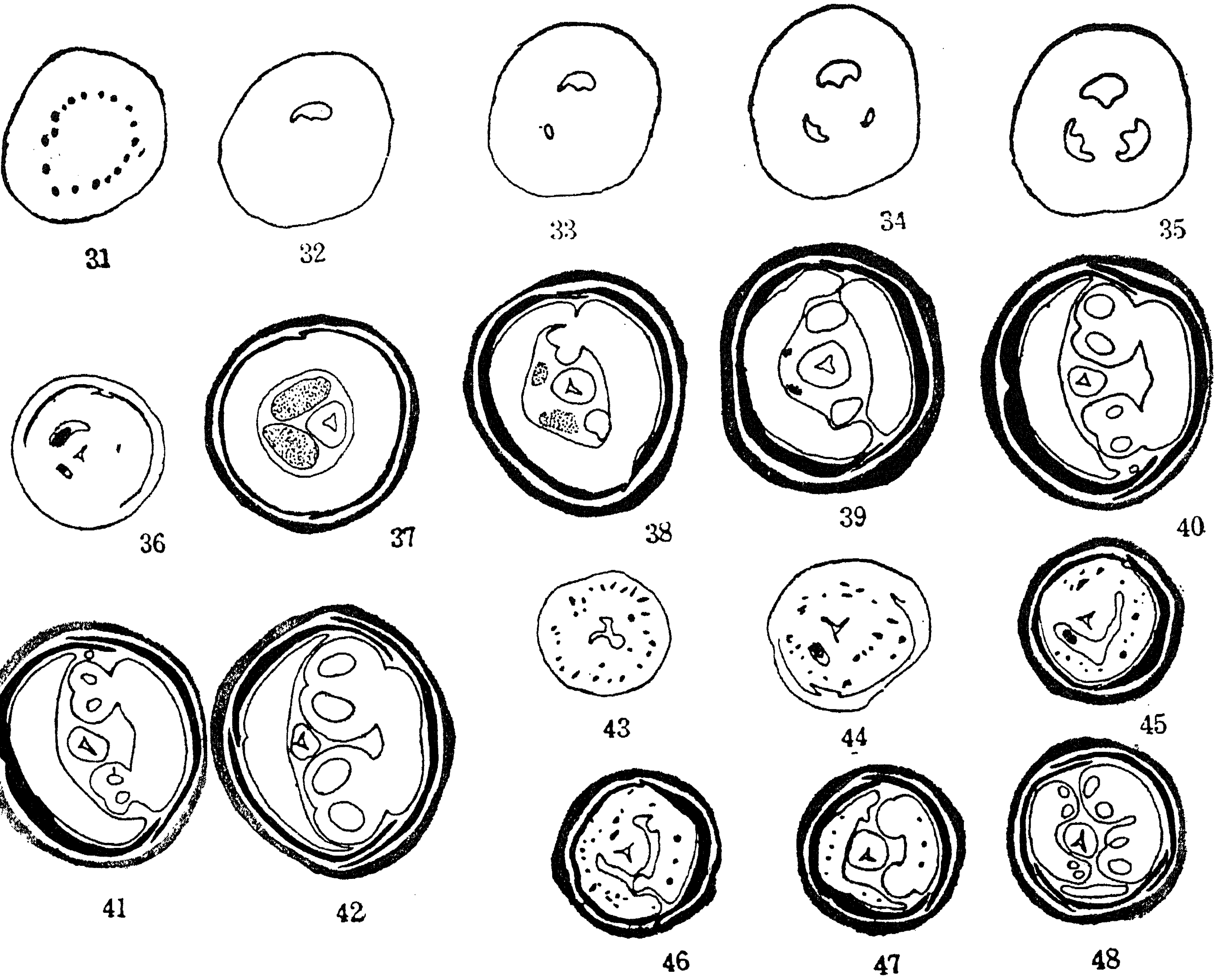
yme undergoes this compression, then we find that the flowers in the flattend inflorescence are arranged in a zig-zag manner. It is such a zig-zag arrangenent that we find in regard to the flowers of each floral group in this species.

of *Alpinia* and there can be no doubt as to their cincinnate arrangement. Support to this is also be gained by the disposition of the bracts which in conformity with the cincinnate arrangement are opposite to one another at successive higher levels.

The question whether it could be a compressed type of racemose inflorescence, such as is contemplated by Thompson (1933) may now be considered. The nearest approach is the spike (Text-Fig. 28) not only because of its apparent resemblance but also of the prevalence of this spikate inflorescence in related families of the Scitamineæ. If an elongated spike, the individual flowers of which are subtended each by a bract, undergoes such a compression as we have assumed in the previous cases, a flat inflorescence resembling the capitulum must be the result. The younger flowers will be in the centre, the successively older flowers towards the periphery. Such an arrangement is not to be found in the present case. Moreover in such a case, the bracts, in keeping with the general arrangement of the flower, will also be circularly disposed. Such however is not the case. The zig-zag arrangement of the flowers with the oldest at the base, instead of the circular arrangement, and the opposite disposition of the bracts indicate that each flower cluster is in reality a scorpioid cyme, highly condensed and flattened out. Of the 5 or 6 flowers in each group, only two usually develop, the rest aborting. That is why in a slightly older condition, we find twin flowers occurring at each nodal region of the inflorescence axis.

VI. Floral Ontogeny

Serial transverse sections were taken of the flower buds at different stages of development, in order to have an idea of the method of origin and differentiation of the parts composing the flower. Text-Figs. 31–42 show an ascending series of transverse sections, *i.e.*, transverse sections taken serially at successively higher levels, commencing from the top of the ovary. Text-Figs. 31–42 are those of a normal flower, while Text-Figs. 43–48 represent those of a flower with two fertile stamens, instead of the usual one. Of this latter type, there were cases more or less of frequent occurrence, and not stray and rare. Text-Fig. 31 is the stalk of the flower showing a number of vascular strands distributed peripherally. Text-Figs. 32–35 represent the ovarian cavities appearing not simultaneously, but in a spiral sequence. Their disappearance also follows the same procedure. This spiral arrangement of the carpels has already been interpreted to be of significance in the matter of the foliar nature of the carpels (Raghavan, 1939). As in the case of *Cratæva* reported in a previous paper (Raghavan and Venkatasubban, 1940) the other floral " whorls " also exhibit a spiral sequence in their origin



TEXT-FIGS. 31–48

FIGS. 31–42. Serial T.S. of a normal flower. Note the appearance of the ovarian cavities spirally in Figs. 32–35. The shaded bodies of Figs. 36–39 are the 'glands' which appear and disappear. × Ca 50. FIG. 37. Same as Plate XVII, Fig. 1. FIG. 38. Same as Plate XVII, Fig. 2. FIGS. 43–48. T.S. of two-stamened flower. Note the presence of only one 'gland' (shaded structure). × Ca 35.

and differentiation. And the carpels composing the gynæcium, only conform to this general rule, adhered to by the other floral members. Text-Fig. 36 shows the top of the ovary and from now upward, the differentiation of the other floral members is to be seen. Sepals are differentiated constituting a single tubular structure, surrounding or enclosing all the other floral parts except the ovary, which being inferior is below it. The posterior petal is the outermost (Text-Fig. 37) and no deviation from this was ever seen. The labellum (Text-Figs. 38–39) next gradually differentiates itself. It is especially with regard to this that the flower-buds of different stages of development were examined. Even the earliest possible stage did not reveal the superposed dual or double nature of this organ. No staminodes were present. The two lateral rounded structures in Text-Fig. 41 and Pl. XVII, Fig. 3, may at first be interpreted as staminodes, but these are only the inrolled marginal tips of the labellum. The posterior fertile stamen likewise makes its appearance. About the same time two structures are differentiated, also in a spiral order in an antero-lateral plane (Text-Figs. 36–39 and Pl. XVII, Figs. 1–2). Particular care was taken to ensure that these, unlike the staminode-like structures referred to previously, were not portions of other organs. These whose nature will be discussed elsewhere, are tentatively called the glands. They are quite independent of the other floral organs. Their appearance and disappearance as seen in serial sections are shown in Text-Figs. 36–40. These two antero-lateral glands together with the posterior fertile stamen would appear to form a natural whorl.

The plan of construction of the flower with two fertile stamens is essentially the same. The other floral whorls are differentiated in the usual manner. But along with the usual fertile stamen formed posteriorly, there is another differentiated in a position which may be described as antero-lateral (Text-Figs. 43–48 and Pl. XVII, Figs. 4–7). This anther however is not so well formed as the usual posterior one. By its side, there appears and disappears a small structure. Two things are worthy of note: Firstly that in this type of flower, the two prominent glands usually present as a rule in the normal flower, are conspicuous by their absence; but instead only one structure, smaller than the usual gland, appears alongside of the second fertile stamen. Secondly, the labellum in this type of flower (Pl. Fig. 7 and Text-Fig. 48) is much smaller than in the normal flower. The interpretation and the significance thereof will be discussed elsewhere.

VII. The Labellum: A Discussion of its Morphology

The morphology of the labellum in the Zingiberaceæ has been the subject of much discussion. The generally accepted view is that of Payer (1857) and Van Tiegham (1868). This is based on the trimerous plan of floral construction. They regard the labellum as a part of the inner staminal whorl, forming the two antero-laterals. The posterior one of the same whorl forms the single fertile stamen. The outer staminal whorl is composed of the postero-lateral staminodes while the anterior member of this inner staminal whorl is suppressed. The other view is that of Brown (1830). It regards the labellum as a member of the outer staminal whorl with the two staminodes. The inner whorl is said to be made up of the fertile posterior stamen and the two antero-lateral glands which are present very commonly among the Zingiberaceæ.

The first view supposes the labellum to be really dual in nature, so that the inner whorl is made up of the three members, *i.e.*, the labellum (2 members) and the posterior fertile stamen. It may also be noted that the glands upon which Brown's theory is built is ignored altogether. If the dual nature of the labellum is conceded, then a serious difficulty will beset Brown's concept and that is, the inner whorl will then consist of four members—the two staminodes and the labellum (2 Nos.) and this will seriously affect the trimerous plan of floral construction. Moreover the plan of alternating position of successive floral whorls would require the members of the outer staminal whorl to be opposite to those of the sepal whorl and not to those of the petals as it would be the case, if we were to accept the double nature of the labellum. This difficulty was solved by Brown by considering the labellum as a unitary structure and not composed of two members of the inner whorl.

In addition to these two views, there has been put forward recently yet another theory (Gregory, 1936) which in essence may be regarded as a modification of Payer's concept. This view regards the labellum neither as a single nor as a dual structure, but as an organ composed of three members, the structure corresponding to the midrib portion being considered as the third member. This together with the two staminodes forms the outer staminal whorl, the fertile stamen and the antero-lateral members of the labellum forming the inner whorl. The main virtue of this theory is that all the members of the two staminal whorls are accounted for and there is no need to regard any organs as being suppressed. The presence of the glands is noticed, but no importance is attached to them.

The edifice upon which this concept is based is mainly anatomical. At the region, according to the author, where the bundles of all the members are seen, there are three groups of vascular strands for each floral whorl. The outermost sepal whorl has more bundles, the alternating petal whorl has also a series of nine bundles in three groups. Alternating with these and opposite to the sepal whorl are three groups of (two each) bundles for the two staminodes and the central portion of the labellum, regarded by the author as the third member thereof. Alternating with these is another group of three (also two bundles in each group) supplying the inner staminal whorl; *i.e.*, the posterior fertile stamen and the two antero-lateral members of the labellum. It is also said that the origin of the bundles to these two staminal whorls is different. At the pedicel region, there are twelve vascular strands, three forming a central group and nine forming the peripheral bundles, the latter form the sepal strands. The central group divides further contributing to the petals, and to the inner staminal whorl. In a similar manner the outer staminal whorl is supplied by a continuation of the peripheral sepal groups. In other words, the bundle groups opposite to the sepals (those supplying the inner staminal whorl, made up of the two staminodes and the " midrib " of the labellum) are a continuation of the peripheral groups on the same radii while those opposite the petals, *i.e.*, the inner staminal whorl (the fertile stamen and the antero-lateral members of the labellum), originate from the central group. Thus all the six members of the two staminal whorls are accounted for and the plan of construction of the flower is not in any way affected. Not only do the floral whorls alternate with one another but their respective vascular supplies also exhibit this alternating arrangement so far as their origin is concerned.

In the present study anatomical evidence is not made use of for the elucidation of the morphology of the labellum. Only such ontogenetic evidence as will be useful in the discussion is let in, and the wide prevalence of what may be regarded as abnormal flowers, has been taken advantage of in venturing to offer an interpretation.

The first question is, what evidence have we for regarding the labellum as being composed of two members? Apart from the anatomical evidence that may or may not be accepted, the only other reliable evidence is that of ontogeny. We have examined sections of very young flower buds and we have not found any sign on the basis of ontogeny for the dual nature of the labellum. At the early stage of development there must be some evidence or other to show that it is made up of two members. Such a free double stage may not exist for a long time and the fusion may almost be congenital. But there must be evidence in an ontogenitic study even of this congenital fusion. As in the case of a polycarpellary syncarpous pistil a critical examination of the ontogenetic stages has revealed (Raghavan, 1939) the individual existence of the carpels and the ultimate formation of a syncarpous ovary by the marginal fusion of the carpellary leaves, so also in this case, must be seen at the earlier stages, evidence of the dual nature of the labellum. When this is so, there is very little ground for accepting the view that the labellum is made up of three members. The support for this concept, derived from the venation of the labellum may not be of much avail. This would involve the belief that the middle portion is a separate member, wherein, only the vascular strands have persisted while the other portions have perished. What evidence have we to take it for granted that while the rest of the labellum has ceased to exist, the vascular bundles alone have persisted? It is this same what may be termed the doctrine of the conservatism of vascular bundles that has been responsible for regarding every stout fibro-vascular cord running longitudinally as the midrib of a carpel and the propounding of the theory of carpel polymorphism. The 'fantastic' nature of such conception has been well brought about and discussed by Parkin (1926, 1933) and the same arguments may well apply in this case also.

Moreover the anatomical work of Arber (1933) has shown that a 'rudimentary external form was found to correspond to a vascular system which is equally or even more rudimentary; indeed an organ which retains some trace of its normal external form may yet show a complete lack of vascular tissue'. When this is so, there is no justification to hold that the vascular cord alone has survived while the rest of the labellum has gone as Gregory's (1936) concept would have us believe.

Support to this is also found to be in a note by Joshi in the latest number of the *Annals* (*Ann. Bot.*, New Series, Vol. IV, No. 15, p. 669) where he describes the anatomy of some abnormal flowers of *Gagea fascicularis*. These have five perianth leaves, five stamens and two carpels and they are derived from the normal flowers by the loss of one of the inner perianth leaves, one stamen and one carpel. The study of the vascular system of this flower showed the total absence of any rudimentary vascular traces of the lost parts. It is therefore clear then, that no bundles persist after the organ which they supplied has ceased to exist. When this is the case with a flower not separated even by one generation from the normal flowers, there is little ground for supposing the vascular cord alone persisting even though the 'third member of the labellum' had disappeared many generations ago.

An ontogenetic study of normal as well as the so-called abnormal flowers in this specis of *Alpinia* indicates certain facts on the basis of which the structure of the flower, especially the morphology of the labellum, could be indicated.

The posterior petal is the outermost petal and the fertile stamen is also posterior as it should be. Serial transverse sections of young buds have revealed the unmistakable presence of two structures situated antero-laterally. They are very prominent to start with but are not continued as far upwards as the anther. They soon disappear in transverse sections taken at successively higher levels. They are situated internal to the labellum and together with the fertile stamen would form a natural whorl of three structures. To our mind these are the two glands of Brown (1830) which along with the fertile stamen constitute the inner staminal whorl. The outer whorl is made up by the anterior labellum and the two postero-lateral staminodes; the latter however may or may not be present.

A description of the flower of the genus *Zingiber* as given in the 'genera Plantarum' (Bentham and Hooker, 1880) may now be briefly recalled with advantage. It says that there is a short cylindrical tubular three-lobed calyx, the corolla tube cylindrical and the lateral staminodes are connate with the labellum or may be wanting. The labellum is considered a single unit, but is bifid or in two parts. Sometimes the staminodes are petaloid. In the present case, Text-Figs. 41 and Pl. XVII, Fig. 3 show two small rounded structures appearing at particular level and connate with the labellum and which at first sight may be taken up for the posterio-lateral staminodes. But a critical examination of the serial sections has shown that these are only the in-rolled ends of the labellum. So that in this case the staminodes are absent. The outer staminal whorl is therefore represented by the labellum and the absent staminodes. Rendle (1904) has however adopted the Eichlerian concept and says that the morphology of the flower has been the subject of much discussion especially as regards the part played by the labellum. The outer whorl of stamens may be suppressed as in *Costus* or *Renealmia*, but is generally represented by two lateral staminodes, the development of which shows a great variety. The inner staminal whorl is complete, the median stamen is fertile while the lateral pair unite to form the labellum.

Let us see now, if a critical study of the so-called abnormal flowers gives us support for the position we have taken as regards the labellum. In these flowers, there are two fertile stamens whose position would confuse us if we saw only the opened flower. Only by a close ontogenetic study is it possible to have a correct idea of their real position and their significance. The two fertile stamens at first sight appear to be side by side. One of these two is the usual one found just below the posterior overlapping petal. The occurrence of an additional stamen adjoining to this may not be easily explained except that it is likely to be a case of a bifurcation of the stamen primordium—something like the 'dedoublément' of Payer (1857). But a careful examination of the serial sections indicates that the additional stamen's real position is in the anterior side slightly towards one side. The two glands which are found in normal flowers are antero-lateral and it is just in the place occupied by one of these that this additional fertile stamen occurs. In other words, one of the two antero-lateral glands has become staminiferous. If this premise is correct, then we should find the other gland in its usual position inasmuch as it has not undergone any trans formation. This is exactly what we find. Text-Figs. 44–46 and Pl. XVII, Figs. 4–6 show the appearance and disappearance of one of these glands, whereas in the place of the other gland we find the additional fertile stamen. This stamen compared to the normal stamen is smaller.

It will also be seen from a comparison of Figs. 3 and 7 of Plate XVII that the labellum in these two-fertile-stamened flowers is much smaller than in the normal flowers. We find after an exhaustive search for an explanation that it is a consequence of spatial necessity. The space which was practically free, having been occupied by one of the two small glands, has now come to be occupied by a large anther, so that there is no place for the labellum to grow in that lateral direction. So much so, the labellum is confined practically to the space lying between the two anthers (Text-Fig. 48).

The transformation of one of these glands into a stamen supports the conclusion previously arrived at—that the inner staminal whorl is composed of the two glands and the fertile stamen. In other words the so-called glands are morphologically equivalent to stamens. We are not quite happy about the term gland which usually carries with it no morphological significance. But for want of a better term and so as to conform to the old terminology of Brown (1830) the same expression has been retained.

It will be of great benefit and interest to digress a little and discuss at some length the views of Thompson (1933) in so far as they pertain to the Zingiberous flowering. His Figs. 103 A–R are those of a flower of *Zingiber officianale*, showing descending transverse sections. The remarkable feature is that organs (Nos. 18 and 19 of his Figs.) appear and disappear exactly like the glands of this paper. But he calls these the stylodes and they are members of the floral organs· from which the accepted style is composed. His Fig. 104 gives an idea of his concept of the floral structure of *Zingiber*. The bract and the three sepals are as usual. The petals come in for a good deal of modification. The original petals are 5, 6 and 8 with 9 and 10 united with 7. That is the overlapping posterior petal of our figures, become a compound petal, made up of three units. The labellum is also a compound structure, being a fusion product of 8, 11 and 13. The stylar components and the stylodes are numbered 14–19. It would appear from this that the flower is composed of (1) a whorl of 3 sepals (2, 3 and 4); (2) two whorls of petals, 5, 6 and 7 and 8, 9 and 10 (7, 9 and 10 forming a compound petal and 8 is the central portion of the labellum); (3) one staminal whorl 11, 12 and 13 (of which 12 is the fertile stamen, 11 and 13 are the lateral components of the labellum); (4) the first three stylar components are 14, 15, 16; the additional stylar primordia are 17, 18 and 19. But 14, 15 and 17 become confluent with 17 as the prominent member of this union. 18 and 19 enlarge, are separated from the stylar dome and are considered to be stylodes. These according to him are the staminodes of Rendle (1904).

So far as this point is concerned, it will be found from a comparison of the figures in the present paper with those of Thompson (1933), his stylodes, 18 and 19 occupy the same position in the flower as do the so-called glands of this paper. They occupy an antero-lateral position. Rendle's staminodes on the other hand occupy the postero-lateral position. It does not seem therefore quite appropriate to equate the so-called stylodes occupying an antero-lateral position with the staminodes which are postero-lateral in their placement. It might have been more appropriate to say that the so-called glands of Brown are in reality the stylodes. But so far as our observations go, we are not in a position to conceive of these as the stylar components. Nor is there any evidence in the present material to consider the posterior petal as compound, being made up of three components.

Thompson's concept would lead to the idea of a portion of the labellum (the middle, No. 8) being part of the inner petal whorl while the lateral components form part of the staminal whorl. Gregory's (1936) interpretation is that the midrib portion is part of the outer-staminal whorl (along with the two staminodes) the inner whorl being made up of the two lateral components of the labellum and the fertile stamen. As has been shown already there is no clear evidence to regard the labellum as being made up of even two members, much less of three.

As regards the so-called stylar components, we have recognized only two glands. Even in Thompson's Fig. 103, only these two (18 and 19) are shown, the others are not shown in the serial transverse sections. Presumably they are emergences whose presence is implied rather than explicit. Even in the diagrammatic representation (Fig. 104) these two 18 and 19 are shown quite different from and bigger than the others (14–17). The reason for this is not clear. There is no evidence in this species of the presence of stylodes and we see no reason, so far as this material is concerned, to take up the view other than the one that has been elaborated, namely, that these are glands which, together with the fertile stamen, form the inner staminal whorl; the labellum is single which together with the staminodes which may or may not be present, form the outer andrœcial whorl.

VIII. Summary

The diploid chromosome number of *Alpinia calcarata* Rosc., is found to be 48.

Prochromosomes are present and their behaviour in mitosis is described. They are found to be the persistent chromatic portions adjacent to the centromeres. Their mitotic cycle is essentially the same as that of the normal chromosomes. There is no evidence to consider these as non-chromonematic.

The pollen tetrads are organized in a linear fashion. T-shaped tetrads are also common.

The embryo-sac develops in a normal manner from a hypodermal archesporium from which a primary parietal cell is cut off. There is usually only one layer of wall cells. The primary parietal cells do not usually undergo any further pariclinal division. Degeneration of the embryo-sac is met with very frequently and at all stages. Development beyond the 8-nucleate stage has not been met with. There is a haustorial-like attenuation of the antipodal end of the embryo-sac.

The ontogeny of the flower has been studied with special reference to the morphology of the labellum.

The labellum is considered to be a single structure and forms the anterior member of the outer staminal whorl, the two postero-lateral staminodes being absent. The inner staminal whorl is made up of the posterior fertile stamen and the two antero-lateral glands.

The frequent occurrence of flowers with two fertile stamens is interpreted on this basis.

The nature of the inflorescence is discussed and it is considered to be a scorpiod cyme.

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PLATE XVII

Photomicrographs

FIGS. 1–3.—Transverse sections of normal flower at successively higher levels from the top of the ovary. Note the appearance and disappearance of the ' glands ' in Figs. 1 and 2.

FIG. 3.—The two rounded staminode-like bodies are only the inrolled ends of the labellum.

FIGS. 4–7.—Serial T.S. of two-stamened flower. Note that there is only one " gland", the other having become staminiferous. Note also that the second stamen is smaller, as also the labellum.

FIG. 8.—The anticlinal division of the primary parietal cell of the archesporium of the ovule.

FIG. 9.—Dyad Stage.

FIG. 10.—Mature embryo-sac with the haustorium-like antipodal end.

FIG. 11.—T.S. of a portion of the anther. Note the intrusive tapetum and 5 or 6 layers of wall cells.

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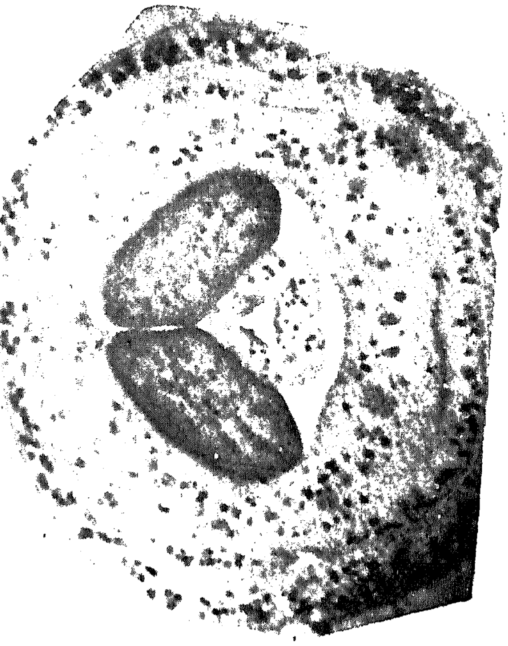

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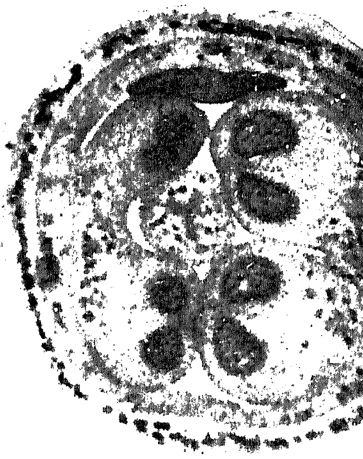

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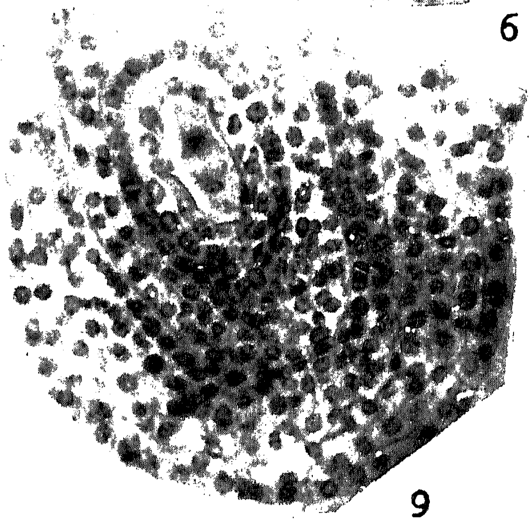

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