

Growth and Development of the Banana Plant

3. A. The Origin of the Inflorescence and the Development of the Flowers

B. The Structure and Development of the Fruit

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With eleven Plates

ABSTRACT

In this paper, which is presented in two parts, the growth and development of the banana plant have been examined from the standpoint of the origin of the inflorescence and the development of the flowers (Part A) and the structure and development of the fruit (Part B). First the main centres of growth in these structures are located and the manner of their development is presented. Thereafter, attention is focused upon the salient events which determine the alternative courses of development with a view to designating the chemical and physiological stimuli that may be required.

PART A

The vegetative shoot apex, situated at ground level, has a broad and somewhat quiescent central dome of meristem. When flowering ensues the shoot apex becomes elongated and produces a series of bracts, spirally arranged, and each of these only partially encircles the axis. The bracts, unlike the leaves, have in each axil a tangentially extended, crescent-shaped, meristematic, cushion-like body, i.e. the primordial 'hand', from which the flowers differentiate simultaneously in a double row. The flowers in one row alternate with those in the other although those in a given row develop simultaneously and not in succession. By the activity of an intercalary meristem, which is situated at its base, the hand is pushed away from the axis. In the analysis of these events, reference is made to hypotheses that might account for the factors involved in the transition from the vegetative to the floral growth. Particular attention is drawn to the recent views of Chailakhjan which require the intervention of two floral stimuli, one being 'gibberellin like', which acts upon the growth and elongation of the main stem, and the other, 'anthesin', which modifies the meristematic regions and induces the formation of flowers.

In the banana plant the floral organs arise as primordia upon the crescent-shaped cushion in the axil of the subtending bract. The floral organs arise in the following sequence: perianth, stamens, and carpels. There is no obvious difference in the origin of the functionally male and the morphologically female flowers. The alternative courses of development of the floral primordia, which are described, must involve an interaction between their innate (genetic) nature and the physiological milieu in which they grow. The latter is, and must be, subject to some degree of regulatory control. The ovary of the female flower is trilobular, which results from the confluence and infolding of the three carpels. The ovary wall shows the adnation of the floral bases to the carpels, typical of an inferior

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ovary. The male flowers have rudimentary ovaries with an interior occupied by numerous ingrowths of the ovary wall.

PART B

The development of both parthenocarpic and seed-bearing bananas has been studied in relation to the time after emergence of the inflorescence from the pseudostem. First the structure of the ovary is described, and attention is drawn to the pulp-initiating cells situated within the inner epidermis of the pericarp and in the septa. In the parthenocarpic banana these cells proliferate from 2 to 4 weeks after emergence; thereafter the growth of the pulp is by cell elongation. These stages are illustrated by photographs. By 12 weeks after emergence the locules are filled by the irregular ingrowths of the pulp parenchyma and the aborted ovules are inconspicuous. The expanding floral axis and the broad septa also contribute to the edible portion of the fruit. Starch appears in the pulp and disappears during fruit maturation.

In its basic structure the seeded banana is similar to the parthenocarpic fruit. The pulp-initiating cells divide only 4 weeks after emergence but the amount of pulp so formed is very small. It mostly develops around the wall of the locules and it presses against the seeds which are large and occupy the bulk of the ovary.

Attention is drawn to the growth induction in the pulp-initiating cells, here associated with parthenocarpy and female sterility, and to the possibility that this may be artificially induced when the factors that govern the behaviour of these cells in seeded and non-seeded bananas respectively are known.

INTRODUCTION

THE fruiting inflorescence or the 'stem' of the banana, which may weigh nearly 90 lb. (as in *Musa acuminata* c.v. Gros Michel), is a familiar object, but it nevertheless presents botanical problems and it is the end result of a remarkable sequence of growth events. An early attempt to illustrate and describe the origin and development of the inflorescence was that of White (1928). More recent works include those of Fahn (1953) and Alexandrowicz (1955), which have been summarized by Simmonds (1959).

This paper will be presented in two parts. The first part will deal with the origin of the inflorescence and the development of the flowers. This account is, therefore, a continuation of the study of the development from the transition of the vegetative shoot apex to the flowering condition which has been described in the previous paper (Barker and Steward, 1962*b*). After presenting the necessary anatomical observations in Part A, those features which appear to be especially significant in the light of current knowledge will be discussed. The second part (B) will describe the structural changes involved in the growth of the fruit from anthesis to maturity. First, a general description of the mature inflorescence of the banana is appropriate.

A. THE ORIGIN OF THE INFLORESCENCE AND THE DEVELOPMENT OF THE FLOWERS

The Tip of the Inflorescence

An inflorescence of the 'Gros Michel' banana about 4 weeks after shooting (i.e. its emergence from the crown of leaves) is massive, and it bears on its

fleshy axis numerous spirally arranged, boat-shaped, crimson coloured bracts. In each axil a hand, comprising two rows of flowers, is borne. White (1928) illustrated by photographs the external appearance of the tip of the inflorescence, as seen in both surface and side views (loc. cit., cf. Figs. 12 and 13). These photographs show the floral bracts, in the axils of which the hand primordia arise. The total number of bracts so produced is very large (of the order of 500 or more), and the lowermost ones are sterile. The next 10 or 12 bracts bear the edible, seedless fruits. These functionally female flowers are conveniently termed fingers. The rest of the hands bear functionally male flowers (in Gros Michel even these are sterile, since the plant is a triploid). Between the edible fingers and the male flowers, a hand of neuter or transitional flowers may, or may not, be encountered.

With a few exceptions, the inflorescence is virtually unlimited in its growth and bears at its tip a 'bud' which encloses the male flowers within closely overlapping bracts. Approximately one such bract opens each day and the flowers therein abscise, leaving a prominent scar on the axis. The inflorescence, which is negatively geotropic and upright before shooting, bends down soon afterwards, and it becomes positively geotropic within 2 weeks from emergence. There are a few exceptions to this geotropic behaviour (see Simmonds, 1959). For example, fe'i banana, *Musa maclayi*, and the ornamental *M. velutina* have an inflorescence which remains upright throughout. The inflorescence with its 'male bud' may grow until it almost touches the ground from an original height of 15–20 ft.; however, the bud is commonly removed in commercial practice.

The massive inflorescence which is described above is differentiated from the tiny shoot apex which is situated almost at the ground level, and its emergence from the crown of leaves is preceded by a great amount of growth in length of the central axis or true stem. The transition from the vegetative to the reproductive phase brings about a marked change in the shape of the growing apex (Barker and Steward, 1962*b*, cf. Pl. 4). In the vegetative state the apical dome is broad (Pl. 1, Fig. 1) and bears one or two leaf primordia which are broad and completely encircle the base of the stem tip (Barker and Steward, 1962*a*, cf. Pl. 1), and the internodes are short or unrecognizable. The first visible change which indicates the transition to the reproductive state is the elongation of the apex to give it a conical appearance (Pl. 1, Figs. 2, 3, 5, 6).

The Bracts, their Origin and Development

The transformed apex shows three tunica layers over the central apical dome (Pl. 1, Fig. 4; Pl. 2, Fig. 7). The bract primordium arises as a small mound, as seen in a longitudinal section, and shows both periclinal and anticlinal divisions of the subepidermal layers (Pl. 2, Figs. 8, 9). The epidermis keeps pace with this increase in volume by anticlinal divisions (Pl. 2, Fig. 10). The bract now elongates and grows almost at right angles to the apex of the inflorescence (Pl. 2, Fig. 11). A transverse section below the apex shows the

bract as a crescent-shaped organ, 8 to 10 cells in thickness (Pl. 4, Fig. 32), which as it grows pushes outward in a radial direction. Due to greater growth on the abaxial side, the bract becomes boat-shaped, i.e. it converges towards the apex (Pl. 1, Figs. 3, 5, 6; and Pl. 2, Figs. 12, 13). As it grows upward and outward, therefore, the bract over-arches and encloses the position which the flowers will later occupy in its axil.

An important distinction between the vegetative apex and that of the inflorescence may be made with respect to the origin and differentiation of the leaf and bract primordia. In transverse sections, cut at approximately the same level, the apex of the inflorescence shows many more bracts than there are leaves on the vegetative axis. Furthermore, while the leaf primordium grows around and completely encloses the axis (cf. Pl. 1 of Barker and Steward, 1962*a*), the bracts do so only partially (Pl. 3, Fig. 32; a similar condition was described diagrammatically by White in Fig. 2 of his paper published in 1928).

The Development of the Flowers

A very characteristic feature of the vegetative shoot of the banana is that no axillary structures develop until relatively very far back from the apex. Moreover, even when the vegetative buds eventually appear, they are not axillary in position but are adventitious (cf. Barker and Steward, 1962*a*). By contrast, the floral apex begins to form axillary structures in very rapid succession, even when the bracts are in a primordial stage of development.

Transverse sections (Pl. 4, Fig. 32) show a crescent-shaped zone of actively dividing cells which arises on the axis and which is enclosed by the bract. In contrast to the bract, this tissue grows more in the radial and tangential directions than in the longitudinal and so forms a cushion on the axis. This growing region, which is conveniently referred to as the 'hand primordium', is designated *hp* in the figures. The cells of the hand primordia are richly cytoplasmic (Pl. 2, Figs. 14, 15, 17), and soon two separate regions of growth are to be seen in a longitudinal section (Pl. 2, Figs. 16, 18). These regions are in fact part of a series of meristematic bulges on the surface of the cushion; bulges which are arranged in two arcs, one within the other. The meristematic bulges are the flower primordia. The members of one row alternate with those of the other (Pl. 4, Fig. 34; also compare White, 1928; loc. cit., Figs. 5, 6, 16). The members of the inner (adaxial) row tend to grow faster than the outer (abaxial) ones (Pl. 2, Figs. 16, 18). A transverse section which passes through the top of the hand at this early stage may, therefore, cut across only the adaxial row of flowers (Pl. 4, Fig. 33); the primordia of the abaxial row will be at a slightly lower level and are slower in development. However, a somewhat more oblique section may show the primordia of both the rows. The sequence of floral development has been illustrated by a series of outline diagrams (Pl. 3, Figs. 19–25) for the sake of clarity.

The different floral organs originate in a regular sequence. Before describ-

ing this, it may be helpful to recapitulate the structure of the adult flower as recently interpreted by Simmonds (1959).

A typical banana flower has a zygomorphic perianth of two whorls, each of which consists of three tepals which are fused in such a way as to form two distinct segments—an adaxial free tepal and a large compound tepal which consists of two minor tepals (lobes) of the inner and three of the outer whorl. The basic pattern of the androecium is 3+3, but in the Musaceae one of the inner three stamens is often absent. The position of this missing stamen is opposite to the adaxial free tepal. The gynoecium is tri-carpellary, the ovary inferior, trilocular, with axile placentae. The three styles are fused and bear a six-lobed stigma.

The floral parts described above arise in the sequence—perianth, stamens, and carpels. In a longitudinal section of a young flower only two perianth lobes can be seen to differentiate on the margin (Pl. 4, Figs. 26–28). The five staminal primordia arise internally to the perianth primordia. After the staminal primordia are put forth, a depression becomes noticeable at the apex of the floral primordium, which is over-arched by the floral parts (Pl. 4, Fig. 30), and it is from the over-arching rim of this depression and on the flanks of the stamen primordia that the three styler primordia make their appearance. The three styles fuse above the depression so as to leave a cavity, and the region below this cavity is destined to become the ovary (Pl. 4, Fig. 31). Due to the incomplete fusion of the base of the styles, a triradiate space remains. The gynoecium usually comprises three carpels, although a bicarpellary condition may be observed somewhat infrequently. The abnormal bicarpellary condition has also been noted by Fahn *et al.* (1961) for the dwarf Cavendish banana as grown in Israel.

Concurrently with the floral development, the hand as a whole grows. As a result of the activity of a zone of meristematic tissue at its base (Pl. 4, Fig. 29), the hand is pushed upwards and away from the axis from which it diverges at an acute angle.

The Contrasted Structure and Development of Male and Female Flowers

The mode of origin of the primordia of the floral organs is the same in the male and female flowers, but the extent to which these structures develop is different in the two cases. In the functionally female flower the stamens do not form anthers and filaments, but they remain as reduced club-shaped structures, whereas in the male flower they develop normally in so far as the formation of filaments and anthers is concerned. However, in Gros Michel, which is triploid and male sterile, pollen grains do not form.

The main feature of the female flower is the development of the ovary which has three locules and a placentation which has been described as axile. This latter condition arises by fusion of three carpels (Pl. 5, Figs. 35 and 36). In each of the three locules there are two rows of anatropous ovules, although, as stated, very occasionally an ovary may have only two carpels. The locules are filled with mucilage secreted by the multicellular hairs which arise from

the placentae and the funiculi. In the case of male flowers, however, the ovary remains short, and very little differentiation occurs within. The region which would normally be occupied by the placentae and the ovules is thrown into a series of folds (ingrowths from the inner ovary wall), which fill the ovarian cavity, but no ovules develop (Pl. 5, Figs. 37, 38). The convoluted margins of the carpels at this stage (Figs. 37, 38) are bordered by glandular secretory cells (i.e. the septal nectaries) which secrete into the cavities where the carpels have not united. This situation is also shown diagrammatically by Fahn *et al.* (1961). The epidermal cells of the infolded margins of the carpels are richly protoplasmic (Pl. 5, Fig. 38) and, as the infoldings gradually shrink, they leave a brown mass. There are no mucilage hairs in the male flowers.

It is interesting that from what were essentially similar floral primordia two distinct types of development may occur. It is, therefore, of great significance to know what is the stimulus that regulates one or the other type of developmental sequence. It seems obvious that this process is subject to some degree of regulatory control because occasionally in nature what would normally be male flowers show a tendency to develop into parthenocarpic fruits (Simmonds, 1959).

Whereas normally the male flowers abscise within a day or two of anthesis, there are some varieties (e.g. Pisang rotan) in which they remain persistently attached. In these cases those male flowers which are closest to the female show the maximum swelling of the ovary. Indeed it is possible that the abscission of the male flowers might be prevented by chemical means and their rudimentary ovaries caused to swell. All these events clearly indicate, however, that there is ultimately some physiological or biochemical method of control of these two contrasted types of development.

Previous References to the Development of Flowers

White (1928) investigated the floral morphology and cytology of several members of the genus *Musa*. Present findings on the origin of the inflorescence and the development of the flower are in general conformity with those of White. However, White's earlier description of the ovary is not now clear, for the contrasted structure and development of the carpels in the male and female flowers is not mentioned. Fahn (1953) has studied the succession of floral primordia in each hand in the dwarf Cavendish banana, *M. acuminata* and *M. balbisiana*. According to Fahn, the flowers in the two tangential rows arise in alternating sequence, 'one in the adaxial being followed by one in the abaxial row'. Further, 'the first primordium to arise is that which becomes the extreme right flower of the adaxial row as arranged in mature hands, the second is its neighbour in the same row, the third is that which becomes the extreme right flower of the abaxial row. . .'. So far as we have been able to observe, the floral primordia arise simultaneously in both the rows of a given hand, and they are not formed in succession as stated by Fahn. This observation is borne out when bracts are removed to reveal the flower primordia which, invariably, are all in the same stage of development in a given row.

*The Stimuli to the Formation of the Inflorescence and the
Development of Flowers*

The physiological stimuli that control the origin of the inflorescence and the development of the flowers of the banana must be complex. The initial transformation of the shoot apex from the vegetative condition to flowering requires a redistribution of growth in the originally broad central apical dome of meristem and to an elevated and strongly tapered cone (cf. Barker and Steward, 1962*b*). In addition, however, there are profound and subsequent changes to be observed in the development of bract primordia and of the inflorescence contrasted with the development of leaf primordia and of the vegetative shoot. In particular, bract primordia have pronounced growing regions in their axils, even as close to the inflorescence apex as they can be observed, whereas leaf primordia in the vegetative shoot do not have buds in the axils. But the physiological stimuli that induce or control the development of banana flowers and fruit must extend far beyond the mere formation of a cushion of meristematic tissue in the axils of the bracts, for, as this grows, it breaks up into smaller lobes of meristematic tissue which are arranged in two rows. Each such bulge is a potential flower, and some further internal stimulus determines the transition into either sterile, parthenocarpic female flowers or to neuter or male flowers. The tendency of these events to occur after the banana plant has produced a given number of leaves (45 in Gros Michel) suggests that the growth-regulating stimuli emerge from the leaves and move upward to the shoot in contrast to the auxins that move only downward.

The march of events in the shoot apex, as it is transformed from the vegetative to the flowering condition, requires stimuli that promote the following:

1. A redistribution of growth in the central dome of the shoot apex leading to activity which causes growth in length of the true stem, whereas this had previously been suppressed.
2. A change in the emphasis upon growth in the foliar organs from that which leads to the massive encircling leaf bases of the pseudostem (cf. Barker and Steward, 1962*a*) to that which merely produces spathe-like floral bracts on the axis of the inflorescence (cf. Barker and Steward, 1962*b*).
3. A release from the inhibition of axillary bud formation, which is a characteristic feature in the vegetative shoot, so that centres of meristematic activity (later destined to be groups of flowers) appear promptly in the axil of each bract. (The further development of the fruit from the flower is considered in Part B.)

The hypothesis of Chailakhjan (summarized in 1961) is suggestive here. Chailakhjan considered the flowering response with special reference to some plants, such as *Rudbeckia*, in which the vegetative shoot adopts a

rosette-habit with compressed internodes—i.e. the terminal growing-point does not lead to conspicuous growth in length—whereas the flowers are borne on an axis which does grow in length. Chailakhjan attributes the flowering response to a double set of stimuli, which originate in the leaves, and are separately needed to control the events of flowering. Lack of either, or both, precludes flowering. Chailakhjan attributes one part of the flowering stimulus to some 'gibberellin-like substance'—i.e. gibberellin-like in the nature of the elicited response, not necessarily in its chemical composition—that promotes stem elongation and internodal growth in the otherwise short shoot of the rosette-like vegetative plant. The other part of the flowering stimulus is attributed to certain 'anthesins' which act specifically upon the metabolism of the meristematic regions to control the formation of flower primordia.

The attraction of this point of view in relation to the banana, however hypothetical the causative agents may be, is that it focuses attention upon at least two events or centres of activity. These are the redistribution of growth and onset of activity in the apex leading to extension growth in the main shoot and the development of centres of meristematic activity in the axils of leafy bracts. That these meristematic centres of axillary growth become flowers, rather than vegetative buds, might (on the hypothesis of Chailakhjan) be regarded as a specific function of the hypothetical 'anthesins'. It is interesting to note that Chailakhjan has had a measure of success in relieving blocks to flowering, which are due to lack of one or other of the required double set of flowering stimuli, by supplying extracts from other plants which have been so stimulated that they can flower. Now that the centres of response in the banana plant may be more precisely designated than hitherto, experiments of this kind could be performed profitably, and experiments could be designed to relieve the blocks to growth in the shoot apex of the vegetative plant by the use of synthetic growth regulators.

The point then of Part A of this paper is to focus attention upon the cardinal events involved in the development of the inflorescence and the flowers in the banana in order that the causative, chemically controlling stimuli may be opened up for investigation. Whether these stimuli are regarded as suppressors of growth in the central apex and the axillary buds of the vegetative shoot, or stimuli to internodal growth and meristematic activity in the axils of bracts, their ultimate chemical basis can be visualized; and if this two-pronged chemical control, on the hypothesis of Chailakhjan, derives ultimately from the leaves, it should be possible either to simulate or to identify it.

This, however, does not exhaust the problems of regulatory control of growth and morphogenesis in the banana. It is one problem to elucidate the mechanism which is required to induce meristematic activity in the axils of bracts in the formation of a meristematic flower-forming cushion; it is still another to know why this cushion breaks up into so many flower primordia; and, having done so, why the flowers that develop for a time are functionally

female though parthenocarpic in their development to fruits, whereas later they are functionally male. In other words, the floral primordia are again subject to further stimuli, in the chemical milieu in which they develop, that will determine their further development into female flowers of the seeded banana; into sterile female flowers which develop parthenocarpically; or into a succession of male flowers which abscise.

It is the purpose of Part B, which follows, to describe the development of the fruit from the flower, so that the salient events which determine the alternative courses of development may at least be designated with a view to their ultimate control.

B. THE STRUCTURE AND DEVELOPMENT OF THE BANANA FRUIT

The foregoing part described the origin of bracts from the inflorescence apex and the differentiation of the flowers in their axils. The present part deals with the major structural changes that ensue during the development of the ovary into a fruit.

Nitsch (1952) has described a fruit as 'the structural entity resulting from the (post-floral) development of the tissues which support the ovules'. Although this physiological definition is often satisfactory, it does not satisfy the requirements of all fruits, and the edible non-seeded banana is one such exception. Here the fruit is parthenocarpic, i.e. it does not require the stimulus of pollination. It may, or may not, possess fertile seed, depending on a variety of cytogenetical factors (Simmonds, 1953). It is now well known that normally the process of fertilization itself and later the seeds furnish the chief source of stimuli for fruit development (Nitsch, 1952; Luckwill, 1953 and 1959*a* and *b*). However, in the edible banana, as indeed in pineapple, this stimulus must come from some other source. An hypothesis is that such parthenocarpic fruits as varieties of grapes, lemons, and oranges possess native auxin content greater than in the unpollinated seeded varieties (Gustafson, 1942). In fact, Steward and Simmonds (1954) have demonstrated that growth substances which induce cell division occur in the extracts of the innermost layers of the pericarp (the pulp-initiating cells) of the parthenocarpic banana. This extract even induced cell proliferation in explants isolated from the secondary phloem of the carrot root.

Two cardinal phases in the growth of a fruit involve growth predominantly by cell division and by cell expansion. The duration of these two phases has been investigated for fruits like the tomato (Houghtaling, 1935), cucurbita (Sinnott, 1942, 1945); apple (Bain and Robertson, 1950; Smith, 1950) and others. In the case of the banana, such detailed information is not available, although the general aspects of the fruit development have been described by Loesecke (1950); Simmonds (1953, 1959).

Two examples of bananas were chosen for a comparative study of the developing fruit. One was a parthenocarpic plant (*M. acuminata* c.v. Pisang lilin), the other was a seeded *M. acuminata*. The former is an important diploid male parent which has been used in the breeding programme in

Trinidad and Jamaica (it is curiously male fertile although female sterile), and the pattern of its development is not markedly different from that of Gros Michel.

The fruits for the investigation were obtained through the courtesy of N. W. Simmonds, formerly of the Tropical School of Agriculture, Trinidad, B.W.I. The materials were fixed at 0, 1, 2, 4, 8, 12 (and 15 in the case of Pisang lilin only) weeks after shooting, in formalin-acetic-alcohol. A few fruits were sectioned by hand and others with a microtome. Camera lucida drawings have been included here to illustrate the gross anatomy, while the cellular details are presented through photographs.

In the parthenocarpic fruit, the principal growth occurs in two ways as the ovary increases both in length and diameter: first by the inward growth of the tissue of the pericarp which borders upon the loculus and secondly by the expansion of the central floral axis, the placentae and the septa. In the final outcome, the entire ovarian cavity is completely obliterated and the central portion of the fruit becomes filled with a soft, fleshy tissue, but the ovules do not develop into seeds. The above events and the formative changes of the fruit are diagrammatically represented in Pl. 6, Figs. 39-48.

In the seeded banana, on the other hand, there is a marked expansion of the axis of the ovary, but it is the seeds that conspicuously contribute to the increase in volume. There is virtually very little pulp in the seeded fruits (Pl. 10, Figs. 64-73).

Developmental Anatomy of a Parthenocarpic Banana (*M. acuminata* c.v. *Pisang lilin*)

Since particular interest attaches to the development of the edible pulp of the parthenocarpic banana, an attempt was made to trace this in more detail with the following results:

(a) At the time of shooting, the young ovary has the structure shown in Pl. 5, Fig. 35 as seen in transverse section, and its wall is to be seen in Pl. 8, Fig. 53.

(b) The epidermis, which consists of a single layer of squarish cells with stomata and a well-defined cuticle on the outer surface, is shown in Pl. 7, Fig. 49.

(c) Six to eleven layers of hypodermal parenchymatous cells occur; most of these contain chloroplasts, while some bear raphides (Fig. 49).

(d) There is a broad region in which the vascular tissues occur. This zone consists of scattered vascular bundles, separated by parenchyma cells. The outer bundles tend to be more fibrous (Pl. 7, Fig. 49), with relatively few vascular elements and, progressively inward, the bundles become less fibrous, have more prominent vascular elements (Fig. 50), and are, in general, surrounded by a ring of large laticiferous elements interspersed with thin-walled parenchymatous cells (Pl. 7, Fig. 50; Pl. 8, Figs. 53-56). Internal to these bundles, which run longitudinally, is a zone of parenchyma with very well-defined air spaces (Figs. 51, 53, 55). This region may be several cells thick.

Inner to the region of parenchyma is a zone in which vascular elements run at right angles to the axis of the fruit (Pl. 6, Figs. 44-48; Pl. 7, Figs. 50-52), they can be seen in a tangential direction, as they pass around the loculus and are connected via the septa to the central floral axis (Figs. 44-48). These parallel bundles are especially surrounded by the laticiferous elements (Figs. 50-52). The outer longitudinal bundles and the inner tangential ones all converge and anastomose at the base of the fruit in the region of the pedicel. At the stylar end of the fruit, however, the peripheral longitudinal bundles pass into the perianth elements and the stamens, whereas the innermost and tangential bundles continue into the stylar region.

(e) The innermost portion of the pericarp is composed of five to seven layers of isodiametric parenchymatous cells which are bounded by an inner epidermis which borders the locule. To the outside there are the tangentially running vascular bundles to which reference has been made. This zone (Fig. 52) contains the pulp-initiating cells with the most actively dividing cells lying immediately below the epidermis (see inset to Fig. 55).

(f) Separating the three locules are the septa (partitions) which have the following structure. In each septum a part of the structure of the pericarp is repeated; that is, it consists of a central portion of parenchyma and it is bordered internally by parallel vascular bundles and, towards the locules, by the epidermis and a few hypodermal pulp-initiating cells. In transverse section a septum is about 50 cells wide (Pl. 9, Fig. 60).

(g) The placental axis consists chiefly of spongy parenchymatous tissue with abundant air space. The parallel vascular bundles of the pericarp which pass into the axis via the septa fuse with the ventral bundles of the carpels which run longitudinally (Pl. 6, Figs. 44-46).

The Development of the Pulp

An examination of the transverse section of an ovary at the time of emergence, and 1 week later, reveals relatively little change, except perhaps a slight enlargement of the cells. However, 2 weeks after emergence the number of pulp cells has definitely increased by cell divisions (Figs. 52, 54). (Mitotic figures were not detected due to inadequate fixation of the material.) There is also an accompanying increase in size of the cells of the rest of the pericarp. By this time the ovules will have almost degenerated (Fig. 45). Somewhat later the pulp-initiating region of the partition also becomes active, and the septum expands into the loculus (Figs. 45, 60, 61).

The increase in cell number in the initiating region of the pulp continues up to about 4 weeks after emergence, when it subsides; thereafter the growth is largely by cell enlargement (Figs. 55, 56 and inset to Fig. 56). At 4 weeks the ovules have become completely disorganized (Fig. 46). A prominent feature is that the activity of the initiating cells of the pulp is not regular and uniform around the circumference, for in places the activity is great and in others it is low; this causes an irregular outline of the pulp which is apparent both in longitudinal and transverse sections (Figs. 55, 56).

While all these events are occurring and the fruit is increasing considerably in diameter, the outer epidermis of the pericarp keeps pace by the enlargement of its cells in the tangential direction.

Thus far the principal events after emergence have been marked by the onset of cell divisions in the pulp-initiating region at 2 weeks, their comparative cessation at 4 weeks, and the progressive growth by cell enlargement thereafter. From 4 to 12 weeks after emergence, the major event in the development of the fruit are as follows: By 8 weeks the locule is nearly filled in by the ingrowth of the pulp (Figs. 47, 57) and by 12 weeks almost entirely so (Figs. 48, 58, 59). Meanwhile by 8 to 12 weeks the floral axis and the septa have greatly expanded (Figs. 47, 48, 62, 63).

Some 12 to 15 weeks after emergence, the air spaces situated around the ring of tangentially oriented vascular bundles expand greatly. It is probable that the increase in diameter of the fruit is at least in part due to this. It is this region of air spaces which gives way when the banana is peeled. When this is done the prominent longitudinal bundles can be seen adhering to the inner portion of the peel, and they leave an impression in the pulp. But in the main the system of tangential bundles remains within the pulp, for it is attached, via the septa, to the placentae.

Starch deposition in the pulp cells commences some 4 weeks after emergence and becomes well established by 8 weeks. The first visible signs of starch deposition are to be seen in the cells of the pulp which are in the vicinity of the vascular bundles. Thereafter, starch accumulation moves centripetally. The signs of starch disappearance can be noted when the fruit is about 12 weeks old; it is rapid after this stage. Some reference has also been made in an earlier paper to the changes that occur during development of the fruit in its content of soluble nitrogen compounds (Steward *et al.*, 1960): these changes may also be correlated with the above account.

The above events concern the fruit of the cultivar Pisang lilin, which is rather small when compared to the fruit of Gros Michel. The main course of events, however, is the same in both. But the amount of pulp developed and the time (in weeks after shooting) of starch deposition, its disappearance, colour development, &c., are somewhat different in the two varieties.

Structure and Development of a Seeded Banana (Musa subsp. burmannica)

The ovary of the seeded banana is not markedly different from that of the parthenocarpic banana at the time of shooting (Fig. 74). The same arbitrary classification into various zones as described for the pericarp of the Pisang lilin banana also holds good for the seeded variety. The two distinguishing characteristics, namely the development of the massive seeds and the small amount of non-edible pulp, are diagrammatically represented in Pl. 10, Figs. 70-73. The external form changes which accompany these are illustrated in Pl. 10, Figs. 64-69 for *Musa acuminata* subsp. *burmannica*.

Figs. 70 and 71 are transverse sections of the fruit 1 and 2 weeks after emergence respectively. Within a week of shooting a marked increase in the

diameter of the ovary and a great enlargement of the ovules, along with an expansion of the septa, and the central floral axis can all be noticed. Figs. 75 and 76 show details at the same stages. There is no change in the pulp-initiating zone. However, 4 weeks after shooting there is a noticeable increase in the number of cells in the pulp-initiating zone (Figs. 72, 77, 78). At this stage the seeds will have enlarged so much that they nearly fill the loculus (Fig. 72). The funiculi appear very prominent. The quantity of pulp produced is rather meagre when compared with that in a parthenocarpic banana fruit of the same age.

In an 8-week-old seeded fruit the pulp tissue remains absent, or, if it is present, it is only 8–10 cells thick, in transverse section, except between the ovules where it makes prominent ingrowths (cf. Figs. 47, 73, 79–81). These ingrowths are broadest where they originate, and they taper as they grow centripetally (Figs. 79–80). Plates of pulp separate the ovules at different levels. This feature is not represented in the transverse sections but can easily be noticed by dissecting a fruit. The seeds become very hard after 8 weeks, and it is virtually impossible to section the fruits. The seeded fruits usually dry up while on the plant, and in some species of bananas, like *M. velutina*, the pericarp splits, thus exposing the central axis bearing a number of black seeds enwrapped in a thin layer of pulp. The break in the pericarp then occurs along the parenchymatous regions outer to the parallel vascular bundles.

Centres of Growth in the Banana Fruit and their Regulatory Control

Every flower in the banana plant originates in much the same way, i.e. as a bulge upon the surface of a meristematic cushion which is destined to form each hand. Moreover, each such bulge gives rise to a primordium which potentially represents a flower. However, alternative courses of development may lead to (a) female flowers with normal ovules, leading to fertile seeds and inedible fruits, (b) female flowers with vestigial ovules and which develop parthenocarpically into edible fruits, and (c) male flowers with either functional or sterile pollen. These alternative courses of development in flowers and fruits must, therefore, be seen as the interaction between the innate nature of the flowers in question and their immediate physiological milieu—i.e. the chemical stimuli to which they are subjected.

Granted that the basic alternative as between ovules which do not develop and ovules which are capable of producing seed, and between anthers with viable or non-viable pollen, has a genetic or cytological basis (cf. Simmonds, 1959), its consequences for growth correlations in the persistent fruits need to be understood. Whereas it is the growth of ovules and seeds that form a large part of the mass of seeded fruits, it is the growth of the innermost part of the pericarp (five to seven layers of parenchyma cells) and of some cells of the septa that function as 'pulp-initiating cells' that contribute to the fleshy mass of the edible fruit. Therefore, in the edible banana it is the *failure*, not the success, of the act of fertilization which permits the ovary to grow and that is

here associated with the induction of growth in the pulp-initiating cells (see pp. 667). By contrast any latent ability to grow, which resides in the cells of these regions in the fertile seeded fruit, must be regarded as suppressed by the presence of normal ovules and fertile seed. The precise location of these events in the developing flower now makes it possible to study growth induction and its suppression in the formative region with a view to simulating, by exogenous means, the controls that operate in the intact plant. These considerations have led to studies of growth induction in tissue explanted from banana fruits, the results of which will be published in a subsequent paper. Such combined morphological and physiological studies, however, hold out the hope that when the course of events is properly understood the parthenocarpic development of the banana fruit may be brought under chemical control—even to the point of inducing this in the male flowers that normally abscise.

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EXPLANATION OF PLATES

a, stamen primordium; *ab*, abaxial flower primordium; *ad*, adaxial flower primordium; *aer*, aerenchyma; *b*, bract; *bp*, bract primordium; *chl*, chlorenchyma; *do*, degenerating ovules; *f*, floral primordium; *h*, hand; *hp*, hand primordium; *im*, intercalary meristem; *l*, latex cells; *lf*, leaf; *m*, mucilage; *mh*, mucilage hairs; *o*, ovule; *oc*, ovarian cavity; *p*, pulp; *pe*, perianth; *pi*, pulp-initiating cells; *pl*, placenta; *pp*, perianth primordium; *ra*, raphides; *s*, seed; *sc*, seed coat; *sg*, starch grains; *sm*, septum; *st*, stylar primordium; *vb*, vascular bundle.

PART A

PLATE 1

FIGS. 1-6. Origin and development of the inflorescence.

FIG. 1. Longitudinal section of the vegetative shoot apex showing leaf primordia. Note the broad apical dome.

FIG. 2. Longitudinal section of the apex at transition from the vegetative to the reproductive state. Bract primordia have already appeared.

FIG. 3. Longitudinal section of the transformed apex. Note the gradual elongation of the apex and the numerous bract primordia with axillary meristematic regions.

FIG. 4. The terminal part of Fig. 2 enlarged to show the three mantle layers, the subapical region and the bract primordia.

FIG. 5. Longitudinal section of the apex of the young inflorescence, showing the differentiation of the hand primordia.

FIG. 6. Same as above but including the well-formed bracts at the base of the figure with hand primordia in their axils.

PLATE 2

FIGS. 7-18. Origin and development of the inflorescence (*cont.*)

FIG. 7. Longitudinal section of the apex of the inflorescence with the young bract primordia on its flanks.

FIGS. 8-9. Margins of the bract primordium enlarged to illustrate the meristematic activity of the subepidermal cells in the initiation of the bract.

- FIGS. 10-12. Stages in the growth of the bract primordium. Note the anticlinal divisions in the epidermis in Fig. 10.
- FIG. 13. Longitudinal section of the inflorescence with bracts and the subtending zones of densely stained cells which mark the differentiation of the hand primordia.
- FIG. 14. The axil of a bract enlarged from the previous figure to show the tangentially oriented cell divisions in the hand primordia.
- FIG. 15. The hand primordium in relation to the bract and the inflorescence axis.
- FIG. 16. Acropetal development of the hand primordia.
- FIGS. 17-18. Stages in the development of the hand and of the distal differentiation of the floral primordia. Note that the adaxial primordium has elongated considerably faster than the abaxial one.

PLATE 3

- FIGS. 19-25. Diagrammatic representation of the growth of the flowers.
- FIG. 19. Longitudinal section of an inflorescence at the level which shows the bulged hand primordium in the axil of the bract.
- FIGS. 20-21. The differentiation of the two rows of floral primordia as bulges at the distal end of the hand primordium.
- FIG. 22. The elongation of the floral primordia in the tangential direction.
- FIG. 23. The origin of the perianth and stamen primordia.
- FIG. 24. The differentiation of the styler primordia with the underlying ovarian cavity.
- FIG. 25. Longitudinal section of a mature flower, showing the arrangement of the floral parts, and cross sections of the flower at the styler end and at the base of the ovary.

PLATE 4

- FIGS. 26-34. Floral development.
- FIGS. 26-28. Longitudinal section of a part of an inflorescence showing differentiation of the perianth and stamen primordia.
- FIG. 29. Basal portion of the hand enlarged to show the intercalary meristem.
- FIG. 30. Longitudinal section of a young flower. Note the origin of the ovarian cavity by the apical fusion of the styler primordia.
- FIG. 31. The same at a later stage of development. By this stage both the style and stamens have elongated.
- FIG. 32. Transverse section near the apex of the inflorescence. Note the differentiation of the crescent-shaped bracts and the hand primordium.
- FIG. 33. Appearance in transverse section of the floral primordia formed as small bulges on the hand primordium.
- FIG. 34. Transverse section through part of flower cluster. Note the alternating arrangement of the two rows of flowers.

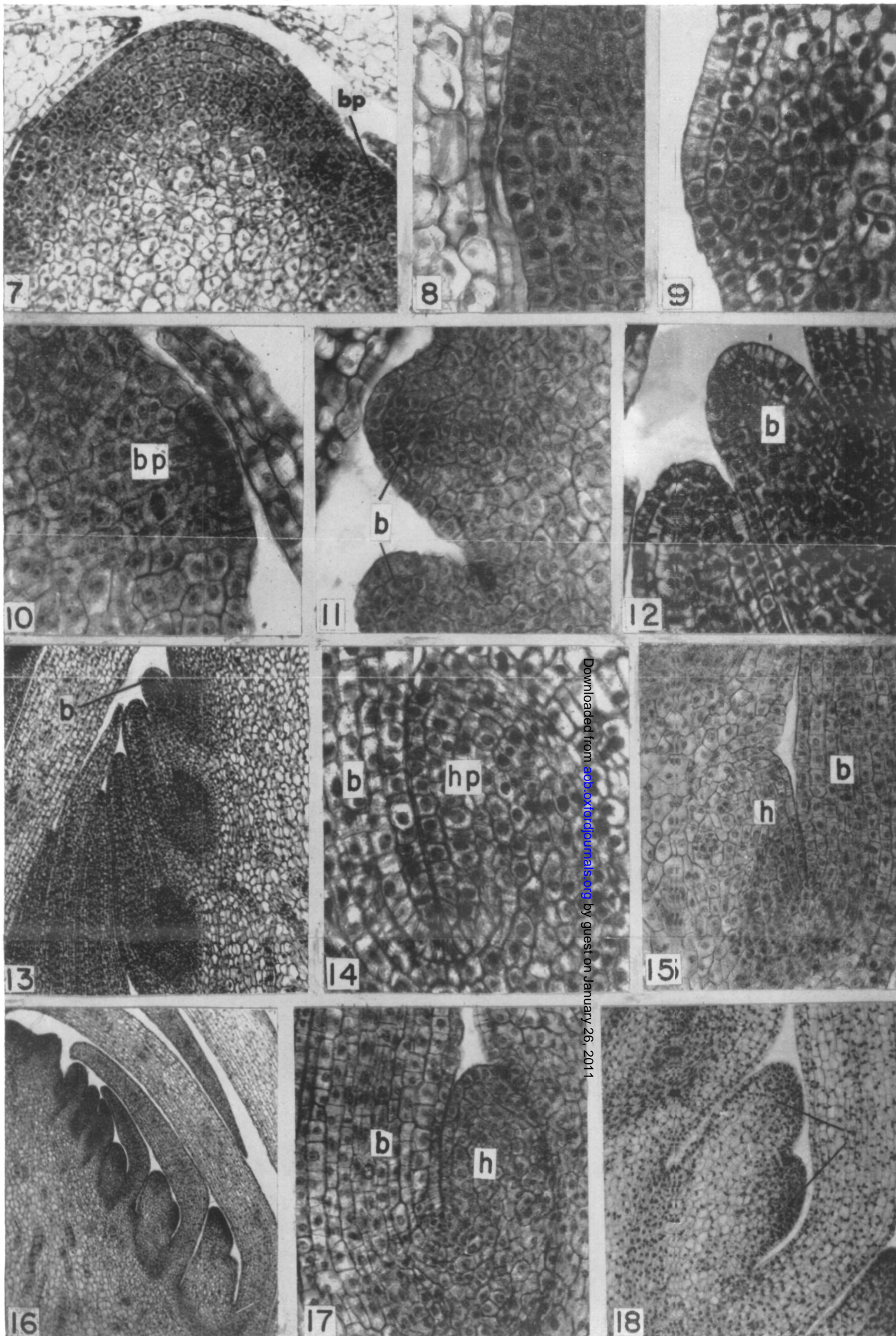
PLATE 5

- FIGS. 35-38. Ovary structure in the female and male flowers.
- FIG. 35. Transverse section of the ovary of the female flower at emergence. Note the locules filled with mucilage hairs.
- FIG. 36. Transverse section of the fully formed female flower with mature ovules and large ovarian cavity.
- FIG. 37. Transverse section of the carpellary region of the male flower at anthesis.
- FIG. 38. Part of Fig. 37 magnified. The epidermal cells of the infolded carpel walls are densely cytoplasmic and constitute secretory cells or nectaries.

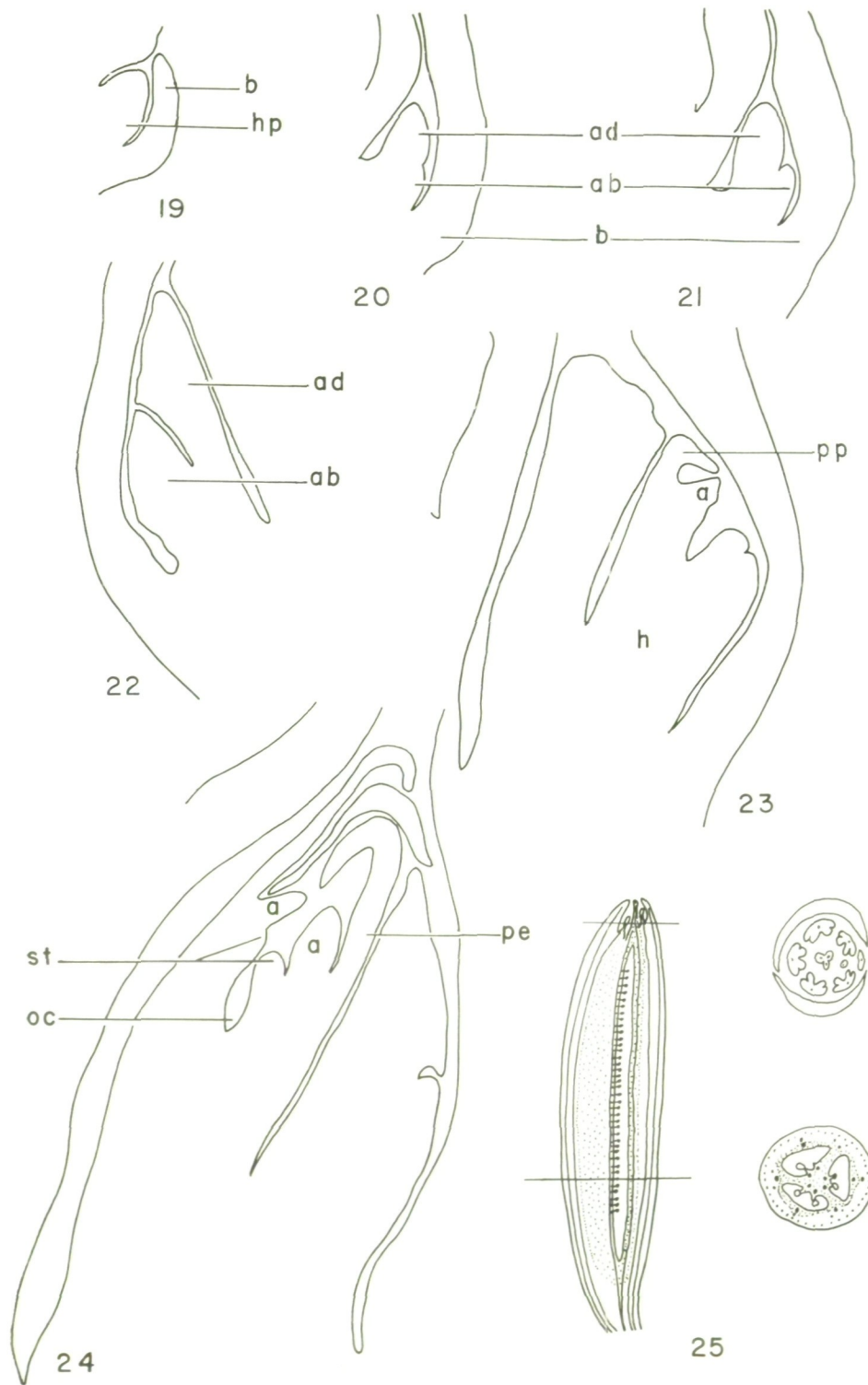
PART B

PLATE 6

- FIGS. 39-48. Structure and development of a parthenocarpic banana (*Musa acuminata* c.v. Pisang lilin).
- FIGS. 39-43. Outline diagrams of the developing fruit at 1, 2, 4, 8, and 12 weeks after emergence respectively.
- FIGS. 44-48. Interpretative diagrams of transverse sections of the fruit at 0, 2, 4, 8, and 12 weeks after emergence showing the pulp invading the ovarian cavity.

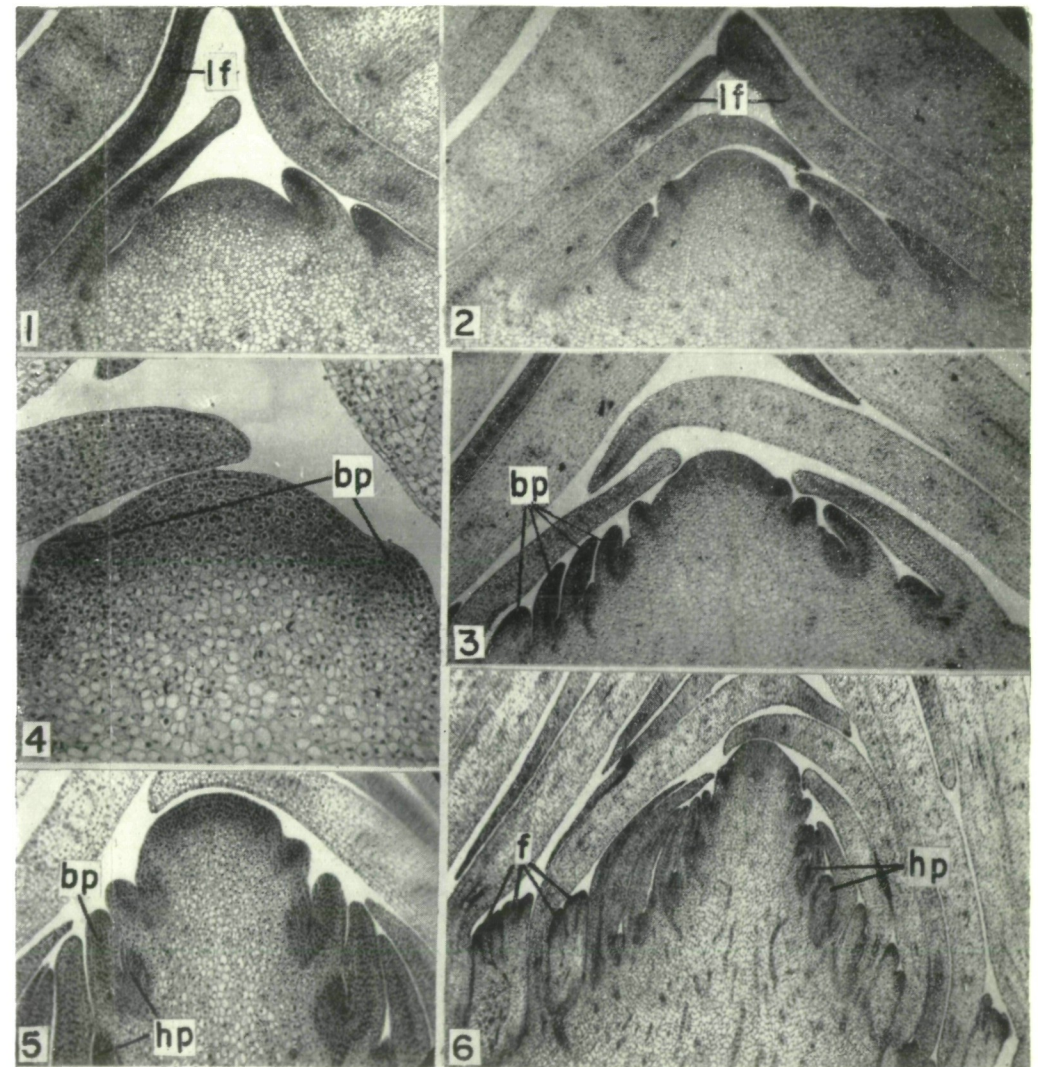


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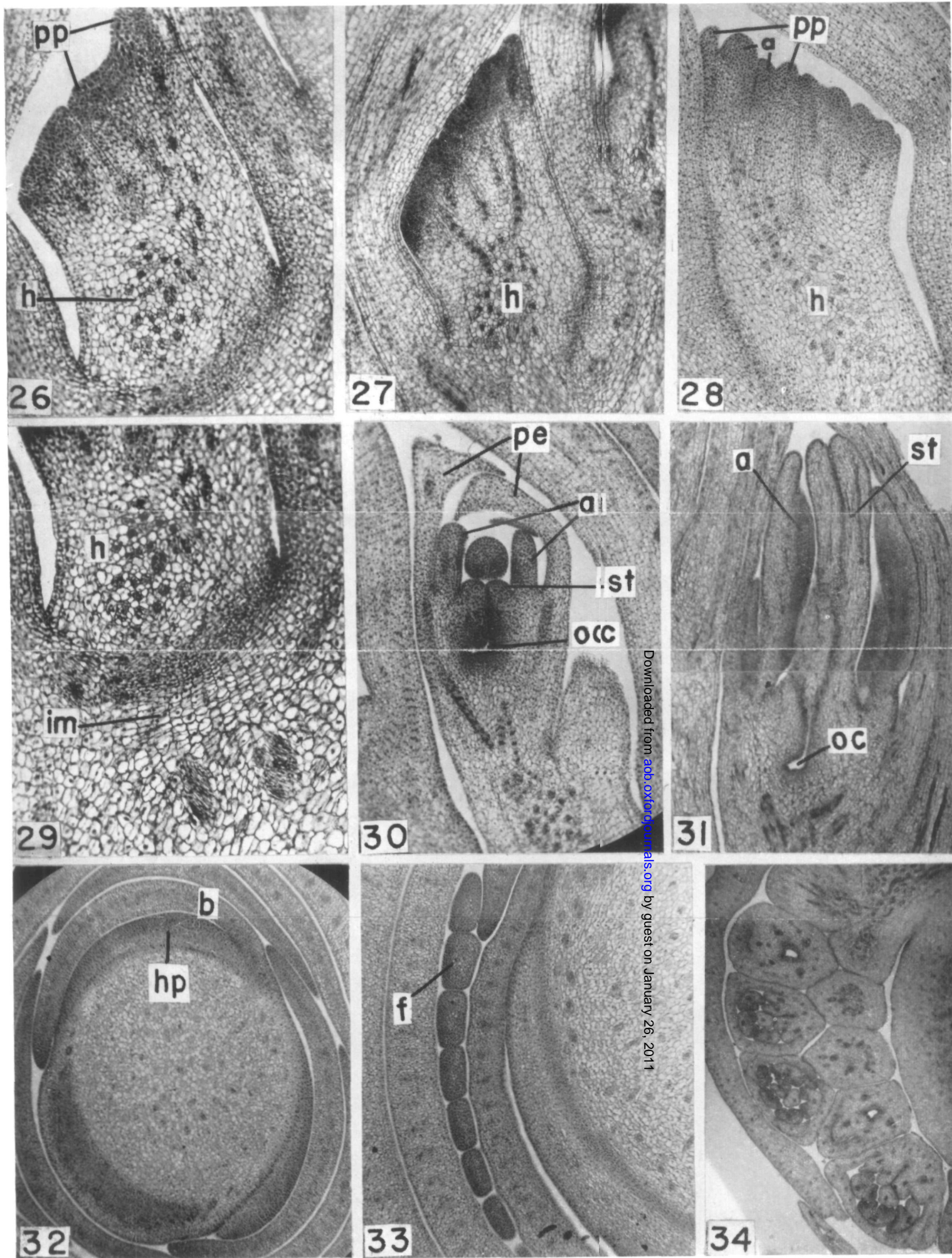


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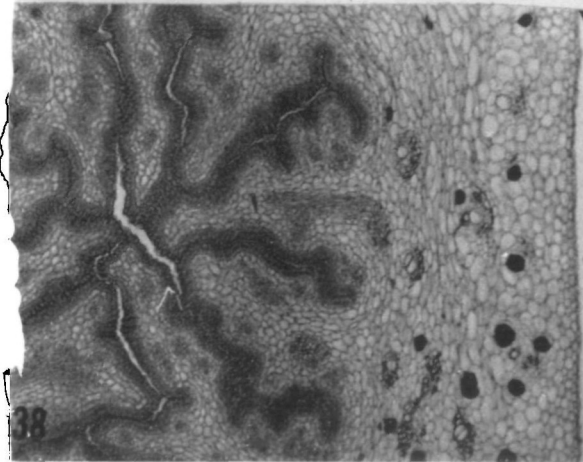
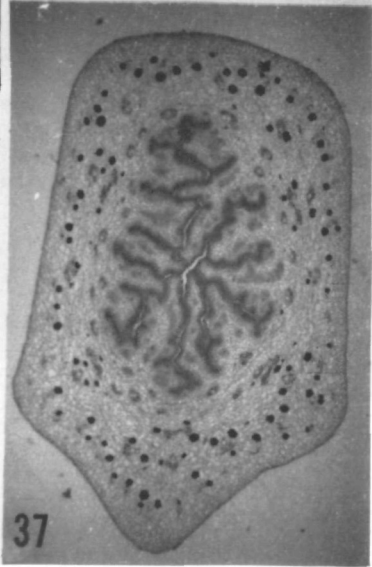
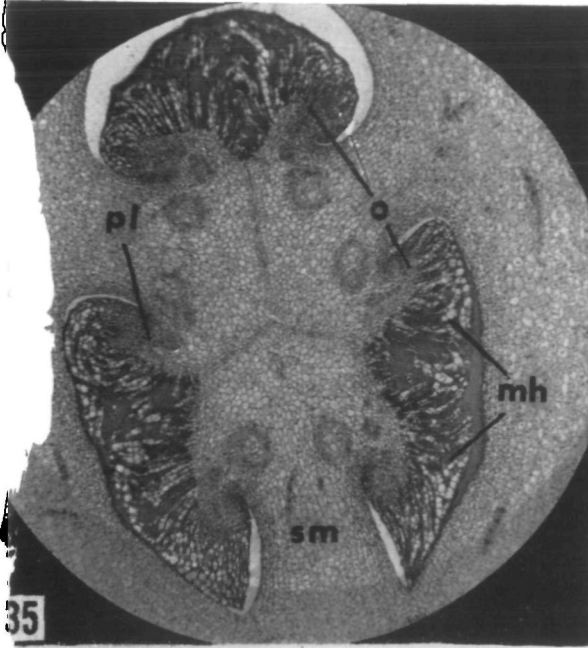
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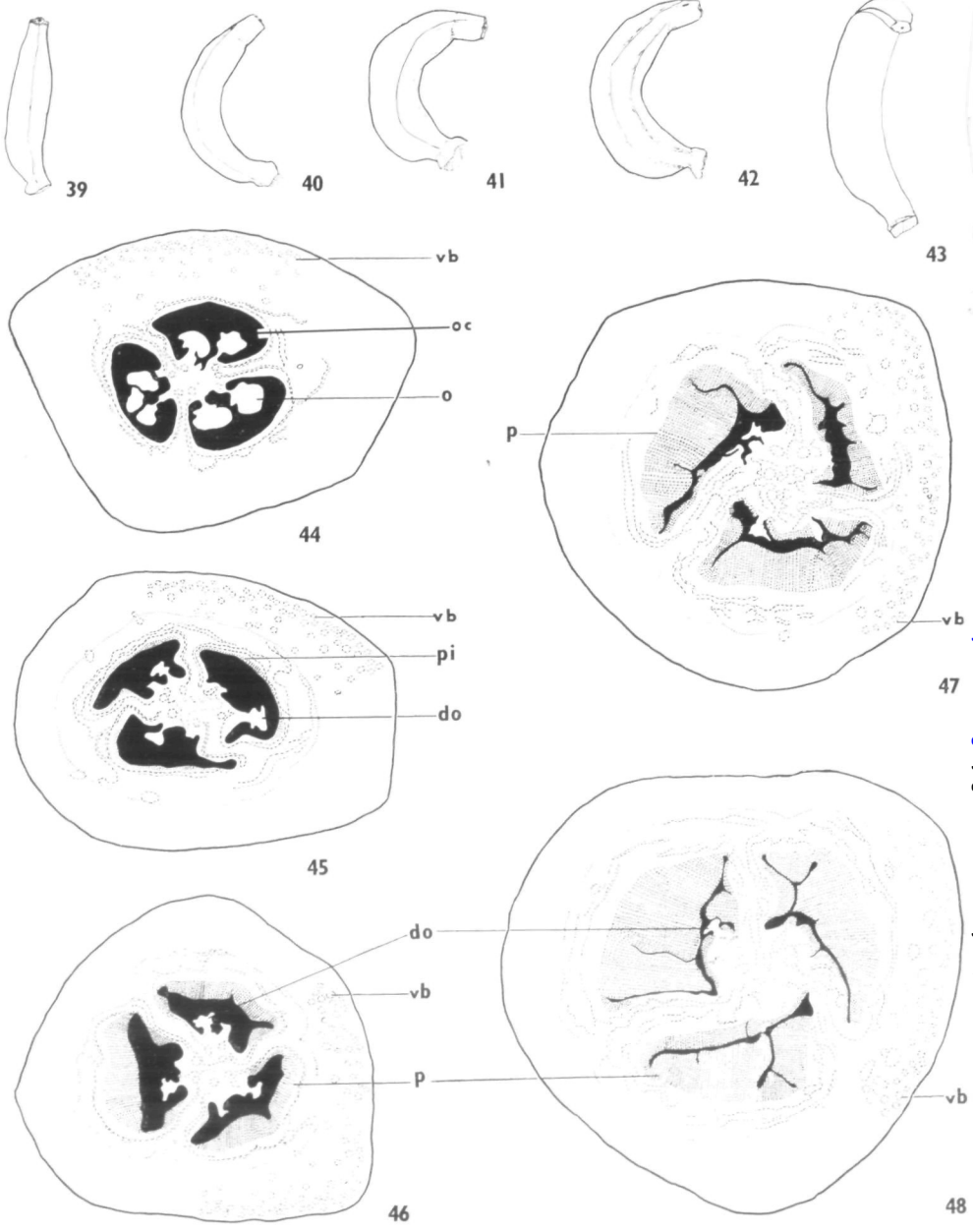
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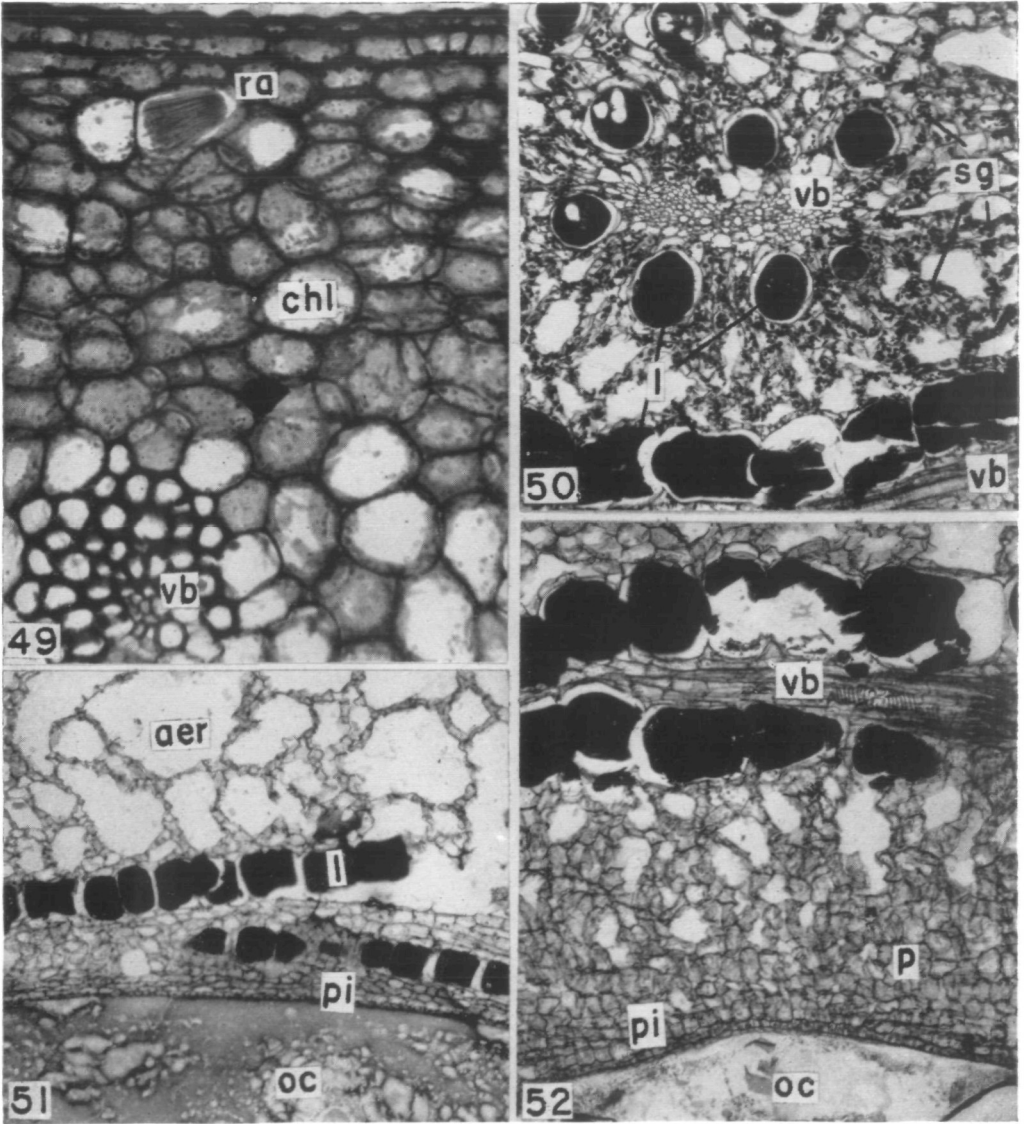


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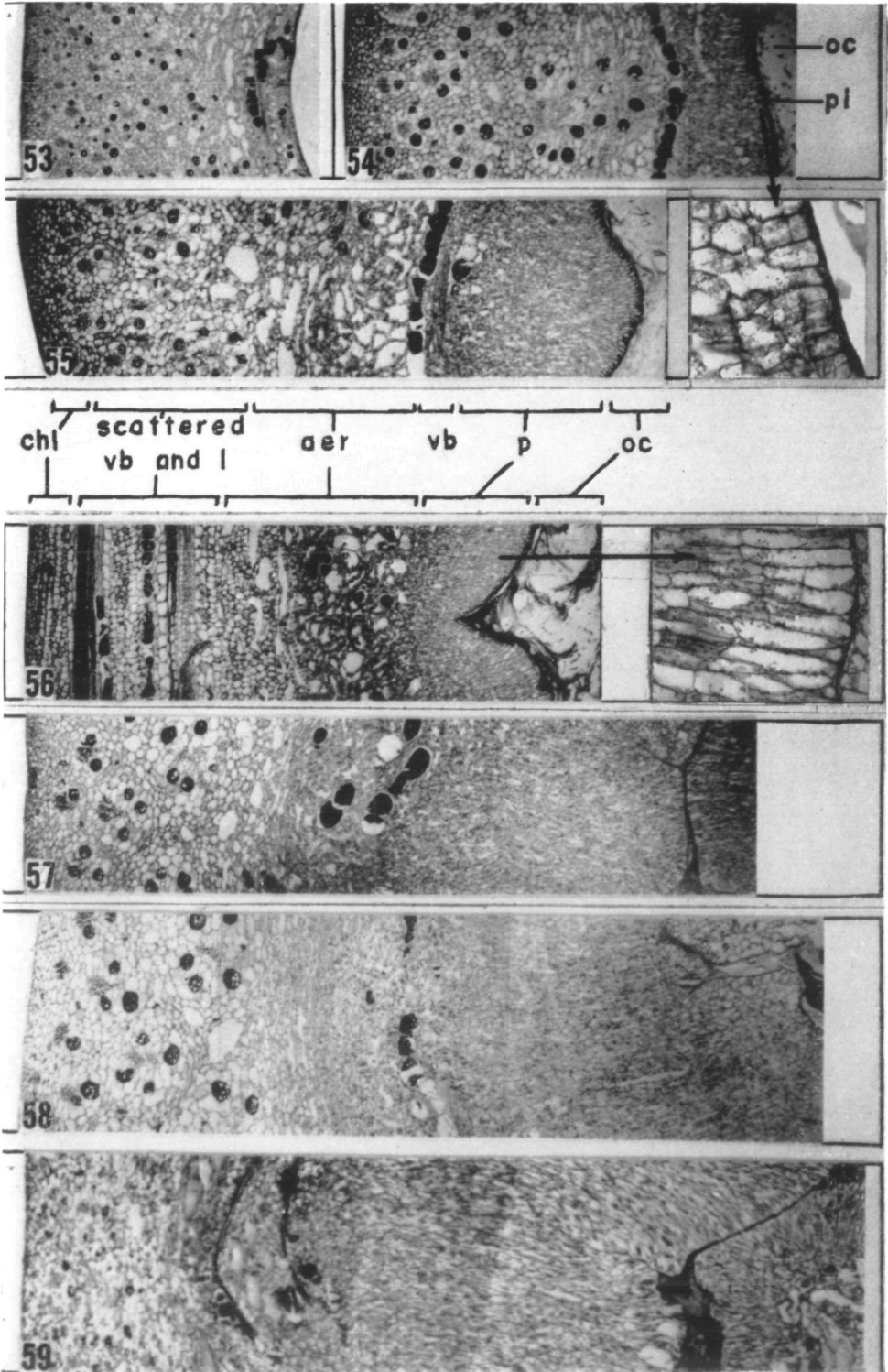


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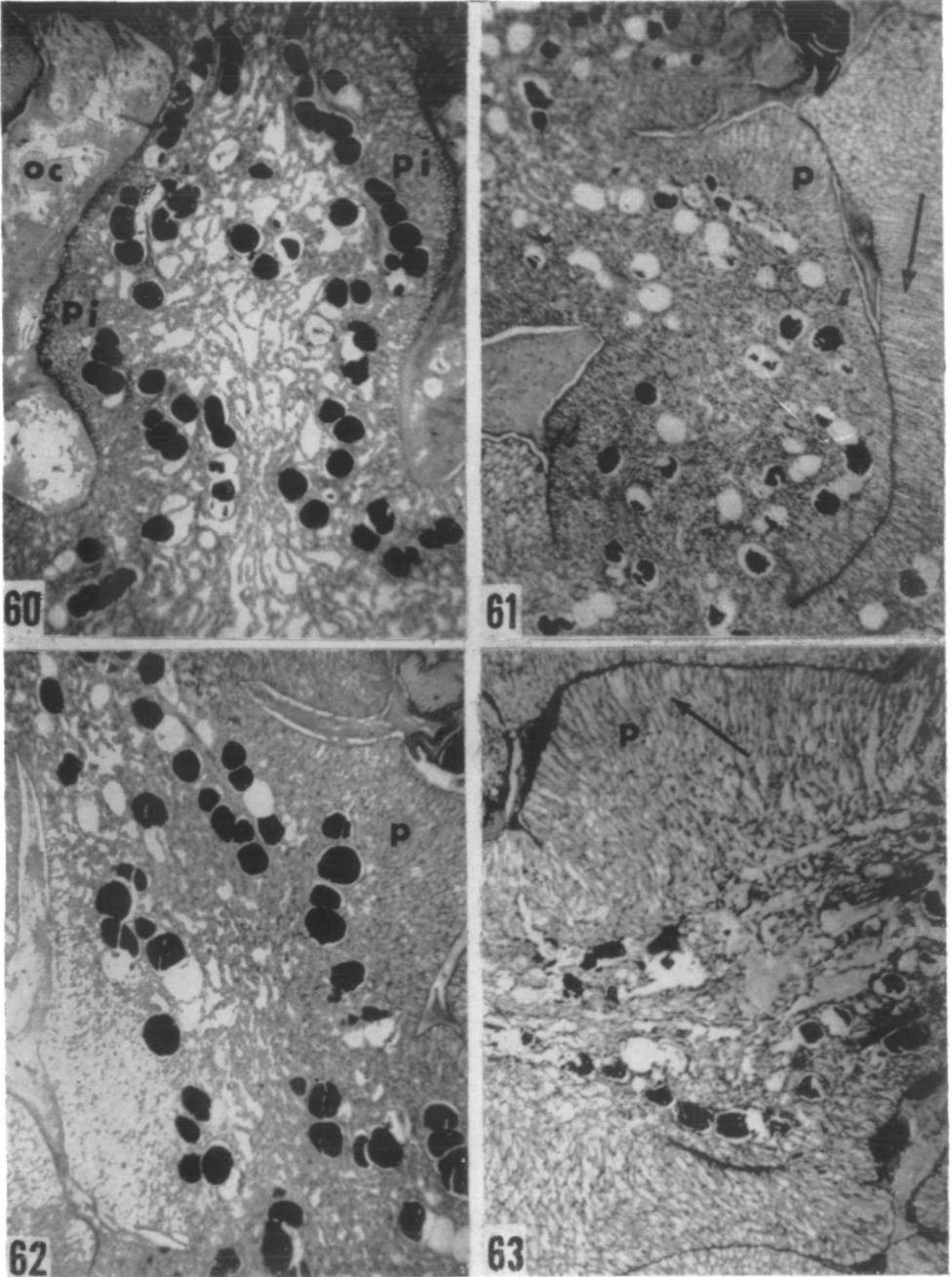
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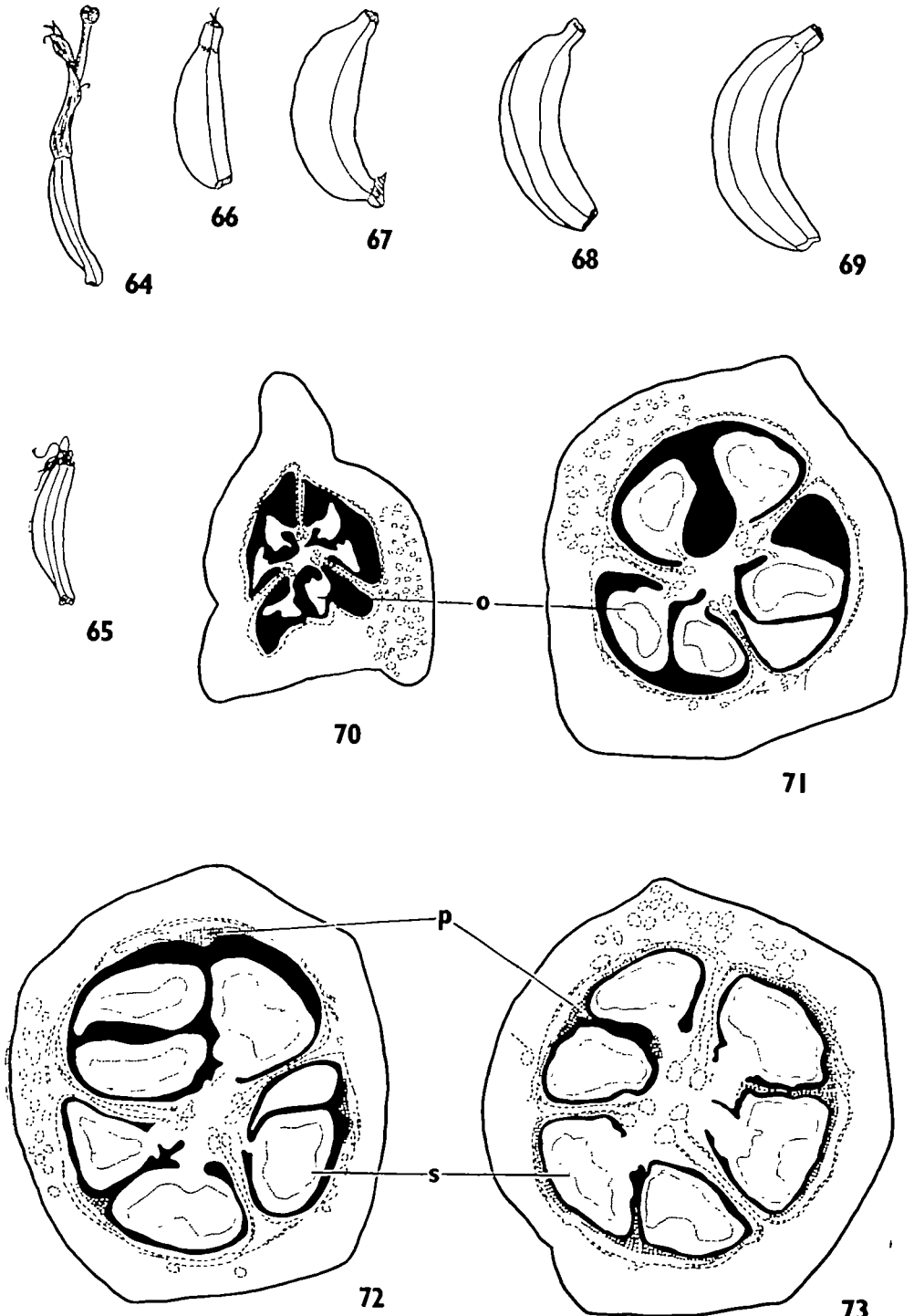
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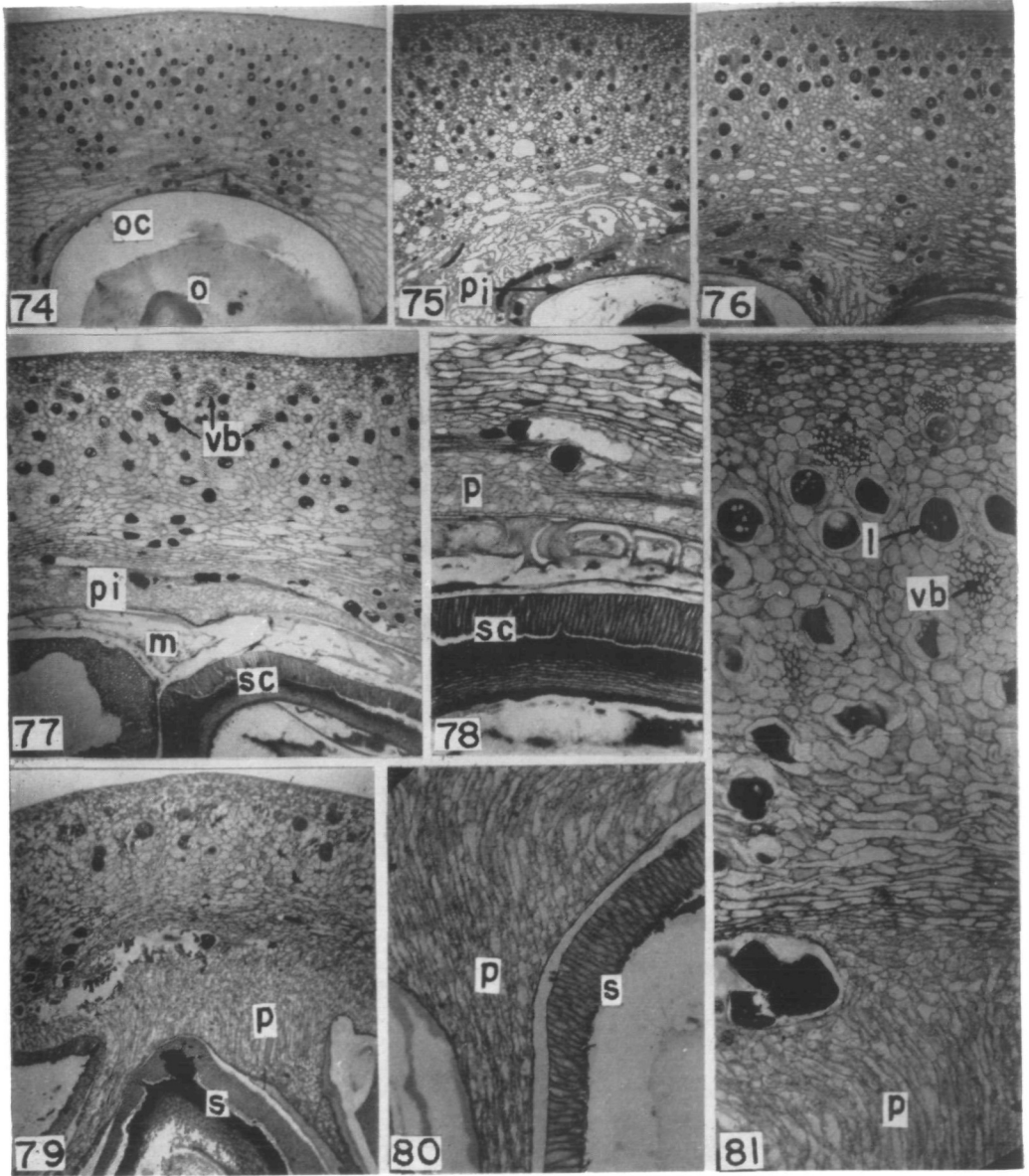


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PLATE 7

- FIGS. 49-52. Structure of the ovary wall of a parthenocarpic banana (*M. acuminata* c.v. Pisang lilin).
- FIG. 49. Outer region of the ovary wall (at emergence) enlarged to show the raphides, chlorenchyma and a vascular bundle.
- FIG. 50. The middle region of the ovary wall enlarged to show the vascular bundles surrounded by latex cells.
- FIG. 51. Innermost region of the ovary wall with aerenchyma, latex cells and the pulp-initiating cells.
- FIG. 52. Same as Fig. 51 but at 2 weeks after emergence. Note the increase in the number of cells in the pulp-initiating zone.

PLATE 8

- FIGS. 53-59. Development of a parthenocarpic banana (*M. acuminata* c.v. Pisang lilin).
- FIGS. 53-55. Transverse sections of parts of pericarp at 0, 2, and 4 weeks after emergence. (Inset to Fig. 55, indicated by arrow, shows first divisions in the subepidermal cells of the inner pericarp which initiate the formation of pulp.)
- FIG. 56. Longitudinal section of pericarp 4 weeks after emergence. Note the irregular invasion of the ovarian cavity by the pulp. (Inset to Fig. 56, indicated by arrow, shows the radial enlargement of pulp cells as the pulp invades the ovarian cavity.)
- FIGS. 57-59. Transverse sections of the pericarp at 8, 12, and 15 weeks after emergence. Note the great increase in the pulp and the compression of the rind.

PLATE 9

- FIGS. 60-63. Changes in the septa during fruit development (*M. acuminata* c.v. Pisang lilin).
- FIG. 60. Transverse section of a septum 2 weeks after emergence. Note the pulp-initiating cells and an arrow which points to elongated pulp cells (cf. inset to Fig. 56).
- FIGS. 61-63. Same as above but 8, 12, and 15 weeks after emergence. The gradual increase in the amount of pulp is clearly to be seen.

PLATE 10

- Structure and development of a seeded banana (*M. acuminata* subsp. *burmannica*).
- FIGS. 64-69. Outline diagrams of the fruit at 0, 1, 2, 4, 8, and 12 weeks after emergence respectively.
- FIGS. 70-73. Transverse sections of the fruit at 0, 2, 4, and 8 weeks after emergence. Note the scanty pulp around the locules and the meagre growth of pulp between the seeds in Fig. 73.

PLATE 11

- Development of a seeded banana (*M. acuminata* subsp. *burmannica*).
- FIG. 74. Part of the ovary wall at emergence.
- FIGS. 75-76. Transverse sections of part of the pericarp of 1- and 2-week-old fruits respectively. A marked expansion of the cells of the pericarp is to be seen.
- FIGS. 77-78. Sections of a 4-week-old fruit magnified to show the pulp-initiating cells. Part of the seed coat, the sclerenchymatous layer, is also visible.
- FIG. 79. A portion of the transverse section of the pericarp 8 weeks after emergence showing the prominent ingrowths of the pulp between the seeds.
- FIG. 80. Enlarged view of the pulp cells in the region of the ingrowth.
- FIG. 81. Transverse section of a part of the pericarp of an 8-week-old fruit magnified to show the cellular details.