# STUDIES IN MUSACEAE—1. *MUSA CARDIOSPERMA* SP. NOV., A FOSSIL BANANA FRUIT FROM THE DECCAN INTERTRAPPEAN SERIES, INDIA

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## ABSTRACT

The paper deals with a petrified fruit of banana from the Deccan Intertrappean beds of Mohgaon Kalan (22° 1′ N; 79° 11′ E) in district Chhindwara, M.P. India. It is the first definite fossil record of *Musa* L. (sensu CHEESMAN, 1947b). It has been referred to the section *Musa* (= *Eumusa*) of the genus *Musa* L. sensu CHEESMAN, LOC. CIT.). However, being of Late Cretaceous or Early Eocene in age, it shows some morphological differences with the living allied species of the genus. These differences may be of some value in unfolding the evolutionary history of the genus.

## INTRODUCTION

*MUSA* L. is a moderately large genus distributed in the moist tropical forests of S.E. Asia and many islands of the Pacific ocean. In recent years much work on the taxonomy and cytogenetics of *Musa* has been done particularly in the Imperial College of Tropical Agriculture, Trinidad. As a result of these studies Cheesman (1947b) has divided this genus into two genera, viz., *Musa* L. and *Ensete* Horan. This division was, however, opposed by Chakravorti (1951) who suggested that *Ensete* should be considered as a sub-genus of *Musa* L.

So far the only known definite record of the old genus *Musa* is the report of *Musa enseteformis* Berry (1925) from the Tertiary of Colombia. But the fossil seeds of *M. enseteformis* belong to *Ensete*. As such I have renamed *Musa enseteformis* Berry as *Ensete berryi* nom. nov. (JAIN, 1960). The present finding of the petrified fruits of banana is the only definite record of *Musa* L. (SENSU CHEESMAN) as a fossil.

## MATERIAL AND METHOD

The material was collected from the Deccan Intertrappean beds of Mohgaon Kalan (22° 1′ N; 79° 11′ E) in district Chhindwara, Madhya Pradesh, India. The present study is based on 10-12 well preserved petrified fruits. The fruits were embedded in two pieces of chert possibly belonging to one parent piece. On breaking and cutting the chert the fruits were cut in various planes. On careful piecing together only two almost complete fruits could be restored from which the measurements of the fruit were taken. One of these fruits and a few fragments of the other specimens were cut and made into thin sections for studying the anatomical details, while the other more or less complete specimen has been retained for the museum to serve as the holotype for the species. From a few other ill-preserved specimens which were unsuitable for other morphological studies, the seeds were extracted by hammering the chert on the other side. In this way about 70-80 seeds were recovered, most of which were injured at places. Only about 25 seeds, coming from different fruits were without apparent injuries. These form the basis for measurements and the study of surface features. Later on some of these seeds were ground into thin sections for studying their morphological details.

## DIAGNOSIS

**Genus** — ***Musa* L.**
**Section** — ***Musa* (=Eumusa of Cheesman 1947b)**
**Species** — ***M. cardiosperma* sp. nov.**

Pls. 1-4, Figs. 1-31; Text-figs. 1-33

Fruits about 10-12 cm. long, 1·2-9·5 cm. in diameter, roughly trigonous with rounded angles or more or less circular in cross section; apex ending abruptly into a short narrow acumen, measuring about 0·5-0·7 cm. in height; base gradually tapering into a short stalk, measuring about 1-1·5 cm. in length, curved at the extreme base. No remains of perianth either at the base or at the apex. Pericarp about 1-1·5 mm. in thickness, thicker in the stalk region; epicarp smooth.

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Seeds arranged somewhat spirally in three vertical rows, one row in each locule, about 12-15 per locule. Each seed shaped more or less like a fist appearing heart-shaped in longitudinal section; (5·5)-6·5-(8) mm. in height (4)-5·5-(7) mm. in width at the widest part and (3)-4·2-(5) mm. in diameter at the waist; general surface minutely striated; abaxial surface more or less convex, rectangular and provided with a shallow transverse groove dividing it externally into 1/3 basal and 2/3 apical part; base more or less semi-circular with prominent hilum and a micropyle situated in a shallow depression in the centre; depression slanting on the adaxial side; adaxial side more or less conical, steeply slanting towards the apex; apical portion more or less flattened with a narrow edge; seed coat highly thickened round the 'collar'. Embryo large, more or less flask-shaped, circular in cross section with its basal part hanging into the albuminous seed cavity, the latter usually empty.

*Holotype* — B.S.I.P. No. 31654.

*Locality* — Mohgaon Kalan, Distt. Chhindwara, M.P. India.

*Horizon* — Deccan Intertrappean Series.

*Age* — Early Eocene.

## DESCRIPTION

### External Morphology

The complete fruit measures about 10-12 cm. in length and about 1·2-1·5 cm. in diameter. It tapers gradually into a short stalk which measures about 1-1·5 cm. in length and is curved at the extreme base (Pl. 1, Figs. 1-2; Text-fig. 1). At the apex the fruit tapers rather abruptly into a short more or less pointed and curved acumen measuring about 0·5 to 0·7 cm. in height (Pl. 1, Fig. 1; Text-fig. 1). There are no remnants of any perianth either at the apex or at the base of the fruit. Externally the fruit is devoid of any hairs, papillae, projections or appendages of any kind or any surface markings. Wherever the epicarp is intact, the surface of the fruit is quite smooth (Pl. 1, Fig. 3; Text-fig. 1), but it appears to be longitudinally striated where the epicarp is destroyed (Pl. 1, Fig. 4; Text-fig. 2a).

In cross section, the fruit is roughly trigonous with rounded angles and more or less convex sides (Pl. 1, Fig. 5; Text-fig. 2b) or more or less circular and variously compressed during fossilization (Pl. 1, Fig. 6). The fruit shows no signs of dehiscence nor have any dehisced fruits been seen and the seeds are always found *in situ*.

The pericarp is quite thick (Pl. 1, Figs. 5-8; Text-figs. 3-4) measuring about 1 mm. at the sides and about 1·5 mm. at the corners. It is more thickened in the stalk region than in the main body of the fruit (Pl. 1, Figs. 7-8; Text-figs. 3-4).

The axis of the fruit is poorly preserved in the stalk region and represented by just a few traces in the body of the fruit (Pl. 1, Figs. 7-8; Text-figs. 3-4). Similarly the septae are represented by a few ill-defined traces in the body of the fruit (Pl. 1, Fig. 7; Text-Fig. 3) and cannot be seen in the stalk region where the pericarp is closely applied to the axis (Pl. 1, Fig. 8; Text-fig. 4).

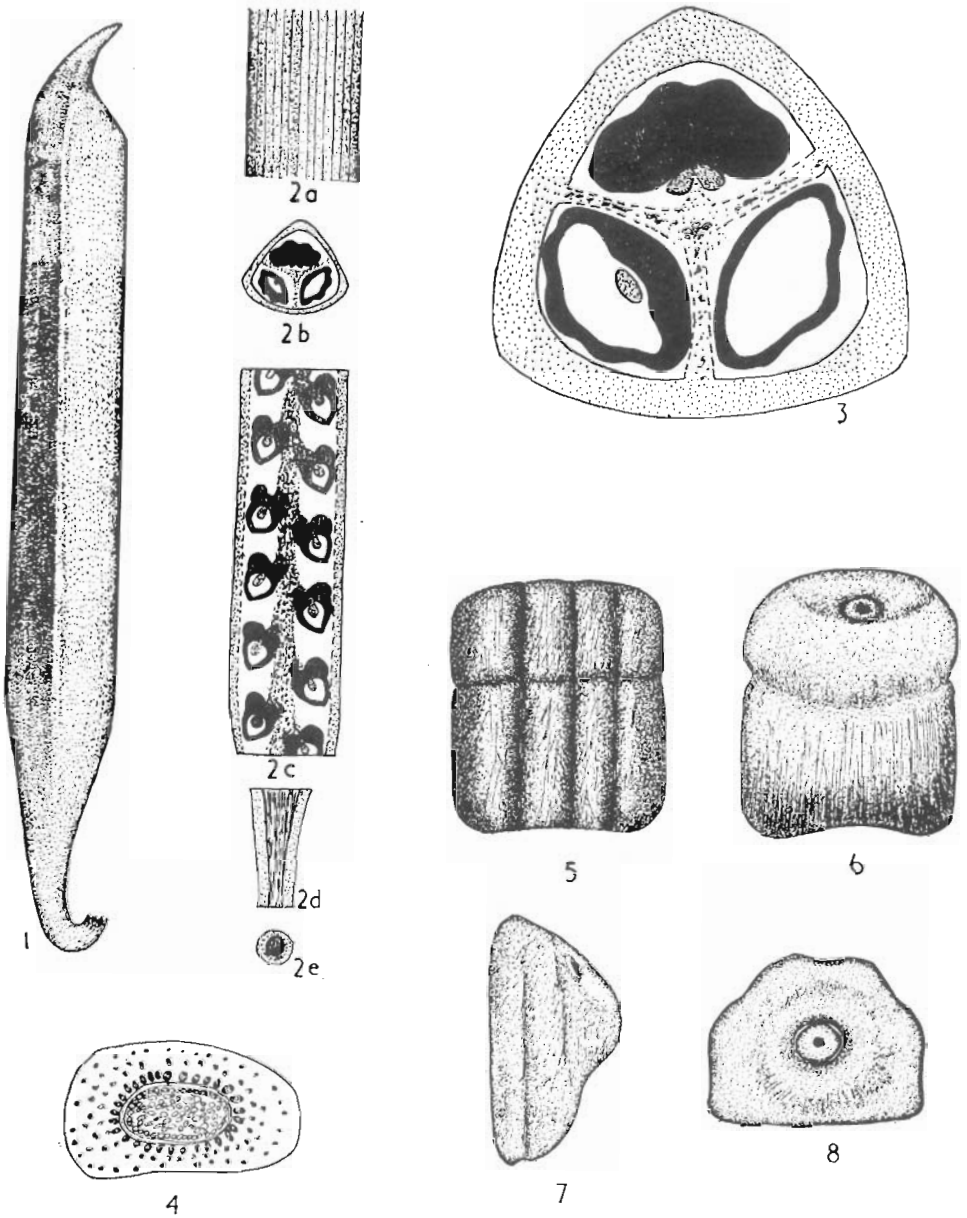
The fruit contains many seeds arranged somewhat spirally in three vertical rows, one row in each locule (Pl. 1, Figs. 1 and 5-7; Text-Figs. 2b, 2c and 3). The seeds, though filling each locule, show no sign of compression and the space left between the seeds is filled with a non-cellular matrix (Pl. 1, Fig. 7; Text-fig. 3). The exact number of seeds is difficult to ascertain but estimating from Plate 1, Figure 1, it appears to be 12-15 per locule. Rarely some abortive seeds are also met with (Pl. 1, Fig. 6), indicating that the number of ovules was probably a little higher than the actual number of seeds produced.

The seeds are not seen directly attached to the axis, but as seen in cross section of the fruit, the hila of the seeds are directed towards the axis indicating central attachment of the seeds or axile placentation of the ovary (Pl. 1, Fig. 6; Text-fig. 3).

Most of the seeds are white but some are reddish-grey. They vary somewhat in size and shape measuring 5·5-8 mm. (average* 6·5 mm.) in height, 4-7 mm. (average 5·5 mm.) in width and 3-5 mm. (average 4·2 mm.) in diameter. Accordingly the shape of the seeds also varies, e.g., the abaxial surface is squarish to rectangular in outline. When rectangular, as is mostly the case, the height is usually more than the width.

The abaxial side of the seed is somewhat convex and divided by an indistinct shallow transverse groove into 1/3 basal part and 2/3 apical part (Pl. 1, Fig. 9; Text-fig. 5). Also running at right angles to this transverse groove, there are 3-4 similar longi-

*These measurements are based on 25 seeds.




*Musa cardiosperma* sp. nov.

TEXT-FIGS. 1-8 — 1, diagrammatic reconstruction of the fruit. × 1. 2, diagrammatic illustration. 2a, surface of the fruit from where the epicarp is missing. 2b, a cross section of the fruit. 2c, median longitudinal section of the fruit. 2d, median longitudinal section of the stalk. 2e, cross section of the stalk. × 1. 3, diagrammatic cross section of the fruit. × 5. 4, diagrammatic cross section of the stalk. × 5. 5, diagrammatic abaxial view of the seed. Note the transverse and longitudinal grooves. × 5. 6, diagrammatic adaxial view of the seed. × 5. 7, diagrammatic lateral view of the seed. × 5. 8, diagrammatic basal view of the seed. × 5.

tudinal grooves on the abaxial surface. Apparently such longitudinal grooves are absent from the adaxial surface of the seed. But a cross section of the seed (PL. 1, FIG. 5; TEXT-FIG. 3) shows similar grooves under the adaxial thickening of the seed coat indicating the initial presence of such grooves later on masked by excessive thickening of the seed coat or perhaps due to adnation of raphae with the seed coat.

The general surface of the seed is finely striated (TEXT-FIGS. 5-8). Opposite the transverse groove, the adaxial side is highly thickened and somewhat raised (PLS. 1-2, FIGS. 10 and 12; TEXT-FIGS. 6 and 8). The 1/3 basal part of the seed lodges a big hilum and a small micropyle at the distal end (PLS. 2-3, FIGS. 11, 18-20; TEXT-FIGS. 6-7). The area lodging the hilum and the micropyle is slightly depressed in the centre (PL. 2, FIG. 11; TEXT-FIG. 7). The depression of the hilum is somewhat slanting towards the axis making the attachment of the seed possible without further elongation of the raphae (PL. 2, FIG. 12; TEXT-FIG. 7). The adaxial side of the seed is somewhat conical in shape and above the transverse groove it is obliquely flattened towards the apex so much so that at the apex only the seed projects a little (PL. 2, FIG. 12; TEXT-FIG. 7). However, the projection of the seed coat (PL. 3, FIG. 22; TEXT-FIGS. 26-28) is not conspicuous enough to be compared to an appendage on the seed.

### Anatomy

(a) *Pericarp* is thick and fleshy. No cuticle or stomata have been observed on the external surface. Internally the pericarp consists of a more or less homogeneous parenchymatous tissue with a few tannin cells and many fibrous and vascular bundles.

The cells of the ground tissue of the pericarp are thin-walled parenchymatous, circular in cross section and vertically elongated as seen in longitudinal section (PL. 2, FIGS. 13-15; TEXT-FIGS. 9 and 11). Sometimes the cells appear to be tangentially flattened in the pericarp of the main body of the fruit (PL. 2, FIG. 15; TEXT-FIG. 10). The outer epidermis consists of the smallest cells in the whole pericarp (PL. 2, FIG. 14; TEXT-FIGS. 10-11). There is no distinct hypodermis but the outermost 3-4 layers of cells below the epidermis consist of cells with walls slightly thicker than those of the inner layers (TEXT-FIGS. 10-11). Rarely, scattered among the cells of the ground tissue, are seen some cells filled with dark brown contents (TEXT-FIG. 10). These may be tanin cells. The inner limits of the pericarp are not clear and appear to merge with the non-cellular matrix inside the fruit (PL. 2, FIGS. 13-14; TEXT-FIG. 11).

The fibrous bundles and the vascular bundles are arranged in a definite order in the pericarp. The fibrous bundles lie towards the outer periphery (PL. 2, FIG. 13; TEXT-FIG, 12) which are responsible for the longitudinally striated appearance of the pericarp from outside when the epicarp is destroyed. The main vascular bundles lie towards the inner periphery of the pericarp. In between the fibrous bundles and the vascular bundles lie smaller vascular bundles. Most of these smaller vascular bundles have no fibrous sheath on the xylem pole while a few others have practically no fibrous sheath on either the xylem or the phloem pole (PL. 2, FIG. 17; TEXT-FIGS. 15-16).

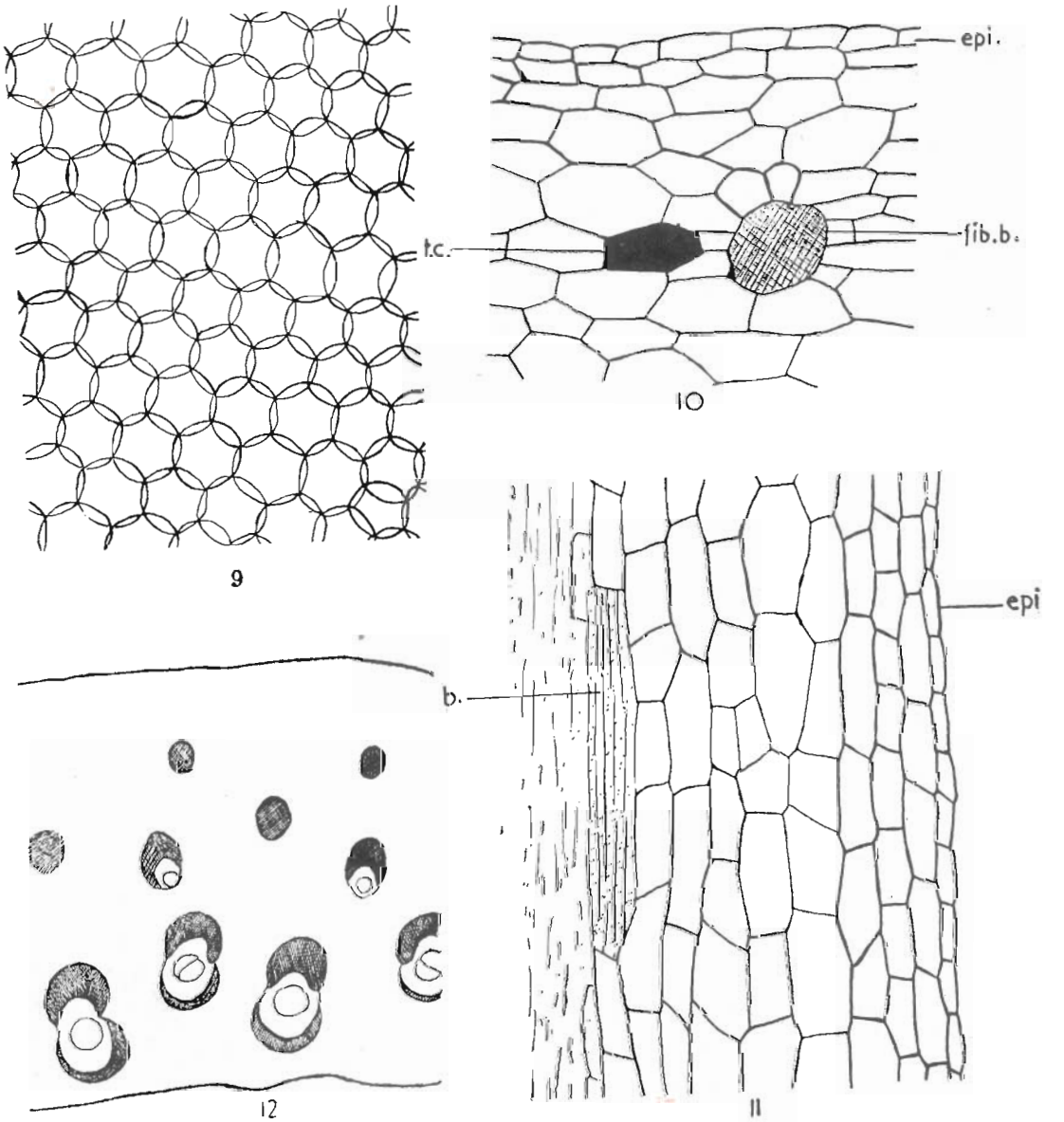
The fibrous bundles are variable in size ranging from 40-150 $\mu$ in diameter. As seen in some cross sections of pericarp of the body of the fruit two or three cells of the pericarp lying just above the fibrous bundles are slightly thickwalled and are never tangentially flattened even where the rest of the cells of the pericarp are flattened (TEXT-FIG. 10). The elements of the fibrous bundles are not very well preserved. However, each fibre measures about 8-12 $\mu$ in diameter and has a small lumen in the centre (PL. 2, FIG. 15; TEXT-FIG. 13). The fibres are very short in length but the exact length of fibres could not be determined due to poor preservation. No inter-fibre pits have been detected.

A typical vascular bundle is elliptical to dumbbell-shaped in cross section being constricted near the junction between the xylem and the phloem (PL. 2, FIG. 16; TEXT-FIG. 14). The inner half of each bundle is slightly wider than the outer. A typical bundle measures about 300 $\mu$ in radial diameter and about 150 $\mu$ in tangential diameter at the widest part. The size of the vascular bundles gradually decreases towards the outer periphery of the pericarp where they measure about 150 $\mu$ in either diameter.

The dominant feature of the vascular bundle is a single conspicuously large conducting element in the metaxylem (PL. 2,

FIG. 16; TEXT-FIG. 14). Sometimes two such elements are seen due to overlapping end walls cut together (PL. 2, FIG. 13; TEXT-FIG. 15). Whether the conducting elements had perforated end walls or not, could not be determined due to poor preservation.

This conducting element is surrounded by 1-2 layers of ill-preserved parenchymatous

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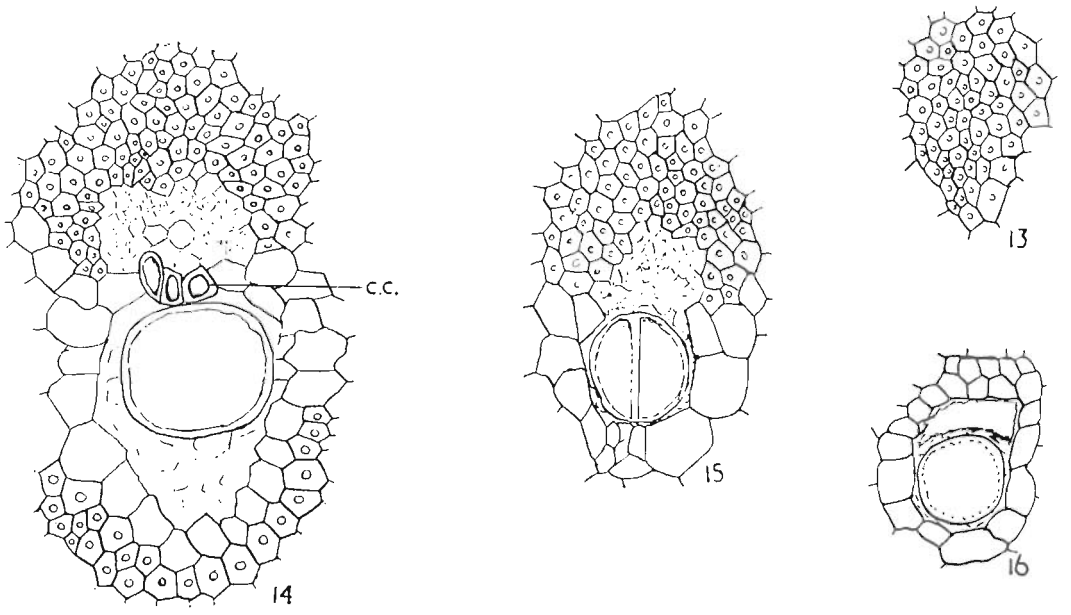
TEXT-FIGS. 9-12— 9, cross section of the cells of ground tissue of the pericarp from the stalk region of the fruit. × 125. 10, cross section of the outer region of the pericarp of a fruit showing ground tissue of tangentially flattened cells, tannin cells (t.c.) and the relation of fibrous bundles (fib.b.) with the adjoining cells. × 125. 11, longitudinal section of the pericarp showing vertical elongation of the cells of the ground tissue. epi.=epidermis and b.=vascular bundle. × 125. 12, semidiagrammatic cross section of the pericarp showing the distribution of fibrous and vascular bundles. × 40.

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TEXT-FIGS. 13-16 — 13, cross section of a fibrous bundle. × 280. 14, cross section of a typical vascular bundle. c.c. = "Commissural connective" or the "late metaxylem elements". × 250. 15, cross section of a vascular bundle with practically no fibrous sheath on the xylem pole. × 250. 16, cross section of a small vascular bundle with no fibrous sheath. × 250.

cells. Between this xylem parenchyma and the phloem are 2-3 small thick-walled elements (PL. 2, FIG. 16; TEXT-FIG. 14). Such elements have been described as "commissural connectives" by Skutch (1927) and "late metaxylem elements" by Tomlinson (1955). No protoxylem elements have been seen.

The phloem is not preserved in these bundles. The bundles are sheathed laterally by one or sometimes two layers of parenchymatous cells. The sheaths are completed on the xylem and phloem poles by fibrous cells. The fibrous sheath on the phloem pole is much more developed than on the xylem pole. On the xylem pole it comprises only 1-2 layers of fibrous cells. Between this fibrous sheath on the xylem pole and the metaxylem the space is filled with shapeless parenchymatous tissue which represents partly the protoxylem and partly a parenchymatous sheath.

The structure of the vascular elements could not be studied because of poor preservation. The composition of the fibrous sheath is identical to that of a fibrous bundle described above.

(b) *Axis*, as pointed out above, is poorly preserved and represented only by a few ill-defined traces of tissue in the main body of the fruit. However, in the stalk region, outlines of the vascular bundles are vaguely marked although the cellular details are not clear (PL. 1, FIG. 8; TEXT-FIG. 4).

(c) *Septa* are not seen in the stalk region. In the body of the fruit they are represented by delicate traces of tissue. No cellular details are available.

(d) *Seed* — A cross or a longitudinal section of the seed taken from any region shows a thick seed coat enclosing an albuminous seed cavity with a well formed embryo near the hilum (PL. 3, FIGS. 22-25; TEXT-FIGS 17-28).

The seed coat is not uniformly thickened. It is so heavily thickened in the hilar region so that only a narrow, small canal-like space is left in which lies the narrow part of the embryo. Thus a 'collar' is formed round the latter (PL. 3, FIGS. 23-25; TEXT-FIGS.

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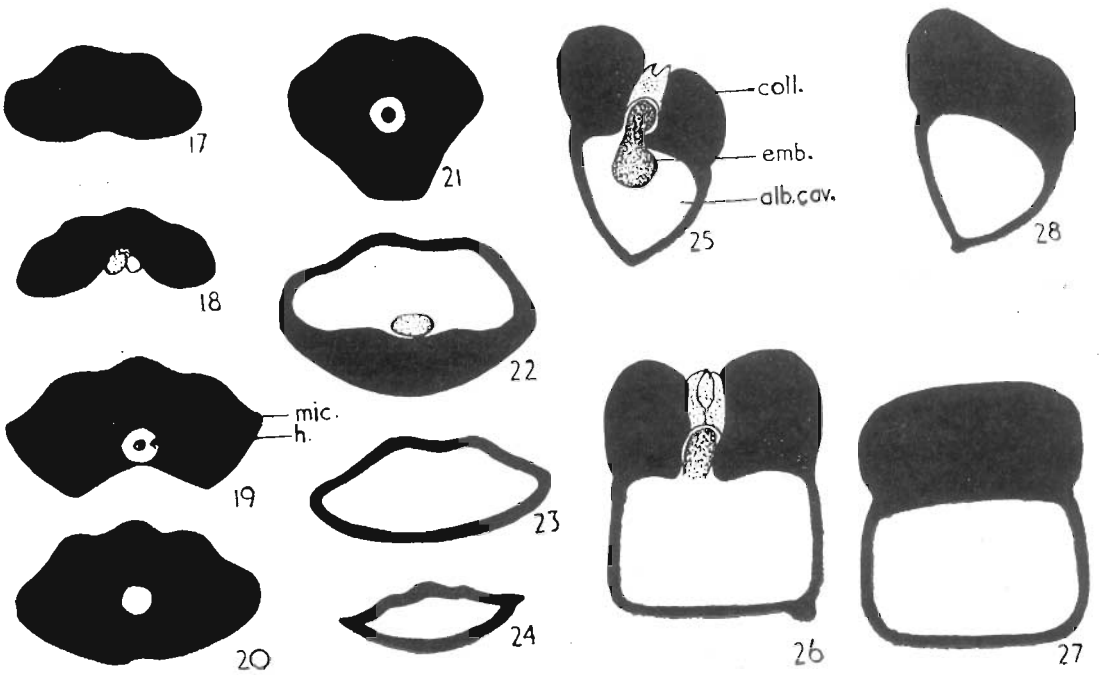



*Musa cardiosperma* sp. nov.

TEXT-FIGS. 17-28 — 17-24, serial cross sections of the seed. h.=hilum and mic.=micropyle. × 5. 25, median longitudinal section of the seed cut parallel to the radial axis alb. cav.=albuminous cavity, emb.=embryo and coll.='collar'. × 5. 26, median longitudinal section of the seed cut right angles to the radial axis showing the vascular supply in the hilar region. × 5. 27, tangential longitudinal section of the seed cut at right angles to the radial axis. × 5. 28, tangential longitudinal section of the seed cut parallel to the radial axis. × 5.

20-21 and 25-26). Due to anatropous orientation of the seed, the thickness of the 'collar' round the hilum is not uniform.

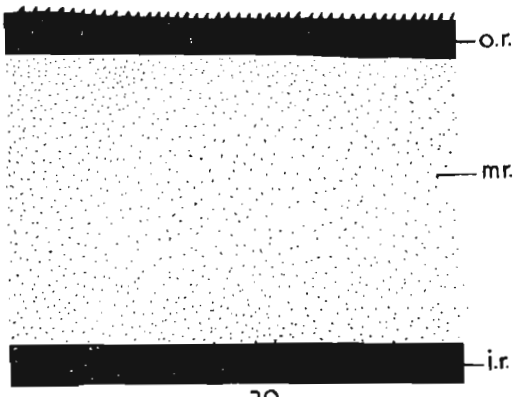
The seed coat consists of three regions, viz., outer, middle and an inner region (PL. 4, FIGS. 26-29; TEXT-FIG. 29). The outer and inner regions are made up of compactly arranged thick-walled cells, whereas the middle is composed of mostly ?thin-walled cells.

In the outer region the epidermis consists of highly thick-walled cells with small lumina (PL. 4, FIG. 28; TEXT-FIG. 30). The wall of almost every alternate cell is radially drawn out into a pointed papilla-like projection. This papillate epidermis renders the seed coat finely striated in surface view. The hypodermis, as seen in a cross section, consists of 1-2 layers of thick-walled isodiametric stone cells with narrow lumen. The inner layers of this region consist of compactly arranged thick-walled polygonal cells with fairly wide lumina. The inner limit of this outer region is marked by the presence of 1-2 layers of thick-walled tangentially elongated cells.

The middle region is variable in thickness. The exaggerated thickening of the seed coat in the hilar region is due to the expansion of this middle region. It consists of mostly ?thin-walled, round to oval cells with a few angular and thick-walled cells scattered among them (PL. 4, FIG. 27; TEXT-FIG. 31).

The inner region is essentially similar to the outer region in structural details with the only difference that the inner epidermis is not papillate like the outer one. The rest of the details are the same.

The vascular supply of the seed is detected only in the hilum region where it makes a small loop parallel to the abaxial surface of the seed before it enters the seed coat (PL. 3, FIG. 25; TEXT-FIG. 26). It has, however, not been seen inside the seed coat.

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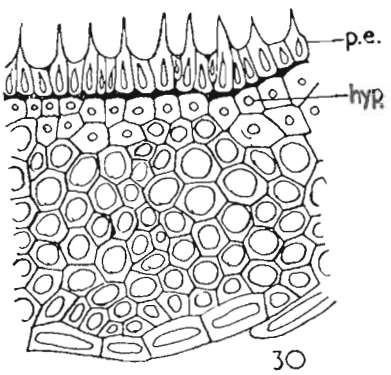


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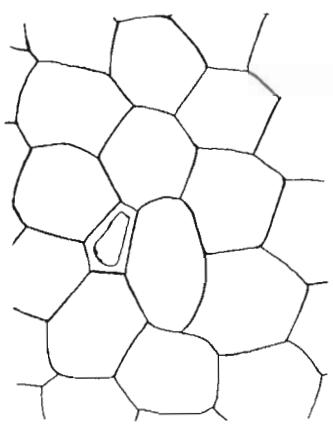

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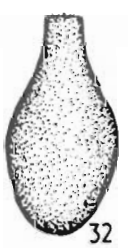

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TEXT-FIGS. 29-33,—29, cross section of the seed coat showing the three regions, viz., outer (o.r.), middle (m.r.), and inner (i.r.) regions. × 40. 30, magnified cross section of the outer region of the seed coat papillate epidermis (p.e.), highly thick-walled hypodermis (hyp.) and the cells of the inner layer. × 300. 31, few cells of the middle region of the seed coat. × 225. 32, entire embryo. × 10. 33, cross section of the embryo. × 10.

In certain angiospermous ovules, there is a space between the outer and an inner integument (MAHESHWARI, 1950). In these fossil seeds there is a narrow longitudinal space in the middle of the seed coat all along the abaxial side (PL. 3, FIG. 23).

Since there are no traces of a second integument or the inner seed coat, the space in the seed coat of these fossil seeds is not homologous to the inter-integumentary space. As this space is on the abaxial side of the seed and the raphae, if at all, seem to have had fused with the seed on the adaxial side, this space possibly does not represent the course of the vascular supply in the seed coat. On the other hand it only seems to be there due to breakage of the cells of the middle layers of the seed coat.

The embryo is fairly large and flask-shaped in outline (PL. 4, FIG. 30; TEXT-FIG. 32). Since no cellular details are present, no structural differentiation, except the form, can be made out. From its narrow end, that lies in the seed cavity surrounded by the 'collar', it hangs with its broader part into the albuminous seed cavity (PL. 3, FIG. 23; TEXT-FIG. 25). It measures about 3 mm. in length and 1·5 cm. in diameter at its broadest part. In cross section it is more or less circular or elliptical due to compression (PL. 4, FIG. 31; TEXT-FIG. 33). The seed cavity is empty or filled with a non-cellular matrix in the fossil. But whether it was filled with endosperm or perisperm of cellular or non-cellular composition, cannot be determined in the fossil stage.

## DISCUSSION

### Morphology

From the above description it is clear that even though there are only delicate traces of three septa and an axis, the fruit had developed from a trilocular syncarpous ovary. Also the large number of seeds, each having the hilum and the micropyle situated side by side, suggests that there were many anatropous ovules per locule arranged in one vertical series in each locule. Further, even though the seeds are not found actually attached to the axis, the fact that their hila were directed towards the axis suggests that the placentation of the parent ovary was axile. However, the absence of any remains of the perianth at the base or the apex of the fruit makes it difficult to determine whether

the fruit had developed from a superior or an inferior ovary. But the distribution of the vascular bundles in the pericarp does not represent the characteristic arrangement of the bundles of a superior ovary where we find the presence of distinct dorsal bundles each representing the mid vein of a carpel. Therefore, it is possible that probably the fruit had developed from an inferior ovary.

The fruit shows no signs of dehiscence nor have any dehisced fruits been seen and the seeds are always found *in situ*. Besides, this the thick pericarp consists of parenchymatous ground tissue indicating the fleshy nature of the indehiscent pericarp supported by a large number of fibrous and vascular bundles. Thus the fruit was a berry. Also as stated above, the seeds show no sign of compression and space left in between the seeds is filled up with a non-cellular matrix. The later appears to be comparable to the pulp of modern bananas. This comparison is supported by the disintegration of the septa and the axis without the effect of crushing by the seeds and merging of the lining of the pericarp with the non-cellular matrix filling the fruit-cavity as is also the case in modern bananas (SIMMONDS, 1953).

A typical vascular bundle is of a kind termed as *Musa*-type by Solereder and Meyer (1930). But according to Tomlinson (1955) the term is inappropriate because of its wide occurrence in Scitamineae. Therefore, he has preferred the use of the term 'Scitaminean bundle', originally used by Futterer (1896). But Dr. C. R. Metcalfe (personal communication) has pointed out that such bundles occur in some palms also. Therefore even the latter term is inappropriate.

The most characteristic feature of these bundles is the single large conducting element in the metaxylem. Whether these conducting elements are vessel-members or tracheids could not be determined due to poor preservation and therefore the use of either of the above terms has been avoided in the description given above. In this connection it is important to note that in *Musa* the vessels are confined to roots only, elsewhere the conducting elements are composed of tracheids only (TOMLINSON, 1959).

As regards the morphology and terminology of the 2-3 small thick-walled elements between the metaxylem and the phloem (PL. 2, FIG. 16; TEXT-FIG. 14), they have been described as "commissural connectives" by Skutch (1927) and "late metaxylem elements" by Tomlinson (1955). Skutch, who had studied the morphology of the leaf of *Musa* found that the lateral extensions of these elements connect similar bundles laterally and, therefore, he employed the term "commissural connectives" for these elements. But Tomlinson, who had studied various vegetative organs found that they do not always behave as "commissural connectives" but remain simply as "late metaxylem elements". Therefore, the latter term appears to be more appropriate than the former.

In the morphology of the seeds the formation of a collar round the monocotyledonous embryo is an important feature characteristic of the seeds of Scitamineae. The shallow basal depression on the seed, which is slanting adaxially, brings the hilum in close contact with the axis making the axile attachment of the seeds possible without elongation of the raphae.

The seed coat is thick but it is much more thickened round the hilum. This thickening is too conspicuous to be neglected in a morphological treatment of the seeds. Apparently this thickening is due to the localized meristematic activity of the outer integument of the seed. This mode of thickening is fundamentally the same as in aril formation in the seeds of many tropical plants. But in aril formation the meristematic activity produces an extra-structure or the "third integument" on the seed (PIJL, 1955; MAHESHWARI, 1950). Whereas in these fossil seeds the divisional activity is confined to the middle layers of the outer integument so that no superstructure is formed on the seed coat and it remains a homogeneous part of the latter. Therefore, it is only an exaggerated localized thickening of the seed coat and not comparable to an aril, arillode or a caruncle.

But nothing is known about the second or the inner integument. It is risky to speculate whether it was initially there and subsequently dissolved or was not preserved in the fossil state or was totally absent. Similarly it is difficult to ascertain whether the seed cavity was filled with endosperm or nucellus (perisperm). Further the large size of the embryo indicates that the emptiness of the seed cavity may be, at least partly, due to the prior consumption of the albumen by the embryo and is not entirely due to its non-preservation in the fossil.

**Identification**

From the monocotyledonous embryo, the monocotyledonous "Scitaminean" vascular bundles scattered in the pericarp and the tricarpellary gynaecium it is evident that it is a Monocotyledon. Though the structure of the vascular bundles directs our attention at once to Scitamineae, yet according to Prof. C. R. Metcalfe (personal communication) such vascular bundles are also found in certain palms. Therefore, while dealing with palaeobotanical material it is rather risky to emphasize such an anatomical character. Taking the over all characters such as a syncarpous, tricarpellary gynaecium, many seeded fruits and albuminous seeds, it is evident that we can search for its relationship in the orders Farinosae, Liliflorae, Microspermae and Scitamineae (LAWRENCE, 1951; RENDLE, 1930; HUTCHINSON, 1959).

The thick testa, comparatively big seeds, 'collar formation' in the seeds and 'Scitaminean-type' of vascular bundles in the pericarp of the fruits, immediately suggests its Scitaminaceous affinities (HUMPHREY, 1896; NETOLITZKY, 1926; BANERJI, 1940).

The Scitamineae of Bentham and Hooker is no longer treated as a single family. It has now been split into four or more families. Generally four families are recognized to constitute this order, viz., Maranthaceae, Cannaceae, Zingiberaceae and 'Musaceae'. The other families recognized by some authors and not accepted by others are Lowiaceae, Strelitziaceae and Heliconiaceae (NAKAI, 1948; HUTCHINSON, 1959; LANE, 1955 etc.). All these families are otherwise treated under Musaceae. However, the opinion is more or less undivided regarding the recognition of Lowiaceae comprising a solitary genus, *Lowia* or *Orchidantha*. Thus in the following discussion this order is treated as comprising five families, viz., Cannaceae, Maranthaceae, Zingiberaceae, Musaceae and Lowiaceae. All the genera treated under the families Strelitziaceae and Heliconiaceae will be treated under Musaceae.

As regards the fossil fruit, the family Cannaceae can be easily eliminated because in this family the fruit is a warty capsule with a few seeds having elongated raphae and crustaceous seed coat. Maranthaceae can be eliminated by virtue of its 3-seeded fruits. Zingiberaceae is a large family but the seeds are always arillate, or 'arilloidate' (HOLTTUM, 1950). Only the genera *Costus* and *Siliquamomum* are worth considering with reference to the fossil fruit. In *Costus*, especially *Costus speciosus*, the seeds are described to possess an arillode (BANERJI, loc. cit.; NETOLITZKY, loc. cit.). In that genus there is a basal cusion on the seed that develops later into an arrillode or a caruncle. The mound-like thickening on these fossil seeds recalls the early stages of development of arillode in *Costus*. But this thickening in *Costus* is externally demarked from the seed coat whereas in the fossil seeds it remains a homogeneous part of the seed coat. Thus the thickening in the fossil seeds is morphologically different from that of the early stages of *Costus*. In *Siliquamomum tonkinense* the fruit becomes nearly as long as the fossil fruit. But the seeds in that genus have an oval or a bilobed distinct aril (WINKLER, 1930). Therefore, the structure of the seeds does not allow the inclusion of this fruit in Zingiberaceae. As regards the anatomical details of this family, the only detailed account is by Tomlinson (1955). However, his paper deals with the anatomy of vegetative parts only. If there is a correlation between the anatomy of vegetative and reproductive organs, we see that whereas the structure of vascular bundles is identical in Musaceae and Zingiberaceae (TOMLINSON, 1955, 1959), the presence of fibrous bundles near the abaxial surface of leaf-sheaths is confined to Musaceae. Similar fibrous bundles are also found towards the outer periphery of the pericarp of this fruit. Although the comparison seems distant, the anatomical considerations also do not allow its inclusion in Zingiberaceae.

In Lowiaceae the seeds have distinct aril.

The only other family of Scitamineae is Musaceae which is considered here to comprise the genera *Strelitzia*, *Ravenala*, *Heliconia* and '*Musa*'. *Heliconia*, which is confined to tropical America, has 3-seeded cocci or rarely 3-seeded indehiscent fruits. In *Strelitzia* and *Ravenala* the fruits are woody capsules with generally a distinct aril. As regards the genus '*Musa*', in the recent years it has been split into two genera, viz., *Ensete* Horan. and *Musa* L. (CHEESMAN, 1947a, b). The fruits of *Ensete* contain a relatively small number of large seeds which are rarely less than one centimeter in diameter. They are irregularly globose and smooth. Also there is, usually, a distinct basal cavity in which is lodged the hilum.

In consideration of these characteristics of *Ensete*, it is clear that this fossil fruit, bearing many small seeds with longitudinal and transverse furrows, heart-like form and with no distinct hilar cavity, cannot belong to *Ensete*. On the contrary all the fundamental morphological and anatomical characters are met with in *Musa* L. (SENSU CHEESMAN).

*Musa* L. is a genus of tropical plants characteristic of rain-forest country. Some species are characteristic plants of secondary bush, while others occur at relatively inaccessible places. They thrive naturally in the rain forests of Ceylon, India, Burma, Thailand, S. China, Indo-China, Malay Peninsula, the whole of the East Indian Archipelago, Queensland and many islands of the Pacific upto Tahiti and Hawaiian islands in the East. It is a moderately large genus, but it is difficult to state the exact number of species it comprises. In a treatise on the taxonomy of this genus, Cheesman (1947b) had identified 30-32 valid species. However, he had suspected that the genus contained 40-50 valid fertile diploid species in the wild state. His estimate has been supported by the more recent work on this genus by Chakravorti (1948a), Matuda (1950), Nakai (1948) and Simmonds (1956).

As regards the systematic arrangement of the species, Cheesman (loc. cit.) has divided them into four sections, viz., 1. *Eumusa* (= *Musa* with reference to article 32 of International Code of Botanical Nomenclature), 2. *Rhodochlamys*, 3. *Australimusa* and 4. *Callimusa*. The sections are distinguished by the differences in the number of chromosomes and the external morphology of the seeds (in *Australimusa* and *Callimusa*) or other organs of the plants (in *Musa* and *Rhodochlamys*).

In *Australimusa* the seeds are sub-globose or more or less dorsoventrally compressed, smooth, striate, tuberculate or irregularly angulate with a marked or obsolete umbo opposite to the hilum corresponding to a perisperm chamber within (CHEESMAN, loc. cit., p. 108). Apart from this account, the seeds of the type species of this section, i.e., *M. texalis*, were also available to me for examination.

So far as the fossil is concerned, the total absence of a perisperm chamber marked externally by an umbo in the fossil seed is opposed to its assignment to *Australimusa*.

In *Callimusa* the seeds are cylindrical, barrel-shaped or top-shaped, marked externally by a transverse line or groove above which they are warted, tubercled or variously patterned, below usually smooth, internally with a well-developed perisperm chamber within, (CHEESMAN, loc. cit., p. 108). Thus *Callimusa* apparently shows some affinities with the fossil fruit in having more or less similar shape of the seeds and presence of a transverse line or groove on the external surface. But with the kindness of Dr. Shepherd, the seeds of two described and four undescribed species of this section (the latter registered as I.R. 273, 285, 302 and 304 in the Banana Research Station, Imperial College of Agriculture, Trinidad, W.I.) were available to me for comparison. After study of this material I found that on these seeds the transverse line or groove is very distinct and regular, the seed-surface is differently patterned above and below it and an empty perisperm cavity is too well defined to have any comparison with the fossil seeds.

In *Rhodochlamys* the seeds are uniform in shape, being dorsoventrally compressed (CHEESMAN, 1949a, b, c). Whereas the seeds in the fossil banana are bigger in vertical height than in cross diameter.

On the other hand most comparable seeds are found in the section *Musa*, particularly in those species that are found in Assam-Burma region. The fossil seeds show maximum resemblance with those of *M. nagnecium* Prain. and an undetermined species belonging to this section, registered as no. 17599 in Botanical Survey of India (PLS. 3-4, FIGS. 23 and 28.) Therefore it can be easily assigned to section *Musa* (= *Eumusa*) of the genus *Musa* L.

### Comparison between the Fossil and Living Fruits of *Musa*

The fossil fruit resembles those of the living species of *Musa* in all the morphological characters of taxonomical significance, e.g., the form of the fruit which is a berry, the size, the organization and the structure of the fruits and seeds. Among some other striking resemblances between this fossil fruit and those of the living species of *Musa*, are:

1. The smooth pericarp of the fossil fruit which appears to be longitudinally striated externally when the epicarp is destroyed (PL. 1, FIGS. 3-4; TEXT-FIGS. 1-2a), exactly as we find in rotten bananas.

2. The axis is poorly represented by a few traces of tissues in the body of the fossil fruit but it fills the entire cavity enclosed by the pericarp in the stalk region (PL. 1, FIGS. 7-8; TEXT-FIGS. 3-4), exactly as we find in the modern edible as well as wild bananas.

3. In the fossil, as also in the modern fruits of *Musa*, delicate traces of tissue represent the septa in the body of the fruit and are not recognizable at all in the stalk region where the axis fills the entire space enclosed by the pericarp.

4. Both in the fossil as well as the living species, there are many seeds in each fruit but they show no sign of compression and the space inside the fruit is partly filled with seeds and the remaining by pulp which appears to have been replaced by rock matrix in the case of fossil fruits.

5. The pericarp is thick and fleshy enclosing a large number of fibre and vascular bundles. Both in the living as well as the fossil fruits, the limit of the lining of the pericarp is not clear which gradually merges into the non-cellular pulp (or matrix in the fossil fruit). Thus the pulp appears to be derived partly by the disintegration of the septa and the axis and partly from the lining of the locules in the fossil fruit as well as in the living species (SIMMONDS, 1953).

6. The fossil seeds have the size and structure characteristic of *Musa* species. The seed coat is thick with a conspicuously large hilum and making a ' collar ' round the embryo both in the living as well as the fossil seeds (PLS. 3-4, FIGS. 22-23 and 27-28).

However, there are some differences in some structural features of the fossil fruit and its modern representatives. They are as follows:

1. The fossil fruit is smaller in diameter than probably any extant species. Correlated with the diameter of the fruit is the space inside filled with pulp and the seeds. The seeds are fewer in the fossil and generally more numerous in the extant species. In some extant species, however, we find nearly as many seeds as in the fossil.

2. The absence of any remnants of the perianth etc. on the top of the fruit is quite striking. In all the extant species there are at least some remnants of a persistent or withered off perianth at the apex of the fruit. This, however, is not a significant character of generic distinction, but it may mean much. For example, now it is not known whether this fossil fruit was produced by a superior or an inferior ovary. But the presence of the remains of perianth at top, if it were there, would have meant that it was produced from an inferior ovary. In this connection it is important to note that it is not necessary that all fruits produced by an inferior ovary must have remains of perianth at the top, e.g., in many genera of Zingiberaceae, where the fruits are produced by inferior ovaries yet have practically no remains of perianth at the top. At the same time there is the possibility that this fossil fruit might have been produced from a superior ovary. In this connection it is important to note that according to Chakravorti (1948b) " the ancestral gynaecium consisted of three carpels which were superior ".

3. The pericarps of the fruits in living species, like all other organs, have articulated laticifers or secretory ducts in the ground tissue and associated with phloem, whereas no articulated laticifers are distinctly traceable in the fossil fruit. According to Dr. C. R. Metcalfe (personal communication) the laticifers are not always easily detected even in the living species. Therefore, it is difficult to be quite sure whether they were altogether absent or not. But, the absence of such a specialized feature would not be surprising from species as primitive as the fossil one. However, there appears to be present some tannin cells in the pericarp of these fossil fruits.

4. The vascular bundles in the pericarp of the extant species are more or less pear-shaped in cross section with highly developed fibrous bundle sheaths on the phloem pole and little or no fibrous sheaths on the xylem pole. Whereas in this fossil fruit the main bundles have both the sheaths well developed, more or less, as we find in the vegetative organs of *Musa spp*. Further there are all stages in the reduction of the vascular bundles with both sheaths to none in this fossil fruit. Evidently, therefore, the difference in the constitution of vascular bundle is only quantitative and more specialized in the extant species.

5. The size of the fossil seeds is not uncomparable with those of the extant species of *Musa*, but the size of the embryo is definitely much larger than in the extant species. This is evidently a case of reduction in the extant species.

Thus it is clear that all the differences between the fossil fruit and the extant species are corresponding to the degree of specializa-

tion. However, the above mentioned differences are subject to revision in view of our present meagre knowledge of the anatomy of the fruits of extant species.


## ACKNOWLEDGEMENTS

I am greatly indebted to Dr. R. N. Lakhanpal for his keen interest and valuable suggestions throughout the progress of this work and going through the manuscript critically. I am also highly thankful to Mr. N. W. Simmonds for his kind help in identification of the section of the genus and obtaining the views and suggestions of Dr. C. R. Metcalfe regarding the anatomy of the fruit. I record my sincere thanks to Dr. K. Shepherd for sending the seeds of *Callimusa* which have greatly helped in assigning the fossil to its proper place within the genus *Musa*.


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## EXPLANATION OF PLATES

PLATE 1

*Musa cardiosperma* sp. nov.

1. Longitudinal (partly tangential and partly median longitudinal) section of a more or less complete fruit broken into three parts. Note the pointed apex (curved acumen), spiral arrangement of the seeds and a short stalk. × 1.

2. Basal half of a longitudinally broken fruit showing the stalk curved at the base. × 1.

3. Surface of the fruit where the epicarp is intact. × 2.

4. Surface of the fruit where the epicarp is missing. Note the longitudinal striations. × 2.

5. Cross section of a fruit showing its trigonous outline with rounded angles, more or less convex sides and thick pericarp. × 5.

6. Cross section of a fruit showing the adaxial direction of the hilum (h.) of the seed and abortive seeds (ab. s.). × 5.

7. Cross section of a fruit showing the delicate traces of the septa (s.) and the axis (a.). × 5.

8. Cross section of stalk showing thick pericarp and the axis filling the entire space enclosed by the pericarp. × 5.

9. Abaxial view of the seed showing the transverse and longitudinal furrows. × 5.

10. Adaxial view of the seed showing the prominent hilum. × 5.

PLATE 2

*Musa cardiosperma* sp. nov.

11. Basal view of the seed showing a prominent hilum in the centre. × 5.

12. Side (lateral) view of the seed showing the slanting depression lodging the hilum, and the raised adaxial side which is steeply slanting on the other end. × 5.

13. Cross section of the pericarp. Note the shape of the cells of the ground tissue, the distribution of vascular (v.b.) and fibrous (f.b.) bundles. × 90.

14. Longitudinal section of the pericarp showing the vertically elongated cells of the ground tissue. × 80.

15. Cross section of a fibrous bundle. × 200.

16. Cross section of a typical vascular bundle. c.c. "Commissural connectives" or the "late metaxylem elements". × 200.

17. Cross section of a vascular bundle with highly reduced fibrous sheaths. × 200.

PLATE 3

*Musa cardiosperma* sp. nov.

18. Cross section of a seed from the extreme basal region. × 10.

19. Cross section of a seed from the sub-basal region. m.=micropyle, h.=hilum. × 10.

20. Cross section of a seed through the 'collar' (Compare it with fig. 21). × 10.

21. Living *Musa sp.* (undetermined species of section *Musa* from Assam registered in Botanical Survey of India as No. 17599). Cross section of a seed through the 'collar' (compare it with fig. 20). × 10.

22. Cross section of a seed from the apex. × 10.

23. Medium longitudinal section of a seed cut parallel to the radial axis. Note the position and comparative size of the embryo (e.). × 10.

24. Living *Musa sp.* (same as fig. 21). Median longitudinal section of a seed (compare it with fig. 23). × 10.

25. *Musa cardiosperma* sp. nov. Median longitudinal section cut at right angles to the radial axis to show the vascular supply of the seed in hilar region. v.s.=vascular supply. × 10.

PLATE 4

*Musa cardiosperma* sp. nov.

26. Longitudinal section of the seed coat showing the papillate outer epidermis and smooth inner epidermis. × 80.

27. Longitudinal section of the seed coat from the hilar region. Note the expanded middle region. × 80.

28. Outer region of the seed coat highly magnified as seen in a cross section. × 600.

29. Few cells of the middle region of the seed coat. × 450.

30. Embryo entire. × 10.

31. Embryo in cross section. × 10.

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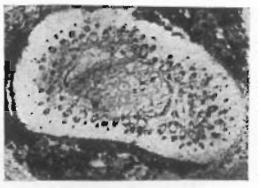

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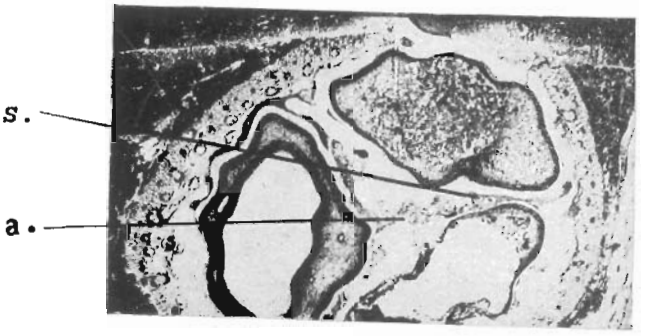


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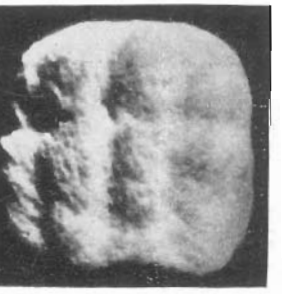

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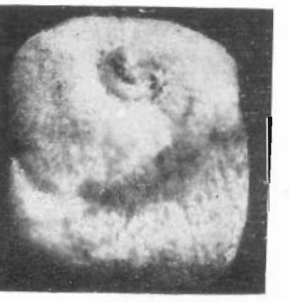

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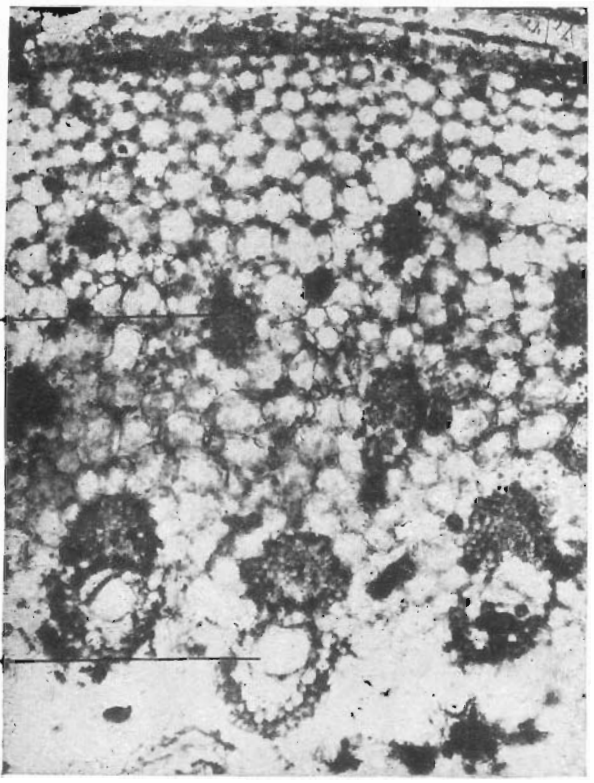


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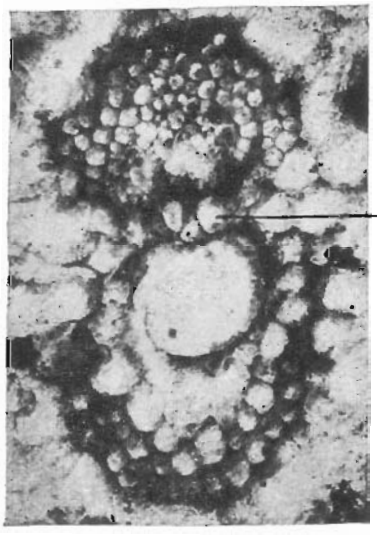


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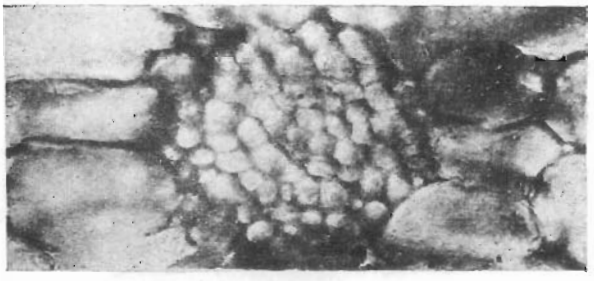

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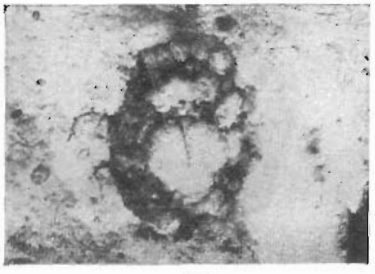

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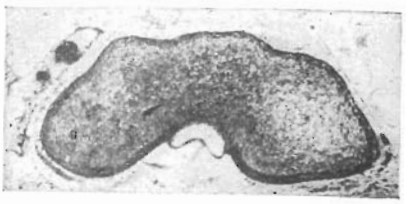

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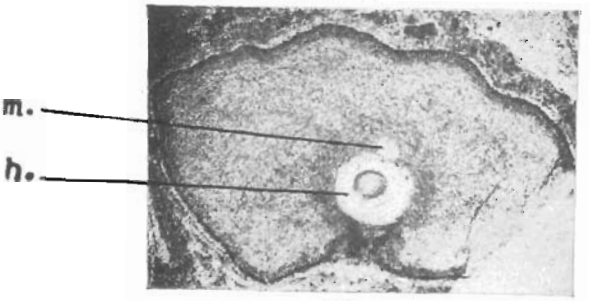


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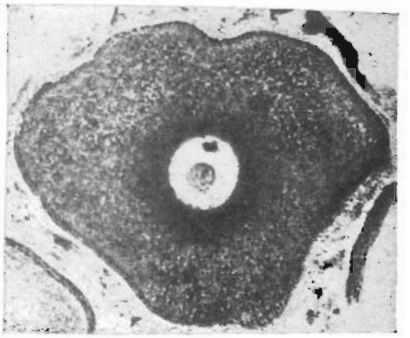

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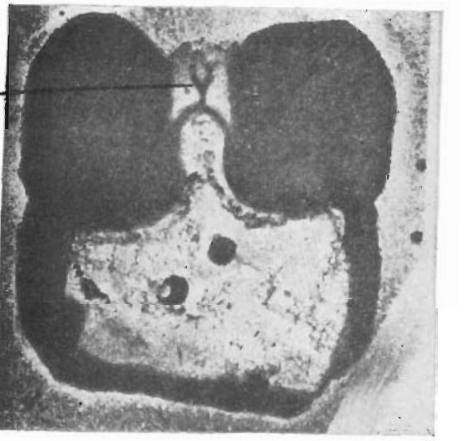


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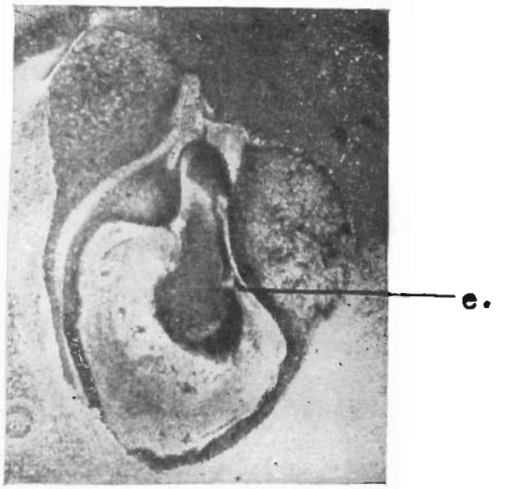


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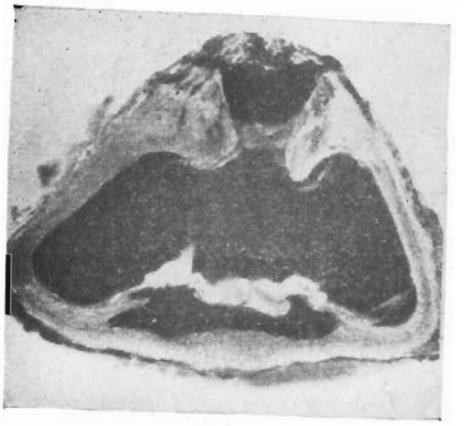

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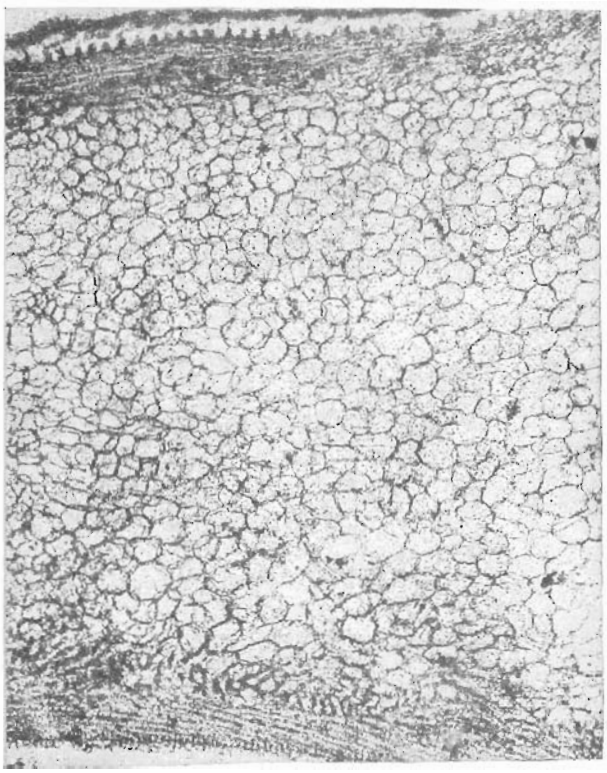

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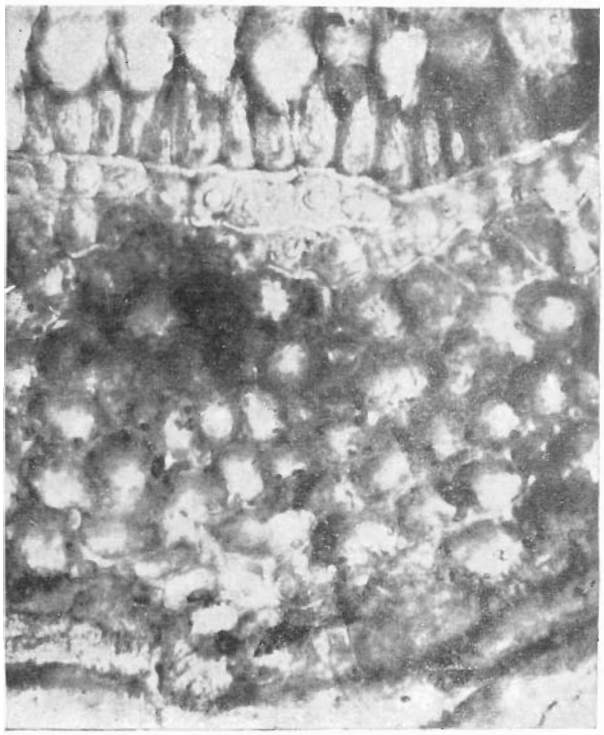

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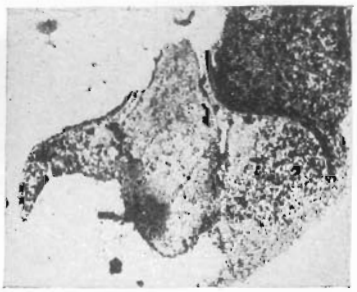

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