ON THE FRUCTIFICATION OF *TRICOCCITES TRIGONUM* RODE FROM THE DECCAN INTERTRAPPEAN SERIES OF INDIA

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ABSTRACT

This paper deals with the investigation of the petrified fructification of *Tricoccites trigonum* Rode, and redescribes the fruit in as much detail as possible. The present material comes from the village Mohgaon Kalan, Chhindwara district of the Madhya Pradesh, India, where the Deccan Intertrappeans are exposed.

The previous diagnosis of the genus and the species is emended. The presence of several ensheathing leaves probably enclosing the fructification is of great interest since their structure resembles most that of *Cyclanthodendron Sahnii* (Rode) Sahni & Surange. The affinities of fruit are discussed but left open. Points of resemblances are noted to Pandanaceae and certain Palmae, e.g. *Attalea*, a 3-locular, 3-seeded drupe. However, it agrees with no existing genus and its classification must remain open until more is learnt.

INTRODUCTION

A PRELIMINARY report of the investigation of the fruit and fructification of *Tricoccites trigonum* Rode was already given by me (CHITALEY, 1956). The fruit *Tricoccites trigonum* Rode is only known from the preliminary descriptions of Rode (1933) and Sahni & Rode (1937), and the fructification has not been described at all, apart from a record by Shukla in 1950 of an axis with twenty fruits.

The present specimens collected by me consist of a few almost complete fruits, a few incomplete ones either exposed in obliquely transverse section or obliquely longitudinal section and two incomplete fructifications with closely packed fruits. They all come from the village Mohgaon Kalan which lies on the latitude 22° 10″N. and longitude 79° 11′ 18″E., in the Chhindwara district of the Madhya Pradesh, India (SAHNI & RODE, 1937). The outcrops of the Deccan Intertrappean Series are to the north-west of the village from whence the specimens came. The age of this series was once regarded as Upper Cretaceous but is now generally regarded as Eocene, and it is of special interest as it contains some of the oldest fully petrified angiospermous flowers and fruits. The present specimens are all petrified in chert, but certain tissues have disappeared.

TECHNIQUE AND METHOD

The ordinary method of slicing the rock at different levels followed by the preparation of thin sections for the microscopical study was used in the investigation, as well as a method mentioned by Chitaley (1955) was also used for studying the serial sections of some of the fruit parts. Etching with HF was also tried to see whether it could reveal more cellular details of the fruit wall and seed contents than the ground sections. Unfortunately, it did not prove successful.

DIAGNOSIS OF *TRICOCCITES* (EMENDED)

Elongated fructification composed of closely packed sessile fruits, enclosed in several ensheathing leaves. Fruit 3-locular, 3-seeded drupe; shape triangular in transverse section, rounded in longitudinal section but with more or less flattened ends. Fruit wall with three main regions; outer region thin, fibrous; middle region broad, divided by radial plates of fibrous tissue alternating with soft tissue or spaces; inner region richly fibrous and thick. Loculi rounded in cross-section occupying the angles of the fruit, with one vertical large seed in each. Seed attached by a placenta extending from the base of the loculus up along its outer edge (embryo not preserved).

DIAGNOSIS OF *TRICOCCITES TRIGONUM* (EMENDED)

Fructification at least 140 mm. long, with crowded fruits on the axis; fruits closely packed in such a way that sides of two adjoining ones fit together. Spathe of two or more sheaths running along the length of the fructification; outermost sheath of fructification 3-4 mm. thick, outer surface longitudinally ribbed; interior showing a single row of air cavities and numerous scattered vascular bundles; bundles with vessels in a single row; epidermal cells of abaxial side radially elongated; underline tissue shows radial plates of fibres separated by parenchyma; ground tissue of parenchyma with scattered thick-walled cells and cells with opaque contents; vascular bundles with a separate inner and outer group of fibres.

Fruit typically 30 mm. long × 30 mm. wide (extremes noted as 30-45 mm. long and 22-40 mm. wide), apex and base typically truncate. Exterior of fruit smooth or obscurely ribbed longitudinally (ribs corresponding to walls of chambers of mesocarp). Mesocarp with about 20 longitudinal chambers about 5-6 mm. tangentially wide and 2·5-3 mm. radially wide (in t.s.), chambers partly occupied by soft tissue. Septa between chambers up to 1 mm. thick. Endocarp solid, fibrous, continued to the centre by fibrous septa, 1-2 mm. thick; core of fruit fibrous and vascular. Specialized flattish tabular cells (? stegmata) abundantly associated with fibrous and vascular bundles. Seed elongated, 16-20 mm. × 6-12 mm., filling the loculus. Testa of three regions; outermost composed of one layer of thin-walled cells elongated in a direction longitudinal to the seed; middle region of about 5-7 layers of isodiametric moderately thick-walled cells with granular contents, innermost region of several layers of thin-walled parenchymatous cells with denser contents.

DESCRIPTION

Fructification — I found two broken specimens of the fructification. One, No. 1, has eight fruits, the other, No. 2, which is less preserved, has ten or more. Neither shows the axis.

Fructification No. 1 is shown in Pl. 1, Fig. 2 and Text-fig. 1A. It is clearly a piece broken tangentially from a larger fossil. Several ensheathing leaves lie pressed together just outside the group of fruits and I, therefore, take this to mark the outer side of the fruits. The peculiar arrangement of the fruits is shown in Text-fig. 1A; I imagine that if we had the whole fructification, the arrangement would appear more elaborate. I do not know if bracts occur subtending individual fruits. I searched but found nothing convincing apart from a small fleshy structure (TEXT-FIG. 1B) in oblique l.s. of the lower end of the fruit. It could equally well be a perianth lobe.

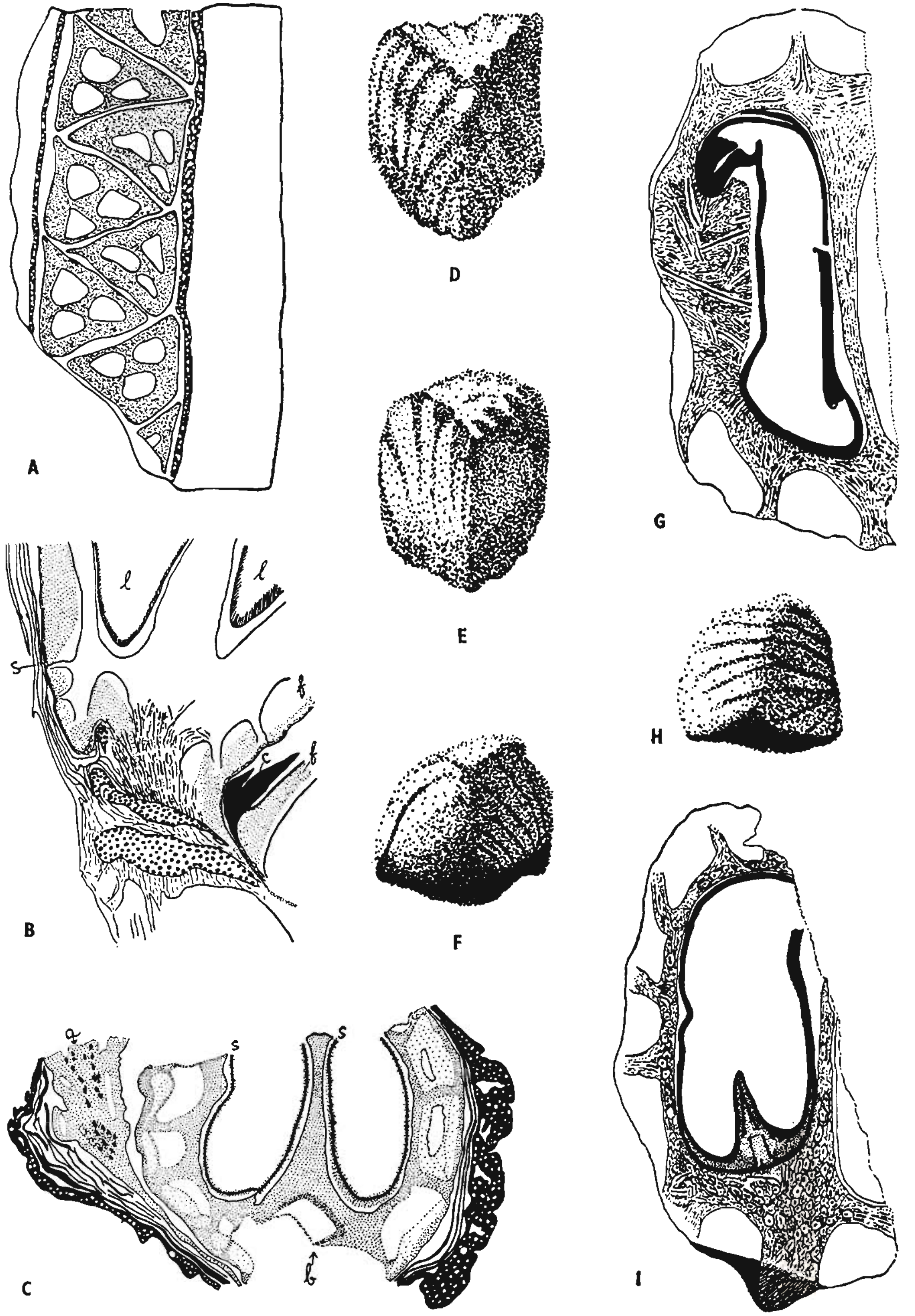
Fructification No. 2 is not illustrated. It shows fruits packed in the same way but its chief value lies in its ensheathing leaves which are just as in fructification No. 1 and thus support the idea that the sheaths belong to the fructification. Fructification No. 2 is a separate fossil for I found it at some distance from fructification No. 1.

Structure of Ensheathing Leaves — In neither fructification is there any organic connection between the tissues of the fruits and sheaths and I imagine that such connection would occur at the fructification axis below the level of the fruits, this part being unknown. All I can say is that the sheaths run along the length of each fragmentary fructification and lie close to the outer side of the fruits (TEXT-FIG. 1, A, C; PL. 1, FIGS. 1, 3). The thick outer sheath in fructification No. 1 is a fragment 14 mm. long and 3·75 mm. thick at its thickest. Its structure in cross-section is shown in Text-fig. 2A, and also the underlying parenchyma and plates of fibres. The parenchymatous ground tissue is thin-walled with distinct intercellular spaces (TEXT-FIG. 2B). Occasional larger cells are reddish brown in both reflected and transmitted light. Other scattered cells in the ground tissue appear white in reflected light and dark in transmitted light (TEXT-FIG. 2, A, B). I suspect this is due to finely divided air cavities. Similar cells are found in the fruit wall. A few scattered fibre masses also occur and some scattered thick-walled cells (TEXT-FIG. 2B) are seen at places. The adaxial epidermis is composed of ordinary flattened cells and the hypodermis is of horizontally elongated cells (TEXT-FIG. 2C).

The inner sheaths are much thinner and less well preserved. They are about 0·2-0·5 mm. thick each and are irregularly overlapping each other.

Outside all these thinner and thicker sheaths and little away from them, there is an additional leaf or sheath which differs in possessing a midrib. Its structure is ill preserved but seems to agree with the other sheaths. I do not know if it is in its original position.

Fruit — I found many isolated fruits in addition to those in the fructifications. The best two are figured in Text-fig. 1, D and E, F and H. Neither end is in the least acute or acuminate as described by Rode (SAHNI & RODE, 1937). I think that Rode's section



TEXT-FIG. 1.

must have been a little off median and so passed through an angle which would make it appear acute or acuminate. Both ends are truncate and are so similar that I could hardly tell them apart in isolated fruits. However, I conclude that the end which shows more vascular tissue in sections is the base. One oblique l.s. of the lower end of the fruit shows a definite parenchymatous scale which might be a perianth member or a bract (TEXT-FIG. 1B). Sections of further fructifications are needed to show the nature of this scale.

Fruit Wall — The epicarp has a one-layered epidermis and a parenchymatous hypodermis of 1-3 layers. Under this is a zone with fibre bundles (TEXT-FIG. 2E). The fibres are surrounded by 1-3 or more layers of cells isodiametric in t.s. in which the contents appear as a ring separated from the wall (TEXT-FIG. 2G). In l.s. they are slightly elliptical and are in uni-multiseriate rows. I suspect they may be stegmata (*see ahead*). Some of these fibre bundles include a tiny vessel.

The mesocarp encloses about 20 (18-21) chambers running along the length of the fruit. In the best preserved fruits, chambers are partly filled with a thin-walled tissue. The inner part of the chamber appears empty but this space may have been caused by shrinkage of the soft tissue (TEXT-FIG. 1C). The soft tissue is parenchymatous and shows intercellular spaces (TEXT-FIG. 2D). Some of the cells have opaque white contents (? air cavities); other cells have reddish contents. The fibrous plates include many longitudinal vascular bundles surrounded by stegma-like cells.

Cells resembling stegmata (TEXT-FIG. 2G) occur around the fibre bundles of the fruit. The endocarp is composed of fibres and a few vascular bundles with vessels. It continues inwards along the fibrous septa to the fibrous central core where vascular bundles are better developed (TEXT-FIG. 2, E, F).

Seed — The three seeds of a fruit are almost of the same size, and each almost fills its loculus. The attachment of the seed appears basal (though there is doubt if I have recognized the base correctly), and the placenta extends up the side along the angle of the fruit. The placenta is richly vascular (TEXT-FIG. 1, G, I). The tissues of the seed coat were studied in various planes of sections. In true transverse section the total thickness is about 0·25 mm., made up of outer, middle and inner regions. Their cells were most satisfactorily seen in a longitudinal section which passed almost tangentially through the testa. The outermost region, separated from the endocarp by a small gap in the fossil and perhaps originally in contact is regarded as the epidermis. It is a single layer of radially elongated prismatic cells (TEXT-FIG. 2H). The middle region consists of about 5-7 layers of parenchymatous cells with rather thick walls and dense contents (TEXT-FIG. 2I). Their shape looks similar in different planes of section. The innermost region is of several layers of thin-walled parenchymatous cells (TEXT-FIG. 2J) with granular contents which also look similar in different planes of section. No other layers in the seed coat were observed and nothing definite was preserved of the contents of any of the seeds.

DISCUSSION

History of Tricoccites trigonum — Dr. Rode collected his type specimen of *Tricoccites*

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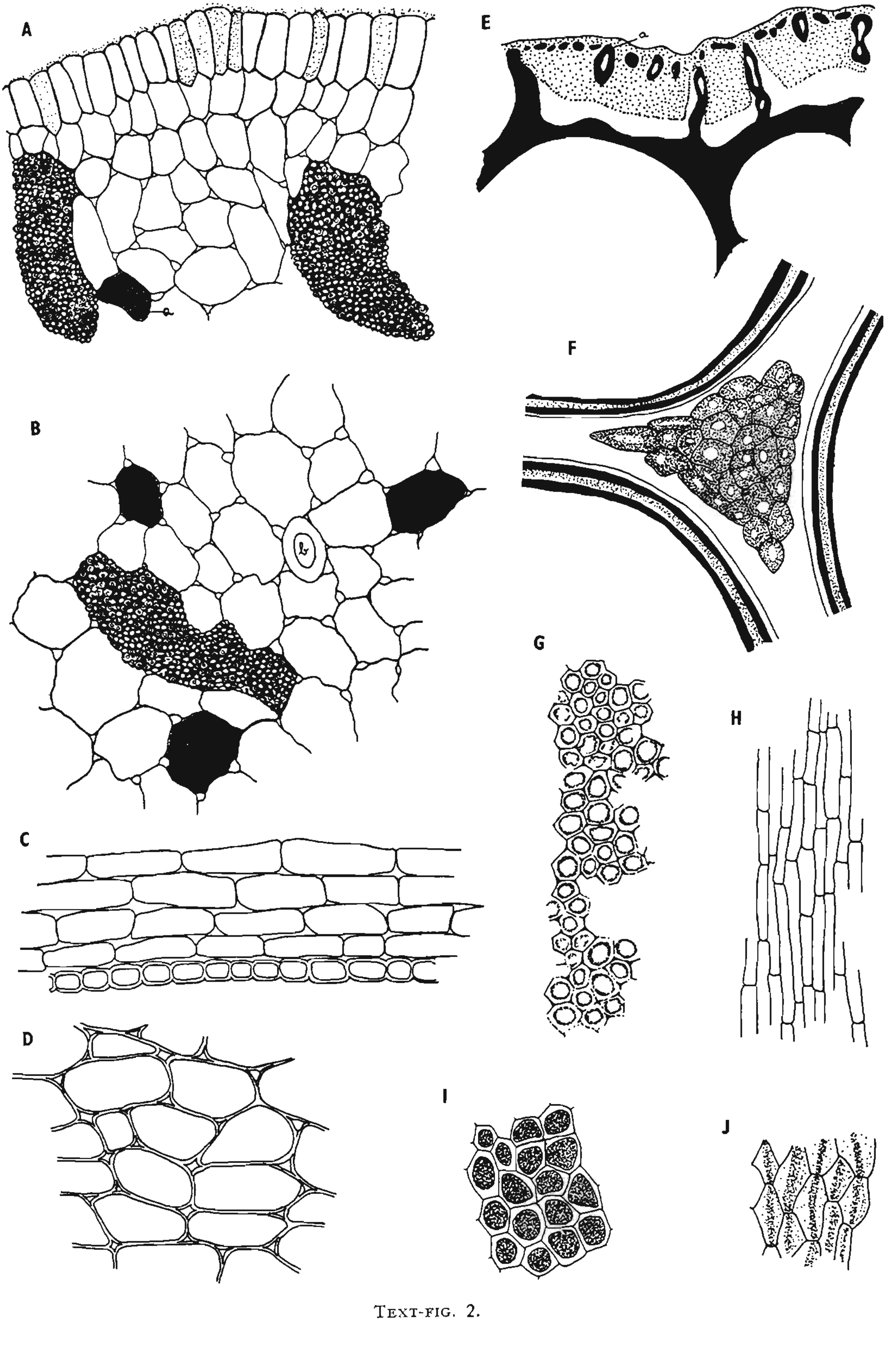
TEXT-FIG. 1 — *Tricoccites trigonum*: A, piece of rock as seen *in situ* showing tangential section of part of No. 1 fructification; individual fruits cut transversely; spathe seen running along both sides of the fruit row. × ½. B, oblique longitudinal section at fruit base showing two loculi (l), fruit wall (f), fleshy structure (? perianth) (c), and sheaths (s). Portion shown with large dark dots shows rock matrix or ? badly preserved axial tissue. × 2·6. C, two fruits in oblique longitudinal sections; fruit *a* in tangential section of fruit wall, fruit *b* with two seeds and chambered wall. Outermost sheath (s) of spathe showing air cavities (large white areas) and dark cells of ground tissue (small white dots). × 1·8. D and E, single fruit (No. 1) in two views showing triangular shape and fine ribs on fruit wall; apex and base indistinguishable, truncate. × *Natural size*. F and H, single fruit (No. 2) seen from two angles showing ribs of fruit wall one of which shows branching (in H, fourth from above). × *Natural size*. G, oblique longitudinal section (more or less tangential) through part of fruit (l) showing highly vascular placental tissue extending from seed base on its lateral surface; seed coat shown dark. × 2·6. I, oblique longitudinal section (more or less radial) through part of fruit (No. 1) showing highly developed vascular tissue in lower end of fruit figure (? base); large vertical seed in loculus showing attachment to fruit wall (endocarp); seed coat shown dark. × 2·6.



TEXT-FIG. 2.

trigonum from Mohgaon Kalan, the locality from which I collected the present material. He regarded it as Euphorbiaceous and named it after *Tricoccus*. In 1934, in a provisional list Professor Sahni renamed it as *Palmocarpon trigonum* (Rode); but in 1937 Sahni and Rode redescribed it under its original name *Tricoccites trigonum*. They gave the original diagnosis with some additional figures and added the remarks " . . . it has nothing whatever to do with the modern *Tricoccus* or indeed with any dicotyledon ". In his Presidential Address at the 27th Indian Science Congress Session, Professor Sahni mentioned the fruit under the name *Tricoccites* (*Palmocarpon*) *trigonum* n. com. with same figures (SAHNI, 1940). Perhaps this may be the same fruit collected and described by Hislop (1861) as " . . . two specimens of a fruit with three large seeds, separated by thin dissepiments which may have belonged to the order of palms ".

The Sheath and the Plant of Origin of Tricoccites — Both fructifications are wrapped in the leafy sheaths, but in neither fragment is there any continuity between the fruits and sheaths. There are two possibilities:

(1) The sheaths are part of the same fossil and spring from the axis below the fruits.
(2) The sheaths lie next the fruits and may have originated from different plants.

Nothing but continuity could prove that the sheaths belonged to the fructifications, although further specimens showing the same association would be suggestive. They should be sought for. It is only if the sheaths belong to the fructification that the remarks below would have any value. They are, therefore, made very briefly.

The sheaths show several striking points of agreement as seen in t.s. with the leaves and leaf sheaths of *Cyclanthodendron Sahnii* (Rode) Sahni & Surange. These include the following:

(1) Both are ribbed (i.e. with crests and furrows) in t.s.
(2) In both the abaxial epidermis is composed of prismatic elongated cells, with flat outer ends but angular inner ends.
(3) In both the hypodermis is of similar oval cells and is followed by elongated plates of fibres separated by similar parenchyma.
(4) The ground tissue in both is of similar parenchyma with a few cells with opaque contents, and same presence of scattered plates of fibres.
(5) Both have large air cavities in the ground tissue.
(6) The vascular bundles are similar in both; the vessels being in a radial row and the fibrous sheath being in separate inner and outer parts of about equal size.
(7) In both the adaxial epidermis is composed of ordinary flattened cells and the adaxial hypodermis is of horizontally elongated cells.

Differences exist in the arrangement of the vascular bundles and air spaces. In *Cyclanthodendron Sahnii* (Rode) Sahni & Surange, the vascular bundles and air spaces are arranged in a definite system whereas in the present specimen the arrangement is not so strict. Also I could not recognize any stegma-like cells around the fibre bundles of the present sheaths. They are said to be abundant in the leaf bundles of *Cyclanthodendron*. The term ' stegmata ' is used for flattish tabular cells which occur next the

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TEXT-FIG. 2 —*Tricoccites trigonum*: A, transverse section of outermost sheath of spathe; the abaxial epidermis of elongated prismatic cells followed by one or two layers of oval cells of ?hypodermis which is followed intermittently by fibrous plates (individual fibres were not distinct for drawing purpose and so shown as in the figure); thin-walled parenchymatous cells of ground tissue with intercellular spaces; one dark cell *a* seen (black). × 225. B, portion of ground tissue of spathe in cross-section; thick-walled cell ?idioblast (*b*); fibrous plate also seen. × 225. C, cross-section of adaxial epidermis of sheath with rows of horizontally elongated cells on inner side. × 225. D, thin-walled parenchyma with intercellular spaces from soft tissue of fruit wall. × 160. E, transverse section of fruit wall with outer epidermis followed by soft tissue (stippled) partially filling the chambers and intermittent small fibrous patches; three large fibrous plates seen separating three chambers. × 5. F, transverse section of fruit core with fibrous bundles (stippled) surrounded by ?stegmata (dark line); each bundle also contains xylem vessel; three layers of seed coats (outer dark, middle stippled and inner dark) also seen in three parts of three loculi. × 15. G, ?stegmata from fruit wall seen in surface view. × 225. H, epidermal cells of seed coat. × 225. I, cells of middle layer of seed coat. × 225. J, cells of innermost layer of seed coat. × 225.

fibre masses (of vascular bundles) and their main character is that they are filled with silica during life (JACKSON, 1916). I do not see how we can recognize original silicification in an organ which has been secondarily silicified and so their recognition in fossil forms may be doubtful. In modern monocotyledonous plants stegmata are to be found in a number of families. They are prominent only in some members of Pandanaceae and in several members of Palmae. They are present (but rare) in some sections I examined at Kew of the Cyclanthaceous genera *Carludovica* and *Cyclanthus*.

The present sheaths are rather poorly preserved and certain fine details may have been missed. It is emphasized again that there is doubt if the sheaths belong to *Tricoccites* and secondly, if they do, that they belong to *Cyclanthodendron*. The matter needs further investigation from better specimens. It is worth this investigation for the fruits are different from those of the living Cyclanthaceae.

Affinities of Tricoccites — The affinities of *Tricoccites* are discussed without any regard to the possibilities that the sheaths belong to it and to *Cyclanthodendron*.

The presence of numerous, small, scattered bundles at the base and in the core of the fruit points to *Tricoccites* being monocotyledonous. The bundles show no trace of secondary wood. Many monocotyledonous families have tricarpellary ovaries. Two families only have members which include the following features: Fructification massive and compact; ovary 3-locular with a single seed per loculus; placentation not axile (probably basal); ripe fruit a drupe; abundance of (? stegmata) around the fibre bundles. These families are Pandanaceae and Palmae.

Pandanaceae — Although the features of *Tricoccites* occur scattered through the family no living member approaches *Tricoccites* closely. Unilocular drupes are more common than trilocular ones, and normally the ovaries have persistent, woody stigmas (WARBURG, 1900). If the ensheathing leaves belong to *Tricoccites*, they are rather against this family because in Pandanaceae there is a single spathe.

Palmae — This huge family has a number of genera with trilocular 3-seeded fruits; for example *Arenga* [where the fruit is, however, a berry with a very small development of hard endocarp (DRUDE, 1889)]. The closest agreement I can find in the fruit is with *Attalea*, a trilocular 3-seeded drupe. There is, however, no generic agreement between the two, for the fruits of *Attalea* form a loose fructification and are of different shape. If the sheath leaves belong to *Tricoccites* they can be readily matched among the palms. It seems likely enough that *Tricoccites* may be an extinct genus of the Palmae but we are ignorant of many important features such as whether there is a perianth (epigynous or hypogynous), whether there are bracts and ignorant also about embryo and endosperm. Information about these might make it closer to the Pandanaceae or might prove that it was unclassifiable in any existing family.

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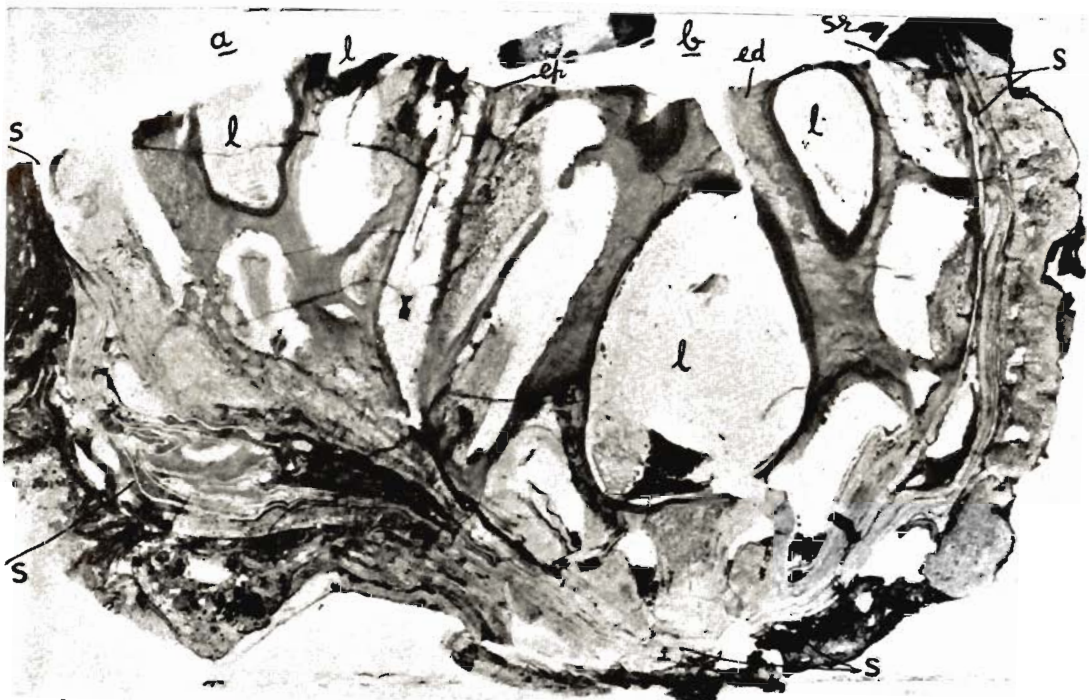

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EXPLANATION OF PLATE 1

1. *Tricoccites trigonum*: obliquely longitudinal section through two fruits *a* and *b*; spathe sheaths (*s*) seen running along the fruit sides and also encircling them from the apical end (bottom side of the figure); fruit wall marked . . . epicarp (*ep*), mesocarp (*sr*), endocarp (*ed*), and loculus (*l*). × 3.

2. *Tricoccites trigonum*: fructification (No. 1) *in situ* as seen embedded in rock. × $\frac{3}{4}$. (Rock sliced, slices present).

3. *Tricoccites trigonum*: tangential section of fructification (No. 1) exhibiting individual fruits in transverse section. Spathe (*s*) seen running along vertically on the two sides of the fruit row. Fruit wall marked . . . epicarp (*ep*), mesocarp (*sr*), endocarp (*ed*), and loculus (*l*). × 1·5.