Infructescences, fruits and seeds of the distinctive fossil palm, *Tricoccites trigonum* K.P. Rode from Mohgaonkalan in Chhindwara District, Madhya Pradesh, India: three-dimensional morphology, and anatomy

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ABSTRACT

Manchester S.R., Kapgate D.K., Ukey R.W. & Wanjari M. 2022. Infructescences, fruits and seeds of the distinctive fossil palm, *Tricoccites trigonum* K.P. Rode from Mohgaonkalan in Chhindwara District, Madhya Pradesh, India: three-dimensional morphology, and anatomy. Geophytology 50(1&2): 49–60.

Infructescences and fruits of the extinct genus *Tricoccites* from the latest Cretaceous of central India were previously studied by optical analysis of fractured surfaces and thin sections. The application of micro-CT scanning now allows for improved documentation of the 3-dimensional morphology. We reconfirm most of the morphological and anatomical features reported previously, including trilocular fruits with one seed per locule and a single cotyledon in each seed, but we also call attention to the presence of a prominent subapical germination pore on the dorsal side of each of the three pyrenes. These characters support assignment of *Tricoccites trigonum* to the *Arecaceae*. The infructescence is composed of closely packed sessile fruits and is unusual in the lack of an obvious central axis or rachis. Spongy tissue arising apically above each locule is interpreted to be stigmatic. The fruit was likely adapted for aquatic dispersal, due to the buoyancy that would have been provided by the longitudinal pericarp cavities.

Keywords: Palm fruits, micro-CT scanning, Maastrichtian, chert, permineralized

INTRODUCTION

The unusual monocot genus *Tricoccites* has been known since the 1930s based on well preserved silicified fruits from the village of Mohgaonkalan in Chhindwara District, Madhya Pradesh, India. The trilocular fruits were named *Tricoccites trigonum* by Rode (1933) who considered them likely to represent *Euphorbiaceae*, but Sahni (1937) reinterpreted them as palm fruits. Chitaley (1956) elaborated on the fruit anatomy and suggested affinities with *Pandanaceae*

or *Arecaceae*. Additional contributions were made by Bonde (1985), who described new material including many expertly ground thin sections of exceptionally well-preserved specimens revealing more details of the fruit and its seed. Some authors noted close association with anatomically preserved pseudostems of the genus *Cyclanthodendron* (Trivedi & Verma 1972, 1978, Biradar & Bonde 1990), but physical connection was not proven. The precise affinities of *Tricoccites* have remained uncertain.

Here we summarize and augment the morphology and anatomy of *Tricoccites trigonum* based on newly recovered infructescences and using new methods of X-ray analysis to revisit the question of its systematic affinities with additional evidence that it belongs to the *Arecaceae*.

MATERIAL AND METHODS

Although angiosperm fruits and seeds have been found at more than 20 different chert sites across central India (Smith et al. 2015), fruits of *Tricoccites* have been recovered only at sites near the villages of Mohgaonkalan and Keria in Chhindwara, Madhya Pradesh, India, where they are locally abundant (Figure 1). We examined specimens at Birbal Sahni Institute of Palaeosciences (BSIP), Agharkar Research Institute, Pune (ARI), and the Cleveland Museum of Natural History, Cleveland, Ohio (CMNH). Newly collected material (Figure 2) was cataloged in the paleobotanical collection of the Florida Museum of Natural History at University of Florida (UF).

Specimens were photographed by reflected light with a Canon Rebel XSI digital SLR camera with an EFS 60 macro lens, or for higher magnification of peel slides, with the same camera mounted on a Nikon Labophot microscope using a fiber optic light source and a white paper background for an optimal combination of reflected and transmitted light. X-ray imagery was obtained with a GE Phoenix V/tome/xm240 CT scanner, located at the University of Florida College of Engineering Nanoscale Research Facility. Depending on size of the chert specimen, scans were set at 200–220 kV and 120-300 mA, obtaining voxel resolutions of 47-61 µm. 2200 images were taken
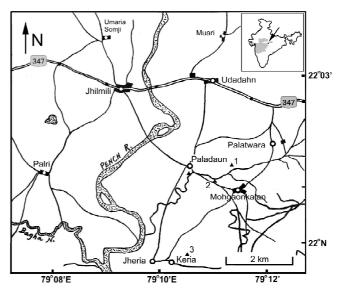

Figure 1. Map updated from Sahni and Rode (1937) showing the location of sites where *Tricoccites* is known including the type locality of Mohgaonkalan. Inset map shows location in relation to the Deccan Traps, shaded gray. Numbered sites include Mohgaonkalan (1 = UF 18311, 2 = UF 19348) and Keria (3 = UF 19329).

through a rotation of 360 degrees with exposure times of 333 or 500 ms. Resulting image stacks were processed with VG Studio Max version 3.1 and Avizo Lite version 9.1 to produce volume renderings, surface renderings, and digital sections. The best example data sets are accessible as TIFF stacks and as 3-D surface renderings at https://morphosource.org under the project "Deccan Plant Reproductive Structures," at Morphosource.org. We studied the following specimens: ARI SDB-5276, CMNH P-3163, 3166, 3776, 3782, 3792, 3795, UF 68964, 69705, 69707, 69708, 71118, 71124, 71125 from Mohgaonkalan and UF 56231, 56232, 56236, 85612 from Keria.

DESCRIPTION

Chitaley (1956) recorded infructescences up to 14 cm long. Newly collected infructescences are up to at least 35 cm long (the longest specimen recovered, Figure 2), but all specimens so far recovered are broken at both ends. Up to 14 closely packed fruits are visible in the 35 cm length. As noted by Chitaley (1956, p. 56) the fruits are crowded, "closely packed in such a way that sides of two adjoining ones fit together." The specimens discussed and illustrated by Chitaley, and those we have studied (e.g. Figure 2.2–13), show the
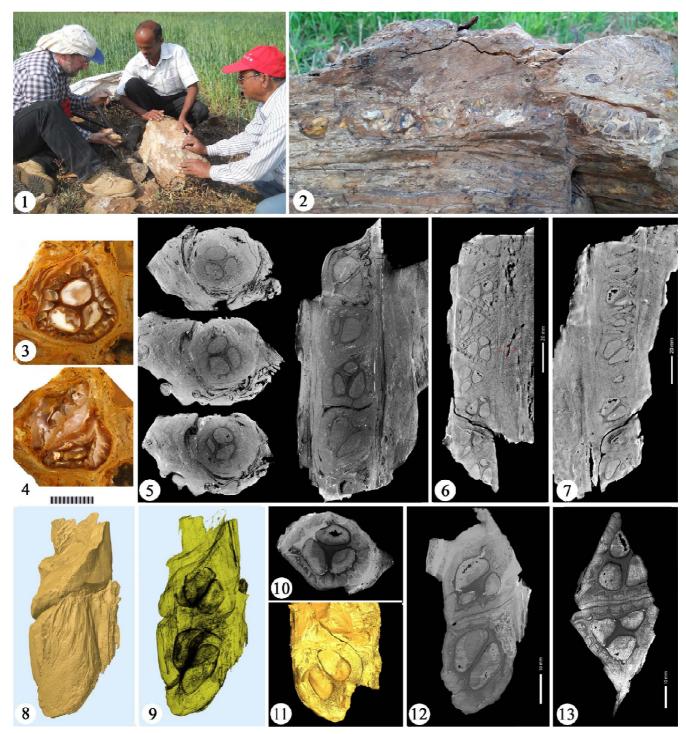
Figure 2. *Tricoccites trigonum* K.P. Rode.
1, 2. Chert boulder in the field near Mohgaonkalan containing infructescences. **3–13.** Specimens obtained from the same boulder by reflected light (3, 4) and micro-CT scanning (5–13). **3.** Physical transverse section of infructescence revealing one of the trilocular fruits, UF 19348-69708. **4.** Another transverse section of same infructescence intercepting two adjacent overlapping fruits. **5.** Successive transverse sections and a longitudinal section, UF19438-69707. **6. 7.** Virtual longitudinal sections of UF19438-68964, with the specimen in two planes rotated about 90 degrees from each other, one plane intercepting the fruits in mostly transverse orientation (6), the other plane intercepting fruits in lateral orientations (7). **8–13.** Two-fruited fragment of the specimen in 6 and 7. **8.** Surface rendering showing rhomboid outline of the fruits. **9.** Translucent rendering showing the positions of pyrenes within the fruits. **10.** Virtual transverse section of fruit. **11.** Surface rendering of naturally fractured specimen with two seeds exposed. **12, 13.** Virtual longitudinal sections in two planes of rotation. Scale bars 1 cm in 4 (applies also to 3), 12, 13, 2 cm in 6, 7.

fruits packed in a single file within a tubular infructescence. Shukla (1950) mentioned a specimen bearing twenty fruits. In longitudinal section, the fruits in that specimen appear to be in two rows (Figure 4.7). However, we infer that this appearance was due to distortion as the infructescence was compressed and starting to disaggregate, because all other infructescences, like those in Figure 2, show the fruits tightly arranged in a single file (see also Chitaley 1956, Plate 1).
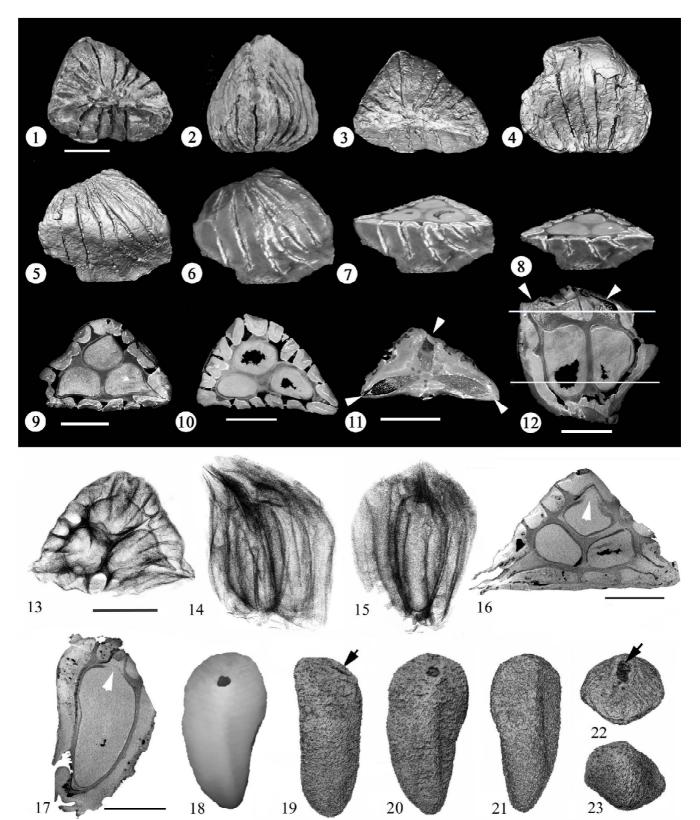
Physical sections and successive micro-CT virtual sections show that the fruits not only are sessile but lack obvious vascular attachment to a common rachis. This makes the mode of attachment and indeed determination of "which way is up" on each fruit somewhat mysterious. Chitaley (1956 p. 59) stated "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." We found enrolled leafy tissue surrounding our infructescences as noted by previous authors, e.g. Chitaley (1956), but could not establish a physical connection and the preservation of the laminar tissue was poor compared to that studied by Biradar and Bonde (1990).

The emended diagnosis of Chitaley (1956) readily applies to the newly collected material as well: "Elongated fructification composed of closely packed sessile fruits, enclosed in several ensheathing leaves. Fruits 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…" Chitaley's emended diagnosis included the statement, "embryo not preserved". Subsequently, Bonde (1985) sectioned fruits with well preserved seeds showing clearly a monocotyledonous embryo of medium size, surrounded by cellular endosperm tissue (refigured here, Figure 4.1, 4–6). It is also worth noting that the seed coat is smooth, not intruded as in those genera of palms with ruminate endosperm.

The prominent lacunae within the pericarp outside of the locules were interpreted by Bonde (1985) as abortive pyrenes, but this hypothesis can be discarded because the structures he interpreted as abortive embryos can be seen to be the somewhat shrunken parenchymatous mesocarp (Figure 4.4; Figure 6.2, 3). The fruits are distinctive in having longitudinal parenchyma-filled lacunae within the pericarp extending from base to apex. There are 16 to 22 of these mesocarp lacunae in the fruits we studied (e.g. Figure 2.3; Figure 3.10; Figure 4.1; Figure 5.2, 12). Each cavity is bounded by exocarp tissue at the surface and fibrous mesocarp tissue that forms longitudinal septations (Figure 6.2, 3). The septations extend from base to apex of the fruit and can be seen as surface grooves in eroded specimens (Figure 3.1–5), because the exocarp can be mostly stripped away so that the

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Figure 3. *Tricoccites trigonum* K.P. Rode.
1–12. A single fruit from Mohgaonkalan showing typical shape, S.D. Chitaley collection, CMNH 3776, viewed by reflected light (1, 2) and micro-CT scanning (3–12). **1.** Basal view showing radiating grooves representing the eroded septations delimiting longitudinal cavities of the pericarp. **2.** Lateral view, with most of exocarp flaked away except left and upper right. **3.** Basal view rotated slightly from 1. **4.** Lateral view showing eroded septations delimiting longitudinal silica-filled lacunae of the pericarp. Exocarp flaked away except at upper right. **5.** Lateral view by surface rendering. **6–9.** The same orientation, volume rendering, with virtual transverse sections at the levels of 9, 10. 9. **10.** Virtual transverse sections at, and below the equator showing the 3 locules, and lacunae of the fruit wall. **11.** Virtual transverse section at apex showing vascular bundles of septum and three radiating arms of spongy tissue that arise above each locule (arrows). **12.** Longitudinal section traversing two of the stigmatic envelopes (arrows). **13–15.** Fruit digitally extracted from chert, rendered translucent to show outlines of the locules, UF 19438-71125A, same specimen as in Figure 5.2–7. **16.** Virtual transverse section, intercepting the germination pore within pyrene (arrow), UF 19438-71118. **17.** The same specimen, virtual longitudinal section intercepting the germination pore (arrow). **18.** The same pyrene, digitally extracted, dorsal view showing germination pore in face view, UF 19438-71118. **19–23.** Pyrene digitally extracted from the fruit in 13-15, UF 19438-71125A, in lateral, dorsal, ventral, apical and basal views. Note germination pore at arrow. Scale bars 1 cm. (bar at 1 applies also to 2–8; bar at 13 applies also to 14, 15; bar at 19 applies also to 20-23).

Figure 3

septations erode preferentially more than the adjacent silica-filled lacunae giving the appearance of surface grooves. The inner mesocarp is formed of interwoven fibers through which sinuous fibrovascular bundles and/ or canals are prolific (Figure 6.2, 5–7). The fibers are arranged in sinuous tracts accompanied by crystalliferous strands (Figure 6.10).

Although placentation was reported as basal, we have not observed obvious attachment between the seed and the locule. Chitaley (1956, p. 59) stated: "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." She considered the placenta to be richly vascular…" but the figures she cited seem to show the vasculature of the mesocarp (as we depict in Figure 6.2, 5–7), rather than of specialized placental tissue. Using sections, both physical and by X-ray methodology, we have not been able to confirm the placentation type.

The layers interpreted as seed coat by Chitaley (1956) are here considered to represent the endocarp or pyrene as is consistent with the morphology of palm fruits (Murray 1973, Romanov et al. 2011, Matsunaga & Smith 2021). Chitaley noted that in transverse section the thickness of this layer is about 0.25 mm and composed of three regions: a uniseriate outermost layer of radially elongated prismatic cells interpreted as epidermis, a middle zone of about 5–7 cells thick of parenchyma with rather thick walls and dense contents, and an innermost layer made up of several layers of thin-walled parenchymatous cells. In addition to these layers, we noticed a faintly preserved inner uniseriate layer of thin-walled cuboidal cells (Figure 6.9). Digital extraction of pyrenes from micro-CT scanned fruits show the external morphology, including a prominent circular germination pore (Figure 3.18-23).

A peculiar feature of the morphology and anatomy of *Tricoccites* that has not received prior attention are the pockets of spongy tissue peripheral to the apex of each locule (see arrows in Figure 4.3, Figure 5.4-6, 15). Under higher magnification (Figure 6.4), this zone is seen to arise within the mesocarp, and is composed of a spongy tissue of thin-walled cells traversed by sinuous tubular strands (Figure 6.8). Transverse sections above the locules intercept three or six vascular bundles situated on the radii between the radiating spongy zones (Figure 3.11; Figure 5.5, 17). We refer to the apical spongy zones as stigmatic pockets, but they are in need of further study. They may represent pollen-tube transmitting tracts (e.g. Castaño et al. 2016; Stauffer et al. 2002) and it is possible that the tubular structures (Figure 6.8) may be pollen tubes. The exocarp separates along the periphery of each of these pockets (Figure 5.4, 13, 24, 6.4), suggesting that these functioned also as germination openings in the pericarp. The germination pore in each pyrene is situated immediately below the stigmatic pocket (Figure 3.16, 17).

DISCUSSION

Affinities

The monocotyledonous affinities of *Tricoccites* are affirmed by the combination of tricarpellate fruits, scattered vascular bundles of the pericarp (Figure 5.5–7), and single cotyledon per seed Figure 3.4–6). Sahni (1937) considered these fruits to represent an extinct kind of palm, but other possibilities have been presented subsequently, including *Pandanaceae* (Chitaley 1956, Bonde 1985), and *Zingiberales* (Biradar & Bonde 1990).

Trivedi and Verma (1972, 1978) published what they considered to be a peduncle bearing fruits of

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Figure 4. 1-6. *Tricoccites trigonum* fruit from Mohgaonkalan in ground thin sections. S.D. Bonde collection, AGI, Pune. **1.** Transverse section near equator of fruit showing three locules with each of the three seeds containing endosperm, SDB5276, slide 26. **2.** Specimen sectioned closer to the apex showing stigmatic pockets (arrows). **3.** Oblique-transverse section near apex of fruit intercepting pericarp lacunae (bottom of figure), and three stigmatic pockets (arrows). **4.** Enlargement from 1, showing receded parenchymatous tissue within each of the pericarp lacunae, and a single seed with a central linear cotyledon within the shrunken mass of endosperm tissue. **5, 6.** Longitudinal slice of a seed showing the single cotyledon (C) and endocarp (E), SDB5276 slide 33. **7.** Longitudinally sectioned infructescence of Shukla 1950 from Mohgaonkalan. BSIP coll. Scale bars 1 cm in 1–5, 7, 2 mm in 6.
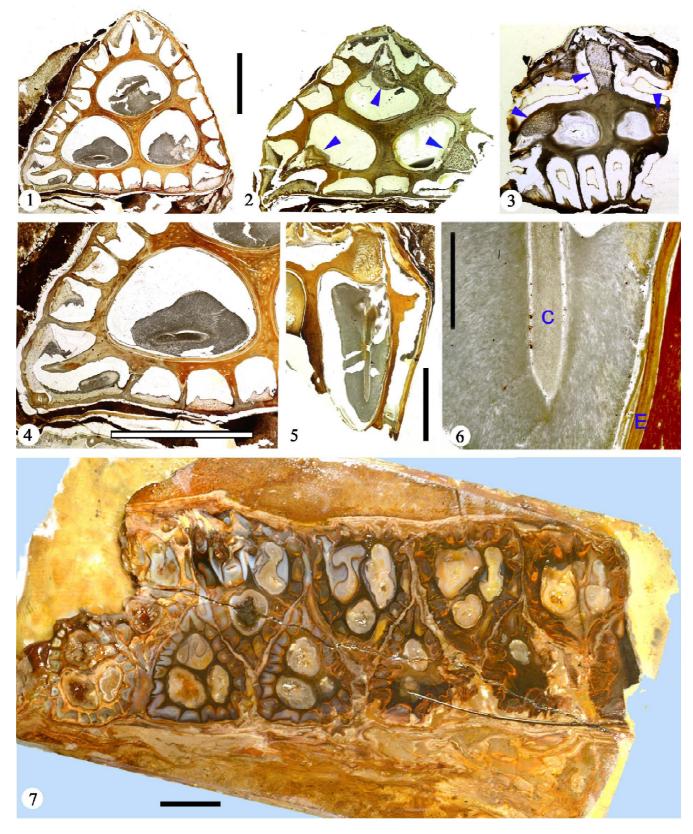
Figure 4

Tricoccites trigonum enclosed by leaf sheaths and showed the anatomical similarities between the peduncle and the pseudostem of *Cyclanthodendron sahnii* Sahni & Surange (Rode 1933; Sahni 1937; Shukla 1950; Sahni & Surange 1953). However, the specimen figured as evidence of attachment does not show physical continuity of tissue and seems instead to be a monocot axis lying adjacent to a fruit. Bonde (1985, p. 65) also mentioned organic connection but did not illustrate specimens with such a connection. The evidence that *Cyclanthodendron* stems and *Tricoccites* represent the same plant thus remains circumstantial, based on close association in the chert. We must remember that there are various other monocot fruits abundant at the same locality including at least four palms and the extinct genera *Momordiocarpon* (see Smith et al. 2021), *Viracarpon* (reviewed, Matsunaga et al. 2018), and *Sahnipushpam* (reviewed, Kapgate et al. 2011) so it is difficult to be certain of the connection between the vegetative and reproductive organs. Among the monocot seeds common at Mohgaonkalan, *Momordiocarpon cardiospermum* (R.K. Jain) Manchester, Kapgate & S.Y. Sm. clearly represents *Zingiberaceae* (Smith et al. 2021), and might be expected to have been borne on a pseudostem like that of *Cyclanthodendron*. The inference that *Tricoccites* is zingiberalean (scitaminean of older literature) (Biradar & Bonde 1990) was based mainly on the assumption that the fruits were borne by *Cyclantodendron* stems, but that remains to be demonstrated.

We reaffirm the affinities of *Tricoccites trigonum* with *Arecaceae*, as recognized early by Sahni (1940). This placement is consistent with the great diversity of fruit morphology known in the family today (Dransfield et al. 2008). Our recognition of a circular germination pore in the pyrene (Figure 3.16-23) reinforces the assignment to *Arecaceae*. Not all palms possess germination pores, but their presence is characteristic of some clades within the family, being particularly useful in recognizing members of the subfamilies *Nypoideae Arecoideae* (Matsunaga & Smith 2021). The position of these apertures, whether basal, lateral or more apical is also informative. In the case of *Tricoccites*, they are dorsal, near the apex.

Although no extant palm shows the same combination of characters, most of its features are not foreign to the family. *Brassiophoenix schumannii, Ptychococcus paradoxus* and *Satranala decussilvae* have similar longitudinal cavities in the pericarp, but differ greatly in other features, e.g. having only a single seed per fruit. *B. schumannii*, and *S. decussilvae* seeds are radially lobed rather than smooth and ellipsoidal. Seeds of *S. decussilvae* have ruminate endosperm. The inflorescence structure of *Tricoccites* resembles the row of sessile flowers, termed acervulus, as seen in the chamaeodorid genus *Synechanthus* (Dransfield et al. 2008). However, a central rachis axis is not observed in otherwise well preserved *Tricoccites* infructescences, so that the mode of attachment of the fruits remains unclear. Also, the structures we call

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Figure 5. *Tricoccites trigonum* fruits in chert from Mohgaonkalan, by micro-CT scanning.
1. Virtual section intercepting two fruits with prominent lacunae in the pericarp, UF 19438-71125. **2–7.** Virtual sections of the left side fruit from 1, UF 19438-71125A. **2.** Nearly equatorial section, showing three equally developed locules; lines indicate the longitudinal planes of section in panels 6 and 7. **3.** Section near the top of the locules. **4.** Section skimming the apex of the locules with three stigmatic pockets (arrows). **5.** Apical section intercepting three-armed stigmatic complex (arrows). **6.** Longitudinal section at orientation indicated in 2, intercepting two of the locules and their adjoining apical stigmatic pockets (arrows). **7.** Tangential section through pericarp showing longitudinal lacunae. **8–17.** Virtual sections of the right side fruit from 1, UF 19438-71125B. **8.** Longitudinal section intercepting two of the locules (each with a central black, empty pocket lined with quartz crystals). Horizontal lines indicate the levels of the transverse sections in 9–17. **9.** Section near base of fruit below the locules. **10.** Section skimming the basal part of the endocarp. **11.** Section in basal 1/5 of fruit intercepting three locules and showing the radiating mesocarp partitions defining lacunae within the pericarp. Note stray seed of *Momordiocarpon cardiospermum* (arrow). **12.** Equatorial section. Note stray seed of *Indovitis chitaleyae* (arrow). **13.** Section approaching the apices of the locules. **14.** Section skimming the apices of the locules. **15.** Section above the locules showing three radiating stigmatic pockets (arrows). **16.** Section at higher level of the stigmatic pockets. **17.** Enlargement from 16. Note three vascular bundles alternating in position with the stigmatic pockets. **18–26.** Virtual sections of a fruit partially exposed at surface of chert, UF 19438-71118. **18.** Longitudinal section intercepting two locules and their apical stigmatic pockets. Horizontal lines indicate the levels of the transverse sections in 19–26. **19–26.** Successive transverse sections from base to apex. Arrows indicate stigmatic complex. Scale bars 1 cm.
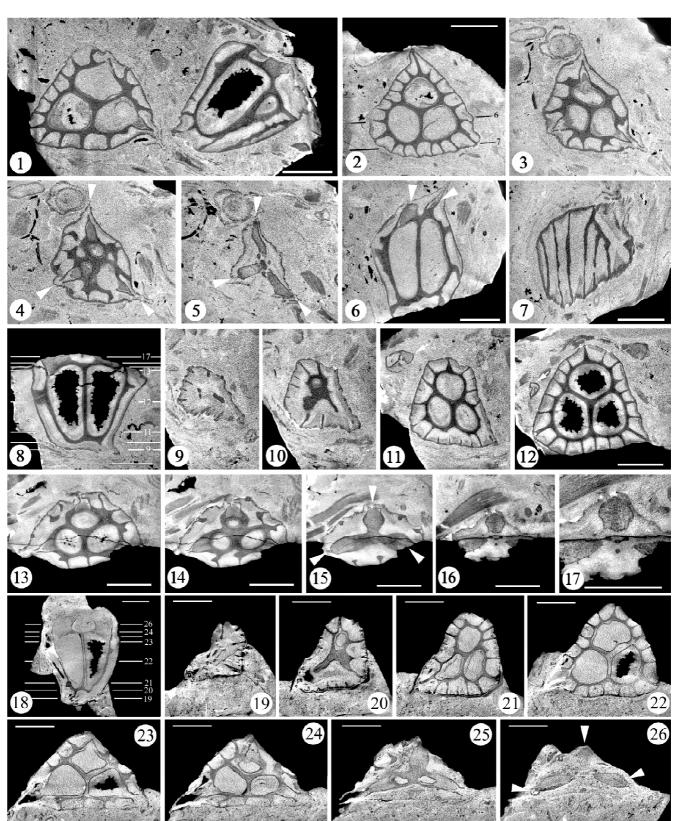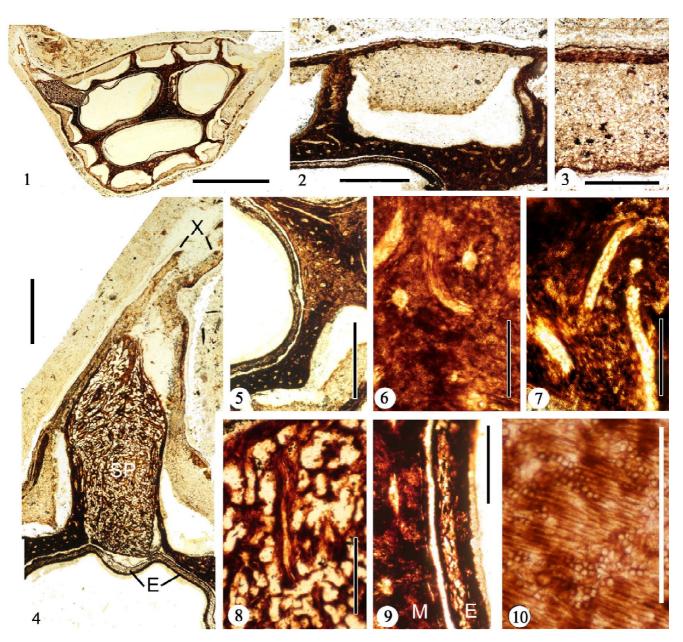
Figure 5

Figure 6. 1–7. *Tricoccites trigonum* fruit sectioned by the acetate peel method for details of anatomy. UF 19329-85612 from Keria. **1.** Somewhat oblique transverse view with plane of section intercepting apical stigmatic pocket upper left. **2.** Detail of pericarp lacuna with parenchymatous tissue adhering to exocarp but receded away from sclerenchymatous layers. Note scattered bundles of the inner mesocarp. **3.** Detail of mesocarp and exocarp. **4.** Detail from 1, showing endocarp (E), exocarp (X), and stigmatic pocket. **5.** Mesocarp with scattered bundles in septa, and endocarp lining the locule. **6–7.** Detail of fibrous mesocarp with sinuous vascular bundle tubes. **8.** Enlargement of tissue from stigmatic pocket. **9.** Histology of mesocarp (M) and endocarp (E). **10.** Detail of mesocarp showing fibers and crystalliferous strands. Scale bars 1 cm in 1; 2 mm in 2, 4; 1 mm in 3, 5–10.

stigmatic pockets may correspond to the pollen tube transmission tract recognized in palms (Castaño et al. 2006; Stauffer et al. 2002). It will be interesting to include *Tricoccites* in a broader phylogenetic analysis of palms taking advantage of the framework presented by Matsunaga and Smith (2021).

Palms were an important component of the Deccan Intertrappean vegetation, represented by vegetative organs such as stems and leaves, and by reproductive structures including fruits, seeds and pollen (Bonde

2006). Co-occurring at the Mohgaonkalan site were at least four other kinds of palm fruits and seeds: 1. *Nypa* (e.g. Chitaley & Nambudiri 1995); 2. *Palmocarpon mohgaoense* U. Prakash (1955) and similar or perhaps conspecific fruits of *P. indicum* U. Prakash (1960), and *Cocos intertrappeansis* G.V. Patil & Upadhye (1984); 3. *Hyphaeneocarpon indicum* Bande, U. Prakash & Ambw. emend. Matsunaga, Manchester, R. Srivast., Kapgate & S.Y. Sm. 2019 (Matsunaga et al. 2019); and 4. *Graminocarpon* Chitaley & Sheikh (Chitaley & Sheikh 1971), the seeds of which have recently been observed to possess germination pores diagnostic of palms (Manchester pers. obs.). We consider *Tricoccites* to be yet another example.

Ecology

We agree with Sahni (1940, p. 15), who concluded that the fruit was adapted for dispersal by water, as evidenced by the longitudinal chambers in the pericarp. A convergent morphology with similar wall cavities occurs in fruits of the North American cornalean species *Nyssa ogechi*. The marsileaceous sporocarps of *Rodeites*, common at Mohgaonkalan (Sahni 1943, Kapgate & Ukey 2014), also indicate a pond or stream environment that would be suitable for aquatic dispersal as is also suggested by the fruits of other palms at the site including *Nypa* (Chitaley 1960, Chitaley & Nambudiri 1995) and *Hyphaeneocarpon* (Bande et al. 1982, Matsunaga et al. 2019).

ACKNOWLEDGEMENTS

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