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Revision of the fossil flower genus *Sahnianthus* Shukla (Myrtales) from the latest Cretaceous Deccan Intertrappean Beds of India

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ABSTRACT. Interbeds of the Deccan traps, ~66 million years old, have long been known to contain cherts with anatomically preserved flowers, fruits and seeds. We studied numerous specimens of *Sahnianthus*, the iconic flower of Deccan Intertrappean cherts, by micro-CT scanning, as well as traditional cellulose acetate peels and scanning electron microscopy of the in-situ pollen, to reconstruct the original floral and pollen morphology. The flowers were collected, in association with fruits of *Enigmocarpon*, from the type locality of Mohgaon Kalan in Chhindwara, Pradesh and other locations in Madhya Pradesh and Maharashtra, Central India. Using micro-CT scans to vary the orientation of virtual sections of complete flowers embedded in chert, we show that nine additional, previously described fossil flower genera represent the same plant and are thus synonyms of *Sahnianthus*. In addition, we suggest that much of the variation observed in the specimens is due to preservation at different developmental stages from bud to maturity. We observed that the epiphyllous stamens are borne in two whorls contrary to prior treatments assuming a single whorl. The number of stamens in each whorl ranges from seven to nine and is equivalent to the number of perianth lobes and ovary locules of the same flower. The pollen is spheroidal and psilate with inconspicuous narrow colpi and a prominent rib-like equatorial thickening of the exine; these features facilitate recognizing the identity of flowers previously assigned to other genera. The combined characters of *Sahnianthus*, together with fruit and seed characters of *Enigmocarpon*, are consistent with placement within, or close to, Lythraceae, as previously suggested.

KEYWORDS: Lythraceae, Late Maastrichtian, Late Cretaceous, Mohgaon Kalan, *Enigmocarpon*

INTRODUCTION

The Deccan intertrappean beds of India are a series of sedimentary layers deposited between basaltic flows extruded during the Late Cretaceous (Maastrichtian) and Paleocene (Danian) as the Indian subcontinent drifted northward over a mantle plume or hotspot in the present-day location of Réunion Island. The period of volcanism bracketed the

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K-Pg boundary (~66.05 MA) extending from about 66.4 to 65.5 million years ago (Renne et al., 2015; Sprain et al., 2019; Schoene et al., 2021). During this time India was isolated from the Gondwanan landmass as it migrated northward and eventually collided with mainland Asia ~50–60 Ma (Rowley, 1996; Hu et al., 2016). Well-preserved fossil plants occur in the intertrappean beds, exposed at sites scattered across central India.

Permineralized plants from the Deccan Intertrappean beds have been studied intensively for nearly a century and have yielded a diverse array of plant remains, including petrified woods, leaves, flowers, fruits, cones, seeds and pollen (Prakash, 1960; Smith et al., 2015). Reproductive organs confirm presence of the families Burseraceae (Kumar et al., 2023; Manchester et al., 2024), Malvaceae (Manchester et al., 2023), Vitaceae (Manchester et al., 2013), Euphorbiaceae (Reback et al., 2022), Phyllanthaceae (Kapgate et al., 2017), Arecaceae (Manchester et al., 2016, 2022; Matsunaga et al., 2019), and Zingiberaceae (Smith et al., 2021). Fruits of *Enigmocarpon* Sahni 1943 and the corresponding flowers of *Sahnianthus* Shukla 1944 have long been considered to represent the myrtalean family Lythraceae (Sahni, 1943; Shukla, 1944), but the precise placement relative to extant genera has remained unclear.

Here we revisit *Sahnianthus*, the iconic flower of the Deccan Intertrappean cherts, first described by Shukla (1944) and documented many times since (e.g. Chitaley, 1955; Dwivedi and Shukla, 1958; Dayal, 1967; Paradkar and Senad, 1984; Kapgate et al., 2016). In addition to specimens published under the name *Sahnianthus*, we found many instances of new generic names being applied to the same kind of flower; we consider those to be junior synonyms. Since their initial investigation (Sahni, 1943; Shukla, 1944) these flowers have been attributed to the Lythraceae, or sometimes to the Sonneratiaceae (Mahabale and Deshpande, 1957), a family more recently subsumed within Lythraceae. The features noted as supporting the familial placement include pedicellate, bisexual, tubular, perigynous, 6–8-valved flowers with calyx constituting about half of the length of the floral tube and axile placentation (Shukla, 1944; Paradkar and Senad, 1984). Additional conforming features were noted in the associated fruits of *Enigmocarpon* (Sahni, 1943; Graham, 2013). In a review of the fossil record of Lythraceae, Graham (2013) accepted the placement of *Sahnianthus* in the family and noted similarities with extant *Koehneria* S.A. Graham, Tobe et Baas 1986 and *Woodfordia* Salisb. 1806, sharing a stipitate superior ovary and non-pseudocolpate pollen. Despite the discovery of many *Sahnianthus* specimens over the decades, and their excellent state of preservation, interpretation of the floral morphology has been challenging because the flowers are preserved in opaque chert that impedes direct observation of all the organs within any one specimen. It is almost impossible to directly count each stamen, so the ranges given in the literature are often under-estimates based only on those on the surface or in peels, or, in some cases, inferred based on the number observed plus an estimate of how many would be expected from the symmetry. In some cases, serial grinding and/or peeling was carried out to reveal features hidden behind the originally exposed surface, but some information is lost in the destructive grinding process (Chitaley, 1955). In addition, the flowers are sometimes distorted by partial compression prior to silicification, and can be preserved at different stages of maturity. The use of x-ray imaging, facilitated by micro-CT scanning, allows us to study entire flowers within the chert non-destructively.

In this article, we call attention to several new sites that have been found to possess *Sahnianthus* and we document the floral morphology with new imagery from micro-CT scanning, as well as transmitted light, and pollen images from transmitted light and scanning electron microscopy. The 3-dimensional morphology of complete flowers, revealed directly for the first time in this article, provides a means of evaluating earlier hypotheses about the floral form, symmetry, merosity of sepals, stamens and carpels, and the extent of variability within these elements. Taking into consideration our current understanding of floral, fruit, seed and pollen morphology, we explore the likely systematic position of *Sahnianthus* relative to extant families of the Myrtales.

MATERIAL AND METHODS

The type locality for *Sahnianthus* is near the village of Mohgaon Kalan (alternative spelling Mohgaonkalan) in Chhindwara, Madhya Pradesh, India (Shukla, 1944), and this area yielded most of the material treated by subsequent authors and in this study. The flowers have also been found at several additional sites collected by D.K. Kapgate and his students and colleagues. These include sites at Keria, Paladaun, and Udadaun, located within a 4 km radius of Mohgaon Kalan in intertrappean beds of the Amarkantak Group. Localities more distant from Mohgaon Kalan include Bhutera, ~10 km to the north (Borkar et al., 2016), Singpur 60 km southwest (Ramteke et al., 2020), and two additional sites to the south: Shibla in Yavatmal at 230 km south (Manchester et al., 2019), and Pudiyal Mohada (Kapgate et al., 2016) in Chandrapur District of Maharashtra, 270 km south of Mohgaon Kalan (Fig. 1). The palynoflora of these sites has been interpreted as Maastrichtian (Kar and Srinivasan, 1998; Samant et al., 2020). At most of these sites the flowers co-occur with *Enigmocarpon*, which are the fruits that probably developed from *Sahnianthus* (Sahni, 1943; Shukla, 1944). Cited specimens are housed at the Florida Museum of Natural History at University of Florida, Gainesville (UF); the Cleveland Museum of Natural History, Cleveland, Ohio (CMNH); and the paleobotanical collection of the University of Kansas, Lawrence (KUPB).

Specimens were discovered by cracking the chert in the field with hammers to expose the flowers in various planes of section depending how the fractures traveled through the chert. In the cases of dark or black chert, brief etching with hydrofluoric acid was used to enhance contrast, making it easier to identify flowers in the samples with the aid of a hand lens. Some of these were sequentially peeled with the cellulose acetate peel technique as modified for hydrofluoric acid for transmitted light microscopy (Joy et al., 1956; Basinger and Rothwell, 1977). Other flowers, still embedded in the chert, were discovered by micro-CT scanning the samples. These were studied in digital sections at various orientations, and digitally extracted to examine the 3-dimensional morphology. For general micro-CT scanning, we used a GE Phoenix V/tome/xm240 CT scanner, at the University of Florida College of Engineering Nanoscale Research Facility. Voltage and current were adjusted to specimen size, with voltage ranging from 100 to 180 kV and current ranging from 50 to 90 µA with up to 2200 images of a single specimen and resolution ranging from 14 to 60 µm. One specimen containing several flowers (UF18311-56214) was also scanned with a Zeiss Versa 620 XRM scanner available at the same facility adjusted for resolution of 11.8 µm. Resulting image stacks were processed with VG StudioMax version 3.1 and Amira version 6.0 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”.

One specimen of tan colored chert bearing several flowers of *Sahnianthus* adjacent to fruits of *Enigmocarpon* was wafered with successive cuts of a Microslice

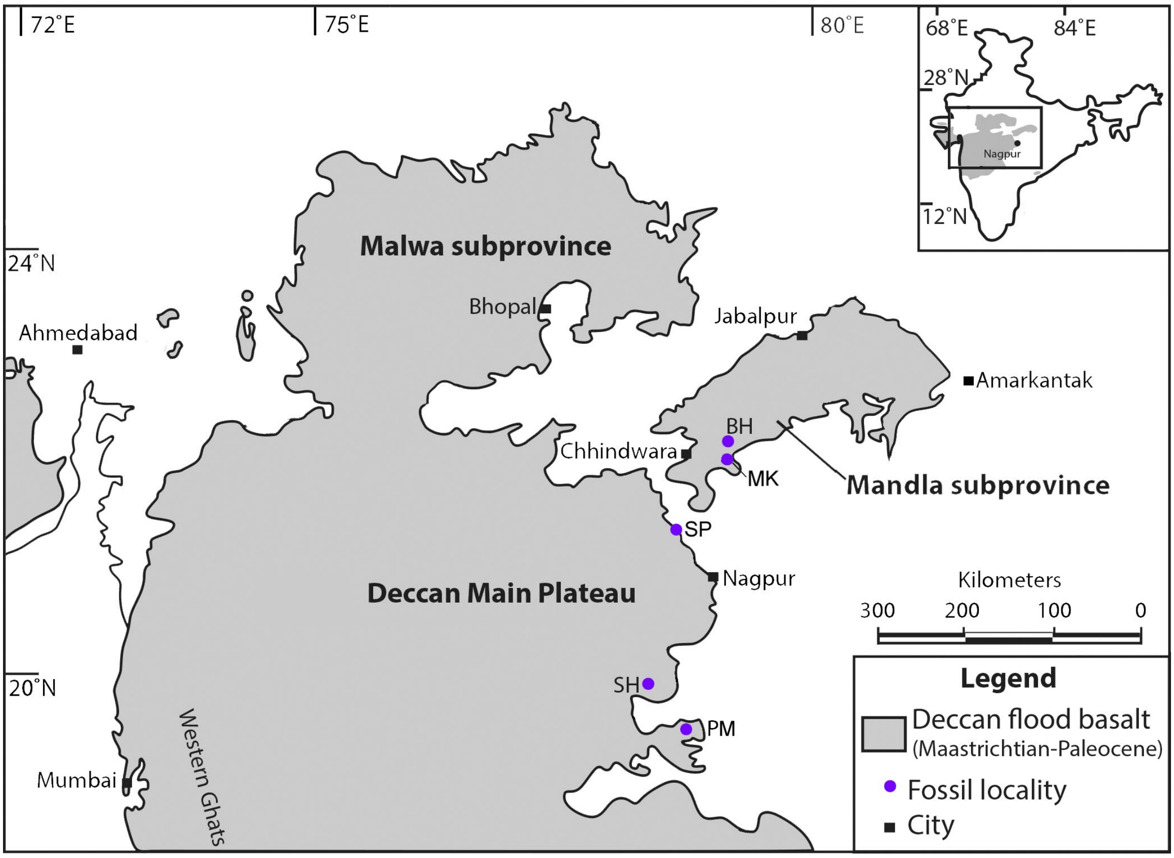


Figure 1. Map showing the distribution of chert localities from which *Sahnianthus* flowers and *Enigmocarpon* fruits have been collected: Bhutera (BH), Mohgaon Kalan (MK), Pudiyal Mohada (PM), Shibla (SH) and Singpur (SP). The site marked as MK also includes nearby Keria, Paladaun, and Udadaun at approximately the same stratigraphic level. Base map from Samant and Mohabey (2009)

II annular diamond blade (kerf loss ~40 µm), to facilitate observations by reflected light while immersed in toluene. We also studied more than 30 specimens for which peels had been prepared and selected a few examples with the best preserved pollen for scanning electron microscopy (SEM). Optical microscopy was done with a Canon XSI digital SLR camera mounted on a Wild Photomacroscope 400, or in some instances with a Keyence VHX-7000N digital microscope with combined reflected and transmitted light.

Samples UF 18311-52592, 68995, 70447 and UF 19329-62709 were studied by SEM, as well as light microscopy. In preparation for SEM, the selected peels were separated from the coverslip and microscope slide using an overnight soak in CitriSolv d-limonene based solvent and then treated in hydrofluoric acid to remove remaining silica. The peels were then mounted on aluminum stubs, sputter-coated with palladium, and scanned with a Hitachi SU5000 Schottky Field-Emission Scanning Electron Microscope at the University of Florida Interdisciplinary Center for Biotechnology Research.

NOMENCLATURE

Although Shukla (1944) provided a diagnosis for his new genus *Sahnianthus*, and described and illustrated 17 specimens in detail, he did not specify a type specimen. However, he argued on morphological grounds, as well as close association in the chert, that this flower actually represented the same species as the fruit described in the preceding year as *Enigmocarpon parijai* Sahni 1943. Following on that conclusion, Shukla stated "I propose to refer the flower to the new genus *Sahnianthus*… The specific name has been retained from the name of the fruit according to the international rules of nomenclature." (Shukla, 1944: p. 33). According to this interesting rationale, the flowers were subsequently referred to as *Sahnianthus parijai* Shukla 1944 (Dwivedi and Shukla, 1958; Paradkar and Senad, 1984). Actually, because the fruits and flower were demonstrated to represent the same plant, both by Sahni (1943) and Shukla (1944), the binomial with priority for the flowers, as well as the fruits, according to the International Rules of Botanical Nomenclature, is *Enigmocarpon parijai* Sahni. For continuity with prior literature, and in keeping with the common practice of applying different fossil generic names for different organs (Cleal and Thomas, 2021), we retain the name *Sahnianthus* for flowers and *Enigmocarpon* for the fruits.

SYSTEMATICS

Family LYTHRACEAE J. St.-Hil. 1805

Genus **Sahnianthus** Shukla 1944

Species **Sahnianthus parijai**
V.B. Shukla 1944

Figs 2–6, 7A, 8–10

Synonymy.

1957 *Sahnianthus dinectrianum* R.K. Shukla; p. 115–116, text-figs 1–4, pl. 15, figs 1–6, pl. 16, figs 8–12.
1971 *Chitaleypushpam mohgaonense* Paradkar; p. 337; pl. 1, figs 1–7, pl. 2, figs 8–11.
1972 *Deccananthus savitrii* Chitaley et U.R. Kate; p. 319, text-figs 1–8, pl. 1, figs 1–6.
1975 *Raoanthus intertrappea* Chitaley et M.Z. Patel; p. 148–149; pl. 1, figs 1–12, pl. 2, figs 13–21, pl. 3, figs 22–32.
2003 *Flosfemina intertrappea* R.K. Kar, K. Ambwani, A. Sahni et P. Sharma; p. 76, fig. 2, pl. 1, figs 1, 2.
2003 *Flosvirulis deccanensis* R.K. Kar, K. Ambwani, A. Sahni et P. Sharma; p. 77, pl. 1, figs 3–7.
2006 *Liliaceopushpum deccanii* Narkhede et G.V. Patil.; p. 22, pl. 1, figs 1–5, pl. 2, figs 1–3; text-figs 1–9.
2010 *Lythraceopushpam mohgaoense* Narkhede, M. Bhowal et S.M. Meshram; p. 4, pl. 1, figs 1–9; text-figs 1–11.
2015 *Menispermaceopushpam amanganjii* Narkhede et B.B Bonde; p. 228, figs 1–4.
2015 *Surangepushpam deccanii* Lanjewar, Puranik et Sakundarwar; p. 330, figs 1–7.

Neotype. Shukla (1944) did not specify a type among the specimens he illustrated, and all of his beautifully photographed specimens were lost before a lectotype could be designated. We here propose a neotype from the same locality, Mohgaon Kalan: UF 18311-52543A (Fig. 2B, C, F), currently deposited in the type paleobotanical collection of the Florida Museum of Natural History, Gainesville, Florida, USA.

Additional specimens studied. UF 19348-73667 [Bhutera], UF 19329-62709a, 70334, 70338, 70767, 87012 [Keria], CMNH-pm 4034, CMNH-pm 3065, KUPB 5837, KUPB 5838, UF 18311-52543, 52592, 53549, 56214d, f, 62708, 62722c, 68993, 68995, 70447, 70449, 71272, 71274, 76413 [Mohgaon Kalan], UF 19506-69602, 70457 [Paladaun], UF 19443-73621, 73633, 73619 [Pudiyal Mohda], UF 19278-69714 [Singpur], UF 19351-62135, 62710, 70428 [Shibla], UF 19527-70305 [Udadaun].

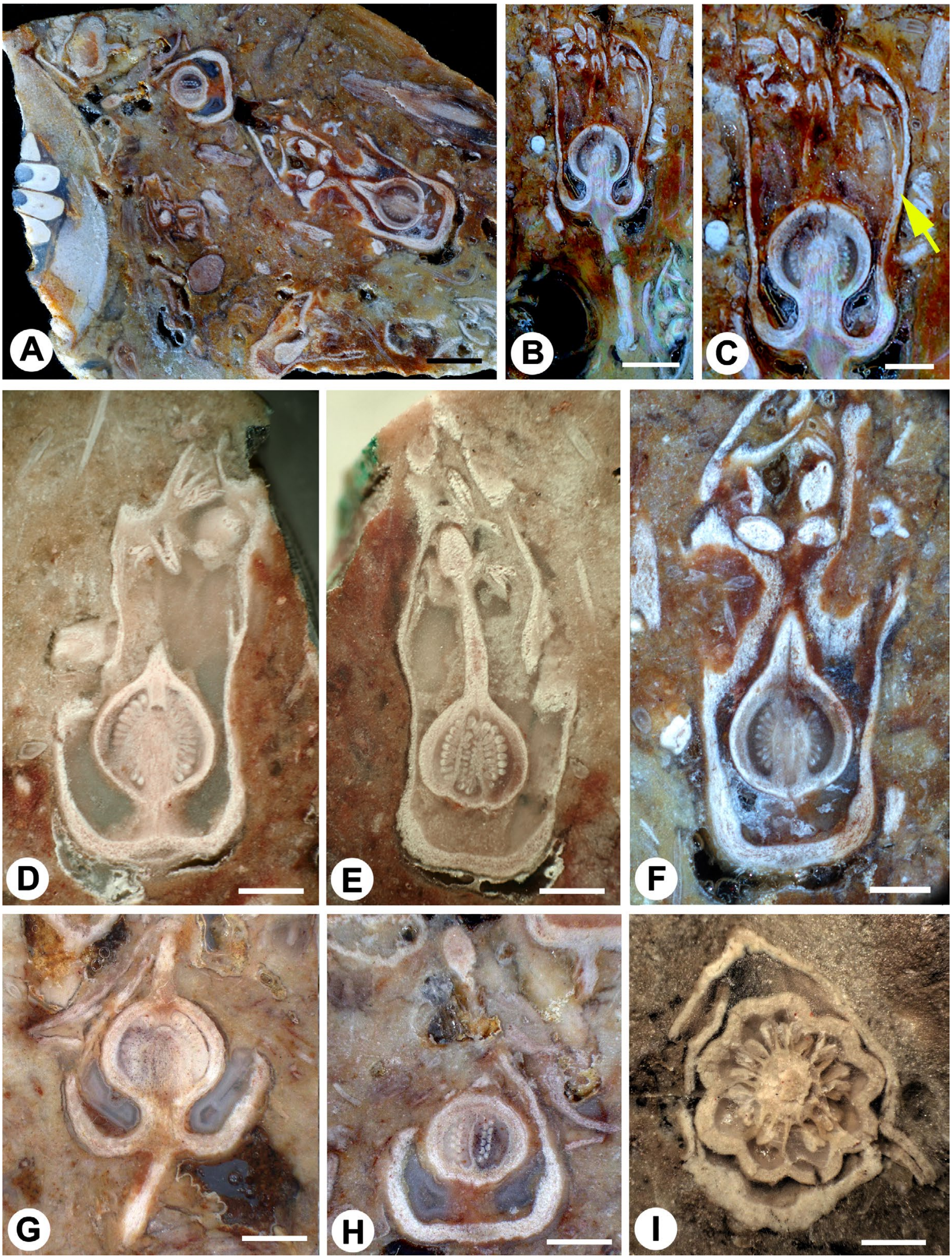


Figure 2. **A**–**I**. *Sahnianthus parijai* V.B. Shukla flowers from Mohgaon Kalan, thin wafers by reflected light. **A**–**H**. Physical sections of a chert specimen containing several *Sahnianthus* flowers, UF 18311-52543; **A**. Several flowers of *Sahnianthus* in different planes of view adjacent to an *Enigmocarpon* fruit with a partial row of seeds (left); **B**. Neotype designated here, flower in longitudinal section with long pedicel, prominent hypanthium and stipitate ovary, UF 18311-52543A; **C**. Detail of same specimen, showing ovules in axile placentation, eleven anthers, and a stamen filament arising from inside of calyx (arrow); **D**. Flower in longitudinal section showing rows of ovules within the ovary, and intercepting at least 4 anthers, UF 18311-52543C; **E**. Same flower as in D, sectioned along the style with elongated capitate stigma; ovary showing at least two thin septa and double rows of ovules in each locule; **F**. Neotype (same flower, as B, C), in a parallel longitudinal slice, showing hypanthium, calyx lobes, gynoecium (sectioned somewhat obliquely, showing the extension of the apical part of the ovary into the style), and at least five anthers; **G**. Flower showing pedicel, hypanthium, stipitate ovary and style, UF 18311-52543B; **H**. The same flower as G, sectioned longitudinally closer to the periphery of the ovary showing two locules, separated by a thin septum, each with two alternating rows of ovules; **I**. Transverse section showing 9-locular ovary with ovules in axile placentation, KUPB 5838. Scale bars = 2 mm in A, B, 1 mm in C–I

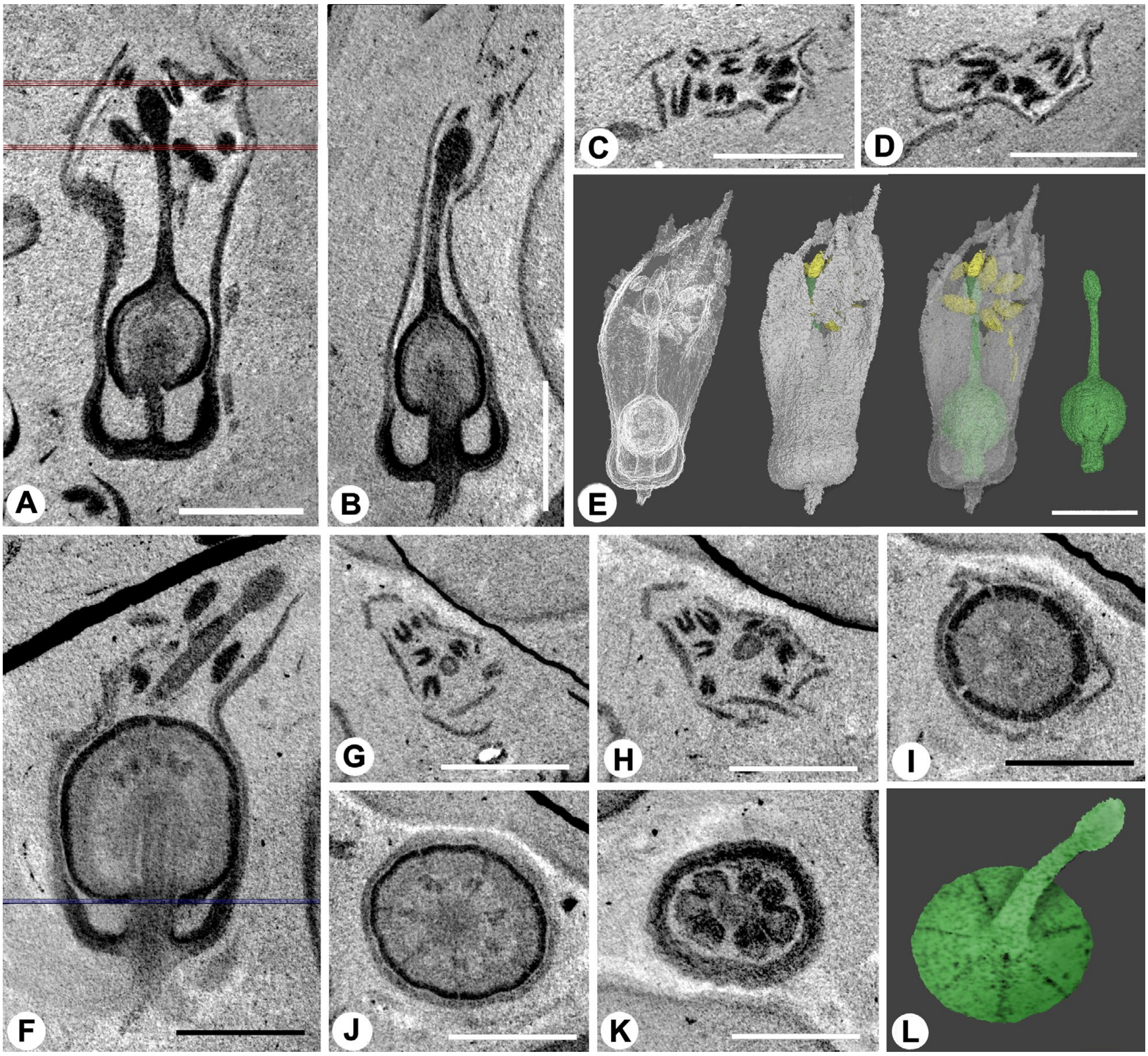


Figure 3. Micro-CT scan digital sections of *Sahnianthus parijai* flowers from Mohgaon Kalan. **A**–**D**. Flower with seven calyx lobes and 14 stamens in longitudinal and transverse sections, UF 18311-56214d; horizontal red lines in longitudinal section A indicate levels of figs C (top level of stamens) and D (lower level of stamens); **E**. The same flower, digitally extracted, depicted with monochrome translucency (left), and with varied translucency highlighting the perianth (light gray), gynoecium (green) and stamens (yellow); gynoecium isolated at right; **F**–**L**. Flower with 7-carpellate fruit, UF 18311-56214e; **F**. Longitudinal section; horizontal blue line indicates level of K; **G**–**K**. Successive transverse sections from near apex to near base; **L**. Apical view of gynoecium digitally extracted from the same flower showing style with elongate stigma, and rounded ovary with incipient capsular dehiscence lines. Scale bars = 2 mm

Emended description. Solitary flowers are borne on long, thick, somewhat curved pedicels that are 4.5–5 mm long and 0.5 mm thick (Figs 2B, 6D). Flower buds are small, 1.5 mm long and 1.4 mm wide (Fig. 5A–D); small flowers are 2.9 mm long and 1.8 mm wide (Fig. 6K), and moderately sized and large flowers that we observed range from 4.0 mm to 7.6 mm in length and from 2.5 mm to 3 mm in width, excluding the pedicel. Shukla (1944) reported his largest specimen as 10.5 mm long and 2.3 mm wide. Flowers are actinomorphic, bisexual, perigynous, and appear elliptical or circular in transverse section depending on the extent of lateral compression. The hypanthium is well developed and thick-walled (Figs 2A–I, 4A–C, 4L–N, 6A–D), with a nectariferous lining in the lower part facing the stipe (Fig. 3 A, B, F). The perianth is arranged in a single whorl (Figs 3C, I, 4K, 5K, L, 6I). The calyx, arising from the top of the hypanthium, is fused basally and is composed of several acute, erect, valvate lobes distally; the length of the calyx lobes is less than half the length of the floral tube. For calyx merosity, we have observed seven (Figs 3C, D, 5K, L), eight (Fig. 4K) and nine lobes (Fig. 5Q, R). Calyx lobes alternate with the carpels (Fig. 4D, H, I). Petals have not been observed in thin sections, peels

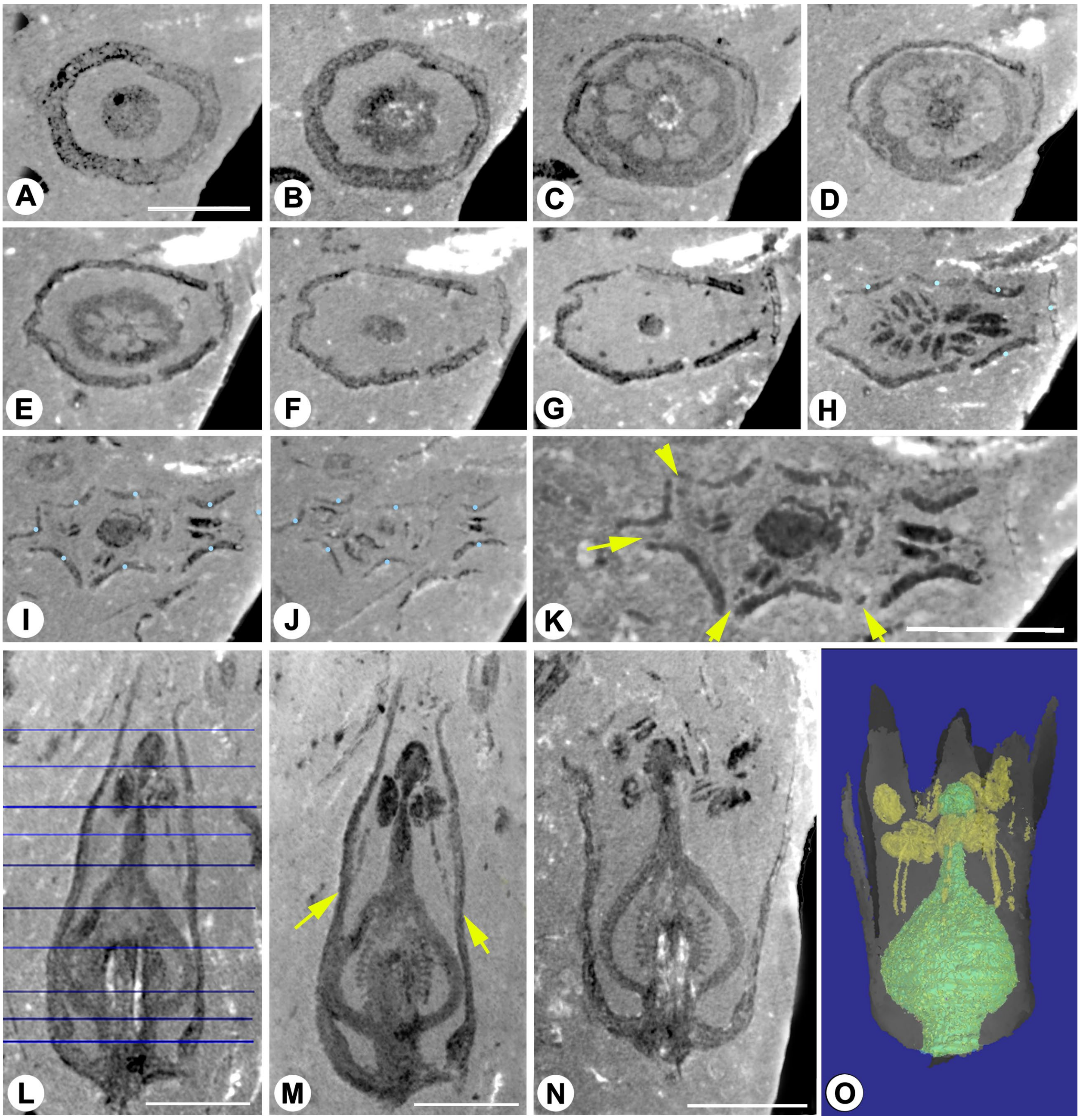


Figure 4. **A–O**. Micro-CT scan imagery of a single *Sahnianthus parijai* flower, UF 19329-70767, Keria. **A–J**. Successive transverse sections from near base of flower to near apex at levels shown by horizontal lines in L; **A**. Stipe surrounded by hypanthium; **B**. Base of ovary surrounded by hypanthium; **C**, **D**. 8-loculed ovary with axile placentation; **E**. Apical part of unilocular ovary; **F**, **G**. Eight stamen filaments arising from inside of hypanthium, surrounding the central style; **H**. Transition from hypanthium to calyx with eight separate concave lobes (blue dot placed at midpoint of each calyx lobe; see successively higher sections I, J for complete count); section traversing lower whorl of eight anthers; **I**. Section at level of stigma, intercepting eight calyx lobes (the one on right poorly visible, aligned with the same structure in G, H; **J**. Calyx lobes spreading, apical portions of top whorl of anthers visible; **K**. Enlargement from I, showing departure of the upper whorl of stamen filaments from notches between calyx lobes (arrows); **L**. Longitudinal section of the same flower with horizontal lines indicating the levels of sections A–J; **M**. Longitudinal section intercepting two of the stamen filaments departing from inside the hypanthium (arrows); **N**. Rotated 90°, showing hypanthium, stipitate ovary, style with elongate stigma, and two levels of anthers; **O**. The same flower digitally extracted from the chert with perianth (gray) rendered translucent, showing gynoecium (green) and stamens (yellow) Scale bars = 2 mm. Scale bar in A applies to B–J; Scale bar in N applies also to O

nor in micro-CT scanning, and no corolla scar is seen so petals are concluded to have been absent (Shukla, 1944; Chitaley, 1955).

The number of stamens is double the number of calyx lobes. Stamens are epitepalous, arising from the calyx in two whorls (e.g. Fig. 2C), the lower set aligned with the middle radial line of each calyx lobe near the top of the hypanthium (Fig. 4G) and the next higher whorl alternating with the first, aligned with the sinuses between calyx lobes (Fig. 4K). The stamens extend to two levels (Figs 2C, 3A,

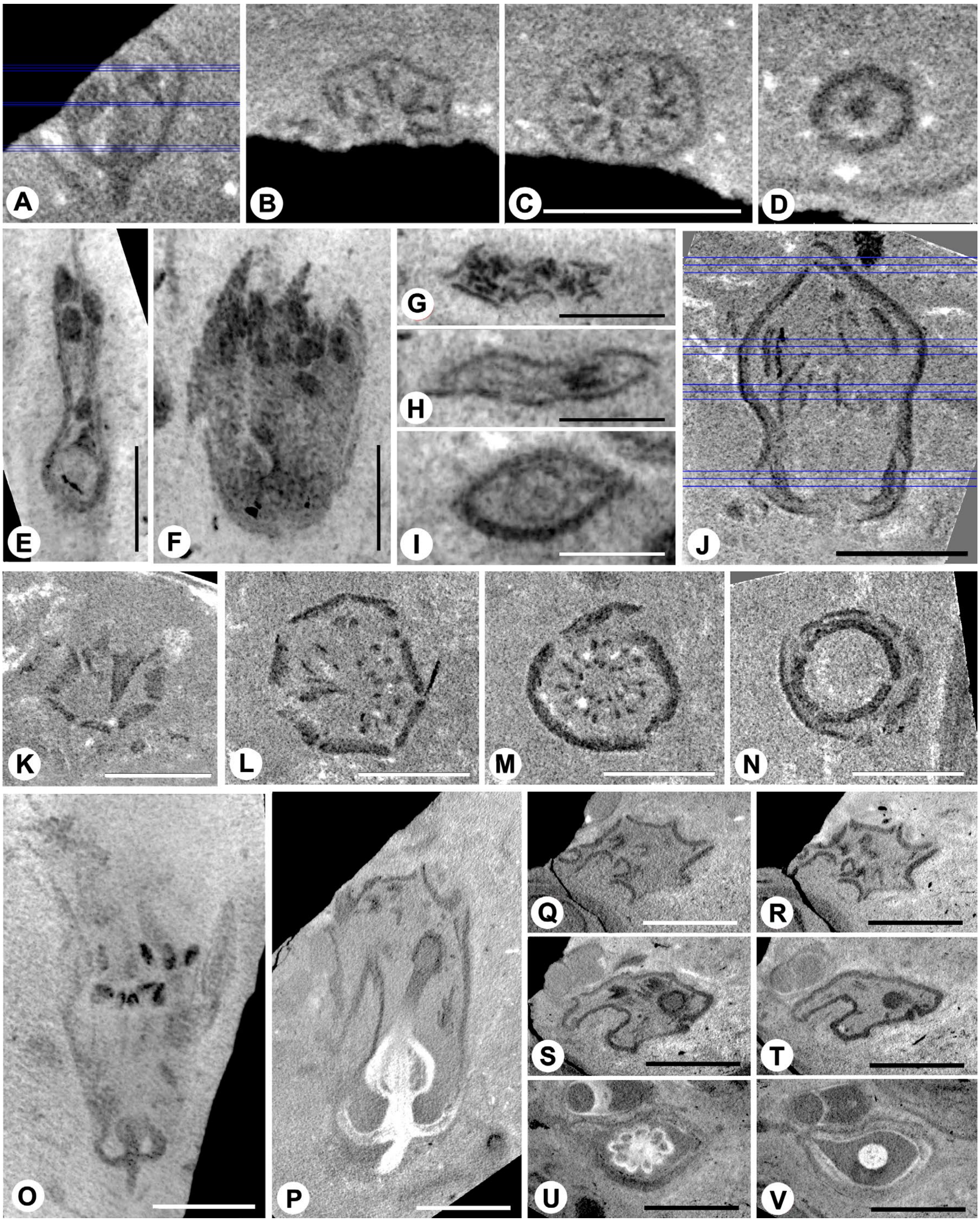


Figure 5. Micro-CT scan imagery of *Sahnianthus parijai* flowers. **A–D**. Young flower, showing two tiers of anthers, UF 18311-62722c; **A**. Longitudinal section, showing pedicel and unopened perianth. Horizontal lines show the levels of section B–D; **B**. Transverse section near apex, intercepting upper whorl of several anthers (about seven inferred from symmetry and successively lower sections); **C**. Transverse section near equator, intercepting lower whorl of seven anthers; **D**. Transverse section near base, intercepting stipe or young ovary and surrounding hypanthium; **E–I**. Laterally compressed flower, UF 18311-76413; **E**. longitudinal section showing three anthers; **F**. Longitudinal section rotated 90° from E, showing at least 10 anthers; **G**. Transverse section near apex, showing nine anthers; **H**. Transverse section at equator, intercepting one of the anthers; **I**. Transverse section through the ovary; **J–M**. Flower from Udadaun, UF 19527-70305; **J**. Longitudinal section, showing continuity of calyx with hypanthium, two levels of anthers apparent. Blue lines show the levels and thickness of sections in K–N; **K**. Transverse section near apex, with one of the calyx lobe tips folded into the plane of section, showing triangular, acute apex. Seven calyx lobes are visible; **L**. Transverse section through upper whorl of about seven anthers, surrounded by seven calyx lobes; **M**. Equatorial transverse section intercepting lower whorl of seven anthers and surrounding hypanthium; **N**. Transverse section near base of ovary; **O**. Longitudinal section of flower from Mohgaon Kalan showing pedicel, hypanthium, stipitate ovary and about ten anthers at two levels, KUPB 5837; **P–V**. Flower with pedicel, hypanthium, and ovary preserved in electron-dense pyrite (white), but apical half of flower organically preserved within the chert. Note style with elongate stigma, UF 18311-56214F; **Q–V**. Successive transverse sections from near apex to near base, showing nine calyx lobes (Q, R), nine locules (U), numerous stamens (Q–S). Scale bars = 2 mm. Scale bar in C applies to A, B, D

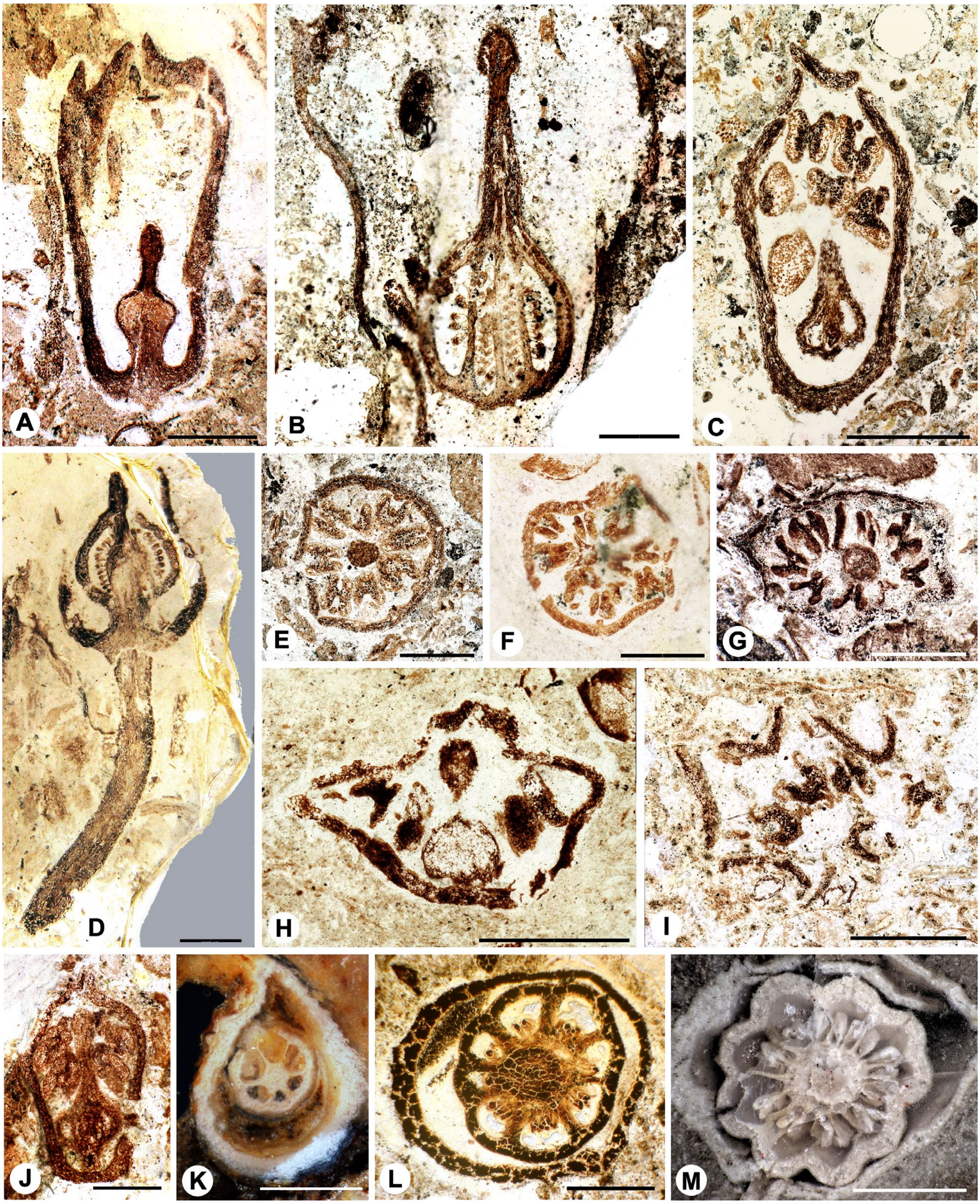


Figure 6. Peel sections (A–J, L) and wafers (K, L) of fossil *Sahnianthus parijai* flowers by transmitted and/or reflected light microscopy. **A**. Longitudinal section with small stipitate ovary and prominent hypanthium, UF 19351-62135, Shibla; **B**. Longitudinal section showing septate ovary with double rows of ovules, and style with elongate capitate stigma, UF 18311-62708; **C**. Oblique longitudinal section showing portion of ovary and six of the anthers, UF 18311-71272; **D**. Longitudinal section showing pedicel, hypanthium, stipe, ovary, style and stigma; Mohgaon Kalan, CMNH-pm 4034; **E**. Transverse section with central style surrounded by eight anthers, and circular hypanthium, UF 18311-71274; **F**. Transverse section showing at least 10 anthers, UF 19329-62709a; **G**. Transverse section with at least nine anthers, UF 18311-53549; **H**. Oblique section intercepting hypanthium, ovary, stigma and four anthers, UF 18311-68995 source of pollen in Fig 8A, C, D; **I**. Flower sectioned near apex, revealing five free convex calyx lobes and four anthers, Shibla, UF 19351-62710; **J**. Flower in longitudinal section with anthers crowded around the style, UF 18311-52592, source for pollen in Fig. 8B; **K**. Transverse section of 6-locular ovary, UF 18311-52543, slide 4; **L**. Transverse section of hypanthium and 8-locular ovary, CMNH-pm 3065; **M**. Ovary in transverse section, enlarged from Fig. 2I, showing nine locules and pairs of stalked ellipsoidal ovules, KUPB 5838. Scale bars = 1 mm

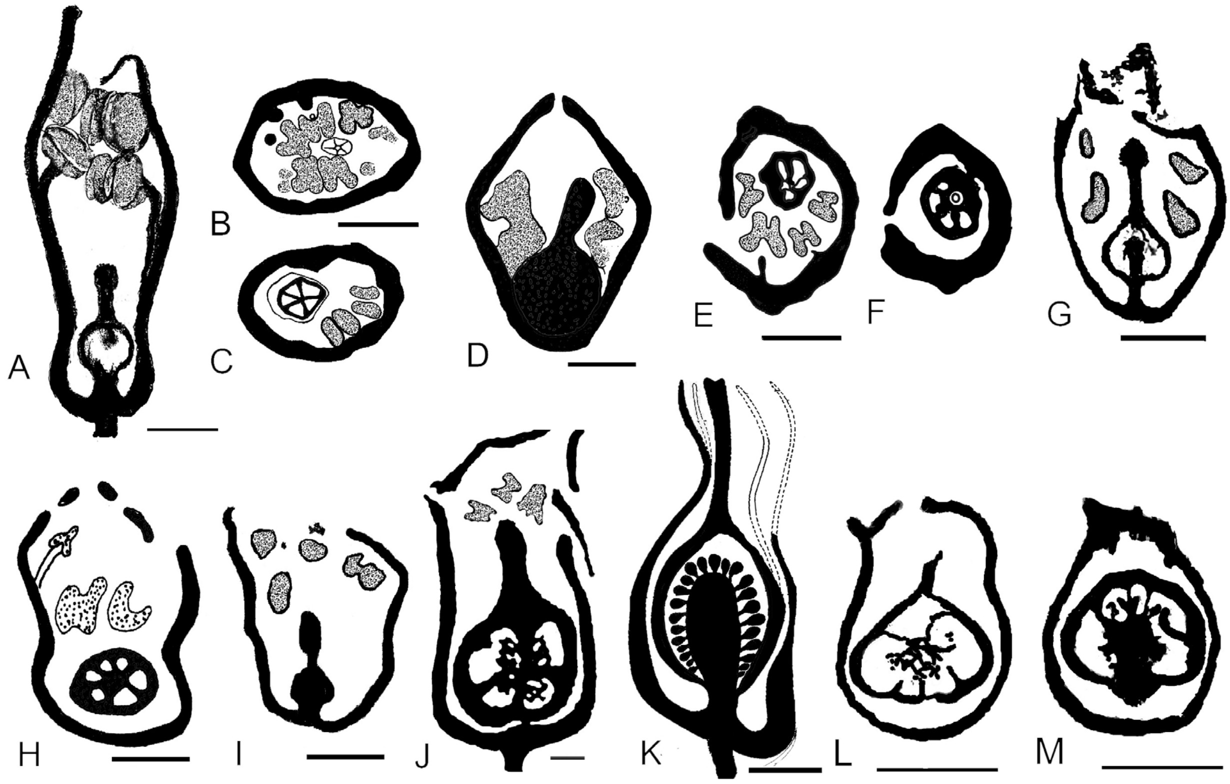


Figure 7. Illustrations of *Sahnianthus parijai* Shukla and synonymous taxa based on illustrations provided in the original publications. **A**. *Sahnianthus parijai* illustration from Shukla (1944); **B**, **C**. *Chitaleypushpam mohgaonense* Paradkar (1971); **D**. *Deccananthus savitrii* Chitaley and Kate (1972); **E**, **F**. *Raoanthus intertrappea* Chitaley, S.D. et M.Z. Patel (1975); **G**. *Surangepushpam deccanii* Lanjewar, Puranik et Sakundarwar (2015); **H**, **I**. *Liliaceopushpum deccanii* Narkhede, S.D. et Patil, G.V. (2006); **J**. *Lythraceopushpam mohgaoense*; **K**. *Flosfemina intertrappea* Kar, R.K., K. Ambwani, A. Sahni et P. Sharma (2003); **L**, **M**. *Menispermaceopushpam amanganjii* Narkhede and G.Y. Patil (2006). Scale bars = 1 mm, calculated from dimensions indicated in the original publications either from the descriptions or as derived from the magnifications indicated in the figure captions

C, E, 5F, P, 7A) with about 8 (6–9) anthers at each level, for a total of 16 (12–18). Their filaments bear versatile, oblong, dorsifixed, anthers, 0.74–1.0 mm long, with longitudinal dehiscence (Figs 2C, 3A, C). In situ pollen is spheroidal to oblate, 8–14 µm in diameter, and triaperturate with narrow colpi. The grains are irregularly collapsed (Figs 8A–D, 9A–D). Both by light microscopy and scanning electron microscopy the exine is seen to be psilate, lacking in ornamentation (Figs 8D, 9C, D). Pseudocolpi are lacking but each grain shows a distinctive belt-like equatorial thickening of the exine, running perpendicular to the colpi, that is visible both in light microscopy and SEM (Figs 8A, D, 9A–D), seen well in the images of Dwivedi and Shukla (1958: pl. 16, fig. 9).

The gynoecium is composed of a stipitate, spherical ovary with a single style and an elongate, barrel-shaped capitate stigma. The stipe is clearly seen in median longitudinal sections (Figs 2C, G, 3A, B, F, 4L–O, 5O, P, 6A, D, J) but can be missed when the section is tangential or oblique (Figs 2E, F, H, 6B, C, 7D, H, L). The stipe ranges from 0.2 mm to 0.7 mm in length and is 0.5 mm in diameter. The ovary body is 1.7–2.8 mm wide and 1.7–2.8 mm high, appearing circular in cross section at and above equator, but the basalmost part has a crenate margin with a convexity corresponding to each locule (Figs 2I, 3K, 4B, 5V, 6M; Shukla, 1944: fig. 23). The number of locules in the ovary can be six (Fig. 6K), seven (Fig. 3K), eight (Figs 4D, 6L), or nine (Fig. 5V) separated by thin septa. The ovary wall is 0.15 mm thick and shows a preformed line of weakness in the central part of each carpel (Figs 2I, 3I, L), coinciding with loculicidal dehiscence in the capsular fruits that mature from *Sahnianthus* flowers. The epidermis of the ovary is made up of slightly elongated cells and is glabrous. Placentation is axile with numerous anatropous ovules (Figs 2D, E, F, H, I, 6B, D, L, M). The placental columella is apically rounded and does not reach to the top of the ovary. Ovules are arranged in two vertical rows in each locule with the two ovules in adjacent rows alternating (Fig. 2H); the same arrangment is seen in the seeds of *Enigmocarpon* (Fig. 12B). Ovules are ellipsoidal, about twice as long as broad (Fig. 4C). The elongate style is 1.4–2.3 mm long and 0.2–0.3 mm wide, terminating in a cylindrical, barrel-shaped capitate stigma, 0.7–0.8 mm long by 0.5 mm wide (Figs 2E, H, 3A, B, F, 5Q, 6B, Shukla, 1944, figs 12, 18, 20), which is particularly well seen in digitally extracted gynoecia (Fig. 3L). Shorter style lengths were presented by Shukla (1944; 0.3–1.3 mm) and Chitaley (1955; 0.35–1.8 mm).

DISCUSSION

NEW OBSERVATIONS CONTRIBUTING TO THE INTERPRETATION OF *SAHNIANTHUS* FLOWERS

Previous investigations of *Sahnianthus* provided excellent anatomical detail and quite reasonable inferences of original floral morphology based on incompletely exposed or sectioned flowers within the chert. Questions

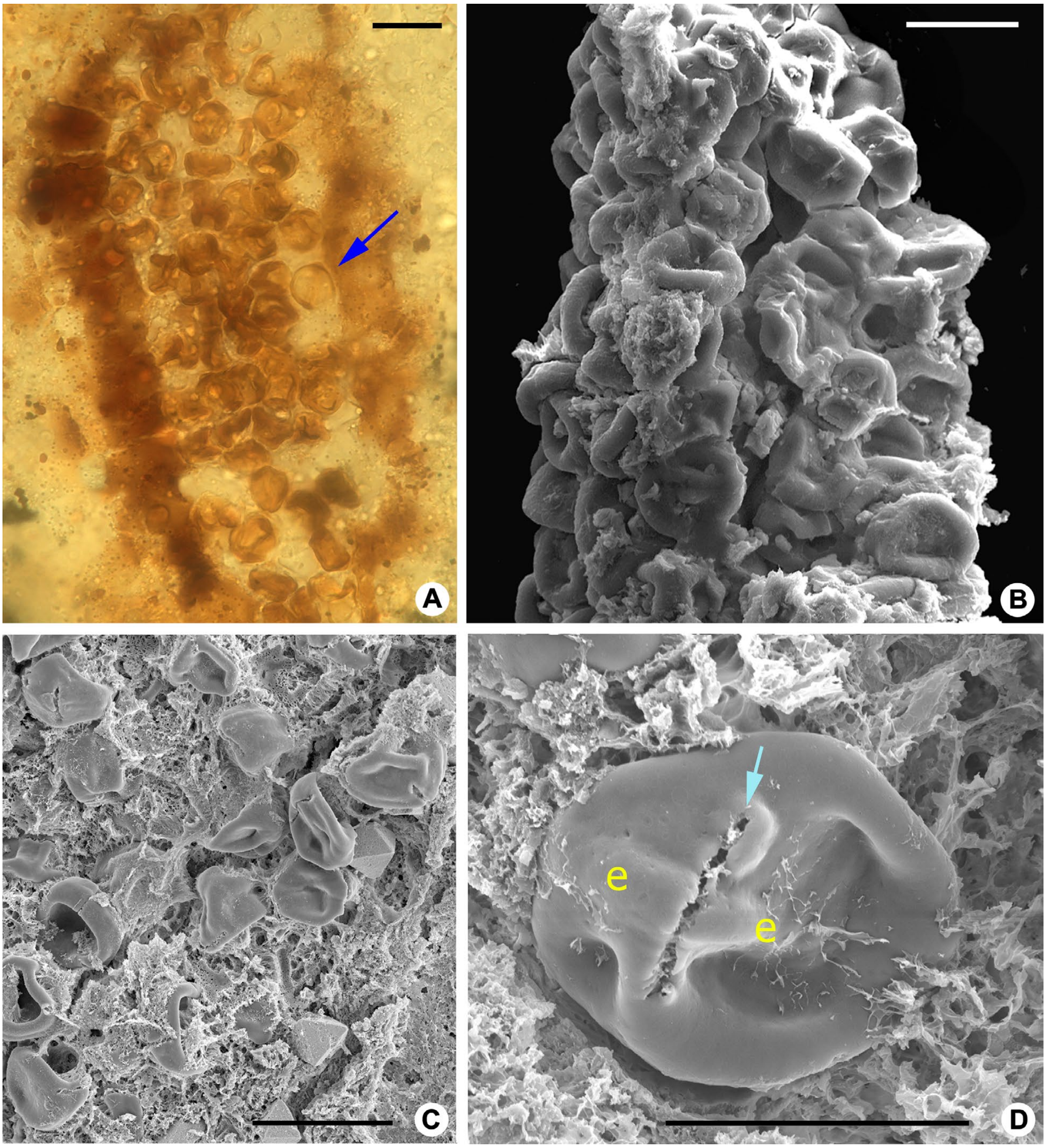


Figure 8. Anther contents of *Sahnianthus parijai*. **A**. Anther from Fig. 6H, enlarged to show pollen grains, transmitted light, UF 18311-68995. Arrow indicates a grain in equatorial view with slightly darker middle line of the equatorial thickening; **B**. Pollen mass from anther of flower in Fig. 6J, SEM, UF 18311-52592; **C**. SEM of pollen from anther in A; **D**. Detail of a pollen grain from C, showing smooth surface, narrow colpus (arrow) and equatorial thickening (e). Scale bars = 20 μm in A–C, 10 μm in D

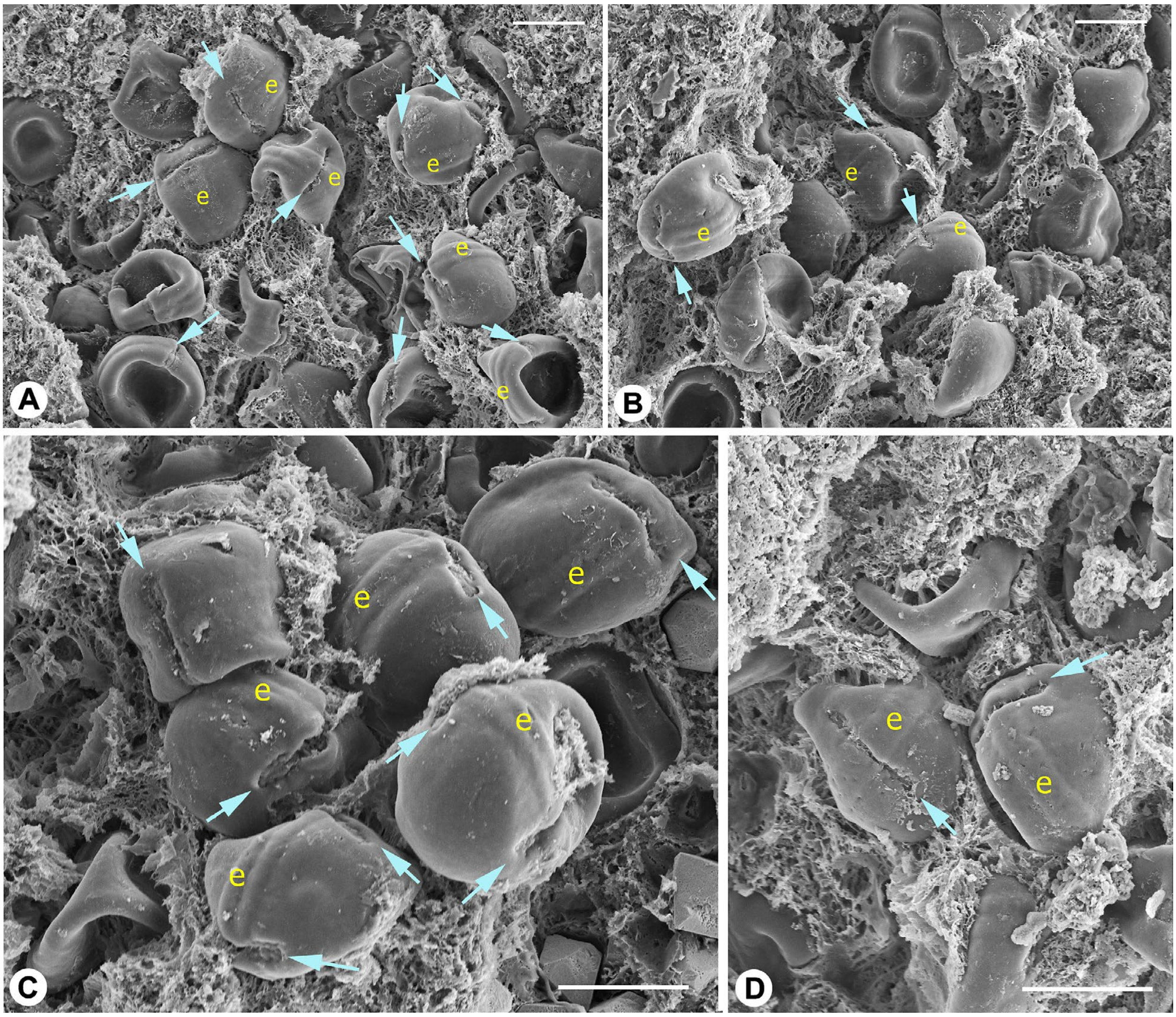


Figure 9. Pollen of *Sahnianthus parijai*. **A**–**D**. SEM of pollen grains from an anther of the flower in Fig 6F, UF 19329-62709a. e = equatorial thickening, arrows indicate colpi. Scale bars = 10 µm

have remained as to the merosity. What is the typical range in number of calyx lobes? What was the actual number of stamens? Are the lower counts (e.g. five) an indication of the lower end of the range in variation, or only reflecting the difficulty to observe the full number of stamens within a flower that is partly hidden inside the opaque chert of the fossil? With the help of micro-CT scanning of flowers completely preserved within the chert, we can now count the total number of elements in each flower to document the extent of variation. We have been able to verify calyces with 7, 8, and 9 lobes and ovaries with 6, 7, 8, and 9 locules (figures cited in preceding description). Our floral diagrams (Fig. 11) reflect this variation. We have not verified specimens with merosity of 5 or 10.

Stamen number and arrangement

The most important departure from prior analyses is our recognition that stamens are borne in two whorls so that the anthers appear in two tiers (Figs 4, 5). This means that a transverse peel showing a cycle of seven stamens (e.g. Fig. 6E) is showing only half of the flower's full set of 14 stamens. Moreover, we were able to confirm that the stamen number is precisely double the number of calyx lobes, with the lower whorl of stamens emerging near the midline of each calyx lobe, and the higher whorl of stamens attaching near the midline of each sinus in the calyx. As far as we have been able to determine, these numbers are also linked to carpel number, so that the specimen with eight calyx lobes, and two whorls of eight stamens, also bears eight locules in its ovary (Fig. 4).

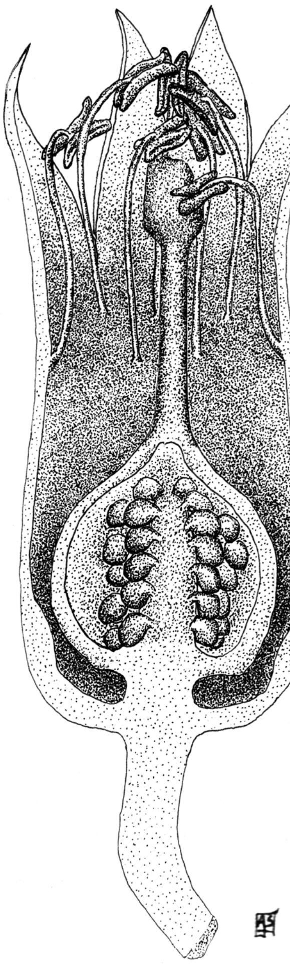


Figure 10. Artistic rendering of *Sahnianthus parijai* flower in longitudinal section showing stipitate ovary, ovules in two rows per locule, style with elongate stigma, and stamens arising in two whorls

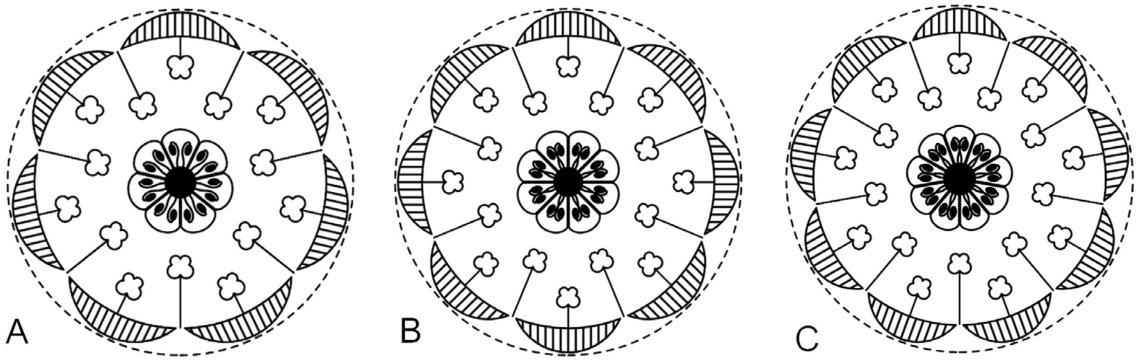
Nectary

RK Shukla (1958), not related to the original author of the genus (VB Shukla), designated a new species of *Sahnianthus* based on a specimen that he interpreted to have a pair of nectaries adjacent to the stipe below the ovary. The nectaries, however, are not clearly seen in the specimen, and what he described appears to be the silica-filled empty space between the base of ovary and hypanthium. It is possible that nectar accumulated in this position, but actual nectaries were not anatomically preserved in the specimen he illustrated. The nectary interpretation was challenged by Dayal (1967) who considered *Sahnianthus dinectrianum* Shukla 1957 of RK Shukla to be a synonym of *S. parijai* of VB Shukla (1944).

The presence of nectaries in *Sahnianthus* has been conjectural. The pouch-like form of the hypanthium has been taken to indicate that nectar may have pooled there (Paradkar and Senad, 1984), but the actual nectary has been difficult to confirm by traditional techniques. Our virtual sections show an electron-dense layer lining the inner part of the hypanthium (e.g. Fig. 3B, F) which corresponds in position to the nectary as observed in some extant Lythraceae (Tobe et al., 1998).

Pollen

Dwivedi and Shukla (1958) described pollen from the anthers, and adhering to the stigma, of a well-preserved *Sahnianthus* flower from Mohgaon Kalan as revealed by transmitted light microscopy of peels. The grains, resolved somewhat more clearly than those of the original specimens shown by Shukla (1944), are spherical and match those shown herein in having a prominent belt-like equatorial thickening (although not mentioned by the authors). Dwivedi and Shukla (1958) noted bulges of the germinal pores, but the aperture type and number were not clearly described or shown. Amazingly, grains found in proximity to the stigma showed distinct pollen tubes, indicating that



☿ [K7 A7+7] G($\underline{7}$) ☿ [K8 A8+8] G($\underline{8}$) ☿ [K9 A9+9] G($\underline{9}$)

Figure 11. **A–C**. Floral diagrams for 7-, 8-, and 9-merous flowers of *Sahnianthus parijai*. Dashed circle represents the hypanthium. Prepared with floral diagram generator, https://kvetnidiagram.8u.cz/oprogramu_en.php

they had germinated. In our specimens, too, the apertures are often obscure, especially by light microscopy, but they form narrow colpi, best visible by SEM (Figs 8C, D, 9C, D) and appear to be tricolpate. It is possible that the grains might be tricolporate but the endoaperture is not obvious. This kind of pollen has also been recovered as dispersed grains from the cherts of Mohgaon Kalan, Bharudpura, and Pudiyal Mohda (Bandana Samant, pers. comm. June 2025).

Heterostyly?

Shukla (1944) described ‘short-styled’ and ‘long-styled’ flowers, and concluded they indicated heterostyly, a feature known in some extant Lythraceae. Flowers of subsumed genera (Fig. 7) also display styles of varying lengths, although specific measurements or ratios are not often included. However, an alternative explanation is that the flowers are preserved in various stages of maturity; those with smaller perianth and ovaries also tend to have shorter styles compared to those with larger perianth and ovary (e.g. Fig. 6A vs 6B; Chitaley, 1955). Chitaley (1955) concluded that the styles elongated rather late in flower development after the pollen had been shed. Evidence for heterostyly remains inconclusive.

Protandry

Several flowers reviewed here have ovaries in ‘young’ condition or an immature state, yet show fully formed anthers with mature pollen grains. This fits earlier observations leading to the conclusion that these flowers were indeed protandrous (Chitaley, 1955).

Zygomorphic vs Actinomorphic flowers?

Paradkar and Senad (1984) cited a gibbous condition observed in some of their specimens [a bulging and swollen side of the flower] as evidence of a spur, which they took to indicate zygomorphy. However, our micro-CT observations indicate that the asymmetry suggested by this spur-like bulge was likely an artifact of oblique section. The bulging condition of the base of the hypanthium appears to be radially symmetrical, and most specimens are apparently actinomorphic. It is difficult to tell if there was some slight zygomorphy, or only some distortion due to the flowers lying on their sides and being somewhat deformed by compression.

Epicalyx, bracts, perianth

Although epicalyx and bracts have been reported previously, the images provided are equivocal. We were unable to confirm the presence of these in the many specimens we observed. We do not agree with the conclusion of Paradkar and Senad (1984) that a corolla was present in *Sahnianthus*. The distinctive crinkled petals typical of the Lythraceae should be preserved if they were originally present, considering the excellent state of preservation of the other organs including stamens, however, none of the peels or micro-CT sections we have observed show any evidence of petals or their detachment scars. They also are absent from specimens studied optically in serial sectioning as already noted by Shukla (1944) and Chitaley (1955). In addition, although we have examined specimens that are in bud condition, anthesis, and senescence, at no point is there any indication of a corolla.

SYNONYMY OF PREVIOUSLY DESCRIBED GENERA WITH *SAHNIANTHUS*

Nine additional genera named from the Deccan flora are here synonymized with *Sahnianthus* based on a suite of shared morphological and anatomical features. Shared features that demonstrate these genera all represent the same taxon, are the combination of a thick-walled hypanthium, a stipitate, multilocular, globular ovary, a single stout style, and stamens attached to inner wall of the hypanthium (Fig. 7). Among the numerous specimens of *Sahnianthus* are flowers that occur in a variety of states of maturity, from small floral buds, to flowers at anthesis to developing or mature fruits. The size discrepancies related to this variation in phenology, combined with differences in preservation and plane of section, may have contributed to the designation of multiple genera for the same plant. Below we highlight the major features found in each former genus and explain how these specimens conform to *Sahnianthus*, arranged in order by year of publication.

1. *Chitaleypushpam mohgaonense* Paradkar 1971 (Fig. 7B, C). The flower of *Chitaleypushpam* shows a prominent, thick hypanthium consistent with that of *Sahnianthus*. It was indicated as not stipitate, however, Fig. 5 of Paradkar (1971) depicts a longitudinal section with a distinct stipe protruding apically from

the hypanthium and pedicel. In situ pollen from the stamens was studied by light microscopy. The grains are smooth, spheroidal, and show equatorial thickening (Paradkar, 1971: pl. 1, fig. 4, pl. 2, fig. 10), like those presented here. The appearance of a five-locular ovary in the description of *C. mohgaonense* is indicated in the provided drawings, but not apparent in the published photos of Paradkar (1971). More details, including images of transversely sectioned gynoecium, were provided by Kokate et al. (2011). Using 3D reconstruction and scanning, the appearance of a five-locular ovary can be recreated with an oblique virtual section of a *Sahnianthus* specimen that actually has eight locules when viewed in truly transverse section. Using this same methodology, serial slices of *Sahnianthus* can be produced where different numbers of stamens appear to be represented (Fig. 4H–J).

2. *Deccananthus savitrii* Chitaley, S.D. et U. R. Kate 1972. *Deccananthus savitrii* (Fig. 7D) was described as having two whorls of perianth, but we interpret the published images to show only a single perianth whorl plus the hypanthium. The inference of petals, which should be crinkled in bud, is not supported by the images provided. The flower measures about 6.3 mm long and 4.5 mm wide, and shows an elongate stigma (Chitaley and Kate, 1972: pl. 1, fig. 4) consistent with that of *Sahnianthus.* The species was described as having six stamens attached to the perianth at two levels and interpreted as two whorls (Chitaley and Kate, 1972: text fig. 4). We agree with the description of two androecial whorls which is consistent with our new observations of *Sahnianthus*, but we infer that there were more stamens in the flower that were not intercepted in the available peels. *D. savitrii* was described as trilocular, but the published photomicrographs provided show the ovary sliced longitudinally rather than transversely so the precise number of septa and locules is not clear; we would infer at least five from the symmetry of the flower. Obliquely sliced ovaries of *Sahnianthus* can appear to have three locules. Pollen grains are 15–20 um in diameter, peroblate, and psilate and resemble those recovered here. However, the photos provided do not support their description of the grains as trichotomosulcate. We consider the type specimen of *D. savitrii* to be an unopened flower of *Sahnianthus parijai.*

3. *Raoanthus intertrappea* Chitaley, S.D. et M.Z. Patel 1975. *Raoanthus intertrappea* (Fig. 7E, F) was described based on a single specimen about 2 mm wide, but of unknown length, which was serially ground and peeled in oblique-transverse orientation, clearly showing a 7-locular ovary and many dorsifixed anthers on filaments arising from the perianth lobes. The authors indicated nine perianth lobes, but we only count seven based on their serial diagrams (e.g. their figs 19 and 28). Chitaley and Patel (1975) reported the androecium to consist of nine stamens in one whorl. However, a study of their serial transverse section diagrams reveals two sets of stamens with a circle of at least six anthers in the lower part of the flower, at and below the base of the style (their figs 15 to 18, including tips of some anthers that are also seen below in their figs 7–14), and a separate circle of six different anthers at a higher level above the top of the style (their figs 25–30). Probably the flower bore at least 12 stamens; 14 might be expected based on our count of the carpels and perianth lobes. Additionally, *Raoanthus* was described as zygomorphic in contrast to actinomorphic *Sahnianthus*; however, the images indicate flattening prior to fossilization. This taphonomic alteration, together with the obliquity of sections, seems to be responsible for the superficial appearance of zygomorphy, because the organs other than the perianth appear to be actinomorphic. The lack of a gibbous perianth and absence of capitate stigma may be accounted for by the early stage of maturity of the flower, as noted by the authors in their remark on the young condition of the ovary (Chitaley and Patel, 1975).

4. *Flosfemina intertrappea* R.K. Kar, K. Ambwani, A. Sahni et P. Sharma 2003. The flowers described under this name show the characteristic thick-walled hypanthium and stipitate ovary of *Sahnianthus* (Fig. 7K, Kar et al., 2003). Although described as having two whorls of perianth, this is not convincingly documented in the photos. The ovary was described as unilocular, but a transverse, rather than longitudinal section would be needed to reveal the septa and multilocular gynoecium expected for *Sahnianthus*. The ovules are seen to be attached to the central column, as is also seen in *Sahnianthus* (Figs 3F, 6B, D), but we interpret their placentation as axile, rather than free central. When the orientation of virtual planes of sections are manipulated within a 3D framework, some

sections of *Sahnianthus* can be observed that appear to be lacking stamens (Fig. 4F, G) and may appear unilocular (Fig. 5N), and as such, supplied images of *Flosfemina* are not convincing of its suggested unisexuality and single locule. The misinterpretation can be attributed to the lack of access to CT scan at that time and/or the distortion of the flower during fossilization.

5. *Flosvirulis deccanensis* Kar, R.K., K. Ambwani, A. Sahni et P. Sharma 2003. This genus was described based on a single specimen in a transverse cut near the upper part of the flower intercepting the stamens and surrounding calyx. Although claimed to be a unisexual staminate flower, no images are provided of the lower part of the flower which would be expected to include the ovary. The in situ pollen, which Kar et al. (2003) illustrate nicely in their pl. 1, fig. 4 resembles that already described from *Sahnianthus* by Dwivedi and Shukla (1958: pl. 16, figs 9–13), and those shown herein from *Sahnianthus* specimens (Figs 8, 9). Pollen grains are psilate and were described as subtriangular-subcircular, tricolporate, anguloaperturate, with exine up to 2 µm thick. Although not mentioned, their images (Kar et al., 2003: pl. 1, figs 4 and 5) show nicely the distinct equatorial rib-like thickening that we consider to be diagnostic of *Sahnianthus*.

6. *Menispermaceopushpam amanganjii* Narkhede, S.D. et B.B Bonde 2015 (Fig. 7L, M). The specimen was exposed in an oblique section transecting the hypanthium and five locules of the ovary but missing the level of the stamens. We do not agree with the interpretation that the flower was unisexual, because the plane of section did not pass through the upper part of the flower where the anthers would be situated. The assignment to Menispermaceae is refuted by the occurrence of axile placentation and multiple ovules per locule.

7. *Liliaceopushpam deccanii* Narkhede, S.D. et Patil, G.V. 2006 (Fig. 7H, I). The stipitate ovary, elongate capitate stigma, and epiphyllous positioning of the stamens just below the open margin of the hypanthium link these flowers with *Sahnianthus*. The ovary in the depicted transverse section of *Liliaceopushpam* shows six locules, separated by six radiating septa; the interpretation of three false septa is not supported by the published figures. Due to the oblique exposure surface and seemingly sharp bend between the upper perianth and ovary, many characteristics of this specimen are difficult to resolve. While three anthers are specified in the species description, as noted above, it is possible to slice a fossil *Sahnianthus* in such a way that it appears only three anthers are visible. Moreover, the original image (Narkhede and Patil, 2006: pl. 1, fig. 5) appears to show portions of more than three anthers, due to the serial section and strongly oblique angle (Fig. 7I). For these reasons, there are insufficient differences between *L. deccanii* and *Sahnianthus* to treat them separately.

8. *Lythraceopushpam mohgaoense* Narkhede, S.D., M. Bhowal et S.M. Meshram 2010 (Fig. 7J). The flower described under this name corresponds to *Sahnianthus* in its stipitate ovary, axile placentation, and epiphyllous anthers, but was described as having only five locules compared to the higher numbers (6–9) in *Sahnianthus*. Also, in contrast to the double longitudinal rows of ovules per locule typical in *Sahnianthus*, this specimen was interpreted as having a single row. We suggest that the discrepancy in locule number can be attributed to the oblique angle of sectioning (Fig. 7J). Using micro-CT scanning and 3D reconstruction, the appearance of a five-locular ovary can be recreated, where the specimen of *Sahnianthus* studied indeed has eight locules when viewed in transverse section. The perianth of *Lythraceopushpam* was noted to be valvate, similar to *Sahnianthus* with a smaller extent of unfused perianth (free tips in contrast to an upper 1/3 in *Sahnianthus*). This difference may be attributed to the immature state of the flower, as noted by the authors (Narkhede et al., 2010). Difference in stamen number (indicated as 7–8 for *Lythraceopushpam*), can be attributed to the study of an incompletely peeled specimen. Unless a complete flower is peeled all the way through, or observed by micro-CT scan, it is easy to underestimate the full number of stamens.

9. *Surangepushpam deccanii* Lanjewar, Puranik et Sakundarwar 2015 (Fig. 7G). *Surangepushpam deccanii* was interpreted as having a 2-whorled perianth and only four stamens which were indicated as being in two whorls. However, the structures interpreted as two whorls of perianth appear more likely to represent part of the thick hypanthium in the lower portion, and the sepals in the upper portion; no petals are visible. The longitudinal section intercepts both an upper and a lower whorl of stamens, but it is not possible from the available sections to know how many stamens there were in total. *Surangepushpam* was

characterized as zygomorphic; however, as in *Raoanthus* discussed above this determination could be due to taphonomic compression upon fossilization or oblique section of fracture.

Genus ***Enigmocarpon*** Sahni 1943

Species ***Engimocarpon parijai*** Sahni 1943

Figs 12, 13

Synonymy.

1977 *Enigmocarpon sahnii* Chitaley et Kate; p. 397, pls 1, 2.

2002 *Duabangocarpon deccanii* Kadoo et Kolhe; p. 45, figs 3, 4.

2016 *Enigmocarpon chandrapurense* Kapgate, Patil, et Gedam (nomen nudum; no holotype specified); p. 71, figs 5–8.

2016 *Premnocarpon mohgaoanii* Dighe et Kokate; p. 23–27 (isolated seeds).

Epitypes, designated here: CMNH 3785 (Fig. 12A), CMNH 3793 (Fig. 12G), UF 18311-53764 (Fig. 12F), UF 18311-70361 (Fig. 12G), UF 18311-53470 (Fig. 13A, B), UF 18311-62157 (Fig. 13E-M).

Additional specimens studied: CMNH 3775, 3779, 24773; UF 18311-52551, 53765,

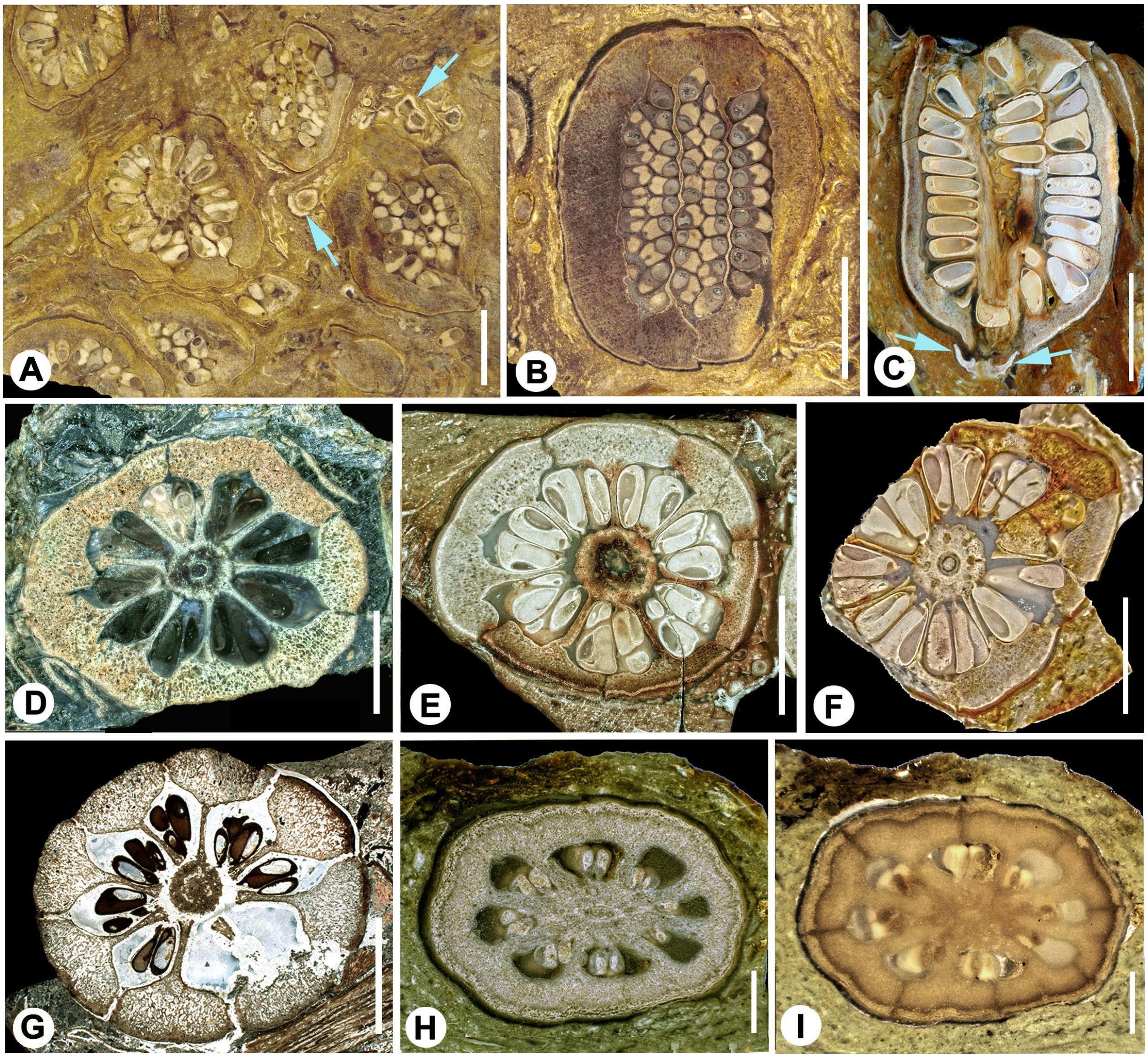


Figure 12. *Enigmocarpon parijai* fruits, both mature (A–G) and immature (H, I) from Mohgaon Kalan except as noted. **A**. Slice of chert intercepting at least six *Enigmocarpon* fruits with adjacent flowers of *Sahnianthus* (arrows), CMNH 3785; **B**. Tangential longitudinal section of a fruit showing three of the locules, each with two rows of seeds separated by thin septa, CMNH 3793; **C**. Longitudinal section with persistent hypanthium at base (arrow), UF 18311-53765; **D–G**. Transverse sections showing capsular organization with loculicidal lines of separation between valves; **D**. Nine locules, UF 19348-58595, from Bhutera; **E**. Seven locules, UF 18311-53764; **F**. Eight locules, UF 18311-52551; **G**. Eight locules, UF 18311-70361; **H**. Immature fruit in transverse section showing ovules in axile placentation, UF 18311-53765; **I**. The same section immersed in xylene, revealing the loculicidal separation planes (dark radial lines). Scale bars = 5 mm in A–G, 1 mm in H, I

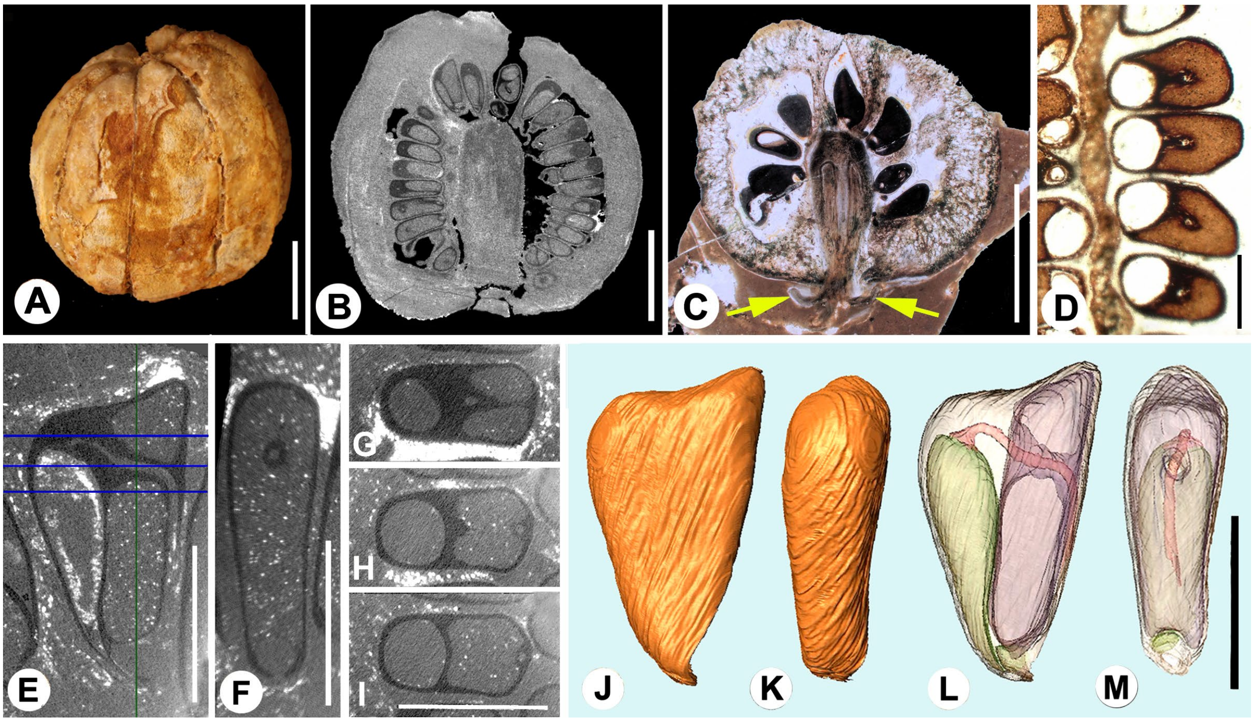


Figure 13. *Enigmocarpon parijai* fruits and seeds from Mohgaon Kalan except as indicated. **A**. Fruit physically isolated from the matrix showing external grooves between the carpels, UF 18311-53470; **B**. Micro-CT scan virtual longitudinal section of the same specimen, showing seeds attached to central column that does not extend fully to the apex; **C**. Physical longitudinal section, with persistent hypanthium at base (arrows), UF 18311-53775; **D**. Seeds aligned within locules separated by a septum. Note raphe canals, UF 19506-70569, Paladaun; **E–L**. Detail of seed intact within fruit, micro-CT scan, UF 18311-62157; **E**. Sagittal section, with vertical and horizontal lines indicating the planes of section in F–I; **F**. Coronal section with raphe canal in upper one-third; **G–I**. Successive transverse sections from near apex toward equator, embryo chamber on left; **J–M**. Digitally extracted seed in lateral views showing surface (diagonal lines are artifacts of processing), with translucency in L, M, to show course of the raphe bundle passing between the two chambers, UF 18311-62157A. Scale bars = 5 mm in A–C, 1 mm in D–L

53775, 56214, 76412, 19348-70343, 70362 [Mohgaon Kalan]; UF 19329-70330, 70333 [Keria]; UF 19348-58595 [Bhutera]; UF 19506-70569 [Paladaun]; UF 19443-71268 [Pudiyal Mohada]; UF 19278-69722 [Singpur], UF 19527-70323, 70324, 73730 [Udadaun].

Enigmocarpon parijai fruits, commonly found in association with *Sahnianthus* flowers in the same chert pieces (e.g. Figs 2A, 12A), have been well described and illustrated previously (Sahni, 1943; Dwivedi, 1956; Chitaley and Kate, 1977). They are thick-walled loculicidal capsules with seven to ten locules (Fig. 12A, D–H). The fruit is subglobose (oblate to prolate with polar length to equatorial width ratio of 0.9 to 1.6), and relatively large, typically 1.2–1.7 cm in diameter and 1.1–1.8 cm high, although smaller immature fruits about half a cm in diameter co-occur (Fig. 12H, I) which closely resemble the ovaries of *Sahnianthus* (e.g. Fig. 3J). The hypanthium and stipe, also characteristic of *Sahnianthus*, commonly persist at base of fruit (Figs 12C, 13C). The radiating septa are thin (Fig. 12D, G). Placentation is axile from a central column that extends from base to about ¾ of the distance to the apex (Fig. 13B, C). Seeds are borne alternately in two vertical rows within each locule with up to ten seeds in each row (Fig. 12B, C). Seeds are anatropous, rounded triangular in lateral view, irregularly ellipsoidal in transverse view, 1.9–2.7 mm high, 0.6–0.9 mm wide, and 1.0–1.8 mm deep. The seed includes a prominent pocket of spongy mesotesta and a smaller cavity containing the embryo (Fig. 13B, D–I). The large embryo is well preserved in specimens figured and described by (Biradar and Mahabale, 1976), showing straight cotyledons. The raphe extends along the periphery of the seed from the hilum about two thirds the seed length, then curves inward, along the sagittal plane, passing through the spongy tissue to connect with the chalazal end of the embryo cavity (Fig. 13E, L, M). A pocket of spongy tissue separated from the embryo cavity has been shown also in seeds of Eocene and extant *Decodon* (Cevallos-Ferriz and Stockey, 1988), but the germination valve delimited by a layer of enlarged cells as seen in *Decodon* is not present in *Enigmocarpon*.

PHYLOGENETIC RELATIONSHIP TO MYRTALES

Features of *Sahnianthus* and *Enigmocarpon* consistent with the order Myrtales include presence of a hypanthium, a syncarpous gynoecium with a single style, and axile placentation, stamens positioned on the inner surface of the hypanthium below the separation of calyx lobes, in two tiers (i.e. diplostemony), and a nectary lining the base of the hypanthium (Dahlgren and Thorne, 1984). These features are depicted in the diagramatic reconstruction and floral diagrams (Figs 10, 11). The strikingly flexible 6–9-merosity found in *Sahnianthus* also occurs in several extant lythraceous genera and some other myrtalean genera. Diplostemony, observed in *Sahnianthus*, is a widespread ordinal characteristic (Dahlgren and Thorne, 1984).

Within families of the order Myrtales, the perigynous flower with a superior ovary is found in most Lythraceae, as it is in *Sahnianthus*, whereas in most Onagraceae (sister family to the Lythraceae), and in Myrtaceae, flowers are epigynous with an inferior ovary. Protandry, as observed in *Sahnianthus*, also appears to be the usual condition in extant Lythraceae (Graham, 2007). *Sahnianthus* and several of the genera synonymized above were previously compared favorably to the Lythraceae (Shukla, 1944; Chitaley and Patel, 1975; Paradkar and Senad, 1984; Narkhede et al., 2010).

DNA sequence phylogenetic analyses of the Myrtales using a 353 nuclear loci supermatrix (Maurin et al., 2021) and the phylogenetic analysis of whole plastome sequences of the 28 currently recognized extant genera of Lythraceae (Inglis et al., 2003) are congruent in the recognition of two major clades within the family, and provide a basis for investigating phenotypic characters presented earlier (e.g. Graham and Graham, 2014; Graham et al., 1993, 2005). Summary descriptions of the genera and their distribution are given in Graham (2007). Unfortunately, the morphological character suites do not align well with the relationships inferred from the genomic data, so it seems that most of the characters that might have seemed useful for assessing the relationships of *Sahnianthus* (Table 1) are homoplasious.

Many characteristic features observed in *Sahnianthus* occur in one or more extant genera of Lythraceae, but the distribution of these characters is scattered, not confined to a particular clade (Table 1). The hypanthium is persistent, as in all genera of Lythraceae except *Physocalymma*. Calyx lobes are erect (rather than reflexed as in *Koehneria*) and pedicels are long (Fig. 6D) as in many of the genera. Other shared features included absence of petals (*Didiplis*, *Lythrum* in part, *Peplis*, *Tetrataxis*); ovary stipitate (*Adenaria*, *Decodon*, *Galpinia*, *Gyrosphragma*, *Koehneria*, *Lafoensia*, *Lagerstroemia*, *Pehria*, *Sonneratia*; Graham and Graham, 2014); ovary developing into a loculicidal capsule (e.g. *Cuphea*, *Duabanga*, *Lafoensia*, *Lagerstroemia*, *Pehria*; Graham and Graham, 2014; also in the Miocene genus *Shirleya* Pigg et DeVore 2005, rather than as an irregularly splitting or septicidal capsule, or as a berry-like fruit (*Capuronia*, *Punica*) or indehiscent drupe (*Trapa*). The stigma is capitate, which is a feature seen in some extant genera, contrasting with the punctate condition which is also common in the family (Table 1). The elongated, barrel-shaped form of the stigma is not known among extant myrtalean taxa.

The nectary lining the lower hypanthium, seen here in Fig. 3A, B, F, is comparable to that shown nicely in the longitudinal section of *Koehneria* (fig. 7 in Graham et al., 1986). Nectaries are present in the majority of genera of the Lythraceae and can occur on the gynoecium or at the base of the floral tube, or at the tube-gynoecium junction; when lining the floral tube the nectariferous tissue may extend upwards distally as far as to the base of the stamens, or may be confined just to the lower half (Tobe et al., 1998).

Although we recognize significant similarities to Lythraceae, there are also differences, especially in the in the distinctive barrel shape of the stigma and unique morphology of the pollen (Graham et al., 1985, 1987, 1990). Pollen in other families of Myrtales has been reviewed by Patel et al. (1984), but none of them show the combination of extremely psilate grains and equatorial thickening of the exine observed in *Sahnianthus*. Most extant genera have colporate apertures rather than strictly colpate pollen. The fruits and seeds of *Sahnianthus*, which take the name *Enigmocarpon*, are also compatible with Lythraceae, but do not match closely to a particular extant genus (Graham, 2013).

The genus *Ludwigia* (Onagraceae; sister to rest of Onagraceae) was used as the single outgroup in the inference of Lythraceae phylogeny

Table 1. Comparison of selected morphological characters for *Sahnianthus* and extant genera of Lythraceae. Data compiled from Cavalcanti et al. (2022), Graham (2007), Graham and Graham (2014), Graham et al. (1993), and Tobe et al. (1998)

	Clade[1]	Merosity[2]	Calyx lobe length[3]	Petals	Stamen whorls	Nectary position[4]	Ovary position	Ovary stipitate	Indument	Stigma[5]	Fruit type
Sahnianthus	?	6–9	short	–	2	jct	superior	+	+/–	elongate barrel	loc. capsule
Adenaria	1	4	short	+	2	ft	superior	+	–	bifid	irreg. capsule
Ammannia	2	4	short	+	2	jct	superior	–	–	capitate	irreg. capsule
Capuronia	1	6	short	+	1	ft	superior	–	–	bifid	indehiscent
Cuphea	1	6	short	+	2	jct	superior	–	+	capitate	loc. capsule
Decodon	2	5	short	+	2	gyn	superior	–	+/–	small capitate	loc. capsule
Didiplis	2	4	short	–	1	jct	superior	–	–	punctate	irreg. capsule
Diplusodon	1	6	short	+	2+	–	superior	–	+	small capitate	sept. capsule
Duabanga	2	4	long	+	1 or 2	jct	inferior to semi	–	+/–	capitate	loc. capsule
Galpinia	1	5–6	short	+	1	jct	superior	–	–	punctate	irreg. capsule
Ginoria	2	4–6	long	+	2	–	superior	–	–	punctate	sept. capsule
Gyrosphragma	1	6	short	+	1	jct	superior	+	+	small capitate	circums. capsule
Heimia	2	5–6	long	+	2	–	superior	–	–	capitate	loc. capsule
Koehneria	1	6	long	+	2	jct	superior	+	+	punctate	sept. capsule
Lafoensia	1	8–16	long	+	2	ft	superior	+	–	large capitate	loc. capsule
Lagerstroemia	2	6	long	+	2[6]	–	superior	–	+/–	punctate	loc. capsule
Lawsonia	2	4	long	+	1	–	superior	–	–	punctate	irreg. capsule
Lourtella	1	4	short	+	2	ft	superior	–	+	punctate	irreg. capsule
Lythrum	2	6	short	+	2	jct	superior	–	+/–	capitate	sept. capsule
Pehria	1	4	short	+	2	ft	superior	+	+	punctate	loc. capsule
Pemphis	1	6	short	+	2	ft	superior	–	+	bifid	circums. capsule
Physocalymma	1	8	long	+	2	–	superior	–	–	small capitate	irreg. capsule
Pleurophora	1	6	short	+	2 (or 1)	jct	superior	–	+	small capitate	irreg. capsule
Punica	1	5–8	short	+	2+	jct	inferior to semi	–	–	punctate	irregular splitting
Rotala	2	4	short	+	1	jct	superior	–	–	small capitate	sept. capsule
Sonneratia	2	4–8	long	+	2	jct	inferior to semi	–	–	large capitate	indehiscent berry
Tetrataxis	2	4	long	–	1	ft	superior	–	–	large capitate	sept. capsule
Trapa	2	4	long	+	1	jct	inferior to semi	–	+	bifid	horned drupe
Woodfordia	1	6	short	+	2	jct	superior	+/–	+	bifid	irreg. capsule

[1] Assignment to major clades 1 and 2 of Inglis et al. (2023).

[2] Merosity of perianth whorls.

[3] Relative calyx lobe length: short = less than 25% total floral tube length, long = more than 33%.

[4] Nectary position: ft = floral tube, gyn = gynoecium, jct = junction of floral tube and gynoecium (Tobe et al., 1998).

[5] Bifid stigmas can appear capitate, then split to two lobes in late stage.

[6] In *Lagerstroemia* many stamens usually, inserted at base of ovary appearing like a single whorl, but two filament lengths and two pollen types produced.

by Inglis et al. (2023). Several features in *Ludwigia* are shared with *Rotala* (Lythraceae) and also occur in *Sahnianthus*: flowers that are hermaphroditic, actinomorphic, pedicellate; sepals persisting after anthesis; petals absent (in some species of *Rotala*); stamens twice as many as sepals in two subequal tiers or of two filament lengths; anthers versatile; ovary with as many locules as sepals, a capitate stigma, and capsular fruits. The similarities raise the question of whether *Ludwigia* or another early member of the Onagraceae might be considered related to or confused with *Sahnianthus*. *Ludwigia*, however, has a fully inferior ovary and pollen with viscin threads, characters exclusive to and diagnostic of the Onagraceae, neither of which is found in *Sahnianthus* or any genus of the Lythraceae. Given the Late Cretaceous age, and the isolation of India from other land masses at that time, it is not surprising that *Sahnianthus* probably represents a mosaic taxon combining characters not found today within a modern genus or perhaps even within a modern infrafamilial clade.

BIOGEOGRAPHIC IMPLICATIONS

Inglis et al. (2003) inferred biogeographic history of Lythraceae from the phylogenetic relationships of extant genera based on whole plastome phylogeny, with similarities to the nuclear phylogeny of Maurin et al. (2021) and their modern-day distributions. Their analysis indicates two deeply branching major clades in the Lythraceae. One major clade accommodates shrubby and arboreal genera of South America and Africa found in seasonally dry environments, in some cases with relatively large, often winged, seeds: *Cuphea* P. Browne 1756, *Gyrosphragma* T.B. Cavalc. et M.G. Facco 2022, *Pleurophora* D. Don 1831, *Adenaria* Kunth 1824, *Pehria* Sprague 1923, *Koehneria*, *Woodfordia* Salisb. 1806, *Diplusodon* Pohl 1827, *Physocalymma* Pohl 1827, *Lourtella* S.A. Graham, Baas et Tobe 1987, *Lafoensia* Vand. 1788, *Capuronia* Lourteig 1960, *Galpinia* N.E. Br. 1894, *Punica* L. 1753, and *Pemphis* J.R. Forst. et G. Forst. 1776.

The second major clade of Inglis et al. (2023) includes North American, Asian, African and several nearly cosmopolitan genera of herbaceous, shrubby and arboreal genera, often inhabiting humid or aquatic environments, several with smaller seeds anatomically suited to water dispersal: *Ammannia* L. 1753, *Lawsonia* L. 1753, *Tetrataxis* Hook. f. 1867, *Ginoria* Jacq. 1760, *Trapa* L. 1753, *Sonneratia* L.f. 1782, *Duabanga* 1835, *Lagerstroemia* L. 1759, *Lythrum* L. 1753, *Decodon* J.F. Gmel 1791, *Didiplis* Raf. 1833, *Rotala* L. 1771, and *Heimia* Link et Otto 1822.

Inglis et al. (2023) hypothesized that the Lythraceae dispersed early in the Late Cretaceous from South America to North America with subsequent expansion in the Late Cretaceous of a North American lineage through Laurasia to Africa via a boreotropical route. Two later expansions of South American clades to Africa in the Paleocene and Eocene, respectively, were also hypothesized. Despite the richness of characters preserved in *Sahnianthus*, its phylogenetic position relative to the two major clades recognized by Inglis et al. (2023) remains uncertain. Although it shows the presence of a distinctive genus allied to Lythraceae in the latest Cretaceous of India, it neither confirms nor refutes the biogeographic hypotheses of Inglis et al. (2023).

The two oldest fossils, recognized as extant genera of the Lythraceae, are isolated seeds of *Decodon* from the Late Cretaceous Cerro del Pueblo Formation, Coahuila of northern Mexico (late Campanian, 73.5 Ma per Eberth et al., 2004) described by Estrada-Ruiz et al. (2009); and dispersed pollen of *Lythrum* in North America and *Peplis* (distinguished by the authors from *Lythrum*) in Asia, dated to the mid-Late Cretaceous at ~70 Ma (Grímsson et al., 2011). Thus, the Lythraceae were already widespread in the Northern Hemisphere even before our earliest records of *Sahnianthus* (~66 Ma).

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